

**ECOLOGY AND CHEMISTRY OF SMALL MAMMALS AND THE IMPLICATIONS FOR  
UNDERSTANDING THEIR PALEOECOLOGY AND ENVIRONMENTS**

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## Abstract

Fundamental goals of paleoecologists and modern ecologists is to understand the evolutionary and ecological patterns in modern and ancient biodiversity. Diet is one ecological trait species may evolve or vary to exploit food resources and increase their fitness. Stable isotope analysis is one method used to infer diet and is transferable between modern and fossil populations. Stable isotope analysis has not been commonly applied to small mammals, mostly because of sampling limitations. Here, three studies focus on furthering our understanding of small mammal ecology and serve as a baseline comparison for interpreting similar data from the fossil record.

Chapter 1 illustrates that small mammals varied their diets independently and indicate granivores focused on C<sub>4</sub> derived resources, generalists consumed resources readily available, and an invertivore focused on invertebrates. Results indicate that intermediate  $\delta^{13}\text{C}$  values between C<sub>3</sub> and C<sub>4</sub> resources are likely from integrating multiple resources through direct consumption and invertivory. Therefore, interpreting  $\delta^{13}\text{C}$  values from consumers in the fossil record must be interpreted with caution.

Chapters 2 and 3 include a  $\delta^{13}\text{C}$  dataset that expands to the regional scale and assess how rodent partition C<sub>3</sub> and C<sub>4</sub> resources as C<sub>4</sub> biomass on the landscape varies. Small mammals mostly rely on C<sub>3</sub> derived resources, but there are some spatial and ecological tendencies with granivores incorporating the most C<sub>4</sub> derived resources and varied with C<sub>4</sub> biomass. Climate variables explained some variance in C<sub>4</sub> consumption for some species, while other species' diets were not explained by climate. Seasonality metrics were the best predictors of C<sub>4</sub> consumption and  $\delta^{13}\text{C}$  values in rodent hairs were more positive during peak C<sub>4</sub> growing seasons.

Chapter 4 estimates temperature and precipitation using the area extant species' geographic ranges overlap today and then applied to ancient faunas where the same species co-occur. Temperature and precipitation estimates for Pleistocene-Holocene localities reflect the general warming during this transition and interpolated temperature and precipitation for climate intervals illustrate deviating spatial gradients through time. The culmination of work presented here greatly improves our understanding of small mammal ecology and sets a baseline for testing modes of evolution and ecology in the fossil record.

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## INTRODUCTION

Modern grasslands of the southern Great Plains are dominated by grasses that use the C<sub>4</sub> photosynthetic pathway. Most plants use either the C<sub>3</sub> (trees, shrubs, cool growing season grasses) or C<sub>4</sub> (primarily warm growing season grasses) photosynthetic pathways, and understanding the origin of C<sub>4</sub>-dominated grasslands occupies a diverse community of Earth and life scientists. The geological history of these grasslands has been examined using various proxies (e.g., paleosols Fox and Koch, 2004; Fox et al., 2011, Fox et al., 2011b), isotopic composition and ecomorphology of large mammalian herbivores (Passey et al., 2002) phytoliths (Strömberg, 2004). C<sub>4</sub> grassland expansion is a Neogene phenomenon, but the timing varies in different regions and aspects of the ecological impacts are still poorly known.

Herbivorous small mammals (rodents, lagomorphs) are important grassland engineers that consume seeds and seedlings, altering plant community structure and diversity (Weltzin et al., 1997; Manson et al., 2001) and compete with large bodied herbivores for food resources (Johnston and Anthony, 2008). Soil mixing by burrowing also affects plant communities by altering nutrient cycling (Reichman and Seabloom, 2002). More omnivorous small mammal species increase trophic complexity in communities by preying on arthropods, and all small mammals are important food resources for secondary consumers. Given the bottom-up and top-down influences of small mammals in grassland ecosystems, determining the paleoecology of small mammals is critical to our understanding of the evolution of C<sub>4</sub>-dominated grasslands ecosystems.

Understanding the response of communities to long-term patterns of environmental change is a fundamental goal of paleoecology, but difficult to assess without independent environmental and faunal records. The Meade Basin (southwest Kansas) meets this requirement and is an ideal location for studying rodent community response to long-term environmental change. A detailed isotopic record from paleosol carbonates indicates that C<sub>4</sub> grasses increased from characteristic Miocene levels (0-20%, 9-12 Ma) to modern abundance for the region (ca. 75%) by 1 Ma (Fox et al., 2011). Over the same interval, local climate became cooler and/or wetter (Fox et al., 2011b) consistent with global cooling (Zachos et al., 2001) and the onset of Northern Hemisphere glaciation at 2.7 Ma.

Stable isotopes are critical tools for reconstructing mammalian diets in the fossil record. Paleodiet datasets are typically interpreted based on our understanding of the modern environment and working hypotheses of ancient ecosystems. With the development of laser ablation-isotope ratio mass spectrometry, analyzing small mammal teeth (e.g. rodents and lagomorphs) has become available and permits trophic analyses of ancient ecosystems to include small mammals. However, our understanding of isotopic variation on the landscape today is limited and hinders our ability to adequately interpret similar data from the fossil record.

Here, I have addressed these limitations by using modern rodents and their environments to provide the background we need to interpret the fossil record. I approach our limited understanding from multiple spatial and temporal scales to evaluate small mammal ecology, specifically diet, using stable isotopes.

In **Chapter One**, I characterize the food web of primary and secondary consumers in the C<sub>4</sub>-dominated shortgrass prairie utilizing stable isotope and associated mixing models to estimate diets. Rodent stable isotope mixing models estimate different dietary categories within locally trapping small mammals. Furthermore, I investigate seasonal dietary changes and the potential responses to a short-term climate event. These results are put into context by comparing rodent diets to those of orthopterans from the same study period and previously published stomach contents of small mammals near the Great Plains. The findings presented here are important for their methodology in assessing small mammal food webs and determining the influence of seasonality, climate events, and invertivory on small mammal diets at the local scale. Overall these will serve as a time zero fauna that will be compared to similar data types from fossil small mammals collected in the surrounding area of the trapping location.

In **Chapter Two** I expand the spatial and temporal scale to investigate how rodent diets vary across the Great Plains in relation to metrics of C<sub>4</sub> primary production. I utilize museum specimens collected across the southern Great Plains and analyze hair for stable isotopes. I determine that dietary responses to C<sub>4</sub> production are species specific with most species consuming more C<sub>3</sub> than C<sub>4</sub> derived resources. Most species do not have significant relationships with C<sub>4</sub> metrics, but some species (mostly granivores and a rootivore) do. The measured carbon isotope values are then used to predict diet carbon isotope values across the Great Plains for each species, diet category, and the entire dataset. The resulting predication maps reflect similar spatial

patterns found for C<sub>4</sub> plant biomass across the Great Plains. These data begin describing the variation among rodent diets and how they may vary on the landscape and will aid in our interpretation of similar datasets from monitoring programs and fossil assemblages.

Building upon the museum voucher dataset, **Chapter Three** investigates the relationship between small mammal diets and climate in the southern Great Plains. This space for time substitution simulates how diets may change in response to future climate change if their diets vary with climate. Land cover type is also included in the analysis to determine if individuals'  $\delta^{13}\text{C}$  values reflect their biome habitat. The grasslands of the Great Plains are the main focus but some immediately adjacent ecoregions (forests and deserts) are also included for comparison. Anthropogenically modified ecoregions are also included as developed or cultivated lands and carbon isotope values of hair from within those regions are compared to natural land covers of grasslands, shrublands, and forests. Combined climate variables do explain more  $\delta^{13}\text{C}$  variance in hair than any C<sub>4</sub> metric alone. The common climate variables of mean annual temperature and mean annual precipitation were not good predictors of  $\delta^{13}\text{C}$  when used as the only dependent variables.

The first three chapters of this dissertation focus on the ecology (i.e. diet) of small mammals and will serve as analogs for interpreting similar data from the fossil record. We can use the fossil record to test hypotheses about modes of evolution such as the Red Queen Hypothesis (Van Valen, 1973) and the Court Jester Hypothesis (Barnosky, 2001). To test these hypotheses, future collaborative research will include stable isotope analysis of fossil remains to indicate diet and independent climate proxies by analyzing the paleosol sediments encapsulating the small mammal remains. The modern analyses presented here provide an understanding of stable isotope values in small mammals' tissues with spatial and temporal controls. Furthermore, we consider potential food resources and the resulting isotopic composition in small mammal tissues. With the datasets we can interpret the fossil record and test the influence of biotic and abiotic factors on small mammal ecology and evolution.

Reconstructing climate in the Great Plains has been a difficult task because of minimal amounts of common paleoclimate records (e.g. lake cores, pollen, phytoliths, and speleothems). New geochemical techniques (e.g. clumped isotopes and compound specific analysis) are being developed and applied to sediments in the Great Plains and

may yield new climate records for the region. Most previous climate records in the Great Plains have consisted of bulk isotope analysis of carbonates (e.g. Fox et al., 2012) or lithologic descriptions and some pollen records in the northern Great Plains (see Meltzer and Holliday, 2010 for a review). Another method used to estimate environment is to use the area of sympatry (the geographic area a suite of species co-occur). If the relationship between species and climate found today is the same as in the past, then the climate within the geographic area where extant species from a fossil fauna co-occur today (i.e. area of sympatry, AOS) could be used to estimate paleoclimate (Semken, 1966; Graham and Semken, 1987).

The AOS methodology has been used through the years, but it has never been quantitatively assessed for accuracy or precision. In **Chapter Four**, I revisit the AOS method and subject it to sensitivity tests to validate the method, and determine its accuracy and precision. Upon conclusion of quantifying and calibrating the method, mean annual temperature and mean annual precipitation are calculated for ancient faunas dispersed throughout the Great Plains and extend back one million years. The paleoclimate reconstructions are then compared to global and regional climate records of past climate, which show broad agreement during large climate changes such as the transition from the Last Glacial Maximum to the warmer Holocene. Precipitation estimates are highly variable through time, but consistently vary around modern values and indicate no broad temporal trends, which likely may be the real trend for the region. These results indicate that the AOS method can be used to estimate climate for the Great Plains and including additional or newly discovered faunas may help resolve gaps in the temporal or spatial sampling.

In the last section, I discuss the overall findings presented here and their significance in understanding small mammal ecology and evolution. On a broader scale, the methods and scientific design presented here are important for future work and to consider the multiple sources of variations that affect an individual, a population, species, or community. This work provides a baseline for comparisons to interpret similar data with confidence, but is also focused on the Great Plains. Future work should include expanding the dataset to include more taxa and beyond the Great Plains. Community ecology will differ among environments and furthering our understanding of community structure and evolution is a shared goal of paleo and modern ecologists.

## CHAPTER 1

### **Rodent food resource partitioning in a mixed C<sub>3</sub>:C<sub>4</sub> grassland indicated by stable isotopes ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ )**

#### **SUMMARY**

We used stable isotope analysis to understand food resource partitioning among small mammals in sagebrush-grassland and cottonwood riparian macrohabitats in southwest Kansas. Stable isotope analysis can be used to estimate current, monitor future, and reconstruct past diets, however we need a great understanding of how small mammal diets vary with respect to stable isotopes. Rodent trapping and dietary sources (plants and invertebrates) were sampled during four trapping sessions between 2012 and 2014 to capture inter-annual and seasonal variation. We used stable isotope mixing models to estimate dietary contributions of various invertebrate and plant food resources into orthopteran and rodent diets. We found that graminivorous grasshoppers consumed mostly C<sub>3</sub> and C<sub>4</sub> graminoids, while polyphagous orthopterans consumed a mixture of mostly forbs/trees/shrubs and C<sub>3</sub> graminoids. Rodent diet estimates indicate that *P. maniculatus* varied its diet seasonally and inter-annually likely in response to varying food resource availabilities. *O. leucogaster* maintained a relatively constant diet through time composed of mostly invertebrates and supplemented by a mixture of graminoids herbaceous plants. *D. ordii* diets increased C<sub>4</sub> consumption through time and may have been supplemented by graminivorous grasshoppers. We demonstrate that stable isotope analysis can be used to identify food resource partitioning among rodents in the Great Plains and that each varies its diet differently with respect to seasonal and inter-annual environmental variations.

#### **INTRODUCTION**

Impending global climate change will influence biodiversity and drive environmental changes across the globe, but perturbations and biotic responses will differ among ecosystems. Grasslands of the North American Great Plains are projected

to experience general warming and drying with increased frequency of extreme weather events in the future. These climatic changes will force organisms to move their distribution on the landscape to remain in their climatic envelopes, adapt to the changing environment, or perish. In the North American Great Plains, much attention has been given to plants communities, avian flyways, and large herbivore species that roam the grasslands. Here, we focus on small mammals that are critical components of grassland ecosystems and use stable isotope analysis to estimate diets and provide a guideline for interpreting similar data from other localities, future diet monitoring, and reconstructing diet from ancient remains.

Small mammals are grassland engineers that compete with large bodied herbivores for food resources (Johnston and Anthony, 2008) and are vital components of grassland ecosystems as consumers, prey, and bioturbators. Herbivorous small mammals (rodents, lagomorphs) consume seeds and seedlings, altering the plant community structure and diversity (Weltzin et al., 1997) as well as impeding woody plant encroachment into grasslands. More omnivorous small mammal species increase trophic complexity in communities by preying on arthropods, and all small mammals are important food resources for secondary consumers. Many small mammals burrow (e.g. prairie dogs, kangaroo rats, ground squirrels, etc.), which influence plant communities by altering nutrient cycling (Reichman and Seabloom, 2002). Given the bottom-up and top-down impacts of small mammals in grassland ecosystems, determining how small mammals utilize resources is important for understanding how they may respond to impending environmental change.

Diet is one aspect of ecology that small mammals may vary in response to environmental and biotic variations and diet can be estimated using stable isotopes in the consumer's tissues. Consumer tissues reflect the isotopic composition of diet sources with characteristic offsets (Deniro and Epstein, 1978). Food sources can have isotopically distinct distributions such as the difference between plants using the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathways. Mean  $\delta^{13}\text{C}$  of modern North American C<sub>3</sub> plants is -27.5‰ VPDB (range: -19.4‰ to -33.7‰); mean of C<sub>4</sub> plants is -14.5‰ VPDB (range: -12.3 to -16.4‰; after Matson et al., 2012). The isotopic distinction between C<sub>3</sub> and C<sub>4</sub> plants permits ecologists to determine the energy source for consumers and track food resources through the food web.



- 1) **How do small mammals partition food resources within a C<sub>4</sub>-dominated grassland ecosystem with respect to stable isotopes?** Multiple species live within grassland communities, and understanding their interspecific interactions is a fundamental aspect of modern and ancient ecology. Diet is one aspect that species may modify in relation to the presence and absence of other species (e.g. Flake, 1973; Hallett, 1982; Lafferty et al., 2014) or in response to environmental variables. Diet can be determined using various methods (i.e. stomach contents, observational, and scat) in the modern and each has associated advantages and caveats. We utilize stable isotopes here because of their integration of diet over time, relatively non-invasive tissue sampling, and compatibility with the fossil record. Stable isotopes are one of the primary techniques for indicating diet, but our minimal characterization of how diets vary on the modern landscape, with respect to stable isotopes, hinders our ability to interpret the fossil record. Based on previous work we expect some species in our study area to focus on graminoids (e.g. heteromyids on grasses and sedges), foliage (e.g. voles on forbs), invertebrates (i.e. *Onychomys* on grasshoppers), and other rodents (e.g. *Peromyscus*) with generalized diets.
- 2) **How do small mammal diets seasonally vary?** Some small mammals vary their diets by modifying the consumption of various plant parts (leaves, stems, seeds) and arthropods (e.g. Flake, 1973; Hope and Parmenter, 2007; Reid et al., 2014) in response to different food resource availabilities. Consumed vegetation consists of different photosynthetic pathways (C<sub>3</sub>, C<sub>4</sub>, and CAM), which can be determined based on their carbon isotope values (O'leary, 1981; 1988). Here, we use carbon stable isotopes to compare seasonal consumption of C<sub>3</sub> and C<sub>4</sub> graminoids, forbs, trees, and shrubs, which may vary because of differing growing seasons for each plant species. For example, C<sub>3</sub> and C<sub>4</sub> plants have different growing seasons with C<sub>3</sub> plant growth peaking early-mid summer, while C<sub>4</sub> grasses peak in mid-late summer (see Ehleringer et al., 1997). Small mammal seed consumption is likely greatest in the fall and during the winter months when invertebrates and new foliage are minimal (Flake, 1973). Therefore, we expect isotopic signatures of rodent tissues in the spring to reflect decreased invertebrate and increased graminoid (seed producers) consumption relative to other seasons. Furthermore, we hypothesize that C<sub>3</sub>-derived resources would be

utilized most in spring/early-summer and decrease throughout the year after they have reached peak production. Consumption of C<sub>4</sub>-derived resources would be lowest in the spring and increase throughout the course of the year in line with their annual productivity.

- 3) **What is the impact of invertivory (invertebrate predation) on consumer  $\delta^{13}\text{C}$  values?** Stable isotope analysis of fossil material is typically restricted to  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  analyses and commonly  $\delta^{13}\text{C}$  values are used to estimate the relative proportions C<sub>3</sub> and C<sub>4</sub> derived resources are consumed. Organic tissues are readily available in modern ecosystems for analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (an indicator of trophic position), which will provide a better estimate of food resource utilization than a single stable isotope. We will use  $\delta^{15}\text{N}$  values to indicate secondary consumers and evaluate how trophic position influences our interpretation of  $\delta^{13}\text{C}$  values. We hypothesize that increasing invertivory (indicated by more positive  $\delta^{15}\text{N}$  values) will integrate more C<sub>3</sub> and C<sub>4</sub> resources resulting in intermediate  $\delta^{13}\text{C}$  values between C<sub>3</sub> and C<sub>4</sub> derived resources.
- 4) **Do small mammal diets reflect the ratio of C<sub>3</sub>:C<sub>4</sub> plants in their macrohabitats?** Paleobiologists have used  $\delta^{13}\text{C}$  values in fossil specimens to indicate of the relative proportions of C<sub>3</sub>:C<sub>4</sub> plant biomass on the surrounding landscape. Large-bodied herbivores indicate large-scale patterns of environmental change in space and through time (Passey et al., 2002), but lack the ability to resolve finer resolution variability of landscape heterogeneity. Small mammals have smaller home ranges (Harestad and Bunnell, 1979), therefore consume food resources within close proximities. Small mammal diets may reflect the macrohabitats and collectively the heterogeneous landscape. Our study addresses this question by determining if diets vary with macrohabitats that differ in relative abundances of C<sub>3</sub> and C<sub>4</sub> plants.

## METHODS

*Study Area.*- We conducted small mammal trapping on the XIT Ranch, a privately owned ranch south of Meade, Kansas and along the Cimarron River near the Kansas-Oklahoma border. Southwest Kansas boasts a semiarid steppe climate that receives precipitation below potential evapotranspiration and characterized by hot

summers and cold winters. Mean annual precipitation is 514 mm/yr and mean annual temperature is 13.4°C (Liberal, KS; ~40km west of study area). Precipitation varies throughout the year with more than 70% of the precipitation occurring between May and October (NOAA, 2015). Diurnal temperature can vary by as much as 20°C between day and night. The average low of the coldest month is -6.4°C (January) and the average high temperature for the hottest month is 34.2°C (July).

Trapping grids were established at XIT Ranch because of the numerous fossil localities in the area rich with small mammal remains (e.g. Martin and Fairbanks, 1999; Martin et al., 2008). The study area is dominated by extensive shortgrass prairie abundant with sagebrush and this habitat is only interrupted by riparian zones along the Cimarron River or small arroyos. We targeted the sagebrush-grasslands and cottonwood riparian habitats because they should represent two local end-members in the amount of C<sub>4</sub> plant biomass contributed to soil organic matter (SOM). Additional trapping grids were established in other habitats such as open river terraces (grass-sedge dominated with some tamarisk), tamarisk-dominated river terraces (thick tamarisk coverage and grass-sedge understory), and mixed short-grass prairie (grass dominated) as part of a biodiversity survey for the area. All trapping grids were established on lands opened to grazing by commercial cattle and horses year-round. Grazing pressure was estimated to be high evidenced by the reduced number of grasses reaching inflorescence except in small exclosures or grasses protected from grazing by shrubs.

*Small mammal trapping.* – Small mammal trapping grids were deployed in June 2012, June 2013, October 2013, and May 2014 to capture inter-annual and seasonal variations of food availabilities and diets. The South Cimarron, Cottonwood Transition, and Sagebrush trapping grids were deployed each session except the Sagebrush grid, which was established in summer 2013. Trapping grids contained stations placed 15 m (Sagebrush and Cottonwood grids) or 10 m (South Cimarron) apart (Figure 1) and a Sherman live trap (H. B. Sherman Traps, Inc., Tallahassee, Florida) was placed within one meter of each station. Traps were baited at dusk with rolled-oats and peanut butter, checked at daybreak the following morning, and trap doors were left closed during the day. A handful of cotton/polyester fill was placed in traps to provide insulation for the mice during cold nights in May and October. Trapping grids were set and baited for at least three consecutive nights during each trapping session.

Upon capture, individuals were identified to species, and the sex, reproductive status, and age were recorded. Individuals were weighed and measured for body, tail, ear, and hind foot lengths for identification confirmation, body size estimates, and age classification. A hair sample (~2 mg) was collected from the dorsal posterior of each individual and cut with scissors at the base of the hair include nearly entire guard hairs, but did not pull hairs in order to minimize pain and discomfort. Hair samples were collected in May, June, and October to incorporate variations in diet due to food availability and seasonal differences. Hair samples in May would reflect food consumed during the onset of the C<sub>3</sub> growing season. Mid-summer samples would reflect the transition from the C<sub>3</sub> growing season into the warmer C<sub>4</sub> growing season. Samples collected in September reflect late summer diets when C<sub>4</sub> plants dominate the grassland. Each individual received an ear tag (self-piercing ear tag, model no. 1500-1; National Band and Tag Company, Newport, Kentucky) with a unique identifier to ensure the same individual was not sampled twice in the same trapping session and to track diet within the same individual through time. Our trapping methods and procedures are in accordance with the American Society of Mammalogists (Sikes et al., 2011) and approved by the University of Minnesota Institutional Animal Care and Use Committee. A Scientific, Education, or Exhibition Wildlife Permit was obtained from the Kansas Department of Wildlife, Parks, and Tourism (Permit Nos. SC-115-2012, SC-124-2013, SC-111-2014).

*Food resource sampling.*- A minimum of two specimens were collected for the ten most abundant plants within each trapping grid and macrohabitat during each trapping session. Plant specimens were pressed within coin envelopes, dried, and identified to species or to the lowest classification possible. Due to heavy grazing and severe drought (Hoerling et al., 2014), many samples were limited in their identification because they lacked inflorescences required for adequate identification to the species level. Plants specimens were dissected to extract seeds, flowers, leaves, and stems for isotopic analysis. Different plant parts were analyzed to determine variability among plant components. Consumer's may prefer particular plant parts (e.g. seeds or leaves), but that may vary throughout the year depending on the growing season.

Invertebrates were collected by sweep netting for 30 seconds within each trapping grid. Each 30 sec sampling covered a distance of ~30 m and multiple samples were collected in each macrohabitat. Additional pit fall traps were placed at night to

target other invertebrates such as beetles and ants. Each trap was constructed with a 16 oz. plastic cup buried in the ground such that the top of the cup was flush with the ground and the cup was filled with ~4 oz. of water. Traps were set at dusk and any captures were collected at dawn the following morning. Individuals were identified to a minimum taxonomic level of order, but identified to the lowest possible level.

*Soil sampling.*- SOM integrates above and belowground organic matter over time (years to hundreds of years) and therefore, SOM  $\delta^{13}\text{C}$  values provide a weighted average  $\delta^{13}\text{C}$  value of the overlying vegetation biomass and reflects the relative proportions of the overlying  $\text{C}_3$  and  $\text{C}_4$  biomass. Within each trapping grid, superimposed soil samples (up to 30 cm deep) were collected from an excavated soil pit.

*Sample preparation and isotope analysis.*- Invertebrates were dried in the field and then fully desiccated in a 60°C oven (~48 hrs) in the laboratory. Before stable isotope analysis, invertebrates were dissected to harvest hind legs and heads for analysis to reach sufficient for sample size. Legs and heads were then placed in 2:1 chloroform:methanol mixture, sonicated for 30 minutes, and then the solvent was decanted off. The solvent rinse was repeated and then rinsed with Millipore water three times and left to dry in a 60°C oven (~48 hrs). To minimize the inclusion of chitin, a subsample of muscle was extracted from hind legs and weighed (~1.2 mg) into a tin capsule. Plants were dried in the field and then fully desiccated in a 60°C (~48 hrs) oven before plant parts were dissected from specimens and then homogenized by grinding with mortar and pestle. Multiple seeds were either ground or whole seeds were combined to reach a target mass of ~2 mg and weighed into a tin capsule.

Hair samples were cleaned following the procedure outlined in Schwertl et al. (2008) to remove dirt, lipids, and any oils. Briefly, samples were soaked and rinsed in deionized water, followed by soaking for three hours in a 2:1 chloroform:methanol mixture, and then rinsed three times with deionized water. Finally, samples were soaked in deionized water (30 mins) and rinsed with deionized water, followed by drying in a 60°C oven (~48 hrs). For each sample, 0.7 – 1 mg of hair was weighed into a tin capsule.

Soil samples collected in the field were dried in a 60°C oven and then homogenized by mortar and pestle. Samples were acidified with 0.5M HCl, rinsed with deionized water three times, and then allowed to oven dry (~48 hrs). Samples were then

re-homogenized with mortar and pestle followed by weighing into tin capsules (the weighed mass varied depending on each sample's total organic matter).

Carbon and nitrogen isotopes and elemental compositions (wt% C and wt% N) were determined by combustion of sample and tin in a Costech 4010 Elemental Analyzer coupled to a Thermo-Finnegan Delta V Plus mass spectrometer. The resulting gases were analyzed for elemental concentrations of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  ratios, expressed in standard  $\delta$  notation as the permil difference between the ratios in a sample and a standard material differential from international standards for these isotope ratios (VPDB for carbon and atmospheric  $\text{N}_2$  for nitrogen). All analyses were conducted in the University of Minnesota Stable Isotope Laboratory. Based on replicate analyses of laboratory standards, precision for  $\delta^{13}\text{C}$  analyses is  $<0.15\text{‰}$  and  $<0.2\text{‰}$  for  $\delta^{15}\text{N}$  analyses.

*Stable isotope mixing models.* - Stable isotope mixing models are increasingly used to quantify consumer diets and estimate probability distributions of food resource contributions (see review by Phillips et al., 2014). There are increasingly more mixing model options (Hopkins and Ferguson, 2012; Phillips et al., 2014) and we elected to use Stable Isotope Mixing in R (SIAR). SIAR is a Bayesian stable isotope mixing model developed by Parnell et al. (2010) and is capable of accounting for concentration dependence (differences in elemental concentrations of C and N in the food resources). This is particularly important in our study because elemental concentrations vary among the potential food resources (particularly between invertebrates and plants) and could greatly influence mixing models if concentrations were not included (see Phillips and Koch, 2012; Phillips et al., 2014).

In addition to estimating rodent diets, we conducted stable isotope mixing models for graminivorous and polyphagous orthopterans. Orthopterans were abundant invertebrates and most particularly during summer trapping sessions and were most dramatically abundant during the summer of 2012. We wanted to determine diet estimates for orthopterans to gain a better understanding of how carbon is transferred through the food web and which carbon sources contribute to orthopteran diets and subsequently into invertivore diets. Orthopterans were divided into polyphagous (i.e. mixed vegetation consumers including a sagebrush and a Chenopodiaceae specialist) and graminivorous (i.e. grasses and/or sedges consumers) diet categories. The dietary sources were restricted to functional groupings described below for forbs/trees/shrubs,

C<sub>3</sub> graminoids, and C<sub>4</sub> graminoids. A mixing model was conducted for orthopterans captured in each macrohabitat and contained all possible data, including isotopic data from orthopterans and plants collected during all four trapping sessions.

We conducted isotope mixing models for *Peromyscus maniculatus* captured in the cottonwood riparian macrohabitat and models for *Dipodomys ordii* and *Onychomys leucogaster* in the sagebrush-grassland macrohabitat, which combines individuals captured within the South Cimarron and Sagebrush trapping grids but occupied the sagebrush-grassland macrohabitat. These three species were captured in adequate abundances and in multiple seasons allowing for sufficient overall and seasonal diet analyses. We conducted four mixing models with the first model incorporating all individuals for the three rodent species and food resources collected during the entire study as a general diet assessment. This broad scale model mimics analyzing a fossil assemblage composed of remains aggregated through space and time. Subsequent mixing models then partitioned analyses by species and macrohabitat (See Appendix X for model inputs).

Plant food resources were separated into C<sub>3</sub> and C<sub>4</sub> graminoids, FTS (forbs, trees, and shrubs), and plants with the CAM photosynthetic pathway. Plant food resources were composed of specimens from within each macrohabitat, but isotope values were again aggregated over time for each macrohabitat. Food availability may have changed throughout the year, but the most common and abundant plants remained constant and many seeds remain available after their growing season has passed. Plant production was stimulated by episodic precipitation throughout the year during the drought stricken years altering defined growing seasons. Furthermore, some rodents are known to cache seeds (e.g. *D. ordii*) and consume them throughout the year. Therefore, any uneven temporal distribution of seed production was likely minimized throughout the year.

The Invertebrate food resource for rodents was composed of invertebrates captured within the corresponding macrohabitat and individuals were aggregated across trapping seasons. Carbon and nitrogen isotope values for invertebrates did not differ among trapping sessions within macrohabitats, but did differ between the cottonwood and sagebrush-grassland macrohabitats, particularly with respect to nitrogen isotope values.

Within each diet analysis, all possible food resources are assumed to be included in the model, but potentially food resources may not have been included such as some invertebrates (e.g. nocturnal species, larvae, and spiders), rare plants that did not fall within our sampling scheme, or other possible food items (e.g. fungi and eggs). Plants and fungi in low abundances on the landscape are unlikely to contribute significant proportions to a consumer's overall diet relative to other available food sources. If egg predation does occur it is likely to be rare enough to not significantly contribute to the overall diet. We are confident that we have captured the majority of food resources that are readily available to small mammals in our trapping grids.

Diet-tissue discrimination factors are required inputs for the mixing models and SIAR allows different values to be applied to each food resource. Diet-tissue discrimination factors can be highly variable and species specific (Caut et al., 2009). Most discrimination factors (i.e.  $\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{diet}} = \Delta^{13}\text{C}$ ) are determined during feeding trials and/or based on monoculture diets, which may not entirely reflect wild populations. Small mammal diet-tissue discrimination factors are few and typically focus on soft tissues such as muscle, blood, or organs. Of our captured species, only *Peromyscus maniculatus* has been the subject of a diet-hair enrichment study (Miller et al., 2008). We combined data from multiple studies and calculated median  $\Delta^{13}\text{C}$  and  $\Delta^{15}\text{N}$  values and applied the same values to all food resources for all taxa (Table 1). All rodent taxa in this study were treated the same given the minimal data on discrimination factors. Therefore, we chose to use median values of  $1.1 \pm 2.6\text{‰}$  for carbon and  $2.6 \pm 1.8\text{‰}$  for nitrogen (Table 1). For the orthopteran mixing models, we again calculated median discrimination values based on published values in the literature and used values of  $1.3 \pm 2.6\text{‰}$  for carbon and  $2.1 \pm 2.4\text{‰}$  for nitrogen (Table 1).

Dietary proteins are preferentially routed towards synthesizing the consumer's proteinaceous tissues such as the structural proteins for hair keratin (Ambrose and Norr, 1993). Diet analyses may be biased towards protein rich resources, however elemental concentrations in diet resources account for some of this bias because protein sources (e.g. invertebrates) contain more nitrogen than most plant parts (e.g. leaves, stems, seeds). Another factor influencing isotope analyses is hair growth through time. Hair records an individual's isotopic composition at the time of synthesis and remains inert thereafter. Therefore, analysis of hair segments integrate isotope values over some length of time depending on hair lengths and growth rates. Mice undergo one or two



major molting periods in spring and/or fall and some XIT Ranch individuals were observed to be molting in October 2013. Some continuous hair growth has been observed between the two main molting periods in *P. maniculatus* (Collins, 1923; Tabacaru et al., 2011), indicating that hair is recording diet throughout the year. Molting periods for *D. ordii* were found to be extremely variable throughout the year and most occurring in July followed by more in October (Quay, 1953).

## RESULTS

*Trapping success and habitat associations.*- Rodent trap success varied among macrohabitats and seasons. The greatest trap success and abundances occurred in the cottonwoods macrohabitat (Table 2 and 3, Figure 2) reflecting high population abundances of *P. maniculatus* and its known trap-happy demeanor (Otis, 1975). Captures increased from summer 2012 and peaked in October 2013, which occurred after some rainfall returned and at the end of the annual growing season when rodent populations are likely to be at their highest because of food production throughout the growing season. Captures and trap success decreased in spring 2014, but still remained greater than summer 2012. *P. maniculatus* most commonly inhabited the cottonwoods riparian macrohabitat followed by other riparian areas. Additional *P. maniculatus* individuals were captured in the sagebrush-grassland macrohabitat in spring 2014. *D. ordii* and *O. leucogaster* were only captured within the sagebrush-grassland macrohabitat. These two species occurred in the Cottonwood Transition grid during the fall 2013 and spring 2014 trapping sessions, but were only captured within the sagebrush-grassland macrohabitat of the trapping grid.

*$\delta^{13}C$  and  $\delta^{15}N$  values.*- The  $\delta^{13}C$  and  $\delta^{15}N$  values for plants (Table 4) indicated that  $C_3$  and  $C_4$  plants were present in both main macrohabitats (cottonwoods and sagebrush-grassland). The cottonwoods by biomass are likely dominated by  $C_3$  plants, particularly cottonwood trees (*Populus deltoides*) that drop leaves, seeds, and woody branches that contribute to the underlying SOM. Sagebrush-grasslands are dominated by  $C_3$  sagebrush (*Artemisia filifolia*) and  $C_4$  grasses (*Bouteloua gracilis*, *Bouteloua dactyloides*, *Chloris verticillata*, *Panicum obtusum*, *Pascopyrum smithii*), but other  $C_3$  grasses are also common (*Bromus tectorum*, *Elymus canadensis*). Carbon isotope

analyses of SOM from soil pits confirmed our assumption that the cottonwood riparian macrohabitat, by biomass, has a greater C<sub>3</sub> component in comparison to the sagebrush-grasslands macrohabitat (Figure 3). SOM δ<sup>13</sup>C values become more positive with depth in both cottonwoods and sagebrush-grassland macrohabitats, which is a common feature of prairie soils (Johnson et al., 2011). In the top 30 cm of each profile, cottonwood soil has a δ<sup>13</sup>C value ~2.5‰ more negative than values from a similar depth in the sagebrush-grassland (Figure 3). The offset in δ<sup>13</sup>C values between the two soil profiles remains through the top 30 cm of the soil profiles. The δ<sup>15</sup>N values in the cottonwoods are more positive than those in the sagebrush-grassland, which indicates differences in baseline δ<sup>15</sup>N values that begin the trophic position ladder.

The difference in δ<sup>15</sup>N baselines also becomes evident when plotting isotopic values of all plants, invertebrates, and rodents (Figure 4). Combining data from all macrohabitats, *P. maniculatus* has more positive δ<sup>15</sup>N values than *O. leucogaster*. This differs from our expectation based on the published literature indicating that *O. leucogaster* should boast the most positive δ<sup>15</sup>N values because of its affinity for regular invertebrate consumption. However, *P. maniculatus* was captured in the cottonwood riparian macrohabitat, which had the more positive δ<sup>15</sup>N baseline than the sagebrush-grassland where *O. leucogaster* was captured. This illustrates the importance of normalizing consumer δ<sup>15</sup>N values with either median plant values or the uppermost SOM.

*Stable isotope mixing models.* - We first conducted mixing models for herbivorous orthopterans that a potential food source for rodents and a possible energy flow intermediate between plants and rodents. Diet estimates for graminivorous orthopterans indicate their diets are composed mostly of C<sub>3</sub> or C<sub>4</sub> graminoids and supplemented by FTS and their diets do not differ between those captured in the cottonwood riparian versus those in the sagebrush grassland (Figure 5). FTS plants and C<sub>3</sub> graminoids make up the majority of polyphagous orthopteran diets and almost exclusively in the cottonwood riparian macrohabitat (Figure 5 and Appendix VI). However, C<sub>4</sub> graminoids contribute more to polyphagous diets in the sagebrush-grassland at the expense of the FTS diet source. Also of interest is the difference between the more positive δ<sup>15</sup>N values in orthopterans from the cottonwood riparian macrohabitat versus the sagebrush grassland (Figure 5, Appendix VI, and Table 4). This is the same pattern found in rodent nitrogen isotope values (Figure 4) and plant values grouped by macrohabitat (Table 4).

The modeled diet estimates for rodents vary by species, macrohabitat, and time (Figure 6 and Appendix VII). *P. maniculatus* diets in 2012 were composed of mostly FTS and C<sub>3</sub> graminoids followed by equal proportions of the three invertebrate groups (Figure 6). *P. maniculatus* individuals increased C<sub>4</sub> graminoid and CAM consumption from summer 2012 to spring 2014 while FTS and C<sub>3</sub> graminoids became less important over that time period. Estimates for invertivore consumption varied among all trapping sessions with no apparent trend through time.

Within the sagebrush-grassland, *O. leucogaster* invertebrate consumption remained constant through time relative to estimates for *P. maniculatus* and *D. ordii* (Figure 6). Polyphagous orthopterans and other invertebrates were favored for consumption over graminivorous orthopterans. Consumption of FTS plants and C<sub>3</sub> graminoids decreased through time potentially in favor of more C<sub>4</sub> graminoids or CAM plants.

Diet estimates for *D. ordii* indicate C<sub>4</sub> graminoids and CAM plants consistently make up diet and their consumption increased through time (Figure 6, Appendix VII). C<sub>3</sub> plant consumption (FTS and C<sub>3</sub> graminoids) decreased through time and was generally less than 10% throughout the duration of the study. Invertebrate consumption also decreased through time except for consumption of graminivorous grasshoppers, which was constant except for low consumption in spring 2014.

Isotope mixing models for *Chaetodipus hispidus*, *Reithrodontomys megalotis*, *Neotoma micropus*, *Xerospermophilus spilosoma*, and *Lepus californicus* were not conducted because of their small sample sizes and attempts to estimate food resource contributions resulted in indistinguishable estimates for all resources. Therefore, our discussion focuses on the habitat associations and isotope mixing models for *P. maniculatus*, *O. leucogaster*, and *D. ordii*.

## DISCUSSION

*Habitat associations.*- Hallet (1982) found no significant habitat associations for *P. maniculatus*, and given its extensive geographic distribution across most of North America, populations can be found in many different habitats. The localized spatial distribution of *P. maniculatus* individuals on the XIT Ranch may be a response to the severe 2012 drought that significantly reduced primary productivity in the region

(Hoerling et al., 2014). *P. maniculatus* populations may have retracted and sought refuge within the cottonwood macrohabitat that is abundant in fallen logs, leaves, and other vegetation that provide beneficial resources such as canopy cover (protection from predators), nesting sites, or food resources. The population within the cottonwood macrohabitat increased as precipitation returned. As precipitation returned to the area, primary productivity (i.e. food availability) in the sagebrush-grassland macrohabitat increased and potentially provided more food, nesting, and canopy cover resources that were suitable for *P. maniculatus*. More *P. maniculatus* in later trapping sessions were captured in the sagebrush-grassland macrohabitat, but still in low abundances and we hypothesize that once drought conditions are relieved that *P. maniculatus* individuals will inhabit the sagebrush-grassland.

*D. ordii* was exclusively captured within the sagebrush-grassland macrohabitat and agrees with previous studies identifying their preference for shrubs and open habitat for quick movement (Hallett, 1982, Cramer and Willig, 2002). Open habitats are preferred by *D. ordii* during summer months to potentially avoid predation by snakes, which are most active during the summer (Cramer and Willig, 2002). Furthermore, *D. ordii* typically inhabit sandy-loam soils that permit easy extensive burrowing ( $253 \pm 233$  cm deep, Reynolds and Wakkinen, 1987; Alcoze and Zimmerman, 1973) required for protection from predators and harsh weather conditions of extreme hot-dry summers and cold winters.

*D. ordii* and *O. leucogaster* were both found exclusively in the sagebrush-grassland macrohabitat. Interspecific interactions among rodents may cause individuals to deviate from their preferred habitats in addition to other predatory pressures from snakes or raptors, for example. Rebar and Conley, (1983) suggested *O. leucogaster* may force *D. ordii* into more open habitats, however both species co-occurred in the open sagebrush-grasslands in our study. Whether competition between the two species or predation by *O. leucogaster* on *D. ordii* produced the previously observed patterns, their overlapping distributions found on the XIT Ranch suggests minimal to no negative interactions between the two species. Moreover, our diet analyses (see below) bolsters this assessment evidenced by *O. leucogaster* focused on consuming more invertebrates and  $C_3$  plants than *D. ordii*, which consumed mostly  $C_4$  graminoids, CAM plants, and a minor component of invertebrates. While *D. ordii* and *O. leucogaster* diets do not substantially overlap (in isotope space or in diet estimates), future diet studies for each

species without the presence of the other are needed to fully address interspecific competition between *D. ordii* and *O. leucogaster*.

*Stable isotope values.* – Our field study contains, as predicted, a mixture of C<sub>3</sub> and C<sub>4</sub> plants evidenced by their carbon isotope values that are distinctly different. Interestingly, the CAM plants plot within only C<sub>4</sub> isotope space, when we would typically expect them to lie between the C<sub>3</sub> and C<sub>4</sub> endmembers. The similar carbon isotope values for C<sub>4</sub> graminoids and CAM plants may influence the mixing models by attributing a greater proportion to the CAM plants that might otherwise be attributed to C<sub>4</sub> graminoids. However, the CAM plants have a more positive  $\delta^{15}\text{N}$  value that also would help differentiate between the two resources in the diet models.

Differences in baseline  $\delta^{15}\text{N}$  values have been documented in aquatic (e.g. Vander Zanden, and Rasmussen, 1999; Post, 2002; Casey and Post, 2011) and terrestrial systems (e.g. Casey and Post, 2011; Woodcock et al, 2012; Korobushkin et al., 2014). In our study there are distinct differences in  $\delta^{15}\text{N}$  values between plants, SOM, and consumers from the two macrohabitats. Directly comparing  $\delta^{15}\text{N}$  values between macrohabitats can result in misleading interpretations of trophic position if the baseline  $\delta^{15}\text{N}$  value is not considered for each macrohabitat. In this study, *P. maniculatus* would be at a higher trophic position than *O. leucogaster*, which is known to be an invertivore. *P. maniculatus* may consume comparable amounts of invertebrates, their diets are more variable based on available food resources. Additionally, the orthopterans in our study would be placed at different trophic positions even though they are all herbivores and should be at the same trophic position. For these reasons, researchers must be careful about indicating trophic position without considering the isotopic baseline. The median value of food resources (i.e. stable isotope mixing models), plants (Woodcock et al., 2012), or leaf litter (Korobushkin et al., 2014) can be used to normalize  $\delta^{15}\text{N}$  values in terrestrial ecosystems, however these can require multiple samples and may be seasonally biased. We suggest that the  $\delta^{15}\text{N}$  value of the uppermost SOM could also be used to normalize consumer values for a macrohabitat because SOM integrates organic input from the overlying vegetation and provides an averaged value across seasons.

*Mixing models.*– Overall, orthopteran diet estimates indicate the different feeding strategies of graminivorous and polyphagous orthopterans. Graminivorous orthopterans focused on consuming graminoids (both C<sub>3</sub> and C<sub>4</sub>) and potentially also various portions

of forbs/trees/shrubs. Polyphagous orthopterans were expected to eat a variety of plant resources and results indicate they focused on consuming forbs/tree/shrubs and C<sub>3</sub> graminoids and consumed more C<sub>4</sub> graminoids in the sagebrush-grassland where C<sub>4</sub> plants were more abundant. With respect to their position in the food web, orthopteran consumers are the first level of integrating C<sub>3</sub> and C<sub>4</sub> derived resources given most individuals have  $\delta^{13}\text{C}$  values intermediate between C<sub>3</sub> and C<sub>4</sub> plants (Figure 4). There is still some isotopic separation between graminivorous and polyphagous orthopterans, but the difference is diminished relative to the difference of C<sub>3</sub> and C<sub>4</sub> mean  $\delta^{13}\text{C}$  values. Presumably, invertivores (e.g. *O. leucogaster*) would then integrate C<sub>3</sub> and C<sub>4</sub> derived resources again by consuming invertebrates in addition to directly consuming plant matter.

Stable isotope mixing models estimate our three focal taxa have different overall diets and respond to food resource availability in different ways. *P. maniculatus* has the most variable diet by consuming variable proportions of all seven food resources throughout the study period. *P. maniculatus* increased C<sub>4</sub> consumption throughout the study and generally consumed more C<sub>4</sub> plants than C<sub>3</sub> plants each trapping session except in summer 2012. Increased C<sub>4</sub> consumption may be from *P. maniculatus* using habitat edges along the cottonwood riparian macrohabitat where seeds may consolidate after being blown in from the open sagebrush-grassland providing highly accessible seeds (Cramer and Willig, 2002; Lobo et al., 2013). C<sub>4</sub> plant consumption may also have increased as C<sub>4</sub> seed availability increased when precipitation returned to the region following the 2012 severe drought. *P. maniculatus* consumed their greatest proportion of C<sub>4</sub> plants (largest increase in C<sub>4</sub> graminoids) in spring 2014, which reflects late winter/early spring diets when seed caches are heavily relied upon because plant foliage and invertebrate availabilities are low (Flake, 1973). Given low invertebrate availability in the spring, a decrease in invertebrate consumption was expected for *P. maniculatus*, and our mixing model estimates invertebrate consumption decreased between fall 2013 and spring 2014 except for graminivorous grasshoppers, which isotopically overlap with C<sub>4</sub> graminoids leaving the potential for misappropriation between the two sources.

*P. maniculatus* diets were expected to be variable based on previous research (Flake, 1973 and therein Hamilton (1941), Jameson (1952), Williams (1959), Johnson (1961), and Whitaker (1966)) that suggest *P. maniculatus* to be a highly opportunistic forager that eats the most readily available plant and animal matter. The model

estimates for invertebrate consumption by *P. maniculatus* are similar to proportions (37% animal) calculated by Flake (1973) based on the stomach contents of individuals from a short-grass prairie in eastern Colorado (Pawnee National Grassland) (See Table 5). Furthermore, the variable diets exhibits by *P. maniculatus* in Meade, Kansas additional research that suggest *P. maniculatus*' highly variable diet may contribute to its widespread geographic distribution (i.e. Williams, 1956; Flake, 1973). Their generalist lifestyle and diet may buffer their susceptibility to extreme climate events or prolonged environmental change that may persist for tens to thousands of years. Documenting *P. maniculatus* as a generalist using stable isotopes is important for recognizing possible generalists in the fossil record to study how they coped with shifting biomes and food resources through time.

*O. leucogaster* diets were dominated by the three invertebrate food sources and supplemented by various mixtures of C<sub>3</sub> and C<sub>4</sub> plants. Invertebrate consumption varied around 20% for polyphagous orthopterans and other invertebrates, while graminivorous orthopterans contributed about another 10%. A diet composed of ~50% invertebrates corroborates similar estimates from *O. leucogaster* stomach contents that estimated their diet to be 60% animal (Flake, 1973; Best et al., 1993; Hope and Parmenter, 2008) (See Table 5). During the duration of the study *O. leucogaster* diets did not reduce the overall amount of invertebrate contribution in their diets, including in the spring when a invertebrate consumption was expected to decrease (Flake, 1973). However, small increases in C<sub>4</sub> graminoid and CAM consumption may indicate increase seed dependence during the winter and early spring when invertebrate and new plant growth are low.

The granivorous *D. ordii* has be documented to consume seeds in proportions that deviate from seed availabilities on the landscape suggesting seed preferences (Alcoze and Zimmerman, 1973). *D. ordii* diets were relatively constant with C<sub>4</sub> graminoids and CAM plants being the most important components and increased during the study period. Contributions of polyphagous and other invertebrates contributed little to *D. ordii* diets, however graminivorous orthopterans were estimated to contribute an average of ~20% each trapping session, which is greater than the 4.4% Hope and Parmenter (2007) found based on stomach contents of individuals in New Mexico. The discrepancy between diet estimates may be the result of C<sub>4</sub> graminoids and granivorous orthopterans having some overlap in isotope space leading to some misallocation of diet

sources. Alternatively, there may be a difference because hair and stomach contents are recording different portions of an individual's diet. Stomach contents include all foods most recently consumed, but does not differentiate between bulk diet and protein diet. Hair is a protein that most closely reflects an individual's protein diet because of preferential routing of dietary proteins into the consumer's protein synthesis (Ambrose and Norr, 1993). The greater proportion of diet allocated to graminivorous invertebrates could be the result of invertebrates providing a high protein diet source, which is then preferentially routing into protein synthesis, such as keratin. This helps illustrate that a resource may contribute little to a species' bulk diet, but its nutritional value meet an individual's nutritional requirements.

All three taxa increased C<sub>4</sub> consumption and decreased C<sub>3</sub> consumption over the course of our study (Figure 5). This shared pattern may be a community-wide dietary response to severe drought that peaked in 2012. We cannot determine if individuals were selecting more C<sub>3</sub> during the severe drought period because of food availability, habitat use, or altered competition pressures without detailed measurements for these covariates or diet analyses before the drought occurred. However, our data illustrate the importance for future long-term (>10 years) studies to capture dietary responses to short term climate events (i.e. 2012 drought) and deep time records to capture global climate changes.

*Diets as indicators of habitat.*- The cottonwood macrohabitat contains a greater input of C<sub>3</sub>-derived organic matter into the soil because of the prominent cottonwood trees and a mixed understory of C<sub>3</sub> forbs, shrubs graminoids, and C<sub>4</sub> graminoids. The SOM δ<sup>13</sup>C values indicate a greater input of C<sub>3</sub> vegetation biomass into the soil in the cottonwood macrohabitat than in the sagebrush-grassland (Figure 3). C<sub>3</sub> and C<sub>4</sub> plants occur in both macrohabitats providing food resources derived from both C<sub>3</sub> and C<sub>4</sub> plants and consumer diets, both orthopterans and rodents, utilize diet resources that are derived from both C<sub>3</sub> and C<sub>4</sub> plants.

Diets in the cottonwood macrohabitat were hypothesized to reflect a greater proportion of C<sub>3</sub> plant biomass relative to diets in the sagebrush-grassland. The rodent diets estimated here do not distinctly reflect their respective macrohabitats. *D. ordii* is likely the best indicator of its environment with its high consumption of C<sub>4</sub> plants, which would be expected for the sagebrush-grassland environment. Future research should include more locations that vary in the relative proportions of C<sub>3</sub>:C<sub>4</sub> biomass on the



landscape to further test whether *D. ordii* diets reflect the relative proportions of C<sub>3</sub>:C<sub>4</sub> biomass on the landscape. *O. leucogaster* and *P. maniculatus* both consumed a greater proportion of invertebrates than *D. ordii* resulting in intermediate  $\delta^{13}\text{C}$  values between plants using the C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways. Invertivory integrates more C<sub>3</sub> and C<sub>4</sub> derived resources resulting in intermediate  $\delta^{13}\text{C}$  values in comparison to a folivores or granivores that may focus more on C<sub>3</sub> or C<sub>4</sub> plants. Furthermore, invertebrates are also integrating plant resources that use the C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways before being potentially consumed by a predatory rodent. For instance, the standard deviation of graminivorous orthopterans  $\delta^{13}\text{C}$  values in the sagebrush grassland is 4.1‰, while the standard deviation of *O. leucogaster*  $\delta^{13}\text{C}$  values is 2.3‰, which aligns with isotopic differences among generalists being smaller than among populations of specialists because of the integration and averaging of multiple sources over space and time (Bearhop et al., 2004; Flaherty and Ben-David, 2010).

Without  $\delta^{15}\text{N}$  values as our trophic position indicator, our intermediate  $\delta^{13}\text{C}$  values could have been interpreted as a mixed diets of direct C<sub>3</sub> and C<sub>4</sub> plant consumption. Interpreting diet types with only  $\delta^{13}\text{C}$  values in modern and fossil studies must be interpreted with caution and combining multiple diet metrics is the best practice to interpret diet categories with confidence.

*Implications for Fossil Record.*- As an analog for interpreting similar data from the fossil record, our results illustrate the importance of modern calibrations in order to interpret similar data from the fossil record. Fossil assemblages are comprised of faunal remains which may be transported some distance and accumulated over time, but can represent the immediate environments around the fossil locality during deposition (Terry, 2010). Using habitat associations documented in the modern, we can disentangle the multiple macrohabitats integrated within the fossil assemblage. Here, we determined that *D. ordii* and *O. leucogaster* preferred open sage-brush grasslands to the cottonwoods, while *P. maniculatus* was most commonly found in the cottonwoods. Our study was limited to one ecosystem within the geographic ranges of the observed species and additional habitat associations throughout a species' geographic range must be included to encompass all habitats that a species may occupy in the past, present, or future. Sampling small mammals across a region may provide greater insight into diet variation along environmental gradients and in turn permit small mammal diets to indicate their environments.

## CONCLUSION

The sagebrush-grassland and cottonwood macrohabitats differed in their baseline  $\delta^{15}\text{N}$  values evidenced by average  $\delta^{15}\text{N}$  values in plants and uppermost SOM. The difference between  $\delta^{15}\text{N}$  baselines signifies that consumer nitrogen values must be normalized before comparisons can be made among macrohabitats. Consumer  $\delta^{15}\text{N}$  values can be normalized by subtracting the local median plant or uppermost SOM value. Alternatively, diet estimates via stable isotope mixing models are comparable among locations because baseline  $\delta^{15}\text{N}$  variability is incorporated within the diet sources.

We have used stable isotopes to characterize the variable diet of a generalist, (*P. maniculatus*), constant diet of an invertivore, (*O. leucogaster*), and a granivorous diet (*D. ordii*) of  $\text{C}_4$  graminoids and CAM plants. *P. maniculatus* occupied a different habitat than *O. leucogaster* and *D. ordii* during our trapping period, but  $\delta^{13}\text{C}$  values among the three taxa did not vary in relation to proportions of  $\text{C}_3:\text{C}_4$  plant biomass in their respective macrohabitats. Invertivory by *P. maniculatus* and *O. leucogaster* integrate multiple resources on the landscape, resulting in intermediate carbon isotope values. *D. ordii* boasted the most positive  $\delta^{13}\text{C}$  values, which may be indicative of the  $\text{C}_4$ -dominated grassland, but a larger spatial scale and variable proportions of  $\text{C}_3:\text{C}_4$  biomass need to be considered in order to further determine if small mammal diets reflect their habitats in regards to carbon isotopes.

Table 1.- Summary of diet-hair discrimination values for rodents and orthopterans based on published literature.

<b>Taxon</b>	<b><math>\Delta^{13}\text{C}</math></b>	<b><math>\Delta^{15}\text{N}</math></b>	<b>Reference</b>
<b>Rodentia</b>			
<i>Clethrionomys gapperi</i>	2.4	2.8	Sare et al. (2005)
<i>Meriones unguiculatus</i>	1.9		Tieszen et al. 1983
<i>Meriones unguiculatus</i>	2.6		Tieszen et al. 1983
<i>Mus musculus</i>	1.1	3.1	DeNiro & Epstein 1978 (C), 1981 (N)
<i>Mus musculus</i>	0.4	1.5	DeNiro & Epstein 1978 (C), 1981 (N)
<i>Mus musculus</i>	1.7	3.2	DeNiro & Epstein 1978 (C), 1981 (N)
<i>Peromyscus leucopus</i>	-1.1	2.9	Demots et al 2010
<i>Peromyscus leucopus</i>	-1.2		Demots et al unpublished (C3 only diet)
<i>Peromyscus leucopus</i>	0.1		Demots et al unpublished (C3 only diet)
<i>Peromyscus maniculatus</i>	0.3	3.3	Miller et al. (2008)
<i>Rattus norvegicus</i>	3.4	2.4	Kurle et al (2014)
<i>Rattus norvegicus</i>	2.1	3.9	Kurle et al (2014)
<i>Rattus norvegicus</i>	2.3	2.9	Kurle et al (2014)
<i>Rattus norvegicus</i>	4.1	2.6	Kurle et al (2014)
<i>Rattus sp.</i>	-2.1	-1.5	Caut et al. 2008
<i>Rattus sp.</i>	-0.6	4.1	Caut et al. 2008
<i>Rattus sp.</i>	-4.2	-1.0	Caut et al. 2008
<i>Rattus sp.</i>	-0.6	-1.0	Caut et al. 2008
<i>Rattus sp.</i>	-4.2	2.1	Caut et al. 2008
<i>Rattus sp.</i>	-2.6	-0.3	Caut et al. 2008
<b>Median</b>	<b>1.1</b>	<b>2.6</b>	
<b>Stdev</b>	<b>2.6</b>	<b>1.8</b>	
<b>n</b>	<b>20</b>	<b>16</b>	
<b>Orthoptera</b>			
<i>Melanoplus sanguinipes</i>	1.6	1.69	DeNiro & Epstein 1978 (C), 1981 (N)
<i>Melanoplus sanguinipes</i>	3.2	-0.75	DeNiro & Epstein 1978 (C), 1981 (N)
<i>Locusta migratoria</i>	-2.5	5.05	Weeb et al. 1998
<i>Locusta migratoria</i>	2.75	2.28	Weeb et al. 1998
<b>Median</b>	<b>1.3</b>	<b>2.1</b>	
<b>Stdev</b>	<b>2.6</b>	<b>2.4</b>	
<b>n</b>	<b>4</b>	<b>4</b>	

Table 2.- Summary of small mammal trapping for four sessions. Cap = Captures; TN = Trapnights; Trap Success = (Cap/TN)\*100

Trapping Grid	2012 Summer			2013 Summer			2013 Fall			2014 Spring		
	Cap	TN	Capture Success (%)	Cap	TN	Capture Success (%)	Cap	TN	Capture Success (%)	Cap	TN	Capture Success (%)
South Cimarron	11	388	2.8	8	138	5.8	10	150	6.7	11	190	5.8
Sagebrush				10	180	5.6	18	180	10.0	17	210	8.1
Cottonwoods Tran.	14	336	4.2	13	163	8.0	30	180	16.7	13	150	8.7
River Plains				1	120	0.8	2	150	1.3			
River Transect	2	68	2.9									
Cottonwood Stand	0	48	0.0									
<b>All Grids per year</b>	<b>27</b>	<b>840</b>	<b>3.2</b>	<b>32</b>	<b>601</b>	<b>5.5</b>	<b>60</b>	<b>670</b>	<b>9.4</b>	<b>41</b>	<b>550</b>	<b>7.4</b>

Table 3 – Summary of small mammal species captured during four trapping sessions. CT = Cottonwood Transition; SC = South Cimarron; RT = River Transect; RP = River Plains; SB = Sagebrush; Rd = Road; CN = Cohen

	2012			2013 Summer					2013 Fall					2014 Spring					Total Sum	
	CT	SC	RT	CT	SC	RP	SB	Rd	SB	SC	CT	RP	Rd	SB	SC	CT	RP	Rd		CN
<i>Chaetodipus hispidus</i>	1	3								1									2	7
<i>Cynomys ludovicianus</i>																				0
<i>Dipodomys ordii</i>		2			7		5		6	2			2	10	5	3				42
<i>Neotoma micropus</i>	1								1											2
<i>Onychomys leucogaster</i>		4			1		5	1	9	7	3		1	5	3	2			2	43
<i>Peromyscus maniculatus</i>	12	2	2	13					1		27	2		2	3	8			12	84
<i>Reithrodontomys megalotis</i>						1													6	7
<i>Sigmodon hispidus</i>																			13	13
<i>Xerospermophilus spilosoma</i>									1											1
<b>Total Sum</b>	<b>14</b>	<b>11</b>	<b>2</b>	<b>13</b>	<b>8</b>	<b>1</b>	<b>10</b>	<b>1</b>	<b>18</b>	<b>10</b>	<b>30</b>	<b>2</b>	<b>3</b>	<b>17</b>	<b>11</b>	<b>13</b>	<b>0</b>	<b>0</b>	<b>35</b>	

Table 4 – Summary statistics for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of food resources used as inputs for diet mixing models. All values are relative to VPDB and atmospheric  $\text{N}_2$  for carbon and nitrogen isotopes, respectively.

INVERTEBRATES		Diet Category	N	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		wt% C		wt% N	
				$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$
<b>Cottonwoods (CT)</b>											
	Other invertebrates	C,N,P,Py	3	-25.1	3.5	8.1	2.0	49.4	4.7	12.4	2.2
	Orthoptera - graminivorous	G	14	-18.7	3.2	5.4	1.8	45.2	5.8	14.0	2.0
	Orthoptera - polyphagous*	Py (Ch,Sa)	8	-24.2	2.1	7.2	2.4	42.6	4.4	12.5	1.9
<b>Sagebrush-grassland (SC/SB)</b>											
	Other invertebrates	C,N,P,Py	7	-18.7	3.3	7.0	3.1	46.2	6.9	13.0	1.7
	Orthoptera - graminivorous	G	10	-17.1	4.1	2.1	1.5	44.9	4.3	14.0	2.2
	Orthoptera - polyphagous*	Py (Ch,Sa)	20	-23.1	1.6	3.6	0.9	45.3	5.0	13.8	2.2
<b>All macrohabitats</b>											
	Other invertebrates	C,N,P,Py	10	-20.6	4.4	7.3	2.7	47.2	6.3	12.9	1.8
	Orthoptera - graminivorous	G	24	-18.1	3.6	4.0	2.4	45.1	5.1	14.0	2.1
	Orthoptera - polyphagous*	Py (Ch,Sa)	28	-23.4	1.8	4.6	2.2	44.5	4.9	13.4	2.2
PLANTS		Functional Group	N	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		wt% C		wt% N	
				$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$
<b>Cottonwoods (CT)</b>											
	Forbs/Trees/Shrub		37	-26.2	4.6	4.7	2.1	41.6	4.3	3.0	1.0
	C <sub>3</sub> graminoids		8	-25.0	3.1	3.7	1.2	39.9	3.9	2.3	0.8
	C <sub>4</sub> graminoids		15	-14.0	0.6	2.2	1.9	41.0	2.3	2.0	1.0
	CAM		2	-13.0	0.1	6.3	1.3	41.7	2.8	2.2	0.3
<b>Sagebrush-grassland (SC/SB)</b>											
	Forbs/Trees/Shrub		45	-26.7	2.6	1.9	2.2	43.2	3.4	2.5	1.0
	C <sub>3</sub> graminoids		7	-26.7	2.1	0.7	1.8	41.4	2.3	2.1	0.9
	C <sub>4</sub> graminoids		13	-14.3	0.9	0.2	1.8	41.2	1.7	1.8	0.8
	CAM		2	-12.8	1.0	1.1	1.4	43.1	9.5	0.8	0.3
<b>All macrohabitats</b>											
	Forbs/Trees/Shrub		82	-26.4	3.6	3.2	2.5	42.5	3.9	2.8	1.0
	C <sub>3</sub> graminoids		15	-25.8	2.7	2.3	2.1	40.6	3.2	2.2	0.8
	C <sub>4</sub> graminoids		28	-14.1	0.7	1.2	2.1	41.1	2.0	1.9	0.9
	CAM		4	-12.9	0.6	3.7	3.2	42.4	5.8	1.5	0.8

Table 5. – Stomach content data summarized for *D. ordii*, *P. maniculatus*, and *O. leucogaster* summarized from published literature. The %Plant category is a combination of %Seed and %GVeg (green vegetation). Percentages are relative to all contents found within the stomach and may not summate to 100% because some material may have been unidentifiable.

<b>Species</b>	<b>N</b>	<b>% Animal</b>	<b>% Plant</b>	<b>% Seed</b>	<b>% GVeg</b>	<b>Source</b>
<i>D. ordii</i>	249	4.4	99.5	16.4	83.1	Flake, 1973; Hope and Parmenter, 2007
<i>P. maniculatus</i>	667	34.7	54.1	11.5	42.6	Williams, 1959; Flake, 1973
<i>O. leucogaster</i>	304	60.8	32.5	22.4	10.0	Flake, 1973; Hope and Parmenter, 2007

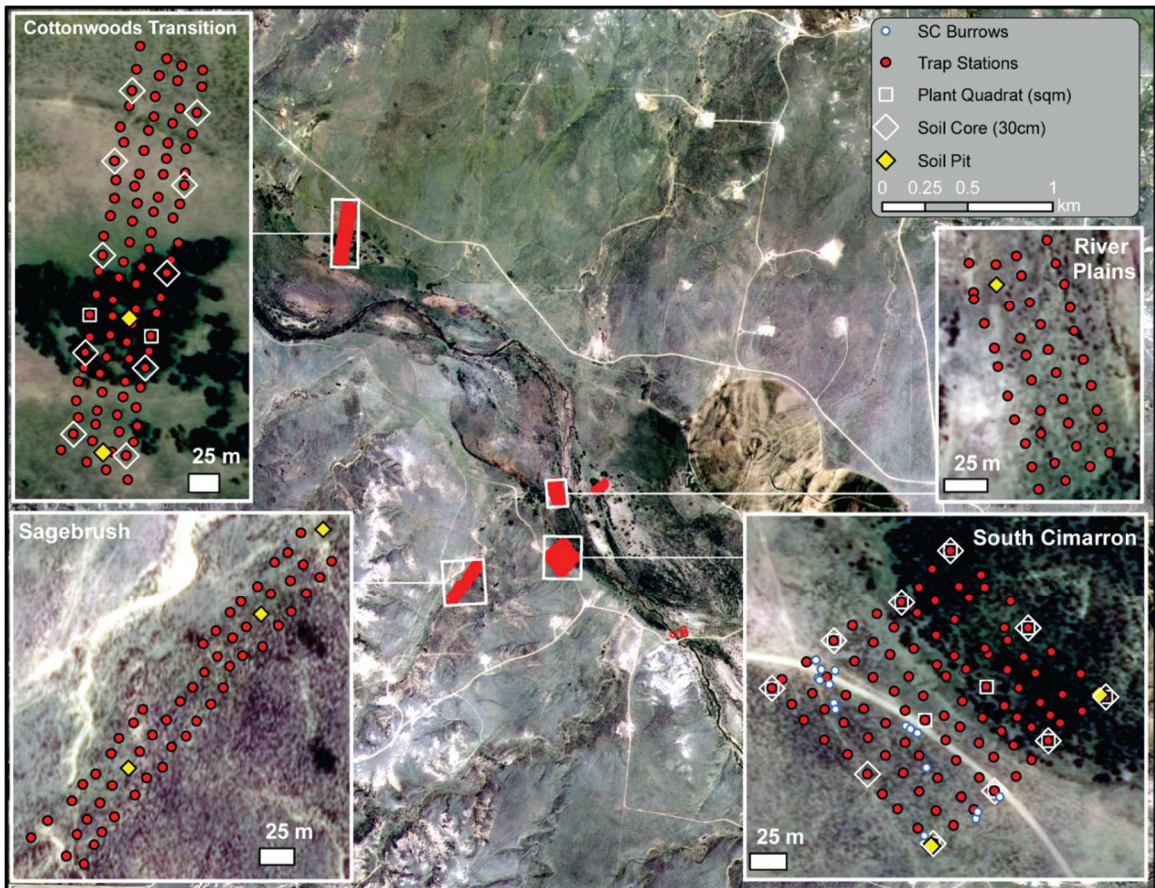


Figure 1 – Locality map of XIT Ranch study area in southwest Kansas (Meade County) and the various trapping grids distributed on the landscape.



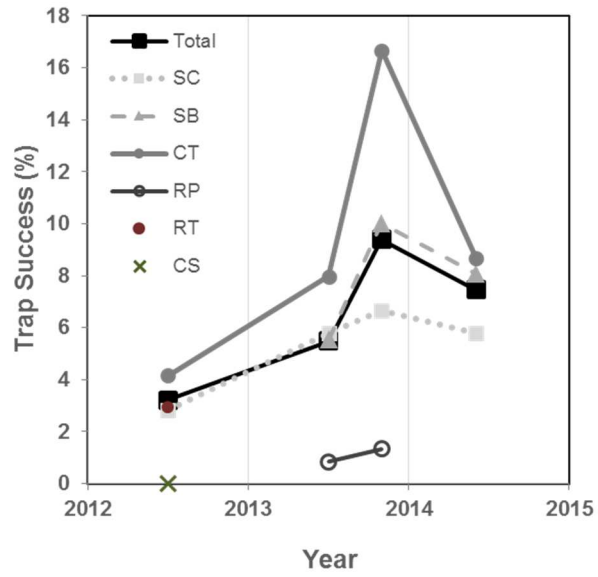


Figure 2 – Trap success (see Table 2) from four field sessions at XIT Ranch. Trapping grids labeled as CS = Cottonwood Stand; RT = River Transect; RP = River Plains; CT = Cottonwood Transition; SB = Sagebrush; SC = South Cimarron; and Total = data combining all trapping grids.

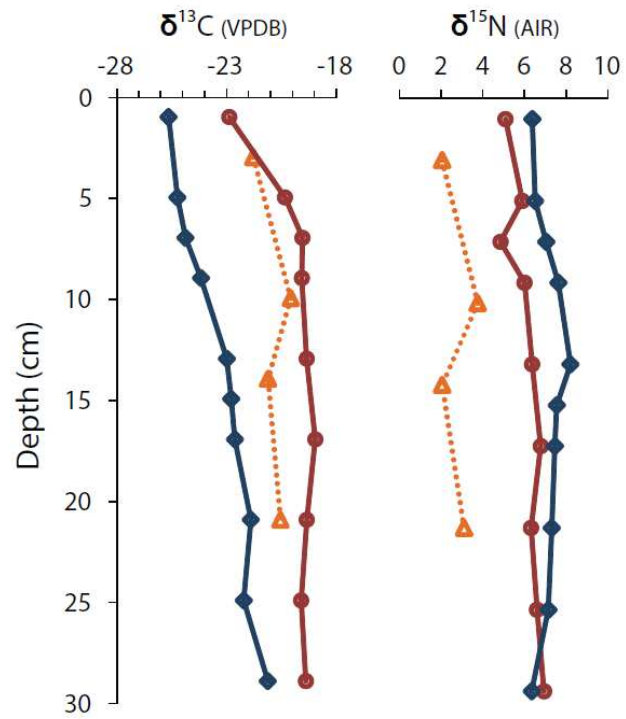


Figure 3 –Soil organic matter (SOM)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  profiles of three soil pits within sagebrush-grassland (red circles), riparian tamarisk-grassland (orange triangles), and cottonwood (blue diamonds) macrohabitats.

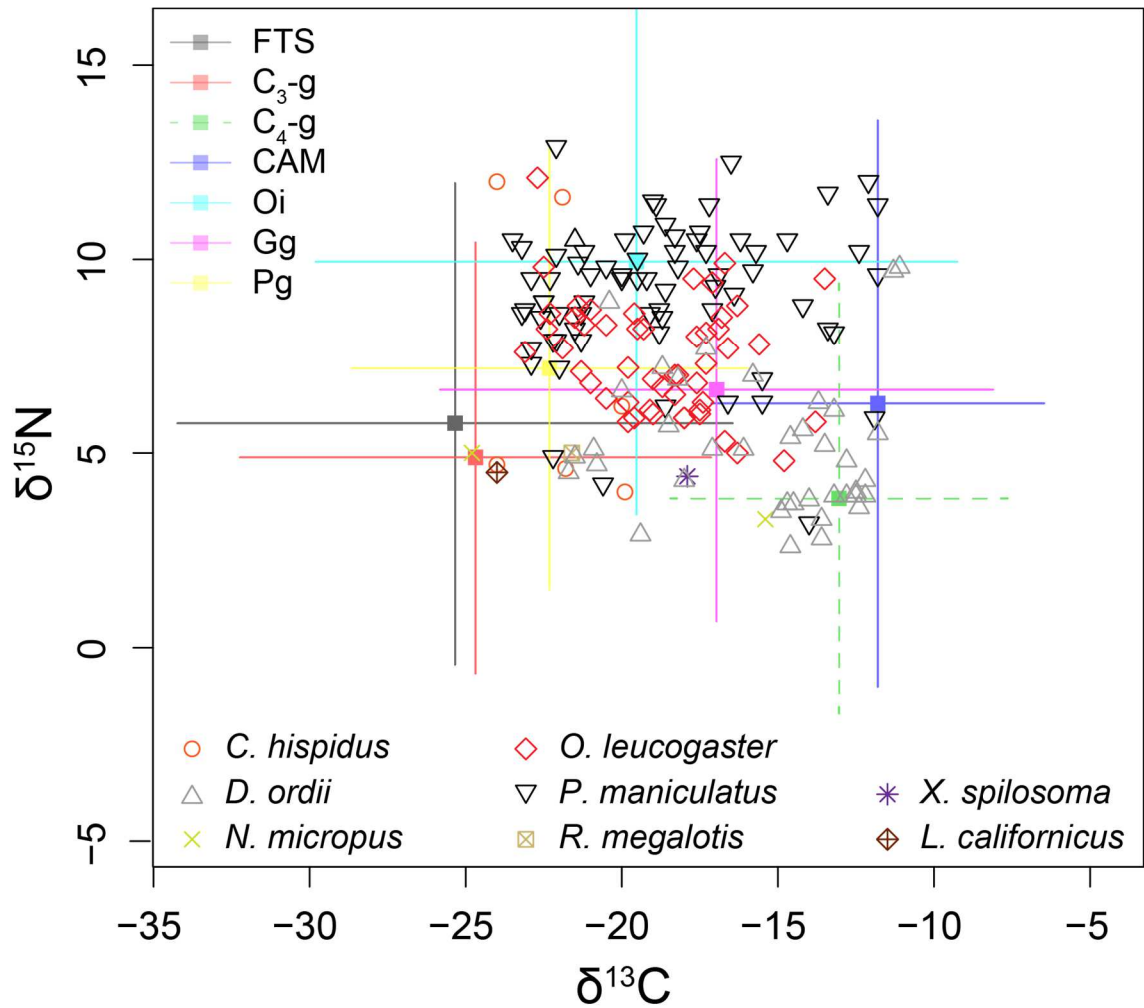


Figure 4 –  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  hair values of all Individuals and all species captured at XIT Ranch, KS and their diet resources (solid symbols). The mean  $\pm$  95% credible intervals of each source are plotted and sources (top left) are FTS = Forbs, Trees, and Shrubs; C<sub>3</sub>-g = C<sub>3</sub>-graminoids; C<sub>4</sub>-g = C<sub>4</sub>-graminoids; CAM = Crassulacean Acid Metabolism; Oi = Other invertebrates; Gg = Graminivorous grasshoppers; Pg = Polyphagous grasshoppers. Note: diet resources are plotted in rodent isotope space.

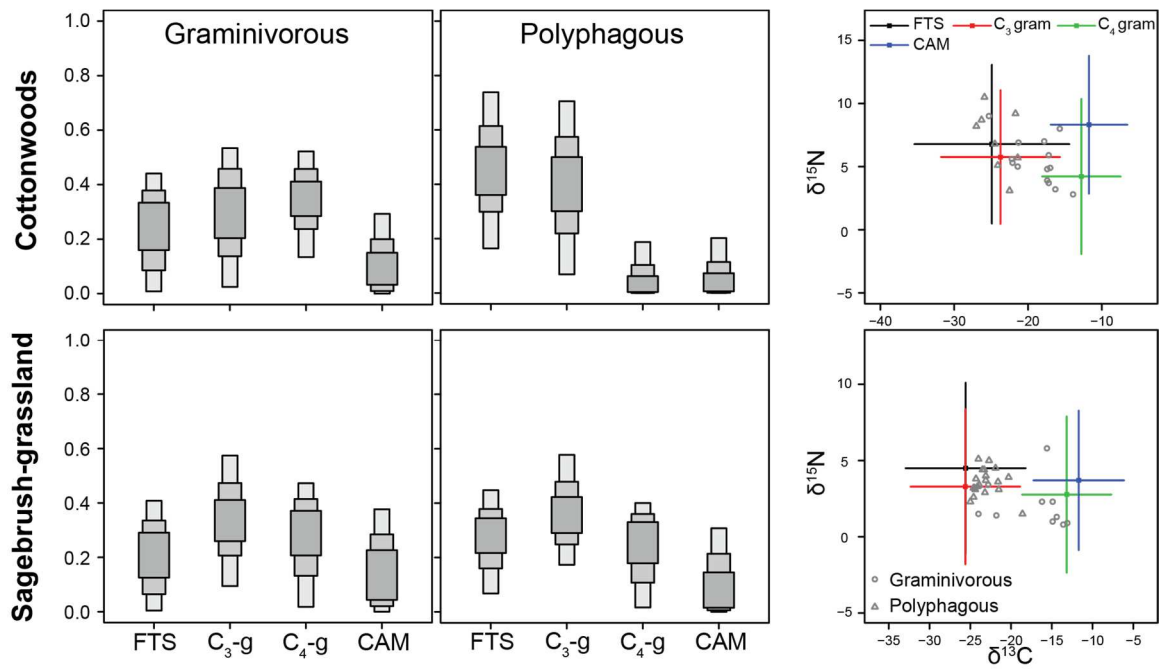


Figure 5 - Results of stable isotope mixing models for graminivorous and polyphagous orthopterans captured in the cottonwoods (top row) and sagebrush-grassland (bottom row) macrohabitats. 95% credible intervals are grouped by potential diet resources. Scatterplots (far right) of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for consumers (gray open symbols) and the mean  $\pm$  95% credible intervals of their potential food sources (source abbreviations are the same as in Figure 4).

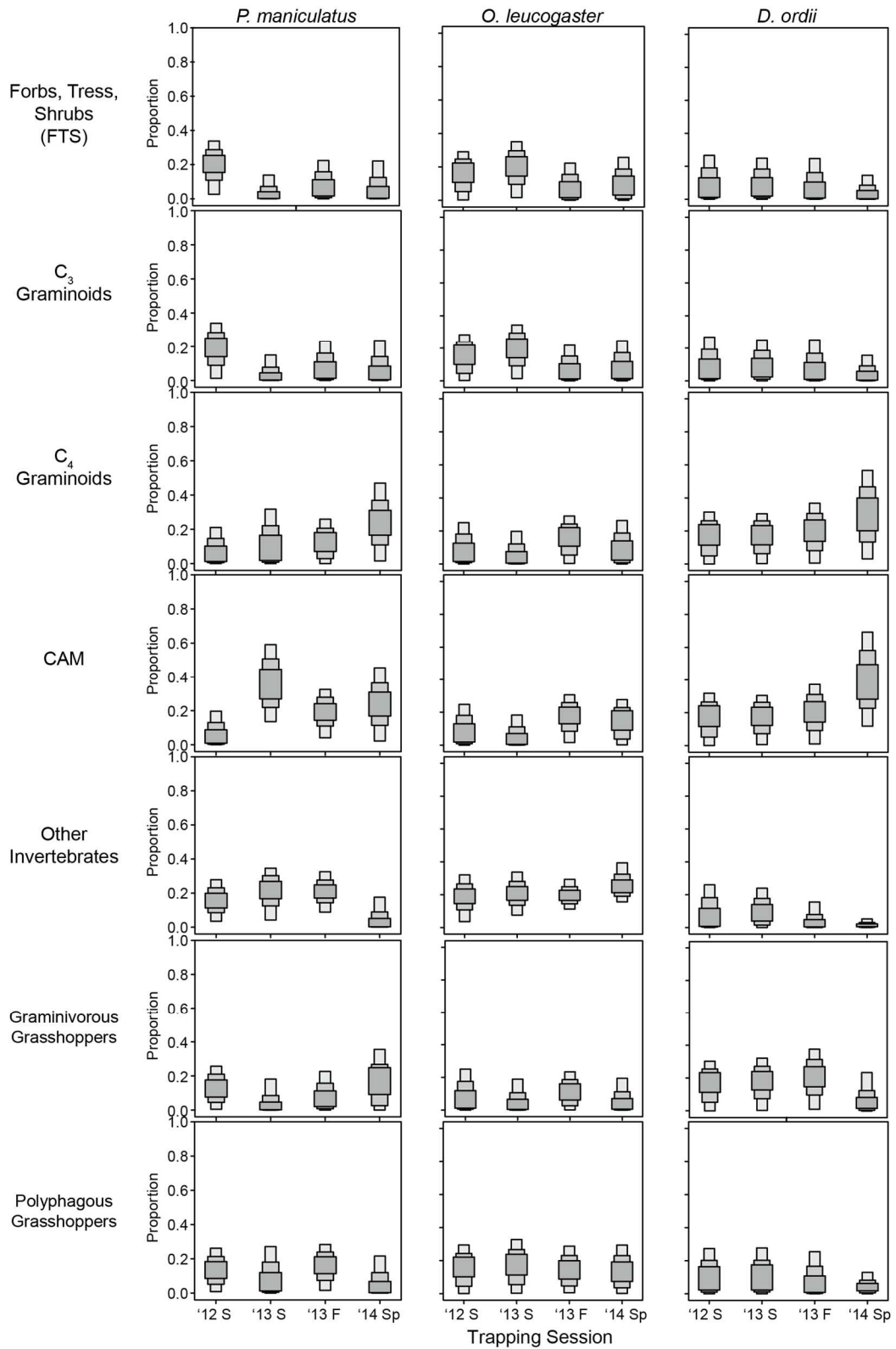


Figure 6 – Results of stable isotope mixing models. 95% credible intervals for *P. maniculatus*, *O. leucogaster*, and *D. ordii* grouped by the different diet resources and plotted through time.

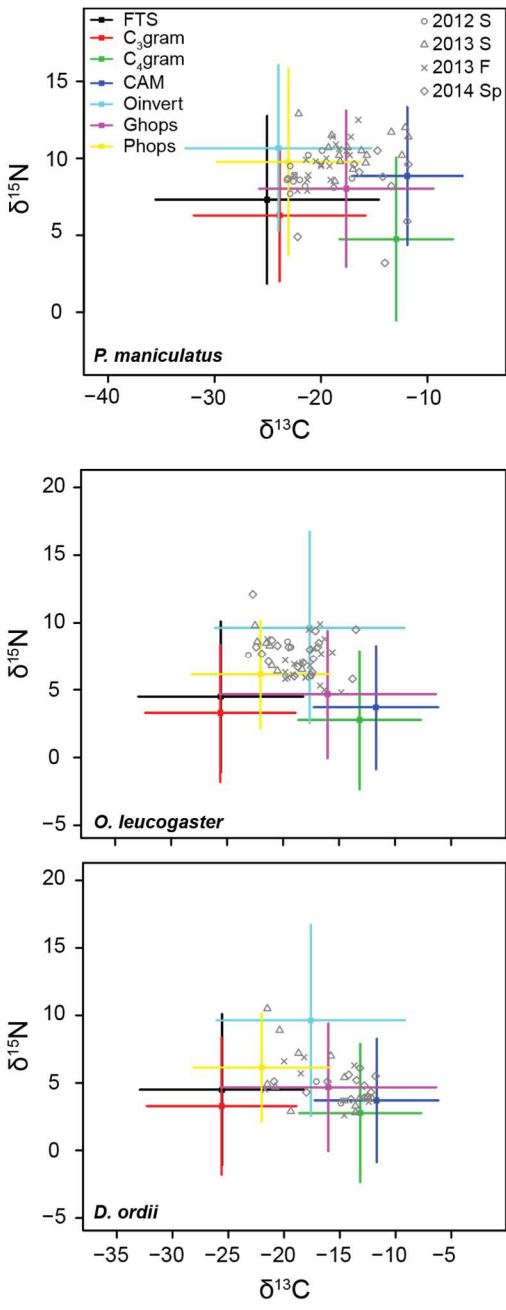


Figure 7 – Scatterplots for *P. maniculatus* (top), *O. leucogaster* (middle), and *D. ordii* (bottom) of their macrohabitat specific diet resources (means  $\pm$  95% credible intervals) and individuals analyzed from all trapping sessions. These panels are the isotope space created for each species' stable isotope mixing model summarized in Figure 6.

## CHAPTER 2

### **Diet variation of rodents in the Great Plains, US: A comparison of diet and C<sub>4</sub> plant distributions**

#### **SUMMARY**

Diet is an ecologic attribute that species will utilize to cope with rapidly changing environments and may be a primary indicator that a population might decline, sustain, or thrive in response to food resources changing over time. We analyzed 534  $\delta^{13}\text{C}$  values from 14 modern rodent species with geographic ranges that span the southern Great Plains and that vary in dietary ecology. Specimens for each species were sampled with uniform spacing across the region and isoscapes of  $\delta^{13}\text{C}$  values were compared statistically to regional patterns of  $\delta^{13}\text{C}$  values of soil organic matter, the percentage of C<sub>4</sub> species, and relative abundance of C<sub>4</sub> plants in the community. Pairwise statistical tests of  $\delta^{13}\text{C}$  values indicate statistically significant differences among both species and dietary categories. Folivores have significantly more negative  $\delta^{13}\text{C}$  values than all other dietary categories, granivores exhibit the most positive  $\delta^{13}\text{C}$  values, and omnivores and rootivores have  $\delta^{13}\text{C}$  values that span the spectrum of diets derived from C<sub>3</sub> and C<sub>4</sub> resources. Insectivores integrate  $\delta^{13}\text{C}$  values of both C<sub>3</sub> and C<sub>4</sub> plants on the landscape resulting in an averaged value of the two resources. Simple linear regression indicates that none of the various C<sub>4</sub> plant metrics explain  $\delta^{13}\text{C}$  in hair for the entire rodent community, however the constructed isoscape of  $\delta^{13}\text{C}$  values in rodent hair does reflect SOM spatial patterns indicating relative proportions of C<sub>3</sub>:C<sub>4</sub> plant biomass. Overall, most species' diets were dominated by C<sub>3</sub> derived resources with only a few species substantially using C<sub>4</sub> resources. A rootivore (*G. bursarius*) and some granivore species (*D. ordii*, *R. megalotis*) and a rootivore incorporated more C<sub>4</sub> resources with increasing C<sub>4</sub> biomass. Granivores incorporated more C<sub>4</sub> derived resources than other dietary categories and the percentage of C<sub>4</sub> derived resources increased with  $\delta^{13}\text{C}$  values of SOM. Furthermore, the difference between median values of granivores and folivores is significantly and highly correlated with SOM  $\delta^{13}\text{C}$  values. Therefore, as C<sub>4</sub> plant resources become more abundant on the landscape, granivores utilize the new niche

space while folivores conserve their dietary niche. These data can be used as a baseline for characterizing dietary shifts in response to climate change and the difference between  $\delta^{13}\text{C}$  of granivores and folivores may be used to estimate  $\text{C}_4$  plant biomass on the landscape in the fossil record.

## INTRODUCTION

Ongoing climate changes are predicted to force biome distributions to shift (e.g. IPCC, 2014) and subsequently pressure mammalian responses to environmental change to maintain their fitness. Diet is an ecologic attribute that species may utilize to cope with rapidly changing environments and could be a primary indicator of a population in decline, sustaining, or thriving in response to changing food resources. However, our understanding of how species partition resources today is limited by the lack of datasets evaluating species' dietary niches at the regional scale, which limits our ability to project outcomes for communities or species' population in the future. This shortfall also hinders our interpretation of the fossil that we can use to determine past responses to environmental change. In order to improve diet projections, a greater characterization of how consumers utilize food resources on the landscape today is required.

Plants utilizing the  $\text{C}_4$  photosynthetic pathway may increase in biomass in the North American Great Plains because they are better adapted to warmer, drier, and extended drought conditions than  $\text{C}_3$  plants. The relative availability of  $\text{C}_3$  and  $\text{C}_4$  food resources on the landscape may change and determining how that may impact mammalian ecology (i.e. diet) is important for assessing a species fitness. Stable isotopes, particularly carbon isotopes, have been used to determine consumer diets due to the anatomical and geochemical differences of  $\text{C}_3$  and  $\text{C}_4$  plants that subsequently result in isotopically distinct  $\delta^{13}\text{C}$  distributions (O'Leary, 1981, DeNiro, 1978). Using a combined knowledge of the consumer tissue  $\delta^{13}\text{C}$  values and an associated discrimination factor (the difference in isotope values between an individual's tissues once equilibrated and diet consumed), it is possible to identify the relative proportions of  $\text{C}_3$  vs  $\text{C}_4$  food resources in a consumer's diet. Large-bodied herbivores (e.g. equids, bovids, or cervids) are commonly evaluated because of their large teeth, thus allowing for convenient sample collection for conventional isotope analysis and their strictly



herbivorous diets allows for simple interpretations. While most attention has focused on large bodied consumers, less attention has been given to small mammals (rodents, lagomorphs, and soricids) that are important components of the ecosystem and boast a greater breadth of diet strategies.

Small mammals have important bottom-up and top-down ecological roles as primary and secondary consumers, bioturbators, and as prey species. Herbivorous small mammals are important grassland engineers that consume seeds and seedlings, altering plant community structure and diversity (Johnson, 1996; Brown et al., 1990). Soil mixing by burrowing also affects plant communities by altering nutrient cycling and soil structure (e.g. Reichman and Seabloom, 2002). More omnivorous species increase trophic complexity in communities by preying on arthropods (e.g. Horner et al., 1965), and all small mammals are important food resources for secondary consumers particularly for raptors, snakes, and fur bearing mammals. Given the bottom-up and top-down influences of small mammals within grassland ecosystems, determining their dietary habits over large spatial scales and multiple habitats is critical towards furthering our overall understanding of small mammal ecology and projecting how small mammals may respond to changing food resources consequently of environmental changes.

The Great Plains, are an ideal ecoregion to begin determining regional dietary patterns because carbon isotopes are used to reflect the relative percent of  $C_4$  plant biomass on the landscape (von Fischer et al., 2008). Grassland community compositions in the Great Plains vary along a latitudinal gradient, with  $C_3$ -dominated grasslands in the north and  $C_4$ -dominated grasslands in the south (Teeri and Stowe, 1976; Paruelo and Lauenroth, 1996; Sage et al., 1999, von Fischer et al., 2008, Figure 8A-C). The turnover of above and below ground plant matter is transformed into soil organic matter (SOM) integrating carbon inputs ( $C_3$  and  $C_4$  plant biomasses) over years to thousands of years. Therefore,  $\delta^{13}C$  values of A-horizon SOM from native prairies have been used to reflect the relative productivity of  $C_3$  vs  $C_4$  plants in the Great Plains (von Fischer et al., 2008). von Fischer et al. (2008) constructed an isoscape (a map consisting of spatially interpolated  $\delta^{13}C$  values) for the Great Plains that provides expected values of  $\delta^{13}C$  ( $\delta^{13}C_e$ ) for the Great Plains and for comparison to rodent diets (Figure 8A). In place of assessing how rodent diets consuming  $C_4$  derived resources through time, we conduct a space for time substitution by assessing how rodent utilize resources across a spatial gradient of varying  $C_4$  biomasses.

We aim to determine small mammal dietary patterns by examining 1) how do species' diets vary in relation to C<sub>4</sub> plant biomass on the landscape; 2) how do species partition C<sub>3</sub> and C<sub>4</sub> derived resources across the southern Great Plains? We address these goals by generating and analyzing a dataset of  $\delta^{13}\text{C}$  values of hair (derived from dietary protein) from rodents across the southern Great Plains.

We utilized hair samples collected from museum voucher specimens to characterize rodent dietary niches with respect to various metrics of C<sub>4</sub> plant distributions and abundances in the southern Great Plains. We hypothesized that some rodent species would consume more C<sub>4</sub> derived resources as C<sub>4</sub> plants become more abundant on the landscape, while other rodent species maintain diets of mostly C<sub>3</sub> derived resources. This model would allow for species' niches to expand to available niche space and reduce intraspecific competition. We assessed the response of rodent diets ( $\delta^{13}\text{C}_d$ ) with respect to expected  $\delta^{13}\text{C}_e$  values and other metrics of C<sub>4</sub> plants such as the relative abundance of C<sub>4</sub> plants (Paruelo and Lauenroth, 1996) and the percentage of C<sub>4</sub> species within the community (Teeri and Stowe, 1976). Lastly, we used the measured  $\delta^{13}\text{C}_d$  values to generate isoscapes of  $\delta^{13}\text{C}_d$  values for the complete dataset, species, and diet categories to predict  $\delta^{13}\text{C}_d$  values across the landscape.

## METHODS

*Museum sampling.*- Specimens from the southern Great Plains were also targeted because of highly accessible museum collections, the spatial variation within expected  $\delta^{13}\text{C}_e$  values, and the region encompasses many Great Plains fossil localities that extend back more than 5 million years and interpreting similar isotopic data in the fossil record will greatly benefit from the results found here. Rodent species were selected to include multiple diet categories (folivores, granivores, insectivores, omnivores, and rootivores), represent different rodent families (Cricetidae, Geomyidae, Heteromyidae, and Sciuridae), and boast fossil records in the Great Plains that will be useful in future studies evaluating mammalian dietary responses to past environmental changes (Table 6).

Museum collections are unique and extensive archives of specimens collected from large geographic areas and at multiple points in time. The large museum collections allow for regional scale analyses of the southern Great Plains without

incurring unnecessary costs and elaborate field campaigns that would have greatly limited the breadth of the study. Furthermore, utilizing geochemically stable tissues like hair, permits using stable isotope analysis to estimate diet for individuals collected over decades.

Museum specimens were procured from the University of Nebraska State Museum (Lincoln, NE), University of Kansas Biodiversity Institute (Lawrence, KS), Oklahoma Museum of Natural History (Norman, OK), and Texas Tech University (Lubbock, TX). Suitable specimens contained georeferencing metadata and were limited to a spatial error equal to a quarter section within the township and range system. Most geographic coordinates were obtained via the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)). For specimens without assigned latitude and longitude coordinates but contained at least a quarter section provided, the latitude and longitude coordinates were then calculated for the centroid of the smallest designated area provided. For each species, specimens were then selected from the pool of suitable specimens to reflect uniform spacing in order to randomly sample the landscape and provide relatively equal weight across the study region (Figure 8D). Deviations from uniform spacing arise from each collections' inherent random sampling of the landscape. Relatively similar spacing was maintained among species resulting in a range of 18 to 55 specimens per species, which varied depending on how much each species' geographic range overlapped with the southern Great Plains. Hair samples (~2 mg) were clipped from the dorsal posterior of specimens in a manner that avoided any obvious damage to the pelage.

*Hair sample preparation and stable isotope analysis.*- Hair samples were cleaned following the procedure outlined in Schwertl et al. (2008) to remove dirt, lipids, and any oils. Briefly, samples were soaked and rinsed in deionized water, followed by soaking for 3 hours in a 2:1 chloroform:methanol mixture, and then rinsed three times with deionized water. Finally, samples were soaked in deionized water and rinsed with deionized water, followed by drying in a 60°C oven. For each sample, 0.7 – 1 mg of hair was weighed into a tin capsule and then combusted in a Costech 4010 Elemental Analyzer coupled to a Thermo-Finnegan Delta V Plus mass spectrometer where the resulting gases were analyzed for elemental concentrations of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  ratios, expressed in standard  $\delta$  notation as the permil difference between the ratios in a sample and a standard material differential from international standards for these isotope ratios (VPDB for carbon and atmospheric  $\text{N}_2$  for nitrogen). All analyses were conducted in the

University of Minnesota Stable Isotope Laboratory. Based on replicate analyses of laboratory standards, precision for  $\delta^{13}\text{C}$  analyses is  $<0.15\text{‰}$  and  $<0.2\text{‰}$  for  $\delta^{15}\text{N}$  analyses.

Measured  $\delta^{13}\text{C}$  values were converted to reflect  $\delta^{13}\text{C}$  value of diet ( $\delta^{13}\text{C}_d$ ) by correcting for experimentally determined enrichments between hair and diet and for the change in  $\delta^{13}\text{C}$  of atmospheric  $\text{CO}_2$ . The choice of diet-tissue enrichment factors was limited to the few experimentally determined enrichments values for rodents. Enrichment factors exist for *Peromyscus maniculatus*, *Peromyscus leucopus*, and a vole (*Myodes gapperi*) not used in this study but taxonomically related to *Microtus ochrogaster* and *Microtus pennsylvanicus*. Using the individual fractionation values available, we used the median enrichment factor of  $1.1\text{‰}$  for all species, which was then subtracted from all raw  $\delta^{13}\text{C}$  values to correct hair values back to diet. We used a general enrichment factor for all taxa in order to treat all species equally given that species specific discrimination values are not available for most taxa. A final correction was made for secular change in the  $\delta^{13}\text{C}$  values of atmospheric  $\text{CO}_2$  based on each specimen's collection date to reach a final  $\delta^{13}\text{C}_d$  value. The appropriate  $\Delta^{13}\text{C}$  correction factor for each year was determined using the equation produced by Long et al., (2005) based on data from Francey et al. (1999).

*Covariate spatial surfaces of C<sub>4</sub> plants.*- The primary covariate for comparison to  $\delta^{13}\text{C}_d$  was  $\delta^{13}\text{C}_e$ , which was determined by reproducing the isoscape (Figure 8A) created by von Fischer et al. (2008) using the reported  $\delta^{13}\text{C}$  data from native prairie locations throughout the Great Plains (for detailed methods, see von Fischer et al, 2008). A map of %C<sub>4</sub> species (%C<sub>4-Species</sub>, Figure 8B) was generated based on Teeri and Stowe (1976) and a map for the relative abundance of C<sub>4</sub> plants (%C<sub>4-abund</sub>) was generated based on Paruelo and Lauenroth (1996) (Figure 8C). All maps were created to produce spatially continuous data for comparison and the same methodology used by von Fischer et al. (2008) was applied to developing maps for %C<sub>4-Species</sub>, %C<sub>4-abund</sub>, and  $\delta^{13}\text{C}_d$ . Each rodent specimen's latitude and longitude coordinates were used to extract a corresponding value of  $\delta^{13}\text{C}_e$ , %C<sub>4-Species</sub>, and %C<sub>4-abund</sub> (Figure 8D).

We analyzed  $\delta^{13}\text{C}_d$  values grouped by land cover classifications, which were assigned to each specimen based on its coordinates. The National Land Cover Database (NLCD) was downloaded for 2006 (Fry et al., 2011) and 2011 (Jin et al., 2013). Both datasets were available for download (<http://www.mrlc.gov/index.php>).

ANOVA was used to determine if differences among species exist followed by pairwise non-parametric Mann Whitney-U tests to determine which species differed from each other. The p-values indicate the probability that any two sets of diets were drawn from the same population and inversely, the confidence level at which dietary differences between two species can be considered to be significantly different. The same statistical analyses were conducted for identifying potential differences among diet categories and land cover types. Parametric (Pearson product moment-correlation coefficient) and non-parametric (Spearman's rho) were used to test for correlation between  $\delta^{13}\text{C}_d$  and covariates. Simple linear regression was conducted between  $\delta^{13}\text{C}_d$  and covariates using all specimens.

*Isoscapes of  $\delta^{13}\text{C}_d$ .*- Geostatistical analyses and prediction maps of  $\delta^{13}\text{C}_d$  values were conducted using the geographic information system software ArcMAP™ 10.2 (ESRI, 2011). Prediction maps (isoscapes) of  $\delta^{13}\text{C}_d$  in rodent hairs were constructed using the complete  $\delta^{13}\text{C}_d$  dataset followed by subsets for each species and diet category. Interpolations, semivariogram plots, and maps of standard error were created using the Geostatistical Analyst tool in ArcMAP™. Interpolations were conducted by including all points as individuals (for instances when two specimens had the same latitude and longitude) and ordinary kriging with two different semivariogram models, spherical and exponential (Johnston et al, 2001). Using the same data, a model was constructed to determine the standard error based on  $\delta^{13}\text{C}_d$  variance and sampling distribution. For each predicted standard error map, an acceptable standard error was selected and used to limit the area of the final prediction maps. Isoscapes were limited by the selected standard errors to avoid over interpretation into areas with poor sampling. Method reports for all predication and standard error maps are available upon request.

## RESULTS

Sampling focused on the southern Great Plains states and included ecoregions that occur within the state boundaries (Figure 8D). A total of 534 specimens were analyzed and  $\delta^{13}\text{C}_d$  values range 22‰ (-32.5‰ to -10.4‰) spanning the C<sub>3</sub> to C<sub>4</sub> spectrum of  $\delta^{13}\text{C}$  values for plants (Table 6). Most samples were from the Greats Plains (N = 478) ecoregion and their  $\delta^{13}\text{C}_d$  values spanned the C<sub>3</sub> and C<sub>4</sub> spectrum (Table 6,

Figure 9). The Eastern Temperate Forests are dominated by C<sub>3</sub> plants and consumer δ<sup>13</sup>C<sub>d</sub> values reflect consumption of mostly C<sub>3</sub> derived resources indicated by a median δ<sup>13</sup>C<sub>d</sub> value of -24.6 ± 3.7‰ (Table 6, Figure 9). Specimens from the North American Deserts are not different from those in the Great Plains, but only represented by 22 individuals.

*Species diets.*- Some species have δ<sup>13</sup>C<sub>d</sub> distributions dominated by C<sub>3</sub> derived resources (*Microtus pennsylvanicus*, *Microtus ochrogaster*, and *Neotoma floridana*), but most species yield δ<sup>13</sup>C<sub>d</sub> values resembling diets with varying mixtures of C<sub>3</sub> and C<sub>4</sub> derived resources (Figure 10, Table 7). There is considerable variation among species and there are statistical differences in δ<sup>13</sup>C<sub>d</sub> values (ANOVA,  $F = 18.52$ ,  $P = <0.001$ ). Pairwise Mann-Whitney U statistical tests of δ<sup>13</sup>C<sub>d</sub> values indicate statistically significant differences among some species (Table 8).

*Diet categories.*- When δ<sup>13</sup>C<sub>d</sub> values are binned by diet categories, two granivores (*D. ordii* and *R. megalotis*) boast the most positive δ<sup>13</sup>C<sub>d</sub> values, but when combined with the other granivore (*C. hispidus*) they have a median δ<sup>13</sup>C<sub>d</sub> value of -19.7 ± 4.4‰. *O. leucogaster* is the only invertivore representative and boasts the most positive δ<sup>13</sup>C<sub>d</sub> values (median = -19.1 ± 2.9‰), followed by the lone rootivore (*G. bursarius*, median = -21.2 ± 4.7), then omnivores (-23.1 ± 2.5‰), and finally folivores (-25.0 ± 3.3‰) (Table 7, Figure 10).

*δ<sup>13</sup>C<sub>d</sub> and covariates.*- Simple linear regression indicates that δ<sup>13</sup>C<sub>e</sub> explains little of the overall δ<sup>13</sup>C<sub>d</sub> variance ( $R^2 = 0.02$ ) and are not correlated (Spearman's rho = 0.156,  $p < 0.001$ ) (Table 9, Figure 11). δ<sup>13</sup>C<sub>d</sub> values range a minimum of 16‰ for most δ<sup>13</sup>C<sub>e</sub> values and the δ<sup>13</sup>C<sub>d</sub>. The δ<sup>13</sup>C<sub>d</sub> variance and range may decrease with δ<sup>13</sup>C<sub>e</sub> values between -19-17‰, however the reduction may be attributed to lower sampling intensity of specimens with δ<sup>13</sup>C<sub>e</sub> values between -19‰ and -17‰ (Figure 11). Other metrics of C<sub>4</sub> plant distribution, %C<sub>4-Species</sub> and %C<sub>4-abund</sub>, also do not explain much variance in δ<sup>13</sup>C<sub>d</sub> values (Table 9).

The weak relationship between δ<sup>13</sup>C<sub>d</sub> and δ<sup>13</sup>C<sub>e</sub> may be the result of species utilizing food resources differently and independently responding to environmental variables. Further analysis of these species specific responses to C<sub>4</sub> abundances will further our understanding of food resources partitioning within communities. Simple linear regression was used to characterize the relationships between δ<sup>13</sup>C<sub>e</sub> values and measured δ<sup>13</sup>C<sub>d</sub> values for each species (Table 9 and Figure 12) and diet category

(Table 9 and Figure 13). The rootivore, *G. bursarius*, exhibits the strongest positive relation ( $m = 2.05$ ,  $p < 0.001$ ,  $R^2 = 0.21$ ) followed by *R. megalotis* ( $m = 1.15$ ,  $p < 0.001$ ,  $R^2 = 0.16$ ) and then *D. ordii* ( $m = 1.95$ ,  $p < 0.001$ ,  $R^2 = 0.14$ ), both granivores. The  $\delta^{13}C_d$  values for the remaining granivore, *C. hispidus*, are positively correlated with  $\delta^{13}C_e$ , however slope ( $m = 1.3$ ) is only significant at  $\alpha = 0.05$  and  $\delta^{13}C_e$  explains a very small fraction  $\delta^{13}C_d$  variance ( $R^2 = 0.08$ ). *N. floridana* is the only species with a significant negative slope between  $\delta^{13}C_d$  and  $\delta^{13}C_e$  ( $m = -0.7$ ,  $p < 0.05$ ), but  $\delta^{13}C_e$  again explains a minimal amount of  $\delta^{13}C_d$  variance ( $R^2 = 0.09$ ). The variance in  $\delta^{13}C_d$  values for all other species are not explained by  $\delta^{13}C_e$ , %C<sub>4</sub>-Species, or %C<sub>4</sub>-abund (Table 9).

Rootivores and invertivores were each represented by one taxon, *G. bursarius* and *O. leucogaster*, respectively, therefore analysis is limited to only that of the species. Granivore  $\delta^{13}C_d$  values have a positive and significant slope ( $m = 1.53$ ,  $p < 0.001$ ) with  $\delta^{13}C_e$  values ( $R^2 = 0.11$ ) (Table 9, Figure 13). In contrast,  $\delta^{13}C_e$  values explain little  $\delta^{13}C_d$  variance in folivore diets ( $R^2 = 0.01$ , Figure 13) and even less for omnivores ( $R^2 = < 0.01$ ) (Table 9).

Folivore and omnivore diets do not vary with  $\delta^{13}C_e$ , but granivore diets ( $\delta^{13}C_G$ ) diverge from folivores ( $\delta^{13}C_F$ ) and are positively correlated with  $\delta^{13}C_e$  (Figure 13). We further evaluated diverging diets of folivores and granivores by calculating median values of  $\delta^{13}C_F$  and  $\delta^{13}C_G$  for every 0.5‰ bin of  $\delta^{13}C_e$  values starting at -18‰ and ending at -14‰. The difference between folivores and granivores ( $\Delta^{13}C_{F-G}$ ) was then calculated by subtracting  $\delta^{13}C_G$  from  $\delta^{13}C_F$ . A simple linear regression through  $\Delta^{13}C_{F-G}$  on  $\delta^{13}C_e$  indicates a significantly positive slope ( $m = 1.64$ ) and the majority of  $\Delta^{13}C_{F-G}$  variance is explained by  $\delta^{13}C_e$  (adjusted  $R^2 = 0.52$ ,  $p = 0.02$ , Figure 14).

*Constructed  $\delta^{13}C_d$  Isoscapes of Rodent Hair.* - The linear regression analyses between  $\delta^{13}C_d$  and  $\delta^{13}C_e$  were restricted to specimens that geographically overlapped with the von Fischer et al. (2008)  $\delta^{13}C$  isoscape, which provided the predicted  $\delta^{13}C_e$  values. Constructed  $\delta^{13}C_d$  isoscapes include specimens not included in regressions with  $\delta^{13}C_e$  because the prediction maps of  $\delta^{13}C_e$  did not extend beyond the Great Plains ecoregion. Ecoregions like the Eastern Temperate Forests are dominated by C<sub>3</sub> plants and rodent diets should reflect the C<sub>3</sub> environments of broadleaf and needleleaf forests. Desert environments were expected to boast  $\delta^{13}C$  distributions similar to those found in mixed grasslands stemming from a mixture of C<sub>3</sub>, C<sub>4</sub>, and CAM plants.

The constructed isoscape of all predicted  $\delta^{13}\text{C}_d$  values illustrates similar spatial trends as those for  $\delta^{13}\text{C}_e$  (Figure 15). The most positive  $\delta^{13}\text{C}_d$  values occur in the southwestern Great Plains and trend along a southwest to northeast bearing as predicted by  $\delta^{13}\text{C}$  values of SOM (Figure 8A, von Fischer et al., 2008). As predicted, more negative  $\delta^{13}\text{C}_d$  values are in northwest Nebraska and along the eastern boundary of the Great Plains, where grasslands transition to temperate forests (Figure 15). Disagreement between  $\delta^{13}\text{C}_e$  and  $\delta^{13}\text{C}_d$  isoscapes occurs in southern Texas likely due to reduced sampling. Incorporation of more specimens and species from the Texas community may yield more positive  $\delta^{13}\text{C}_d$  values.

Species specific maps were generated and clipped by species specific standard error values due to differing spatial sampling and  $\delta^{13}\text{C}_d$  variances (Figure 14 and Appendix XI). Representative species' specific isoscapes illustrate differing dietary variation among species. Some species specific isoscapes indicate the same higher  $\delta^{13}\text{C}$  values along a southwest to northeast transect such as *O. leucogaster* (Figure 16A), *D. ordii* (Figure 16F), and to a lesser degree *P. maniculatus* (Figure 16E). Other taxa boast diets that show minimal variation across the landscape such as *M. ochrogaster* (Figure 16A) and *S. niger* (Figure 16B). Lastly, some species boast distinct dietary transitions such as the *G. bursarius* isoscape (Figure 16C) that depicts a distinct north-south gradient with more positive  $\delta^{13}\text{C}_d$  values in the south and the *P. maniculatus* isoscape that depicts a distinct east to west transition in Oklahoma/Texas reflecting the vegetation transition from temperate forests to short-grass prairies.

Dietary isoscapes were constructed for  $\delta^{13}\text{C}_d$  values of folivores, granivores, and omnivores (Figure 16). Rootivores and insectivores were represented by singular taxa, therefore *Geomys bursarius* and *Onychomys leucogaster* should be referred to for representatives of rootivores and insectivores, respectively (See above). Folivore diets exhibit a general north-south trend with more negative  $\delta^{13}\text{C}_F$  values in the north, however the more positive values in the south may be due to the reduced sampling intensity spatially and fewer analyzed taxa. Granivores boast the distinct trend of more positive  $\delta^{13}\text{C}_G$  values from north Texas to eastern Nebraska. Moreover, granivores indicate relatively increased  $\text{C}_3$  consumption in western Nebraska and eastern Kansas. Granivore  $\delta^{13}\text{C}_G$  values appear to decrease in the very southwest corner of the Great Plains, but this again may be a reduction in sampling intensity. Omnivore  $\delta^{13}\text{C}_d$  values boast the largest range of values and are not correlated with expected  $\delta^{13}\text{C}_e$  values (See



linear regressions above). The blocky interpolation is a reflection of the high  $\delta^{13}\text{C}_d$  variance among neighboring specimens. However, the isoscape for omnivores does predict higher  $\delta^{13}\text{C}_d$  values along the main northeast-southwest transect as previously described.

## DISCUSSION

$\delta^{13}\text{C}_d$  and  $\delta^{13}\text{C}_e$ .- The minimal relations between rodent  $\delta^{13}\text{C}_d$  values and  $\text{C}_4$  vegetation metrics ( $\delta^{13}\text{C}_e$ ,  $\% \text{C}_4\text{-Species}$ , and  $\% \text{C}_4\text{-abund}$ ) may in part be the result of the greater spatial sampling intensity of rodent specimens relative to the inputs for  $\text{C}_4$  vegetation metrics. Increased sampling intensity may include more landscape heterogeneity that is averaged out in lower resolution  $\text{C}_4$  vegetation metrics. Only the  $\delta^{13}\text{C}_e$  metric is specific to the Great Plains and considers the relative proportions of biomass produced between  $\text{C}_3$  and  $\text{C}_4$  plants. The  $\text{C}_4$  metrics ( $\% \text{C}_4\text{-Species}$ , and  $\% \text{C}_4\text{-abund}$ ) encompass North America and may be at the wrong spatial scale and may underestimate differences in plant production (i.e. food production).

We focused on the southern Great Plains, but that spatial scale may not include a large enough gradient between  $\text{C}_3$  only and  $\text{C}_4$ -dominated ecosystems. Including rodent specimens from the northern Great Plains where SOM  $\delta^{13}\text{C}$  values are more negative (-22 to -24.9‰) would increase the environmental gradient from habitats dominated by  $\text{C}_3$  plants to  $\text{C}_4$ -dominated grasslands in the southern Great Plains. We predict that adding communities from more  $\text{C}_3$ -dominated environments (e.g. northern Montana and Saskatchewan) may result in a stronger relationship between community diets and  $\text{C}_4$  vegetation metrics.

The largest source of variation within rodent community diets is the independent responses to food resource availability and their food preferences. We predicted that as  $\text{C}_4$  biomass increased on the landscape that some species would continue to maintain their  $\text{C}_3$  dominated diet while other taxa expanded their diet to include more  $\text{C}_4$  derived resources as they increased on the landscape. Although the linear relationships are weak between  $\delta^{13}\text{C}_d$  and  $\delta^{13}\text{C}_e$ , some species did consume more  $\text{C}_4$  derived resources as  $\text{C}_4$  biomass increased on the landscape (e.g. *D. ordii*, *G. bursarius*, and *R. megalotis*). Other species maintained  $\text{C}_3$  dominated diets such as the *Microtus folivores*. If a greater

range of C<sub>3</sub> to C<sub>4</sub> biomass was included, we hypothesize that the overall variation would decrease dramatically as C<sub>4</sub> plants become less abundant.

*Diet Isoscapes.*- Although  $\delta^{13}\text{C}_e$  did not directly explain much of the overall  $\delta^{13}\text{C}_d$  variance,  $\delta^{13}\text{C}_d$  isoscapes did predict similar spatial trends for the entire rodent community similar to the  $\delta^{13}\text{C}_e$  patterns. The  $\delta^{13}\text{C}_d$  isoscape captures the southwest to northeastern trend of positive  $\delta^{13}\text{C}$  values in SOM (Figure 15). Additionally, the boundary between the Great Plains and the Eastern Temperate Forests becomes evident and would likely continue the transition moving eastward and extend the latitudinal isotopic boundary with additional rodent sampling in Iowa, Missouri, Arkansas, and Alabama. Higher density spatial sampling may help decrease standard errors of the prediction maps and further identify spatial patterns among rodent diet categories within states, but would likely not divulge any new spatial trends at the scale presented here.

Folivores were expected to focus on green vegetation and our results indicate folivores consume mostly C<sub>3</sub> derived resources across the region. Since the other diet categories include multiple forms of C<sub>3</sub> and C<sub>4</sub> derived resources via foliage, seeds, or invertebrates, we would expect these diet categories to respond more strongly to spatial patterns of C<sub>4</sub> abundance and have the potential to be more variable as they vary their diets relative to local food availabilities.

The consistent diets (i.e. folivores, *Microtus pennsylvanicus*, *Neotoma albigula*, *Sciurus niger*), diets varying with C<sub>4</sub> biomass (i.e. granivores, *Dipodomys ordii*, *Geomys bursarius*), and highly variable diets (e.g. omnivores) are consistent with expectations for broad diet categories, but broad dietary categories are only a starting point for assessing small mammal diets. Realistically, rodent diets are variable proportions of foliage, seeds, and invertebrates that vary across space and through time (e.g. Flake, 1973; Best et al., 1993; Hope and Parmenter, 2008; Pineda-Munoz and Alroy, 2014). However, deconstructing an individual's diet to a finer degree would require multiple isotopes from the consumer, isotopic compositions of all the potential food resources, and inputting those parameters into a stable isotope mixing model to reach diet estimates indicating the proportions a diet resource contributed to an individual's diet (e.g. SIAR, Parnell et al., 2010). This type of analysis can only be done at a local spatial scale where diets can vary even between macrohabitats, seasonally, and during short-term (years) climate events. However, multiple local trapping sessions within various macrohabitats and over

time, would permit a detailed analysis and greatly improve our understanding of how species vary their diets on the landscape.

*Habitat utilization.*- Rodents have small home ranges (0.02 to 1.1 ha) in comparison to large bodied herbivores (equids, bovids, and cervids; 59 to 1292 ha) (Harestad and Bunnell, 1979). Small home ranges reduce the probability of averaging isotopic compositions of food resources over large distances or consumers maintaining a specific diet throughout the year by migrating. Smaller home ranges allow small mammal populations to reside within macrohabitats that may be no larger than an individual's home range. Furthermore, species may prefer specific macrohabitats that are the minority habitat in the region and subsequently their diet may not be a good indication of region. While the southern Great Plains are dominated by grasslands, localized pockets of riparian zones (graminoid river terraces and tree stands) persist and provide variable food resources, canopy cover for protection from predators, and microclimates. Therefore, some macrohabitats with a greater proportion of C<sub>3</sub> plants present being may be over represented in comparison to the surrounding C<sub>4</sub>-dominated grasslands that dominate the landscape. The macrohabitat associations may further explain the conservative dietary niches of some taxa (e.g. *Sciurus niger*, *Microtus pennsylvanicus*, *Microtus ochrogaster*, and *Neotoma albigula*) as C<sub>4</sub> plants become more abundant on the landscape. However, some species' dietary niches do reflect transitions among biomes (e.g. *Geomys bursarius*, *Dipodomys ordii*, *Reithrodontomys megalotis*, *Onychomys leucogaster*, and *Peromyscus maniculatus*) and further reinforces the partitioning of niche space by rodents.

*Rodent Community Dynamics.*- This study of 14 species includes multiple lineages and dietary categories. However, the geographic ranges for these species do not uniformly overlap in the region, therefore different species contribute to the community in different regions of the Great Plains. Once the geographic extent of species is reached, potentially another species is available to fill the ecospace void. Presumably, if the same ecological void is filled by a replacement species, the  $\delta^{13}\text{C}_d$  values of the current species and its predecessor are the same.

Increasing the species richness in the dataset would help provide a more complete community picture and provide species specific baselines for comparison in other regions. The broad diet categories (folivores, granivores, and omnivores) were represented equally across the southern Great Plains evidenced by the prediction

outputs covering essentially the same geographic extent. Insectivores and rootivores were limited by their singleton representatives and these categories could use additional species and sampling. However, these diet categories have few species that overlap in the southern Great Plains and the data presented here are some of the most widely distributed species for their respective dietary categories.

*Implications for Assessing Dietary Niches.*- Recently, the development of laser ablation systems has permitted in situ isotopic analysis of small mammal teeth (e.g. rodents, lagomorphs, and soricids) (e.g. Passey et al., 2006; Hynek et al., 2012; Kimura et al., 2013). While laser ablation isotope techniques permit analysis of fossil small mammal teeth (e.g. rodents and lagomorphs), our understanding of isotopic variation in rodents across modern environments is still limited, hindering the interpretation of isotopic data from ancient ecosystems. The dataset presented here is imperative for interpreting similar modern and fossil data with confidence.

## CONCLUSIONS

We have identified that the  $\delta^{13}\text{C}_d$  values of some species and dietary categories vary spatially with respect to ecosystem  $\delta^{13}\text{C}_e$  values. Folivores typically have isotopically more negative  $\delta^{13}\text{C}_d$  values and maintain a similar diet regardless of  $\delta^{13}\text{C}_e$ , MAT, and MAP and only slightly increase in variation with the more positive  $\delta^{13}\text{C}_e$  values. Granivores incorporate generally more  $\text{C}_4$  derived resources than other dietary categories and the percentage of  $\text{C}_4$  derived resources increase with  $\delta^{13}\text{C}_e$ . Furthermore, the difference between median values of granivores and folivores is significantly and highly correlated with  $\delta^{13}\text{C}_e$ , which implies that the  $\Delta^{13}\text{C}_{\text{F-G}}$  value of a fossil community could be used to estimate the  $\% \text{C}_4$  and/or help reconstruct the associated paleoenvironment. Extending the dataset beyond the Great Plains would allow for characterizing more environments potentially identify a stronger relationship between  $\delta^{13}\text{C}_d$  and  $\delta^{13}\text{C}_e$ . The results and patterns we have described can be used as a baseline for monitoring species' diets to determine if their diets change over time in response to changing environments and if they begin to resemble diets from other portions of their dietary niche.

## FUTURE WORK

The research presented here has laid the groundwork for establishing a database that extends temporally and geographically. Specific to the Great Plains, including more individuals from the northern Great Plains that are dominated by cool-season grasses will increase the range of expected  $\delta^{13}\text{C}_e$  values, which will help put the values presented here in a greater perspective. Including a greater proportion of the landscape would subsequently include greater ranges of environmental and climatic variables that would be used to better understand the controls on rodent diets. Other variables like potential evapotranspiration, soil type, number of frost free days, etc., may yield an improved understanding of  $\delta^{13}\text{C}_d$  variance. Furthermore, including more biomes that occur along the boundaries of grasslands, would create a more robust gradient from closed canopy forests to deserts.

Understanding the variation in rodent diets among biomes is important for interpreting similar data from the fossil record. In turn the fossil data can then be used to reconstruct paleoenvironments, or test hypotheses about faunal turnover such as the Red Queen (Van Valen, 1973) and Court Jester (Barnosky, 2001) models. Furthermore, an expanded database and fossil record could be used to further test the niche variation hypothesis (Van Valen, 1965) that predicts greater population variability in species with wider niches. The addition of more species and lineages could be used to address questions about niche conservatism of species and higher taxonomic levels in space and time

Table 6 – Summary statistics of  $\delta^{13}\text{C}_d$  (measured hair valued corrected for diet and secular changes in atmospheric  $\text{CO}_2$  composition through time) values grouped by diet category and ecoregion.

Family	Diet Category	$\delta^{13}\text{C}_d$ (‰)							
		n	mean	sd	median	min	max	range	se
	<b>All Specimens</b>	534	-21.6	4.2	-22.5	-32.5	-10.4	22.0	0.2
	<b>Ecoregion</b>								
	Temperate Sierras	1	-19.8	NA	-19.8	-19.8	-19.8	NA	NA
	Great Plains	478	-21.5	4.2	-22.3	-29.9	-10.4	19.4	0.2
	North American Deserts	22	-21.6	3.7	-22.9	-25.6	-13.3	12.3	0.8
	Eastern Temperate Forests	33	-23.7	3.7	-24.6	-32.5	-12.3	20.1	0.6

Table 7 – Summary statistics of  $\delta^{13}\text{C}_d$  grouped by species. G = Granivore, F = Folivore, I = Invertivore, O = Omnivore.

Family	Species	Diet Category	n	$\delta^{13}\text{C}_d$ (‰)						
				mean	sd	median	min	max	range	se
Cricetidae	<i>Microtus ochrogaster</i>	F	42	-25.9	1.9	-26.3	-29.9	-21.6	8.2	0.3
Cricetidae	<i>Microtus pennsylvanicus</i>	F	18	-26.2	3.7	-27.8	-29.1	-16.3	12.8	0.9
Cricetidae	<i>Neotoma floridana</i>	F	25	-25.2	2.3	-25.8	-28.7	-18.9	9.8	0.5
Cricetidae	<i>Neotoma micropus</i>	F	30	-22.8	3.2	-23.5	-26.5	-15.7	10.8	0.6
Cricetidae	<i>Onychomys leucogaster</i>	I	40	-19.5	2.9	-19.1	-24.8	-13.3	11.5	0.5
Cricetidae	<i>Peromyscus leucopus</i>	O	38	-22.1	4.2	-24.1	-28.7	-12.7	16.0	0.7
Cricetidae	<i>Peromyscus maniculatus</i>	O	55	-21.9	3.8	-22.8	-32.5	-11.9	20.5	0.5
Cricetidae	<i>Reithrodontomys megalotis</i>	G	47	-18.9	3.8	-18.9	-26.1	-12.9	13.1	0.6
Geomyidae	<i>Geomys bursarius</i>	R	34	-20.8	4.7	-21.2	-27.6	-12.9	14.8	0.8
Heteromyidae	<i>Chaetodipus hispidus</i>	G	34	-21.5	3.7	-22.9	-26.5	-12.3	14.1	0.6
Heteromyidae	<i>Dipodomys ordii</i>	G	55	-18.0	4.7	-16.4	-27.5	-10.4	17.1	0.6
Sciuridae	<i>Ictidomys tridecemlineatus</i>	G	47	-20.9	2.8	-21.2	-24.6	-13.2	11.4	0.4
Sciuridae	<i>Sciurus niger</i>	O	29	-23.9	1.8	-24.2	-26.5	-17.5	9.0	0.3
Sciuridae	<i>Sigmodon hispidus</i>	O	40	-21.7	3.1	-21.8	-27.0	-15.3	11.7	0.5
<b>Diet Category</b>										
	Folivore	F	155	-24.1	3.3	-25.0	-29.9	-15.3	14.6	0.3
	Granivore	G	136	-19.2	4.4	-19.7	-27.5	-10.4	17.1	0.4
	Omnivore	O	169	-22.0	3.5	-23.1	-32.5	-11.9	20.5	0.3

Table 8 – Summary of pairwise Mann-Whitney U tests (with Bonferroni corrected p-values) of  $\delta^{13}\text{C}_d$  values among rodent species

Pairwise Mann-Whitney U tests, bonferroni corrected	<i>Microtus pennsylvanicus</i>	<i>Microtus ochrogaster</i>	<i>Neotoma floridana</i>	<i>Sciurus niger</i>	<i>Peromyscus leucopus</i>	<i>Neotoma micropus</i>	<i>Chaetodipus hispidus</i>	<i>Peromyscus maniculatus</i>	<i>Sigmodon hispidus</i>	<i>Geomys bursarius</i>	<i>Ictidomys tridecemlineatus</i>	<i>Onychomys leucogaster</i>	<i>Reithrodontomys megalotis</i>
<i>Microtus ochrogaster</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Neotoma floridana</i>	1	1	-	-	-	-	-	-	-	-	-	-	-
<i>Sciurus niger</i>	0.002	0.002	0.129	-	-	-	-	-	-	-	-	-	-
<i>Peromyscus leucopus</i>	0.002	<0.001	0.032	1	-	-	-	-	-	-	-	-	-
<i>Neotoma micropus</i>	0.006	0.001	0.110	1	1	-	-	-	-	-	-	-	-
<i>Chaetodipus hispidus</i>	0.001	<0.001	0.001	0.419	1	1	-	-	-	-	-	-	-
<i>Peromyscus maniculatus</i>	<0.001	<0.001	0.001	0.767	1	1	1	-	-	-	-	-	-
<i>Sigmodon hispidus</i>	<0.001	<0.001	<0.001	0.220	1	1	1	1	-	-	-	-	-
<i>Geomys bursarius</i>	0.001	<0.001	0.020	1	1	1	1	1	1	-	-	-	-
<i>Ictidomys tridecemlineatus</i>	<0.001	<0.001	<0.001	<0.001	1	0.227	1	1	1	1	-	-	-
<i>Onychomys leucogaster</i>	<0.001	<0.001	<0.001	<0.001	0.043	0.003	0.388	0.027	0.198	1	1	-	-
<i>Reithrodontomys megalotis</i>	<0.001	<0.001	<0.001	<0.001	0.043	0.002	0.238	0.013	0.046	1	0.632	1	-
<i>Dipodomys ordii</i>	<0.001	<0.001	<0.001	<0.001	0.006	<0.001	0.053	0.002	0.009	0.491	0.153	1	1



Table 9 – Summary of simple linear regressions between  $\delta^{13}\text{C}_d$  and  $\text{C}_4$  plant covariates. Diet categories (DC) are the same as in Table 7.

	DC	$\delta^{13}\text{C}_e$ (von Fischer et al., 2007)					%C <sub>4</sub> -Species (Teeri and Stowe, 1976)					%C <sub>4</sub> -abund (Paruelo and Lauenroth, 1996)				
		m	b	R <sup>2</sup>	Adj R <sup>2</sup>	p	m	b	R <sup>2</sup>	Adj R <sup>2</sup>	p	m	b	R <sup>2</sup>	Adj R <sup>2</sup>	p
All Individuals		0.70	-10.58	0.027	0.03	<0.001	0.42	-21.91	0.017	-0.002	0.003	0.05	-24.27	<0.001	0.014	0.773
<i>Chaetodipus hispidus</i>	G	1.28	-1.14	0.106	0.08	0.06	0.00	-21.63	<0.001	-0.031	0.965	8.82	-27.23	0.085	0.056	0.099
<i>Dipodomys ordii</i>	G	1.94	13.26	0.157	<b>0.14</b>	0.00	0.16	-25.79	0.117	0.1	0.011	1.06	-18.65	<0.001	-0.018	0.835
<i>Geomys bursarius</i>	R	2.08	12.25	0.239	<b>0.21</b>	0.00	0.25	-34.39	0.371	<b>0.351</b>	<0.001	-0.84	-20.30	<0.001	-0.031	0.895
<i>Ictidomys tridecemlineatus</i>	O	0.69	-9.91	0.053	<b>0.03</b>	0.12	0.09	-25.73	0.082	<b>0.061</b>	0.051	5.66	-24.53	0.079	0.058	0.056
<i>Microtus ochrogaster</i>	F	0.37	-19.90	0.036	0.01	0.23	0.08	-29.82	0.118	0.096	0.026	1.13	-26.60	0.004	-0.02	0.674
<i>Microtus pennsylvanicus</i>	F	0.44	-19.06	0.012	-0.05	0.67	0.03	-27.29	<0.001	-0.062	0.926	1.24	-26.87	0.001	-0.061	0.880
<i>Neotoma floridana</i>	F	-0.74	-37.26	0.149	0.11	0.08	-0.07	-21.58	0.103	0.064	0.118	-9.81	-19.20	0.214	0.177	0.026
<i>Neotoma micropus</i>	F	-0.94	-37.22	0.060	0.03	0.19	0.10	-29.00	0.051	0.018	0.228	-5.37	-19.50	0.047	0.013	0.248
<i>Onychomys leucogaster</i>	I	0.29	-14.88	0.010	-0.02	0.54	-0.03	-17.72	0.012	-0.014	0.493	0.10	-19.45	<0.001	-0.027	0.981
<i>Peromyscus leucopus</i>	O	0.48	-14.26	0.013	-0.02	0.52	0.06	-25.57	0.041	0.014	0.223	-2.87	-20.41	0.01	-0.018	0.853
<i>Peromyscus maniculatus</i>	O	-0.13	-24.05	0.001	-0.02	0.81	-0.04	-19.85	0.013	-0.006	0.415	0.79	-22.41	<0.001	-0.019	0.853
<i>Reithrodontomys megalotis</i>	G	1.58	6.21	0.186	<b>0.17</b>	0.00	0.03	-20.30	0.007	-0.015	0.565	0.98	-19.39	0.001	-0.021	0.816
<i>Sciurus niger</i>	O	-0.03	-24.44	0.000	-0.04	0.93	-0.03	-22.36	0.026	-0.01	0.404	4.61	-26.77	0.083	0.048	0.137
<i>Sigmodon hispidus</i>	F	-0.33	-27.19	0.010	-0.02	0.57	0.04	-24.14	0.015	-0.011	0.451	1.01	-22.74	0.001	-0.028	0.851
Folivores	F	0.38	-18.25	0.015	0.008	0.144	0.11	-30.05	0.125	<b>0.12</b>	<0.001	0.40	-24.54	<0.001	-0.007	0.861
Granivores	G	1.54	5.45	0.120	<b>0.113</b>	<0.001	0.03	-20.96	0.008	<0.001	0.302	1.11	-19.84	0.001	-0.006	0.705
Omnivores	O	0.25	-18.08	0.005	-0.002	0.394	0.00	-22.23	<0.001	-0.006	0.867	1.98	-23.22	0.006	<0.001	0.335
Rootivore ( <i>G. bursarius</i> )																
Insectivore ( <i>O. leucogaster</i> )																

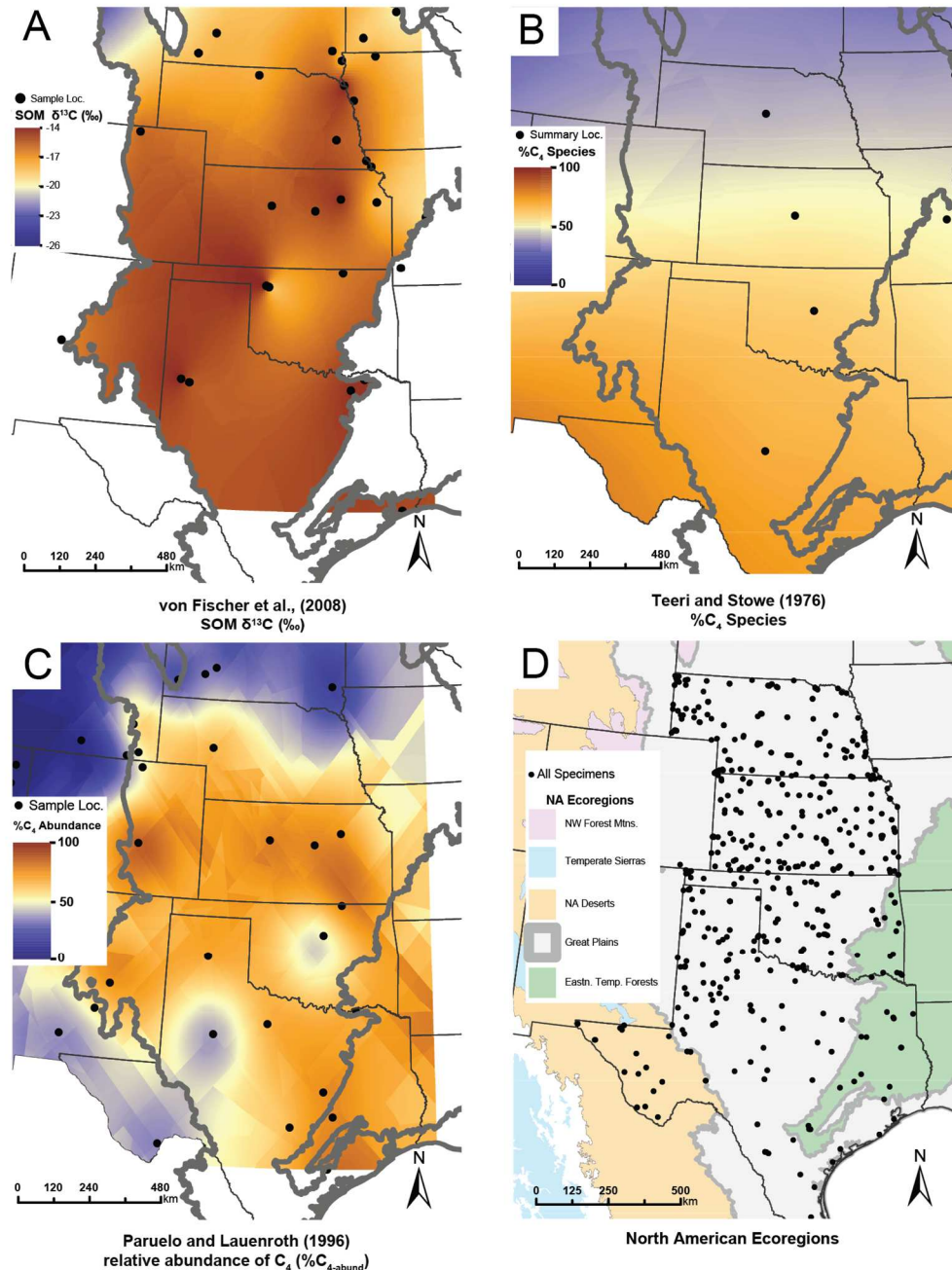


Figure 8 – Metrics of C<sub>4</sub> plant distribution across the southern Great Plains and collection location of museum specimens used in this study. A) Prediction map of  $\delta^{13}\text{C}_e$  values based on SOM matter (after von Fischer et al., 2008); B) %C<sub>4</sub> species (%C<sub>4</sub>-Species) (Teeri and Stowe, 1976); C) relative abundance of C<sub>4</sub> plants (%C<sub>4</sub>-abund) (Paruelo and Lauenroth, 1996); D) Distribution of 534 hairs sampled and analyzed in this study. Sampling focused on specimens within the Great Plains ecoregion, but extended to adjacent ecoregions (Eastern Temperate Forests and North American Deserts) that fell within the state boundaries of Nebraska, Kansas, Oklahoma, or Texas.

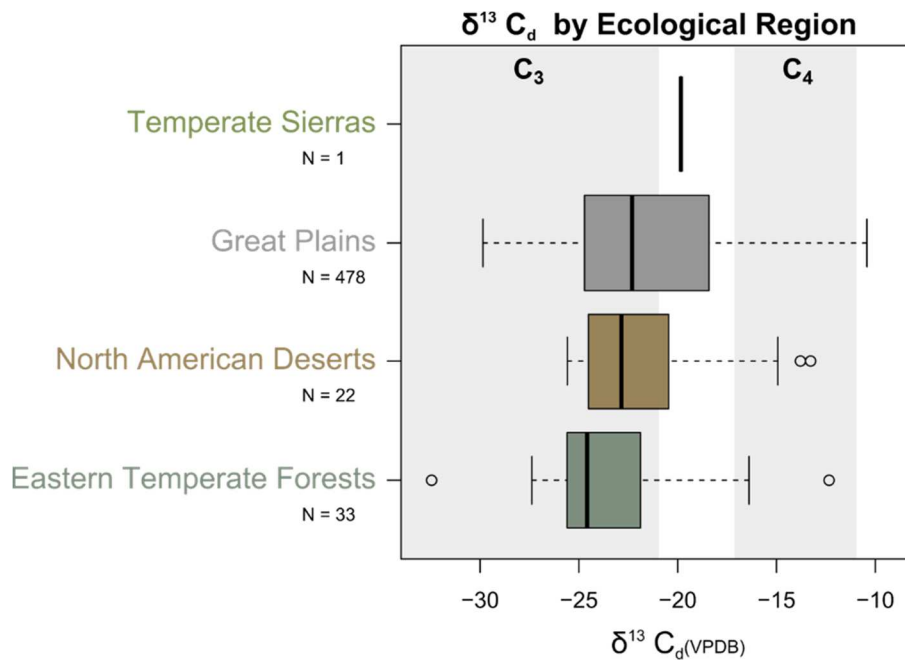


Figure 9 – Box and whisker plots of rodent  $\delta^{13}\text{C}_d$  values from four ecological regions of North America. Boxes indicate the lower and upper quartiles (25% and 75%), whiskers indicate maximum and minimum values, open circles indicate outliers, and the thick bar indicates the median. Vertical gray bars indicate the range of  $\text{C}_3$  and  $\text{C}_4$  values for North American plants (after Matson et al., 2012)

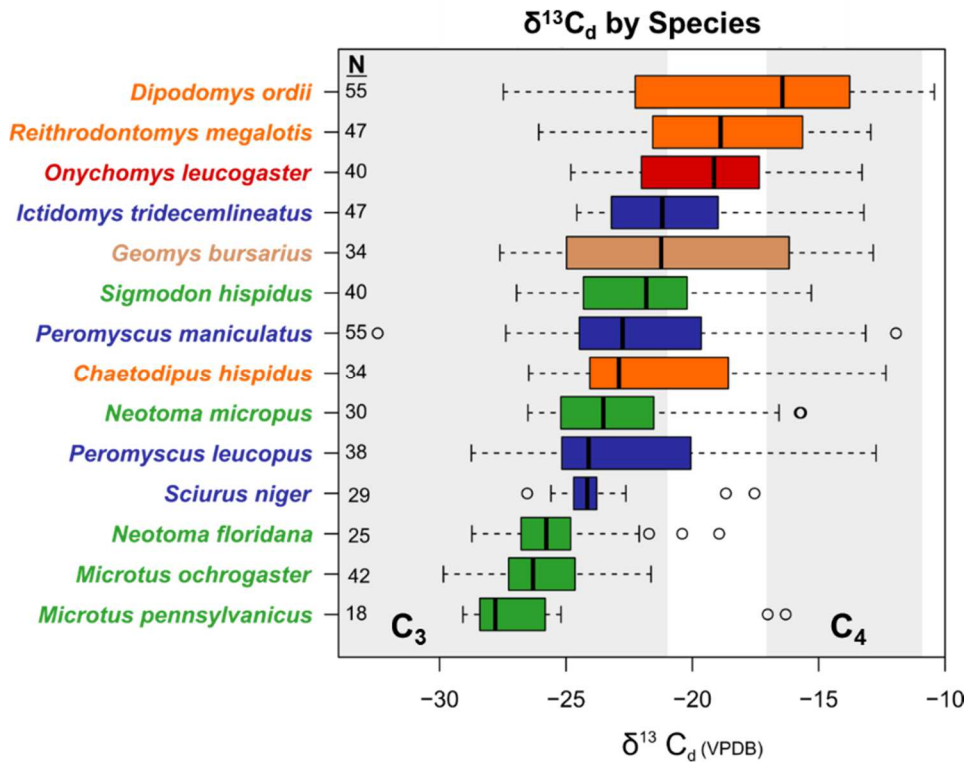


Figure 10 – Box and whisker plots of  $\delta^{13}\text{C}_d$  values grouped by species. Species names and boxes are colored relative to their diet category (see Table 7), Orange = granivore, Red = invertivore, Blue = omnivore, Brown = rootivore, and Green = folivore. Boxes indicate the lower and upper quartiles (25% and 75%), whiskers indicate maximum and minimum values, open circles indicate outliers, and the thick bar indicates the median. Gray bars indicate distribution of  $\delta^{13}\text{C}$  values for North American  $\text{C}_3$  and  $\text{C}_4$  plants (after Matson et al., 2012)

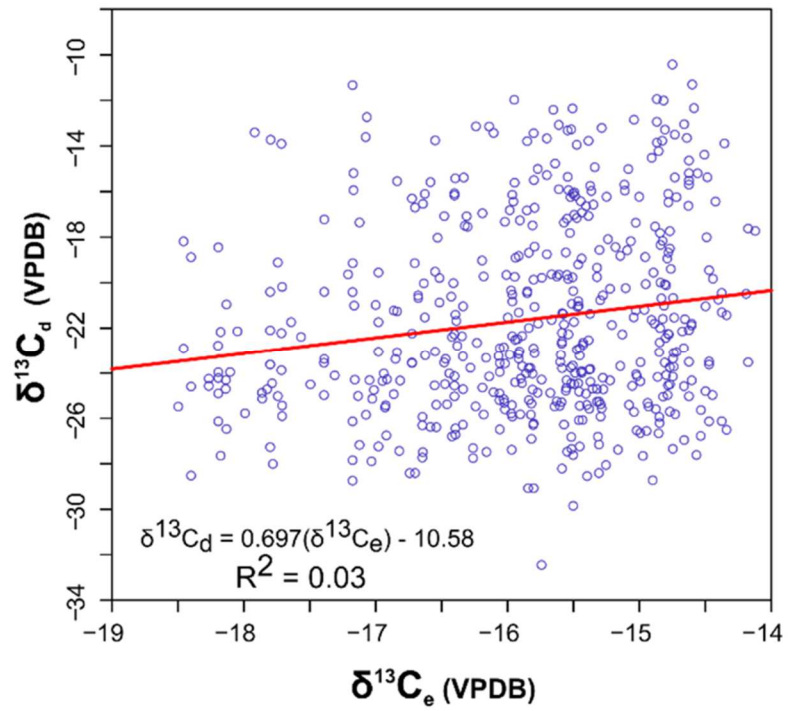


Figure 11 -  $\delta^{13}\text{C}_d$  values plotted relative to  $\delta^{13}\text{C}_e$  values for all specimens. Solid red line indicates simple linear regression between  $\delta^{13}\text{C}_e$  and  $\delta^{13}\text{C}_d$ .

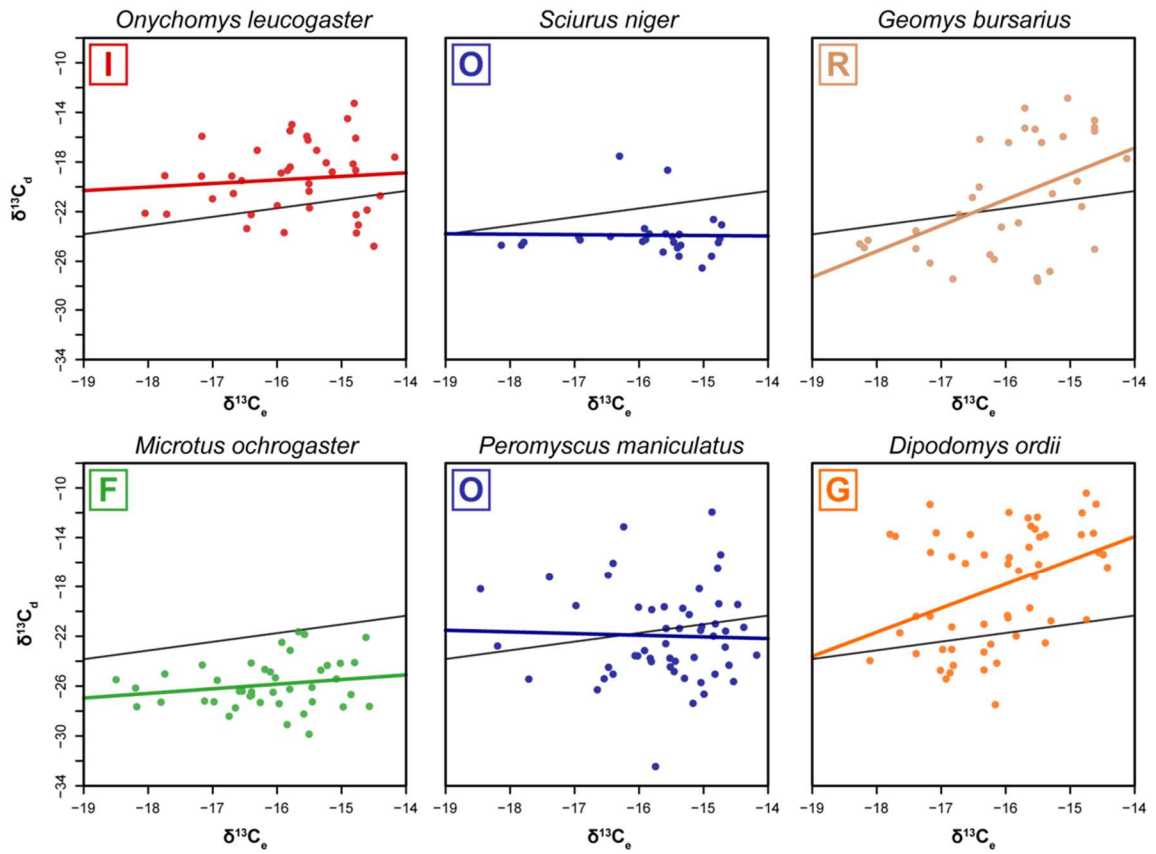


Figure 12 – Example bivariate plots and simple linear regressions between  $\delta^{13}C_d$  and  $\delta^{13}C_e$ . Diet categories are indicated in the upper left corner where I = Insectivore, O = Omnivore, G = Granivore, F = Folivore, and R = Rootivore. Thin black line in all panels is the linear regression for all 534 specimens for comparison to the bolder linear regression line for each species. A) *Onychomys leucogaster*; B) *Sciurus niger*; C) *Geomys bursarius*; D) *Microtus ochrogaster*; E) *Peromyscus maniculatus*; F) *Dipodomys ordii*.

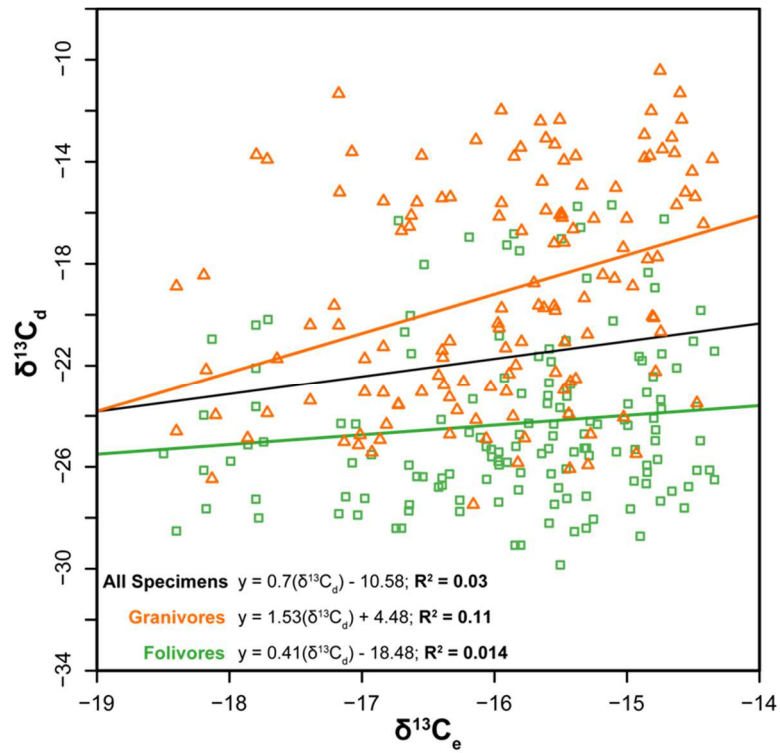


Figure 13 - Dietary  $\delta^{13}C_d$  of folivores (green open squares) and granivores (orange open triangles) against SOM  $\delta^{13}C_e$ . The thin gray line represents simple linear regression for all 534 specimens for comparison to simple linear regression for folivores (bold green line) and granivores (bold orange line).

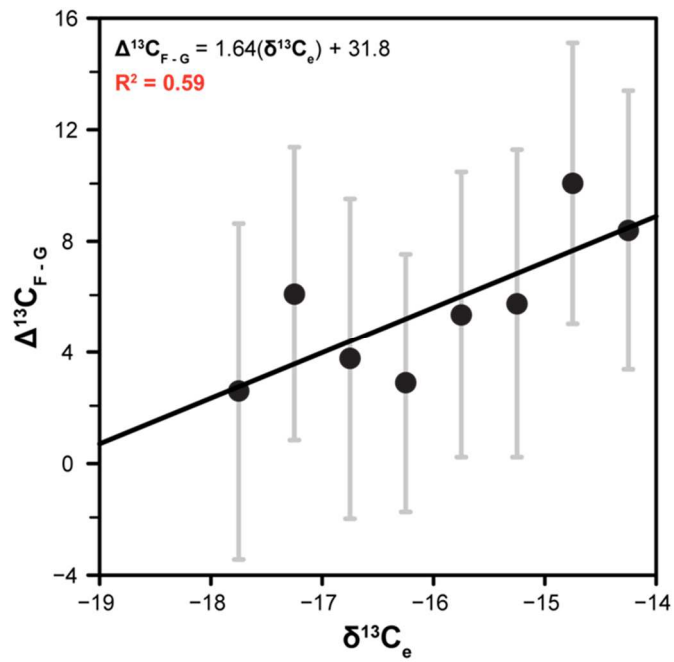


Figure 14  $-\Delta^{13}\text{C}_{\text{f-g}}$  (the difference between median values for folivores and granivores in 0.5‰ bins of  $\delta^{13}\text{C}_e$ ) values  $\pm$  the cumulative  $\sigma$  of folivores and granivores plots against  $\delta^{13}\text{C}_e$  values and a simple linear regression between  $\Delta^{13}\text{C}_{\text{f-g}}$  and  $\delta^{13}\text{C}_e$ .  $\delta^{13}\text{C}_e$  values are the midpoint of each 0.5‰ bin.



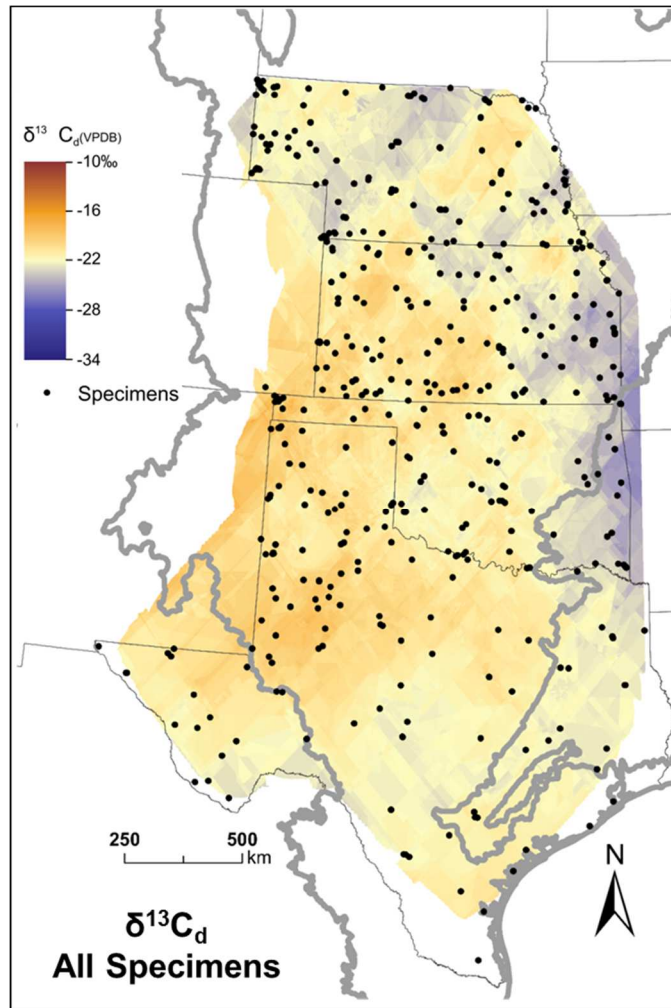


Figure 15 - Constructed  $\delta^{13}C_d$  isoscape for hair from all specimens (N = 534) and all species (N = 14). Thick gray line indicates the boundary of the Great Plains ecoregion.

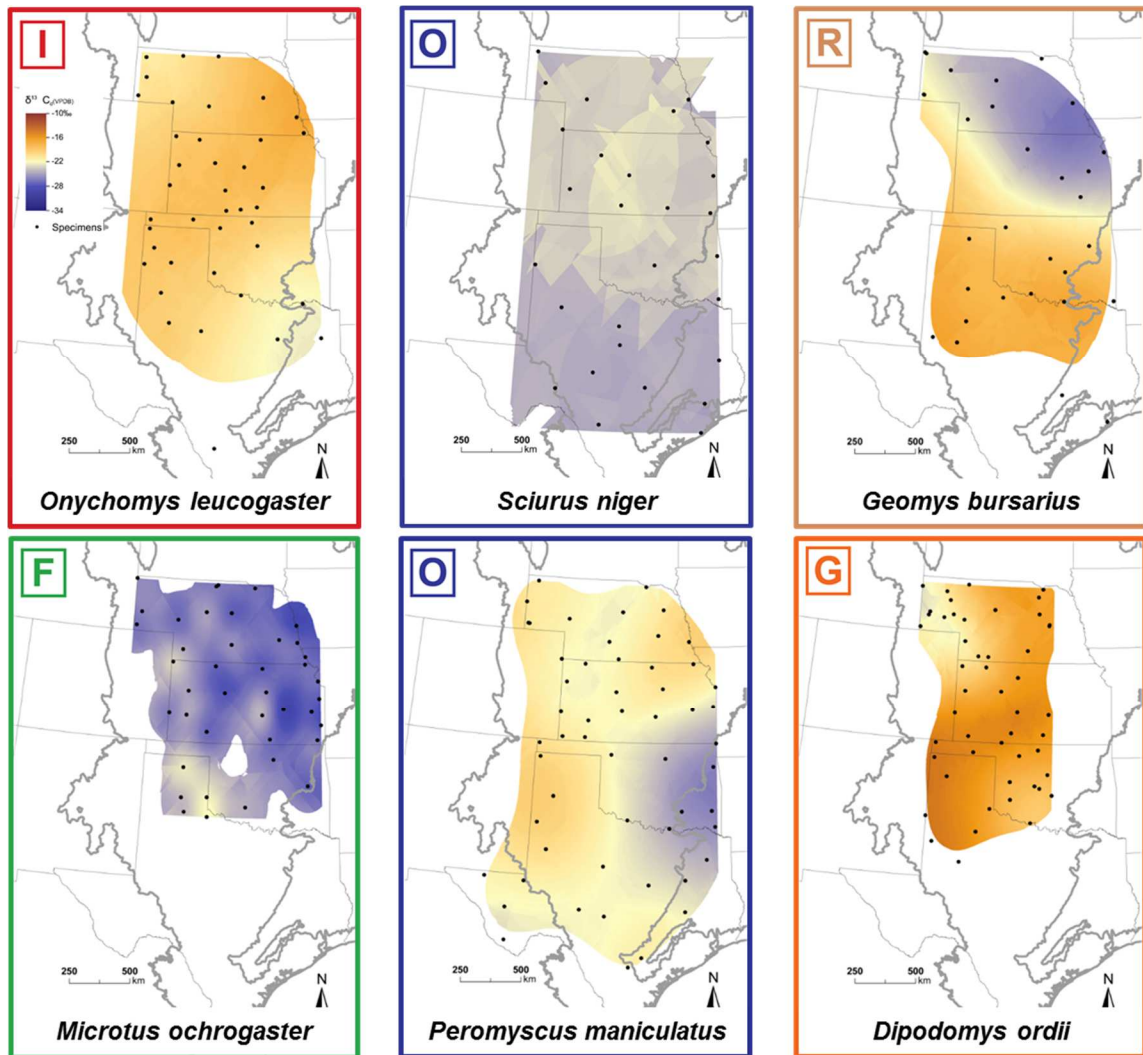


Figure 16 - Constructed  $\delta^{13}\text{C}_d$  isoscapes of hair for A) *Onychomys leucogaster*; B) *Sciurus niger*; C) *Geomys bursarius*; D) *Microtus ochrogaster*; E) *Peromyscus maniculatus*; F) *Dipodomys ordii*. Border colors and text color of letter in upper left corners indicate diet category and are the same as in Figure 12.

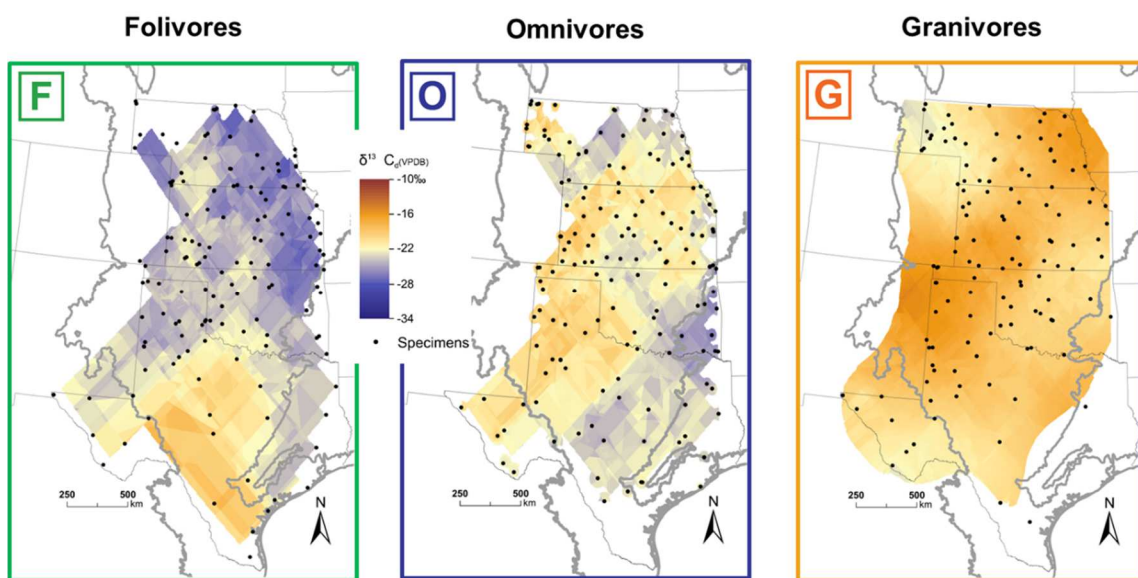


Figure 17 - Constructed isoscapes based on  $\delta^{13}C_a$  values of hair from A) Folivores, B) Omnivores, and C) Granivores.

## CHAPTER 3

### **Diet variation of rodents in the Great Plains, US: Do climate variables and land cover types explain consumption of C<sub>4</sub> derived resources?**

#### **SUMMARY**

Species distribution models do not typically include ecological information (e.g. diet) to assess if species are responding to climate because of physiological constraints or indirectly responding via their interactions with changing food resources. Food resources in grassland ecosystems can be greatly impacted by climate such as the relative proportions of biomass produced by plants using the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathways. Here, we determine if rodent diets vary with climate (e.g. temperature and precipitation) in respect to their consumption of C<sub>3</sub> and C<sub>4</sub> derived resources. Furthermore, land cover types are in part determined by the distribution of temperature and precipitation and we determine if rodent diets differ among land cover types.

We analyzed 534 hairs of 14 species distributed across the southern Great Plains for  $\delta^{13}\text{C}$  values, an indicators of C<sub>3</sub> and C<sub>4</sub> derived resources. We used nine climate least-collinear variables to determine if variation in small mammal diets is explained by climate variables and also binned  $\delta^{13}\text{C}$  values by land cover types. Multiple linear regression models varied in their predictive power, with some explaining up to 53% of the variance in  $\delta^{13}\text{C}_d$  for a species while other models explained only 4% of the variance in  $\delta^{13}\text{C}_d$  for another species. Generally, precipitation metrics were more commonly used as prediction variables than temperature metrics. We explored the predictive power of MAT and MAP and they explained little  $\delta^{13}\text{C}_d$  variance ( $R^2 < 0.01$  and  $R^2 = 0.02$ , respectively). The range of  $\delta^{13}\text{C}$  values from rodent hairs decreases during peak summer months in the central Great Plains potentially in response to primary productivity related to the distribution of rainfall throughout the year. The  $\delta^{13}\text{C}$  values of rodent hairs collected within grasslands span the isotopic spectrum of C<sub>3</sub> and C<sub>4</sub> plant values and the distribution of values is not significantly different from other land cover types. Rodent diets greatly vary in their diets in space, time, and in their responses to biotic and abiotic variables resulting the highly variable diets recorded in their tissues.

## INTRODUCTION

A species' fundamental niche is defined as a set of environmental tolerances that are suitable for a population to persist (Hutchinson, 1957). Species distribution models have been developed to describe patterns of species' occurrences, but also to make predictions of possible occurrences across space and through time (Elith and Leathwick, 2009). As environments on the landscape change, species must track or evolve their niche to avoid extinction (Graham et al., 1996, Martinez-Meyer et al., 2004). Species distribution models (or ecological niche models) typically do not include ecological information to assess if species are responding to climate physiologically or responding indirectly through interactions with changing food resources.

Deviating from their existing dietary niche may consist of altering the relative proportions of their current dietary sources, utilizing new food resources, or conserving their existing diet by migrating to remain aligned with their current food availabilities. Understanding how species utilize food resources along environmental and climatic gradients will improve projections and interpretations of species responses to impending climate change, which is important for environmental managers and policy makers (e.g. IPCC, 2014). Additionally, any relationship between diet and climate can then be tested with the fossil record to assess dietary responses to past environmental change and ultimately hypotheses about modes of evolution like the Court Jester hypothesis (Barnosky, 2001).

Carbon isotopes are commonly used to evaluate the relative proportions  $C_3$  and  $C_4$  derived food resources into diet.  $C_4$  plants are composed of mostly warm-season grasses and some sedges and  $C_3$  plants are composed of trees, shrubs, and cool-season grasses. In the Great Plains,  $C_4$  plant biomass increases along a latitudinal gradient with  $C_4$ -dominated grasslands in the hot-dry southwest to  $C_3$ -dominated grasslands in the northern plains (Teeri and Stow, 1976; Paruelo and Lauenroth, 1996; von Fischer et al., 2008). Carbon stable isotope values from rodent hair indicate some species increase  $C_4$ -plant derived resource consumption as  $C_4$  plant biomass increases on the landscape (See above, Chapter 2). However,  $C_4$ -plant biomass only explains a small amount of a  $\delta^{13}C$  variance in rodent diets and at best, explained 21% of the  $\delta^{13}C$  variance in *Geomys bursarius* (See above, Chapter 2). Therefore, a large proportion of consumer  $\delta^{13}C$  variance remains unexplained and the inclusion of more environmental

and climatic spatial covariates may explain more of the remaining variance in  $\delta^{13}\text{C}$  values.

This study builds upon a regional analysis of mammalian diets indicated by stable isotopes to evaluate mammalian diets in relation to continuous gradients of climate and environments. We aim to answer two main questions: 1) Does climate (e.g. temperature and precipitation) influence the relative proportions of  $\text{C}_3$  and  $\text{C}_4$  derived resources consumed by rodents? 2) Do carbon isotope values of rodent communities differ among land cover types? To address these questions, we analyzed hair from museum voucher specimens to determine diet variation with respect to 19 climatic variables and land cover types.

## METHODS

The southern Great Plains were defined as the region including Nebraska, Kansas, Oklahoma, and Texas. While some remnant native grasslands persist, the Great Plains have been anthropogenically modified over the last 150+ years for crop cultivation, livestock grazing, and urban development. Climatically, the southern Great Plains boast directional temperature and precipitation gradients as mean annual temperature (MAT) varies along a north-south gradient and mean annual precipitation (MAP) varies along an east-west gradient (see Hijmans et al., 2005). Physiographic features of relief and elevation are other potential variables that may influence local climate or rodent ecology, but relief is relatively low and there are no major orographic features present throughout the Great Plains. The lack of significant features minimizes their influence on climate and rodent ecology. Using the available climate gradients, we tested whether different climate variables influence rodent diets indicated by stable isotopes.

*Hair sampling and stable isotope analysis.* - Specimens of 14 rodent species from four Great Plains museum collections (University of Nebraska State Museum, University of Kansas Biodiversity Institute, Oklahoma Museum of Natural History, Texas Tech University) were sampled and analyzed for  $\delta^{13}\text{C}$  values of hair (Haveles Dissertation, Chapter 2). The species represent five diet categories (folivore, granivore, invertivore, omnivore, and rootivore) and four families (Cricetidae, Geomyidae, Heteromyidae, and Sciuridae) (Table 7). Each individual contained georeferenced metadata with a

maximum spatial error equal to a quarter section within the township and range system (~0.65 km<sup>2</sup>) (see Chapter 2 for additional spatial details). Specimens were selected to reflect uniform spacing in order to randomly sample the landscape and deviations from uniform spacing result from each museum's different studies, sampling methodologies, and protocols. Each specimen's geographic coordinates were then used to extract a corresponding value from each climate and land cover covariate.

Hair samples were sampled from the dorsal posterior of each individual, cleaned following the procedure by Schwertl et al. (2008), and analyzed in the University of Minnesota Stable Isotope Laboratory. Measured  $\delta^{13}\text{C}$  values were converted to reflect  $\delta^{13}\text{C}$  of diet ( $\delta^{13}\text{C}_d$ ) by correcting for enrichment between a consumer's tissue and its diet. We applied a diet-hair correction value of 1.1‰, corrected for secular change in the  $\delta^{13}\text{C}$  of atmospheric CO<sub>2</sub> based on collection date to reach a final  $\delta^{13}\text{C}_d$  value (see Chapter 2 for further discussion of corrections).

*Spatial Covariates.* – The WorldClim dataset includes 19 climate surfaces describing temperature and precipitation variation at a resolution of ~1 sqkm (Hijmans et al., 2005, [www.worldclim.org](http://www.worldclim.org)). Many of the climate variables are not independent from each other, therefore we utilized nine variables (Isothermality, Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month, Mean Temperature of Driest Quarter, Mean Annual Precipitation, Precipitation of Driest Month, Precipitation Seasonality, Precipitation of Warmest Quarter, and Precipitation of Coldest Quarter, see Appendices XII-IV) that were previously identified to be the least collinear (Ladd et al., 2014), or previously determined to impact species density (Badgley and Fox, 2000). Multiple linear regression was conducted for  $\delta^{13}\text{C}_d$  on the nine climatic covariates to determine which covariates have statistically significant, unique contributions to the prediction of  $\delta^{13}\text{C}_d$  values. Each species may be responding independently to climate, therefore we began with the same nine climate variables and then used stepwise multiple linear regression to determine which variables produce the optimal model for each species using backward elimination. Backward elimination begins with all nine variables and at each step, a variable is dropped if it does not significantly increase the model's fit. All statistical tests and regressions were conducted in the free statistical program R.

MAT and MAP are commonly estimated for climate modeling research and reconstructing past climate histories (e.g. Kowalski and Dilcher, 2003; van Dam, 2006;

Ivany and Huber, 2012 and sources therein), which are two climate variables we focused on here. In the fossil records, we can use these independent records of climate and rodent diets to study the response of mammals to long-term climate and subsequent environmental changes. These analyses will test whether species conserve their dietary niche through time, or if species utilize different food resources in response to environmental change. First, we must determine if modern rodent diets vary with MAT and/or MAP on the modern landscape to determine the influence these particular climate variables have on rodent diets. Therefore, we conducted separate analyses of rodent  $\delta^{13}\text{C}$  values with MAT and MAP by first running simple linear models.

Digital surfaces of land cover types were downloaded from the National Land Cover Database (NLCD) (Jin et al., 2013; available at <http://www.mrlc.gov/index.php>). Significance of diet differences among land cover types, were established using pairwise non-parametric pairwise Mann Whitney-U tests. The land cover digital surface will permit analyses test if anthropogenic land uses (e.g. cultivation, urbanization, pastures) and/or natural areas (e.g. forest, grassland, shrubland) influence  $\delta^{13}\text{C}$  values (i.e. diet) recorded in rodent hair.

## RESULTS

*Climate and  $\delta^{13}\text{C}_d$ .* - We conducted multiple linear regressions of all  $\delta^{13}\text{C}_d$  values on 19 climate variables to evaluate which combination of variables best predict  $\delta^{13}\text{C}_d$ . Using backward elimination, seven variables were deemed to best explain  $\delta^{13}\text{C}_d$  variation, however with only minimal predictive power ( $R^2_{\text{adj}} = 0.06$ , model p-value  $<0.001$ , Table 10). The seven climate variables that were included were composed of three temperature and four precipitation variables. Five of the seven climate variables were those included as part of the nine least collinear variables.

When limiting the multiple linear regression to start with the nine least collinear climate variables, only MAP and the Maximum Temperature of the Warmest Month remained as significant explanatory variables and explained nearly the same  $\delta^{13}\text{C}_d$  variance as the first model ( $R^2_{\text{adj}} = 0.05$ , model p-value = 0.001, Table 11). A similar result was found between soil organic matter  $\delta^{13}\text{C}$  values (indicative of relative  $\%C_4$ -plant biomass) and all  $\delta^{13}\text{C}_d$  values, which was partially because each species varied



their diet differently across the landscape. To determine the influence of climate on each species, we conducted additional multiple linear regressions for each species.

Subsequent multiple linear regressions for species began with the nine climate variables and we used backward elimination to determine which variables best explained  $\delta^{13}\text{C}_d$  variation. Minimum Temperature of the Coldest Month, Precipitation of Warmest Quarter, and Precipitation of Coldest Quarter were the most common variables followed by Precipitation Seasonality and MAP, and then Precipitation of Driest Month, Mean Temperature of Driest Quarter, and lastly, Isothermality (Table 11). Multiple linear regression models varied in their predictive power, with some explaining 53% and 49% (*Neotoma micropus* and *Geomys bursarius*, respectively) of the variance in  $\delta^{13}\text{C}_d$  while other models explained only 4% and 5% (*Reithrodontomys megalotis* and *Sciurus niger*, respectively) of the variance in  $\delta^{13}\text{C}_d$ . Generally, precipitation metrics were more commonly used as prediction variables than temperature metrics. There was also no combination of variables typically used for species in the same diet category or genus.

*$\delta^{13}\text{C}_d$  vs MAT and MAP.*- MAT and MAP explained little of  $\delta^{13}\text{C}_d$  variance ( $R^2 < 0.01$  and  $R^2 = 0.02$ , respectively). The negative slope between MAP and  $\delta^{13}\text{C}_d$  is statistically significant ( $p < 0.001$ ), however undersampling of higher MAP ( $> 1,000$  mm/yr) may be influencing the slope (Table 12, Figure 18). Among species, only *Geomys bursarius* ( $R^2_{\text{adj}} = 0.29$ ,  $p < 0.001$ ) and *Neotoma micropus* ( $R^2_{\text{adj}} = 0.26$ ,  $p = 0.002$ )  $\delta^{13}\text{C}_d$  values vary significantly with MAT. MAT explains less than 8% of  $\delta^{13}\text{C}_d$  variance for all other species (Table 12). In addition to species, we conducted simple linear regressions between  $\delta^{13}\text{C}_d$  values binned by categories on MAT and MAP climate variables. Folivores were the only diet category to boast a significant ( $p < 0.001$ ) relationship with MAT, which explained 14% ( $R^2_{\text{adj}} = 0.14$ ) of folivore  $\delta^{13}\text{C}_d$  values. The linear relationship between MAP and Omnivore  $\delta^{13}\text{C}_d$  values was significant ( $p < 0.001$ ), but MAP explained little omnivore  $\delta^{13}\text{C}_d$  variance ( $R^2_{\text{adj}} = 0.06$ ).

*Temporal Distribution of  $\delta^{13}\text{C}_d$ .*- The onset of growing seasons vary across the Great Plains in response to variable temperature and precipitation regimes, which may impact seasonal primary productivity and subsequently small mammal diets. We investigated the influence seasonal fluctuations on small mammal diets and their consumption of  $\text{C}_3$ -plant and  $\text{C}_4$ -plant derived resources throughout a year. Specimens were binned by two degrees of latitude between  $43^\circ\text{N}$  and  $27^\circ\text{N}$  and their  $\delta^{13}\text{C}_d$  values were plotted against collection month.  $\text{C}_3$  and  $\text{C}_4$  derived resources were both utilized

throughout the year evidenced by values spanning 16‰ regardless of latitude (Figure 19). The specimen samples size between 31-27°N is small and may result in the diminished range of  $\delta^{13}\text{C}_d$  values in comparison to more northern specimens.

The range of  $\delta^{13}\text{C}_d$  values from specimens occurring between 43°N and 35°N contracts during the middle to late summer months (June – September) and the median values become more positive (Figure 19). The minimum  $\delta^{13}\text{C}_d$  values for 37-35°N individuals increases from June through August before decreasing again in September. Furthermore, the minimum monthly values in 37-35°N are ~2‰ more positive throughout the year than values between 43-37°N. The more positive minimum  $\delta^{13}\text{C}_d$  values during the summer months also appears in latitudinal bins of 39-27°N, 41-39°N, and 43-41°N, but the timing minimum values being trending positive differs among the latitudinal bins. The onset of  $\delta^{13}\text{C}_d$  values contracting during summer months occurs earliest in the most southern (and warmer MAT) latitudinal bin (37-35°N) and then occurs later with more northern (and cooler MAT) latitudinal bins resulting in only a small contraction of values in the 41-41°N latitudinal bin.

*$\delta^{13}\text{C}_d$  and Land Cover.*- Grassland was the best represented land cover type (N = 216) and had the greatest range of  $\delta^{13}\text{C}_d$  values, (-30.1 to -11.4‰, range = 18.7‰, Table 13) and the most positive value (-10.4‰). Anthropogenically modified lands (Developed, Rural, Agricultural) are intermixed within grasslands and characterized by  $\delta^{13}\text{C}_d$  distributions with generally more positive values, including the two most positive median values (Cultivated Crops =  $-20.9 \pm 4.5$ ‰, Developed Land =  $-20.9 \pm 3.5$ ‰)(Table 13B). The more positive values in Developed Land and Cultivated Crops, may be the result of individuals consuming corn (a  $\text{C}_4$  grass) or human food derived from corn. Forests have more negative median  $\delta^{13}\text{C}_d$  values (E. Forests =  $-23.2 \pm 3.5$ ‰, D. Forests =  $-23.4 \pm 3.6$ ‰), but neither forest type is significantly different from grasslands (Table 14). Specimens assigned to the 'Open water' land cover, which no interpretation is possible because of the misclassification resulting from error in spatial coordinates.

## DISCUSSION

*Climate and  $\delta^{13}\text{C}_d$  values.*- Climate variables explain little or zero  $\delta^{13}\text{C}_d$  variance and is partially due to species varying their diets differently along environmental gradients. The larger  $R^2$  values from multiple linear regressions for individual species

supports that some species' diets are related to climate and other species' have no relationship (Table 10). These different responses in utilizing C<sub>3</sub>/C<sub>4</sub> resources suggest small mammals are partitioning food resources and in response to different climate variables.

There are relationships between climate and the  $\delta^{13}\text{C}_d$  values for some species, but there are multiple possible mechanisms at the base of these relationships. We must first acknowledge that the geographic ranges of the species included here, may only partially overlap with our study region, the southern Great Plains. For example, sampled *Microtus pennsylvanicus* specimens are only in Nebraska, which greatly limits the climate gradient those individuals span. We found no relationships between *M. pennsylvanicus*  $\delta^{13}\text{C}_d$  and climate, however we cannot extend that conclusion to the entire range of *M. pennsylvanicus*. If we increased the spatial coverage by including more *M. pennsylvanicus* specimens, we may potentially find that climate does or does not influence the diet of *M. pennsylvanicus*. Our assessments here are only limited to those in the southern Great Plains, but our results setup multiple hypotheses that could be tested by researchers interested in particular taxa that could be tested with increased sampling and reanalysis.

Other species have geographic ranges covering most of the southern Great Plains such as *Sciurus niger* and *Geomys bursarius*. While both species are well sampled across the southern Great Plains (Figure 16), their diets vary differently with SOM  $\delta^{13}\text{C}$  and climate variables. *G. bursarius*  $\delta^{13}\text{C}_d$  values positively varied with SOM  $\delta^{13}\text{C}$  (Chapter 2, Figure 12). Additionally, four climate variables (Table 11) explained 55% of the variance in *G. bursarius*  $\delta^{13}\text{C}_d$  values. Conversely, neither SOM  $\delta^{13}\text{C}$  values (Figure 12) nor any climate variables (Table 11) explained any variance of *S. niger*  $\delta^{13}\text{C}_d$  values. If we were to expand the spatial sampling for these two species, we hypothesize that *G. bursarius* would continue to vary consumption of C<sub>4</sub> derived resources based the proportion of C<sub>4</sub> plants and climate, while *S. niger*  $\delta^{13}\text{C}_d$  values would likely remain constant regardless of increased spatial sampling.

Species with  $\delta^{13}\text{C}_d$  values reflecting change in their consumption of C<sub>3</sub> and C<sub>4</sub> derived resources (e.g. *G. bursarius*, *D. ordii*, *R. megalotis*, *Ictidomys tridecemlineatus*), could have selectively altered their diets because of physiological and/or nutritional requirements to maintain metabolic requirements under different climate regimes. To meet these requirements, they may need to consume different proportions of green

foliage, invertebrates, or seeds resulting in differing  $\delta^{13}\text{C}$  values depending on the ecosystem. Alternatively, food resources (plants and invertebrates) are also distributed on the landscape according to their environmental tolerances. Thus the pool of dietary resources may spatially differ for a rodent species and then indirectly consumes variable proportions of  $\text{C}_3$  and  $\text{C}_4$  derived resources based on the distributions of plants and invertebrates. For example, the invertivore, *O. leucogaster*, is known to consume invertebrates throughout its geographic range, but the pool of invertebrate species varies across that same area. Orthopterans (grasshoppers) have different diet preferences with some focused on graminoids, sagebrush only (*Melanoplus bowditchi*), Chenopodiaceae only (*Melanoplus lakinus*), and others are polyphagous that feed on a variety of graminoids, forbs, and shrubs. The distribution of species ergo their diet preferences, will then influence the diet of invertivores, which then inadvertently change their consumption of  $\text{C}_3$  and  $\text{C}_4$  derived resources.

Small changes in  $\delta^{13}\text{C}_d$  values may also be indicative of  $\text{C}_3$  growing in warmer and drier climates that yield more positive  $\delta^{13}\text{C}$  values than individuals of the same species residing in a cooler and wetter environment. The positive shift in  $\text{C}_3$  plant  $\delta^{13}\text{C}$  values and subsequent consumption of those resources may result in diets that appear to include some  $\text{C}_4$  derived resources, but may only be the result of climate effects. For example, *Microtus ochrogaster*  $\delta^{13}\text{C}_d$  values become more positive with decreasing latitudes, but only slightly increases from an average of  $\sim 27\text{‰}$  to  $\sim 28\text{‰}$  over an area ranging from northern Nebraska to north Texas (Figure 12 and 16). While the trend is apparent it could be increased intake of  $\text{C}_4$  resources, consumption of  $\text{C}_3$  resources with more positive  $\delta^{13}\text{C}$  values due to aridity, or a combination of the two. These scenarios demonstrate the indirect effect climate can have on consumer  $\delta^{13}\text{C}_d$  values even if diet remained constant across the region.

Previous analysis of  $\delta^{13}\text{C}_d$  values in relation to soil organic matter (SOM)  $\delta^{13}\text{C}$  values, an estimate of  $\text{C}_3:\text{C}_4$  plant biomass, yielded similar conclusions with SOM  $\delta^{13}\text{C}$  explaining little  $\delta^{13}\text{C}_d$  variance for all species and individuals combined. However, SOM  $\delta^{13}\text{C}$  values did explain more  $\delta^{13}\text{C}_d$  variance in some species while climate covariates (addressed here) did not explain  $\delta^{13}\text{C}_d$  variance for the same species. Species like *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Sciurus niger* have no significant relationships with any climate variables. *P. maniculatus* is an omnivore and generalist with large dietary variance that may diminish any discernable dietary patterns

with climate (Flake, 1973), but does vary with land cover evidenced by the more negative  $\delta^{13}\text{C}_d$  values along the eastern boundary of the Great Plains with the Eastern Temperate Forests and more positive values along the western boundary of the Great Plains in western Kansas reflecting differences in  $\text{C}_4$  biomass on the landscape (Figure 16). *Reithrodontomys megalotis* did increase  $\text{C}_4$  consumption with increasing  $\text{C}_4$  biomass (Table 9), but climate explained little  $\delta^{13}\text{C}_d$  variance ( $R^2_{\text{adj}} = 0.04$ , Table 11). Lastly, *S. niger* has extremely low  $\delta^{13}\text{C}_d$  variance ( $\sigma = 1.8\text{‰}$ ) considering the spatial extent sampled, suggesting that *S. niger* individuals maintain a very similar diet regardless of environment and climate. The different species relationships between  $\delta^{13}\text{C}_d$  and  $\text{C}_4$  biomass or climate indicate the complexities within small mammal communities and how they utilize and partitioning food resources.

*$\delta^{13}\text{C}_d$  vs MAT and MAP.*- The weak and lack of relationships between  $\delta^{13}\text{C}_d$  and MAT are not unexpected because  $\text{C}_3$  plants can dominate high MAT ecosystems (e.g. tropical rainforests) given sufficient water availability throughout the course of the year. The absence of any relationship in part indicates the overall reliance of most small mammals on  $\text{C}_3$  derived resources. Grasslands dominated by  $\text{C}_4$ -biomass still contain  $\text{C}_3$  graminoids and forbs that provide forage for primary and secondary consumers (See Chapter 1). Furthermore, the reliance on  $\text{C}_3$  derived resource may indicate the importance of riparian zones ( $\text{C}_3$  vegetation dominated) and herbaceous  $\text{C}_3$ -plants within  $\text{C}_4$ -dominated grasslands as rodent dietary resources (Hamilton et al., 2015) and mitigate the influence of climate on rodent diets. Possibly, intermediate variables (e.g. NDVI, seed production, arthropod populations, or canopy cover) between the consumer and climate may provide more explanatory power with a more direct connection to consumers' diet.

The multiple linear regression analyses also indicate that diet variation was best explained by a combination of temperature and precipitation variables, which indicates that the combination of temperature and precipitation is important. Furthermore, most of the climate variables in the multiple regressions are related to seasonal extremes (e.g. Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month, and Precipitation of the Driest Month) or overall seasonality (e.g. Precipitation Seasonality and Isothermality), which suggests seasonal climate might be an important influence on diet.

*Temporal Distribution of  $\delta^{13}C_d$ .*- Our complete dataset includes specimens collected throughout the year, therefore seasonal changes in diet in response to seasonal food availability may contribute to overall diet variation. von Fischer et al. (2008) found that July climate (the month's mean daily high temperature and total rainfall) was the best predictor of %C<sub>4</sub> in the Great Plains. July is in the middle of the C<sub>4</sub> growing season and differences in July climate influence C<sub>4</sub> production and subsequently may influence C<sub>4</sub> consumption by small mammals. Therefore, we would expect C<sub>4</sub> consumption to be greatest in the late summer months when C<sub>4</sub> production has peaked. The onset of the C<sub>4</sub> growing season likely does not occur simultaneously across the Great Plains and varies with latitude, so we would expect C<sub>4</sub> consumption to occur earliest in the south and latest in the north.

We address this latitudinal gradient by binning the dataset into eight latitudinal bins at two degree intervals and then plot  $\delta^{13}C_d$  values by collection month. Our expectation was C<sub>4</sub> consumption would be earlier in the south in comparison to northern latitudes as warm-season grasses (C<sub>4</sub> grasses) become more abundant during the summer months. This pattern does not hold true for latitudes above 41°N or below 35°N, however there is an indication that between 41°N and 35°N (northern Texas and Oklahoma, and all of Kansas) rodents consume more C<sub>4</sub> resources at different times of the year relative to their latitudinal position (Figure 17). Between 37°N and 35°N, rodents consumed a mixture of C<sub>3</sub> and C<sub>4</sub> derived resources yielding  $\delta^{13}C_d$  values varying around an intermediate value and few diets are dominated by C<sub>3</sub> derived resources. Moving two degrees north, (37°N to 39°N), diets become increasingly positive after May until reaching a peak in August, and then decreasing again at the end of the growing season (Figure 17). Moving another two degrees north (39°N to 41°N), a similar temporal pattern emerges except increased C<sub>4</sub> consumption does not occur until after May. The latitudinal pattern does not hold in the northern or southern latitude bins possibly because of the temporal distribution of precipitation throughout the year. Between 41°N and 35°N (where the pattern is most prevalent), precipitation is normally distributed throughout the year and peaking during the summer months of June, July, and August. Above 41°N precipitation is slightly skewed with peak precipitation earlier in the year (May, June). The distribution of precipitation is greatly different below 35°N where the distribution is bimodal with peak precipitation in May/June and September/October. These differences in how precipitation distributed throughout the

year may influence the productivity of C<sub>3</sub> and C<sub>4</sub> plants and ultimately the foraging habits of small mammals. Further work could address this further with monthly small mammal sampling accompanied with precipitation and plant productivity measurements in order to directly determine how diet changes with productivity throughout the year.

The more positive  $\delta^{13}\text{C}_d$  values during the summer months may also be a result of hot-dry conditions that influence plant discrimination between C<sup>12</sup>/C<sup>13</sup> and results in more positive foliar  $\delta^{13}\text{C}$  values under water stress (e.g. Tieszen, 1991; Ladd et al., 2014). Whether more positive  $\delta^{13}\text{C}_d$  values are a result of increased C<sub>4</sub> consumption or water stress is beyond the scope of this study and not possible to test without foliar  $\delta^{13}\text{C}$  values for comparison.

The geographic extent considered here may factor into the minimal explanation of  $\delta^{13}\text{C}_d$  variance by climate variables. Most specimens were collected within the southern Great Plains ecoregion and from grassland habitats. Smaller subsets are from other biomes (evergreen forests, deciduous forests) that occupy different climate space from grasslands (Whittaker, 1970). Expanding the dataset to include a greater range of climates (subsequently more biomes) may yield dietary trends occurring on scales larger than our dataset can detect. Including specimens from the northern Great Plains (C<sub>3</sub>-grass dominated) may result in more discernable relationships between diets and spatial covariates such as %C<sub>4</sub>-plant biomass and climate.

*$\delta^{13}\text{C}_d$  and Land Cover.*- Rodent  $\delta^{13}\text{C}_d$  values from the grasslands boast the largest range of values (19‰) representing the full range of C<sub>3</sub> and C<sub>4</sub> resources available for consumption throughout the Great Plains and therefore encompasses values in all other land covers. Thus grassland carbon isotope values are not different from any other land covers. Shrublands are commonly intermixed with grasslands such as the short grass prairies in western Kansas and throughout north Texas. They are also integrated into the North American Deserts in western Texas that is included in our study. Isotopically, consumers from shrublands have  $\delta^{13}\text{C}_d$  values within the range of grassland carbon isotopes values and with additional sampling of rodent individuals from shrublands in the Great Plains and in North American Deserts will yield a very similar distribution to grasslands with species partitioning food resources. The anthropogenically modified land covers (agricultural and developed) also yield similar carbon isotope values, but individuals from agricultural lands even contain  $\delta^{13}\text{C}_d$  values indicative of C<sub>4</sub> only consumption. We hypothesize these individuals may have been consuming corn, a

common C<sub>4</sub> crop throughout the Great Plains. Various forms of corn are included in a lot of human foods and, we would expect that individuals consuming a lot of human food would have values boasting more positive carbon isotope values (e.g. Hopkins et al., 2012). The temperate evergreen forests yielded mostly carbon isotope values indicative of C<sub>3</sub>-only to C<sub>3</sub>-dominated diets, which would be expected given that these ecosystems are greatly dominated by C<sub>3</sub> vegetation.

The greater variance in rodent diets relative to the broad land cover types may be in part due to the difference in how rodents view their environment. Rodents have small home ranges (0.02 to 1.1 ha) in comparison to large bodied consumers (equids, bovids, and cervids; 59 to 1292 ha) (Harestad and Bunnell, 1979). Small home ranges reduce the potential of averaging food resources over large distances or maintaining a specific diet throughout the year by migrating. Small home ranges allow small mammal populations to reside in isolated macrohabitats that may be no larger than their home range but provides enough resources for the population to maintain fitness. Furthermore, species may prefer specific macrohabitats, but those habitats may be the minority land cover type in the surrounding landscape. That area is then classified as the habitat that covers occupies the majority of some defined squared area (or raster cell). The southern Great Plains are dominated by grasslands, but pockets of riparian zones containing shrubs, grasses, sedges, and trees provide a variety of resources such as canopy cover from predators, nesting sites, and food (Kaufman and Fleharty, 1974; Stamp and Ohmart, 1978; Cramer and Willig, 2002).

A limitation to this study is potentially the use of a single stable isotope as indication of diet. Our main question focused on the overall consumption of resources derived from plants using either the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathways and used  $\delta^{13}\text{C}$  values to indicate the source of assimilated carbon in consumer tissues. However, we cannot determine if the assimilated carbon isotopes for an individual are via direct consumption of primary producers or acquired as secondary or tertiary consumers.

Populations may also alter diets relative to climate, but in a manner that does not change the proportion of C<sub>3</sub> and C<sub>4</sub> derived resources. Instead, consumers may alter their diet by changing the relative proportions of foliage, invertebrates, and seeds consumed. Including a second isotope ( $\delta^{15}\text{N}$ ) could provide some indication of trophic position, which could be used to test if invertebrate consumption varies with climate. However, bulk  $\delta^{15}\text{N}$  values from museum specimens are difficult to interpret because



baseline  $\delta^{15}\text{N}$  values greatly vary on the landscape even between adjacent macrohabitats (Ambrose, 1991; Casey et al., 2011). Normalizing consumer  $\delta^{15}\text{N}$  values to the local  $\delta^{15}\text{N}$  baseline would entail analyzing soils from each specimen's macrohabitat.

Recent analytical developments have led to compound specific isotope analysis of amino acids (CSIA-AA), which could be used to indicate an individual's trophic position based on the isotopic difference between the consumer's essential and non-essential amino acids (McClelland & Montoya 2002, Chikaraishi et al. 2007, Chikaraishi et al., 2009, Popp et al. 2007, Hannides et al. 2009; Lorrain et al., 2009). CSIA-AA would be valuable because it would allow for trophic position determination without analyzing all potential food items. However, this method has recently been developed and applied mostly to marine taxa and would need to be calibrated and verified in terrestrial ecosystems before application.

## CONCLUSIONS

These data are imperative for interpreting similar data in modern and fossil studies. We have identified that combined climate variables can explain some variance in  $\text{C}_4$  consumption for some species, while other species' diets were not explained by climate variables. Most climate variables that contributed towards species specific models best explaining  $\delta^{13}\text{C}_d$  values were generally metrics of seasonality or seasonal extremes. Furthermore, species' with  $\delta^{13}\text{C}_d$  values that varied with climate included representatives from all five diet categories, suggesting that dietary responses to climate are species specific. When specimens are binned by latitude, the range of  $\delta^{13}\text{C}$  values from rodent hairs decreases during peak summer months in the central Great Plains potentially in response to primary productivity related to the distribution of rainfall throughout the year. The  $\delta^{13}\text{C}$  values of rodent hairs collected within grasslands span the isotopic spectrum  $\text{C}_3$  and  $\text{C}_4$  plant values and the distribution of values is not significantly different from other land cover types investigated here. Rodent diets greatly vary in their diets in space, time, and in their responses to biotic and abiotic variables. The results presented here, further our understanding of rodent ecology on temporal and spatial scales that extend beyond other modern diet metrics and lays the ground work for increasing in spatial and temporal scope.

## FUTURE WORK

Our assessments are limited to the southern Great Plains, but our results lay the groundwork for multiple hypotheses to be tested by investigators interested in particular taxa, food webs, ecosystems, or landscape ecology by expanding the ecosystem diversity by including more C<sub>3</sub> grasslands, forests, savannahs, deserts, or rainforests. Extending the dataset beyond the Great Plains would allow for characterizing more climate space and biomes that may produce larger scale diet patterns. Understanding the variation in rodent diets among multiple biomes is important for interpreting similar data from the fossil records. In turn, we can use the fossil record to reconstruct past environments, test models of evolution, or model past ecological responses to environmental change. Larger incorporation of the landscape would subsequently include greater ranges of environmental and climatic variables that would be used to better understand the controls on rodent diets. Other variables like potential evapotranspiration, soil type, number of frost free days, etc., may yield an improved understanding of  $\delta^{13}\text{C}_d$  variance. This spatial database of rodent diets distributed across the Great Plains can serve as the seed to spurn multiple avenues of paleobiology and ecological research.

Table 10.- Results of multiple linear regression with reverse elimination of  $\delta^{13}\text{C}_d$  and beginning with 19 climate variables.

Group	Adj R <sup>2</sup> w/ $\delta^{13}\text{C}_e$ only	R <sup>2</sup>	Adj R <sup>2</sup>	Residual SE	Model p-value	Intercept p-value	Mean Diurnal Range	Isothermality	Min Temp of Coldest Temp	MAP	Precip of Driest Month	Precip of Driest Quarter	Precip of Warmest Quarter
							Bio2	Bio3	Bio6	Bio12	Bio14	Bio17	Bio18
All Specimens (Starting with all Vars)	0.07	0.06	0.06	4.07	<0.001	-14.21	1.04	-47.26	0.51	-0.01	-0.16	0.06	0.02
					0.011	0.011	0.007	0.008	<0.001	0.061	0.138	0.085	0.063

Table 11.- Multiple Linear Regressions between  $\delta^{13}\text{C}_d$  and climate covariates

Species	Trophic	Adj R <sup>2</sup> w/ $\delta^{13}\text{C}_a$ only	R <sup>2</sup>	Adj R <sup>2</sup>	Residual SE	Model p-value	Intercept p-value	Temperature				Precipitation				
								Isothermality	Max Temp of Warmest Month	Min Temp of Coldest Month	Mean Temp of Driest Quart	MAP	Precip of Driest Month	Precip Seasonality	Precip of Warmest Quart	Precip of Coldest Quart
								Bio3	Bio5	Bio6	Bio9	Bio12	Bio14	Bio15	Bio18	Bio19
<i>Chaetodipus hispidus</i>	G	0.08	0.21	0.13	3.47	0.063	-27.6					-0.03			0.08	0.13
<i>Dipodomys ordii</i>	G	0.14	0.30	0.24	4.06	0.001	3.6		0.60			0.087	-0.69	-0.28	0.071	0.042
<i>Geomys bursarius</i>	R	0.21	0.55	0.49	3.332	<0.001	-8.9		0.008			-0.02	0.72	0.065	0.04	-0.14
<i>Ictidomys tridecemlineatus</i>	O	0.03	0.39	0.35	2.26	<0.001	-60.5		0.001			0.012	0.028			0.057
<i>Microtus ochrogaster</i>	F	0.01	0.42	0.38	1.53	0.000	-25.6		1.20				1.14			-0.32
<i>Microtus pennsylvanicus</i>	F	-0.05	0.42	0.10	3.48	0.328	61.6		<0.001				0.002			0.002
<i>Neotoma floridana</i>	F	0.11	0.59	0.53	1.62	0.000	41.0		0.40				0.10		-0.01	
<i>Neotoma micropus</i>	F	0.03	0.36	0.32	2.63	0.002	-1.0		0.000				0.023		0.168	
<i>Onychomys leucogaster</i>	I	-0.02	0.36	0.31	2.40	0.001	-8.4		-3.40				-2.55	0.69		0.80
<i>Peromyscus leucopus</i>	O	-0.02	0.32	0.28	3.60	0.001	-16.2		0.137				0.076	0.259		0.173
<i>Peromyscus maniculatus</i>	O	-0.02	0.10	0.08	3.59	0.018	-18.9		-1.76						-0.03	
<i>Reithrodontomys megalotis</i>	G	0.17	0.16	0.04	3.76	0.281	-82.3		0.000					-0.21	0.001	0.001
<i>Sciurus niger</i>	O	-0.04	0.15	0.05	1.75	0.244	-48.0		0.000					0.001	-0.05	
<i>Sigmodon hispidus</i>	F	-0.02	0.32	0.20	2.76	0.035	-5.5		0.000					-0.22	0.07	0.052
All Specimens			0.05	0.05	4.09	<0.001	-33.6		0.000					0.066	0.000	0.115
									0.43						0.01	0.06
									<0.001						0.125	0.047
															0.178	0.047

Table 12.--Simple Linear Regression between  $\delta^{13}\text{C}_a$  on MAP and MAT

Species	Trophic	Bio1				MAP					
		m	b	R <sup>2</sup>	Adj R <sup>2</sup>	p-value	m	b	R <sup>2</sup>	Adj R <sup>2</sup>	p-value
<i>All Individuals</i>		<b>0.11</b>	<b>-23.0</b>	<b>0.01</b>	<b>0.01</b>	<b>0.046</b>	-0.0030	-19.7	0.03	0.03	<b>&lt;0.001</b>
<i>Chaetodipus hispidus</i>	G	0.18	-24.0	0.03	<0.001	0.35	0.0050	-24.7	0.09	0.06	0.08
<i>Dipodomys ordii</i>	G	<b>0.47</b>	<b>-23.6</b>	<b>0.09</b>	<b>0.07</b>	<b>0.03</b>	0.0041	-20.3	0.01	0.00	0.39
<i>Geomys bursarius</i>	R	<b>0.68</b>	<b>-29.8</b>	<b>0.31</b>	<b>0.29</b>	<b>&lt;0.001</b>	-0.0001	-20.8	<0.001	-0.03	0.97
<i>Ictidomys tridecemlineatus</i>	O	0.32	-24.9	0.08	0.06	0.06	-0.0014	-20.0	0.01	-0.01	0.49
<i>Microtus ochrogaster</i>	F	0.21	-28.4	0.08	0.05	0.07	<b>-0.0032</b>	<b>-23.7</b>	<b>0.13</b>	<b>0.11</b>	<b>0.02</b>
<i>Microtus pennsylvanicus</i>	F	-0.05	-25.6	0.00	-0.06	0.95	-0.0039	-23.7	0.02	-0.04	0.56
<i>Neotoma floridana</i>	F	-0.17	-22.8	0.08	0.04	0.17	-0.0030	-22.9	0.15	0.12	0.05
<i>Neotoma micropus</i>	F	<b>0.87</b>	<b>-35.6</b>	<b>0.29</b>	<b>0.26</b>	<b>0.002</b>	0.0039	-24.7	0.02	-0.01	0.41
<i>Onychomys leucogaster</i>	I	-0.18	-17.1	0.04	0.02	0.21	-0.0022	-18.2	0.02	-0.01	0.38
<i>Peromyscus leucopus</i>	O	0.05	-22.8	0.00	-0.03	0.78	<b>-0.0062</b>	<b>-18.2</b>	<b>0.13</b>	<b>0.11</b>	<b>0.02</b>
<i>Peromyscus maniculatus</i>	O	-0.17	-19.6	0.02	0.01	0.25	<b>-0.0045</b>	<b>-18.9</b>	<b>0.10</b>	<b>0.08</b>	<b>0.02</b>
<i>Reithrodontomys megalotis</i>	G	0.06	-19.6	0.00	-0.02	0.75	0.0002	-18.9	<0.001	-0.02	0.95
<i>Sciurus niger</i>	O	-0.08	-22.7	0.03	-0.01	0.38	-0.0001	-23.8	<0.001	-0.04	0.94
<i>Sigmodon hispidus</i>	F	0.24	-25.4	0.07	0.05	0.09	-0.0004	-21.4	<0.001	-0.03	0.85
Granivores	G	0.1	-20.5	0.01	<0.001	0.36	0.0011	-19.8	<0.001	-0.01	0.59
Folivores	F	<b>0.4</b>	<b>-29.2</b>	<b>0.15</b>	<b>0.14</b>	<b>&lt;0.001</b>	-1.0633	-17.3	0.01	0.01	0.16
Omnivores	O	-0.1	-21.0	0.01	<0.001	0.33	-2.4180	-6.5	0.07	0.06	<0.001
Rootivore (Geomys)	R			see above					see above		
Insectivore (Onychomys)	I			see above					see above		



Table 13.- Summary statistics of  $\delta^{13}\text{C}_d$  values grouped by land cover types. A) All land cover types; B) Land cover types grouped broad classifications. Open water, Wetlands, and Barren Land were not included in pairwise Mann-Whitney U tests because of low sample sizes and misclassification due to error in spatial coordinates (Open Water).

<b>A) Land Use</b>	<b>n</b>	<b>Mean</b>	<b><math>\sigma</math></b>	<b>Median</b>	<b>Min</b>	<b>Max</b>	<b>Range</b>	<b>SE</b>
Wetlands - wood	6	-23.1	5.1	-23.4	-29.1	-15.4	13.7	2.1
Wetlands - Herb	2	-17.2	5.6	-17.2	-21.2	-13.3	7.9	4.0
Shrubland	56	-21.5	3.7	-21.8	-27.5	-13.1	14.4	0.5
Pasture	26	-23.5	3.8	-24.3	-32.5	-16.4	16.1	0.7
Open Water	11	-24.1	4.9	-25.5	-28.7	-11.3	17.4	1.5
Grassland	219	-21.4	4.2	-22.4	-29.9	-10.4	19.4	0.3
Evergreen Forest	22	-23.2	3.5	-24.1	-26.8	-13.3	13.6	0.8
Developed - Open	32	-22.2	3.9	-23.1	-28.4	-13.8	14.6	0.7
Developed - Med	7	-21.2	3.6	-21.8	-24.0	-13.7	10.3	1.4
Developed - Low	14	-19.4	3.7	-19.3	-24.9	-12.3	12.6	1.0
Developed - high	4	-21.0	2.4	-20.9	-24.0	-18.2	5.8	1.2
Deciduous Forest	27	-23.4	3.6	-24.7	-28.0	-12.9	15.2	0.7
Agricultural	107	-20.9	4.5	-21.7	-29.1	-11.9	17.1	0.4
Barren Land	1	-17.3	NA	-17.3	-17.3	-17.3	0.0	NA

<b>B) Land Use</b>	<b>n</b>	<b>Mean</b>	<b><math>\sigma</math></b>	<b>Median</b>	<b>Min</b>	<b>Max</b>	<b>Range</b>	<b>SE</b>
Wetlands	8	-21.6	5.5	-21.1	-29.1	-13.3	15.8	1.9
Shrubland	56	-21.5	3.7	-21.8	-27.5	-13.1	14.4	0.5
Developed - Open	33	-22.1	3.9	-23.1	-28.4	-13.8	14.6	0.7
Pasture	26	-23.5	3.8	-24.3	-32.5	-16.4	16.1	0.7
Open Water	11	-24.1	4.9	-25.5	-28.7	-11.3	17.4	1.5
Grassland	219	-21.4	4.2	-22.4	-29.9	-10.4	19.4	0.3
Evergreen Forest	22	-23.2	3.5	-24.1	-26.8	-13.3	13.6	0.8
Developed	25	-20.2	3.5	-20.9	-24.9	-12.3	12.6	0.7
Deciduous Forest	27	-23.4	3.6	-24.7	-28.0	-12.9	15.2	0.7
Cultivated Crops	107	-20.9	4.5	-21.7	-29.1	-11.9	17.1	0.4

Table 14.- Results of pairwise Mann-Whitney U tests among land cover types

Pairwise comparison of land covers based on 2011 data	Agricultural	Deciduous Forest	Developed	Evergreen Forest	Grassland	Pasture	Rural
Deciduous Forest	0.21	-	-	-	-	-	-
Developed	1	<b>0.02</b>	-	-	-	-	-
Evergreen Forest	0.74	1	<b>0.02</b>	-	-	-	-
Grassland	1	0.36	1	1	-	-	-
Pasture	0.306	1	0.05	1	0.56	-	-
Rural	1	1	0.70	1	1	1	-
Shrubland	1	0.41	1	0.77	1	0.62	1



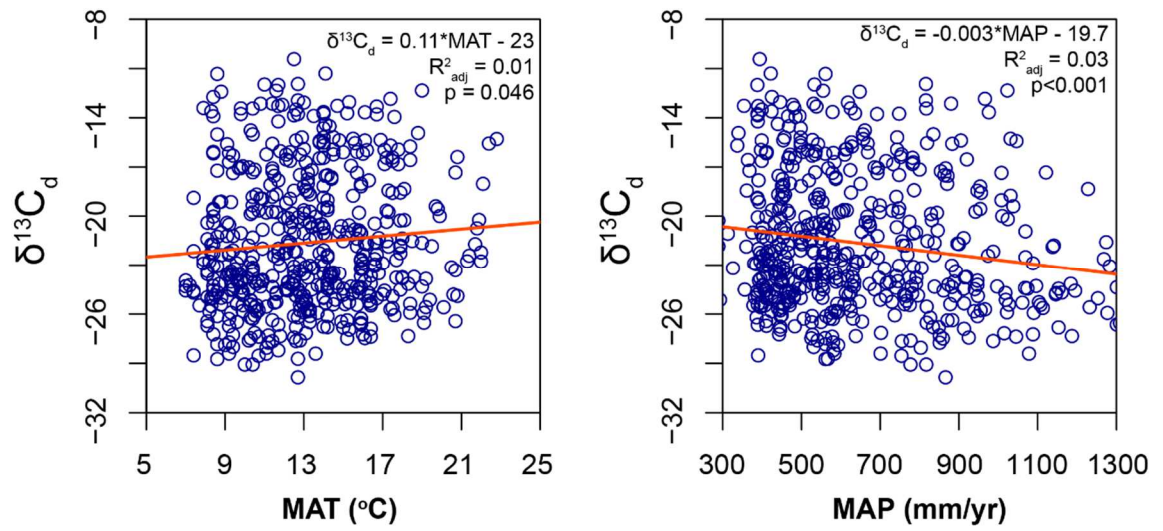
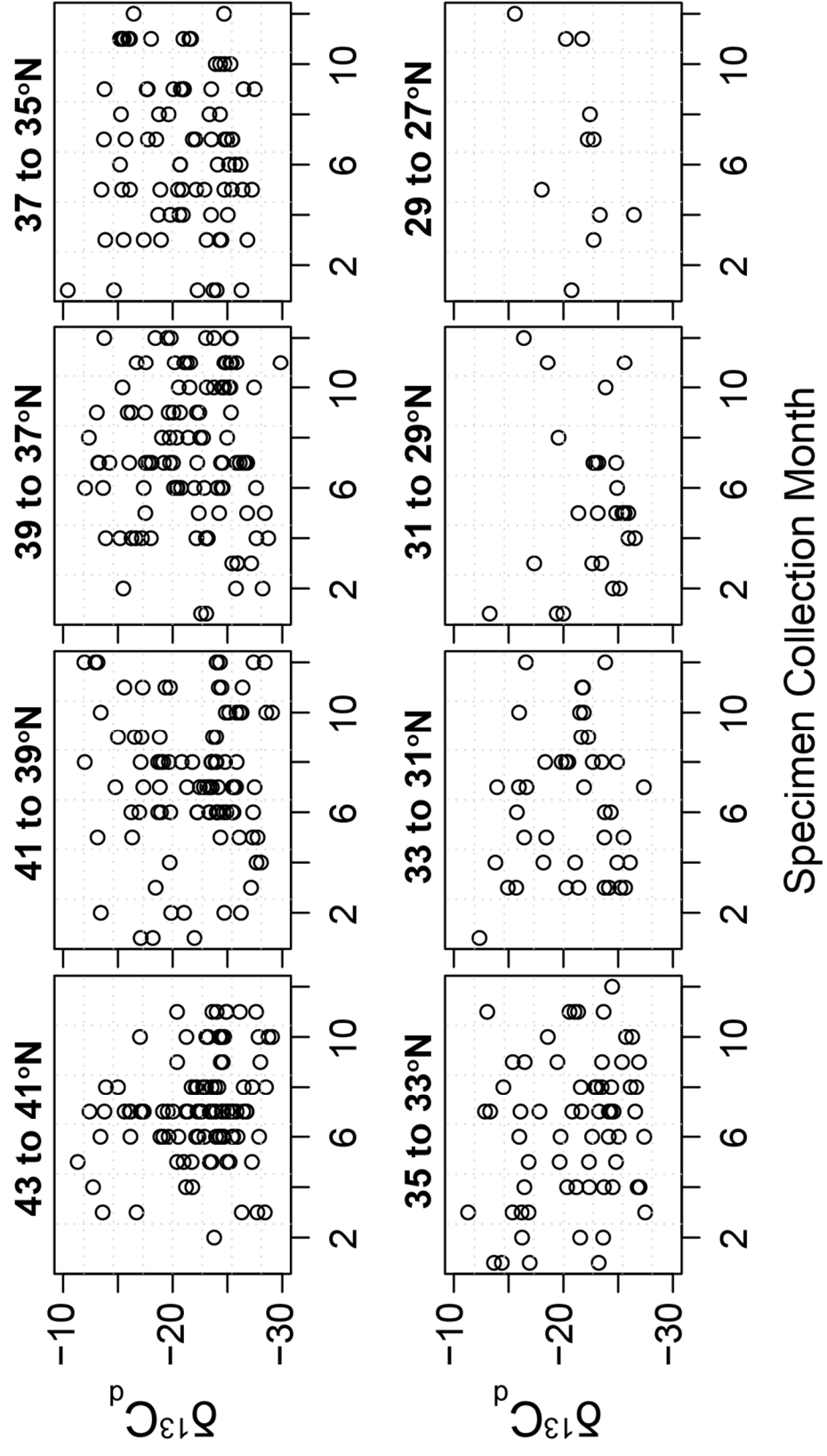


Figure 18.- All  $\delta^{13}\text{C}_d$  values plotted on A) MAT and B) MAP. Red line indicates simple linear regression lines.

Figure 19 —  $\delta^{13}C_d$  values plotted by month of collection and grouped by two degrees of latitude between 43°N and 27°N. Note the lack of negative values during summer months (June through August) in latitudes between 43° and 35°N. The onset of more positive  $\delta^{13}C_d$  values changes with latitude. The onset to more positive values occurs earlier in the south (37-35°N).



## CHAPTER 4

# Reconstructing Quaternary and Holocene Paleoclimates in the Great Plains, USA Using Areas of Sympatry Among Co-occurring Extant Small Mammal Species

### SUMMARY

Geographic distributions of extant terrestrial mammals are determined in part by the climatic conditions tolerated by constituent populations, which is a measure of the ecological niche of the species. Assuming niche conservatism, past populations of a species should have had the same climate tolerances as extant populations, thus where extant species from a fossil fauna co-occur today (i.e. area of sympatry, AOS) could be used to estimate paleoclimate. The Quaternary fossil record of small mammals in the Great Plains is a good test case for this approach as many extant species have multiple occurrences over the last million years.

The AOS methodology has been used in the past but was never quantified or tested for accuracy or precision. Here, we have developed a GIS based method that uses modern species ranges and environmental parameters (i.e., mean annual temperature or MAT and mean annual precipitation or MAP) that relate quantitatively to extant species distributions in North America. Geographic ranges for 92 extant species of rodents, lagomorphs, and soricomorphs were used to determine climatic conditions where species ranges overlap.

The reliability of this method was assessed by varying the number of extant species for a given location used to determine the AOS and the distribution of climate variables in the AOS and then compared estimated and known values. For nine locations spanning the region, we rarefied complete extant species lists to sample sizes of 20, 15, 10, 5, and 3 species and at each sample size estimated climate variables from range overlaps for 1,000 randomly sampled replicates, yielding 5,000 total replicates at each location. Accuracy of climate estimates increased with sample size up to 10 species, but more than 10 species did not improve accuracy substantially. With 10 species, differences from expected values are less than a degree except for the most northern points, but are still within 1.5°C of the expected value. Mean annual precipitation estimates varied in their precision related to the sites actual mean annual

precipitation, but with 10 species, differences from expected values are between 116 and -29 mm/yr.

We estimate MAT and MAP for 460 faunules from 370 fossil localities in the Great Plains that contain at least three extant species. MAT estimates for those faunules reflect general warming between the Last Glacial Maximum and early Holocene. Our faunules extend back one million years, but deciphering general climate trends are difficult over that time period because of few faunules meeting our criteria. MAT estimates in the early Holocene reflect the warmer and near present temperatures, but does not distinctly reflect climate events occurring over 100's of years. Precipitation estimates over the entire one million years does not indicate any long-term or directional trends through time and consistently varies around modern precipitation values.

Time slices of six climate intervals (Last Glacial Maximum, Oldest Dryas, Bølling-Allerød, Younger Dryas, and the early Holocene) were evaluated to determine if temperature and precipitation spatial gradients deviated during the global warming from the Last Glacial Maximum into the Holocene. Temperature and Precipitation estimates indicate a transition from tundra and boreal forests and to more temperate forests and shrublands, which supports previously published interpretations.

The results presented here indicate that the area of sympatry methodology can estimate temperature and precipitation with accuracy and precision based on our sensitivity tests. We applied the method to the greater Great Plains region and the resulting temperature and precipitation estimates reflect global and regional climate change during the Pleistocene and Holocene.

## **INTRODUCTION**

Geographic distributions of extant terrestrial mammals are determined in part by the environmental conditions suitable for a population to persist (Hutchinson, 1957). Assuming niche conservatism (Holt, 2003; Martínez-Meyer, 2004; Peterson et al., 1999; Peterson et al., 2011; Wiens and Graham, 2005), past populations of a species should have had the same climate tolerances as extant populations, thus past biogeographic distributions for extant species might be used to estimate paleoclimate quantitatively. If the relationship between species and climate found today is the same as in the past, then the climate within the geographic area where extant species from a fossil fauna co-occur today (i.e. area of sympatry, AOS) could be used to estimate paleoclimate

(Semken, 1966; Graham and Semken, 1987). The AOS methodology has been applied to many localities in North America and the world to indicate paleoenvironments (e.g. Pfau, 1994; Aaris-Sorensen, 1995; Lyman, 2008; Smith and Polly, 2013). However, the method has not been quantitatively tested for accuracy or precision to produce uncertainty estimates that could be applied to climate estimates in the fossil record. Here, we subject the AOS methodology to a sensitivity test to determine the accuracy and precision of mean annual temperature (MAT) and mean annual precipitation (MAP) estimates.

We will use the North American Great Plains as a test landscape for calibrating the methodology because of multiple reasons. The north-south temperature and east-west precipitation gradients of the Great Plains provide relatively simplified climate gradients that are not substantially influenced by local relief or elevation changes. These physiographic features could add complexity to the climate gradients, but their influences are minimized by focusing on the Great Plains and the immediately surrounding ecoregions. Furthermore, these features would not play a large role as a physical barrier impeding the relocation of a species and their overall distribution. Thus, the major abiotic factors influencing a small mammal distributions in the Great Plains are reduced to climate.

Paleoclimate reconstructions of the Great Plains are difficult because of few common paleoclimate proxies such as lake, pollen, or speleothem records. For example, Meltzer and Holliday (2010) summarize North American climate records that span the Younger Dryas and there is a significant gap in the spatial coverage that spans the central and southern Great Plains (see Fig. 1 within Meltzer and Holliday, 2010). Most climate records for the Great Plains are located in the northern portion or along the western and eastern boundaries leaving the heart of the Great Plains vacant. Developing a paleoclimate proxy for use in the central Great Plains would improve our understanding of how climatic events such as the Last Glacial Maximum (LGM), Oldest Dryas (OD), Bølling-Allerød (BA), and the Younger Dryas (YD) affected ecosystems in the Great Plains. While classic paleoclimate records (e.g. pollen, speleothems, lake cores) are rare in the central Great Plains, there are a number of fauna localities that span millions of years and could be utilized for reconstructing climate using the area of sympatry methodology.

The Quaternary fossil record of small mammals in the Great Plains is a good test case for this approach as many extant species have multiple occurrences over the last

million years. Graham et al. (1987) applied the area-of-sympatry (AOS) across the Great Plains and throughout the Quaternary and were able to categorically detect climatic changes in the region through the last 10,000 years. However, their environment reconstructions were limited to categorically estimating biome types that are difficult to compare to global and regional temperature records.

After validating the use of AOS to estimate Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) in the Great Plains, we apply the AOS method to faunas that extend back one million years. We will examine the resulting climate record for the greater Great Plains region and compare it to global and regional climate records that overlap with various portions of the Pleistocene and Holocene. Lastly, we bin climate reconstructions by major climate events (LGM, OD, BA, YD) and the early Holocene to reconstruct spatial gradients of MAT and MAP across the Great Plains to assess if gradients have deviated through time.

## METHODS

*Data Aggregation.*- Modern MAT and MAP surface layers (1960-1990 averages) were downloaded from the WorldClim dataset (Hijmans et al., 2005; <http://www.worldclim.org/>) and have spatial resolutions of 1 sqkm. The modern geographic ranges for North American mammals were downloaded from the Natureserv website (<http://www.natureserve.org/getData/mammalMaps.jsp>) and only the geographic ranges of rodents, lagomorphs, and soricids were used. We restricted our taxonomic lists to small mammals because of their small home ranges (Harestad and Bunnell, 1979), and non-migratory behavior. Large herbivores can migrate and reside in different regions throughout the year, thus their fossil records may be their summer refuge as opposed to their winter location or year-round residence. By limited our taxonomic lists to small bodied mammals, we assume that individuals were residing in climates suitable for year-round occupation.

To test the AOS methodology, we created a grid of 957 equidistant points across the Great Plains that represent hypothetical fossil localities of the modern landscape (Figure 20). Points span 17.5 (30.3 – 47.8°N) and 15.3 (108.5 - 93.2°W) degrees of latitude and longitude, respectively. A list of extant species was generated for each point by determining which species' geographic ranges overlap each point. We conducted multiple sensitivity tests to validate the methodology and calculate its accuracy and

precision relative to the number of species used. Calculated values of MAT and MAP using the AOS method were compared to values extracted from the surface layers for each point. Surface layers are interpolated values of average monthly climate data from weather stations (see Hijmans et al, 2005 for details). Therefore, the exact MAT and MAP values for a point are not necessarily the absolute true values for a given location, but collectively reflect the overall climate gradients and we use the point values as our target (expected) values for comparison to calculated values using the AOS methodology.

*Method Validation.*- We first applied the AOS method as a best case scenario to a subset of our grid of points by using all possible taxa for each location. Summary statistics (minimum, maximum, range, mean, median, and standard deviation) were then calculated for MAT and MAP within the resulting AOS. A fossil fauna with 100% representation of all co-occurring species at the time of deposition is statistically improbable because of multiple taphonomic effects (e.g. temporal and spatial averaging, sampling biases, preservation biases, etc.). However, this analysis serves as an initial proof of concept to illustrate the method's utility based on the associations between mammalian geographic ranges and climate.

*Sensitivity tests.*- We subjected nine of the grid points to sensitivity tests by simulating fossil assemblages by randomly sampling from each point's respective species list and varying the number (subsets of 3, 5, 10, 15, and 20 species) of taxa used to create the AOS (Figure 20). At each point, 1,000 iterations were conducted for each subset size by randomly subsampling the species list, determining the AOS, and then calculating summary statistics of MAT and MAP. The difference between the points' expected value (described above) and the median value from each replicate was calculated. The standard deviation and standard error were then calculated for the differences of the 1,000 replicates.

*Fossil Assemblages.* – Faunal lists were downloaded from the Neotoma Paleoecology Database (<http://www.neotomadb.org>) and the area of interest included all of the Great Plains localities and other localities between Illinois (~85.8°W) to the east and Arizona (112.2°W) to the west (Figure 21). Localities also extended from northern Minnesota (48.5°N) to southern Texas (29.5°N) (Figure 21). Suitable faunas contained a minimum of three extant species and also included age estimates. Additional faunal lists were also downloaded from the Paleobiology Database (PaleoDB; <https://paleobiodb.org/>) and used the same criteria. Some localities included more than

one fauna (faunule), with their independently determine age. We used the species lists for faunules when possible and the species list for entire locality if ages for the specific faunules were not determined.

We identified 530 faunules from 423 localities with at least three extant species, but not all suites of species are likely to result in an AOS. Failure to produce an AOS may result from species with different climatic envelopes that were time averaged at the locality as environment changes and new species moved into the area. Also, some species may have co-occurred in the past, but their current geographic ranges do not overlap, which are known as 'non-analogue' or 'disharmonious' faunas (Hibbard, 1960; Lundelius et al., 1983; Graham et al., 1987, Graham, 2005). In instances where an AOS was not produced using all species for a fauna, the AOS resulting from using the greatest number of species from the faunal list was used. If only three species composed the faunal list for a fossil locality, but did not produce an AOS, climate was not calculated because the locality no longer met the required three species.

## RESULTS

*Method validation.*- A total of 90 species overlap with at least one point of the continental grid. Calculated values of MAT and MAP using all occurring species for a given point reflects the measured values on the landscape (Figure 22). Linear regression between the expected and calculated values indicate a near 1:1 relationships for both MAT and MAP (Figure 22). These results demonstrate that the AOS produced by co-occurring extant species reflect MAT and MAP and the method could be applied to fossil assemblages. However, using all available species is an ideal situation and improbable with numerous biases associated with fossil assemblages. Therefore, we must determine the accuracy and precision when varying the number of species used to produce the AOS.

*Sensitivity tests.*- Multiple replications of the AOS method indicate that climate estimates are influenced by the number of species used and which taxa were randomly selected (Table 15, Figure 23 and 24). Numerous outliers indicate that some species combinations strongly deviate from the central tendency of the distribution. The differences between expected and calculated MAT values are not normally distributed when using three or five species and the skewness direction changes spatially. MAT estimates from northern points (i.e. 5314 – 5329) underestimate each points' expected



value and calculated values for the southern points (8418 – 8437) overestimate expected values. Calculated MAT values for the central points (6948 – 6963) are close to being normally distributed. We have reported the 97.5% and 2.5% quantiles (Table 15) in place of two standard deviations because of the asymmetric distributions. Furthermore, these upper and lower bounds contain 95% of the sample. The same reporting was done for MAP estimates.

Using three or five species does include a large range of MAT estimates, but the median difference between calculated and expected values is close to zero with the greatest difference being 1.3°C at point 5329. Estimates improve with five species and with 10 species differences from the expected values are less than a degree except for the most northern points, but are still within 1.5°C of the expected value. The difference between the upper and lower bounds are greatly reduced between using five (mean for all points = 5.8°C) and ten species (mean for all points = 2.8°C) (Table 15, Figure 25)

MAP estimates are asymmetrically distributed and vary between points with low variance (Points 5314 and 8418) and high variance (Points 8437, 8427, 6963, and 6955) (Table 15, Figure 24). Point 8418 has the lowest variation and also the lowest expected MAP. Points located in the eastern Great Plains (Points 6963 and 8437) have large differences between the upper and lower bounds and boast the greatest MAP expected values (Figure 24). The difference between the upper and lower bounds is greatly reduced between using five and 10 species and the average difference is nearly in half.

*Fossil Assemblages.* – We identified 530 faunules from 423 localities with at least three extant species. However, not all suites of species resulted in an AOS as we hypothesized. Therefore, MAT and MAP were calculated for a total of 460 faunules from 370 fossil localities in the Great Plains (Figure 21). Localities were also binned by various climate intervals (i.e. LGM, OD, BA, YD, and early Holocene) and span similar geographic space (Figure 21). These intervals will be used to assess how temperature and precipitation gradients may have changed on the landscape and also to estimate the biome types present on the landscape during the each climate interval.

For each faunule, the modern MAT and MAP value was extracted based on the localities' geographic position. Temperature anomalies were then calculated for each faunule by taking the difference between the calculated MAT for the fossil locality and its respective current MAT. Temperature anomalies in the early Holocene (Figure 26A) do not seem to vary with climate events occurring on the decadal or centennial scales and difficult to determine if AOS temperature anomalies capture Holocene climate events like

the Medieval Warm Period (MWP) because of minimal data immediately prior to the MWP and no data after. Global temperature anomalies in the Holocene only range two degrees Celsius while fossil MAT anomalies range mostly between 6 and -8 °C.

Extending further back in time, MAT estimates using the AOS method do reflect the overall warming transition between across the Pleistocene-Holocene boundary (Figure 26 B and C). Figure 26B illustrates the temporal fluctuations in AOS MAT anomalies relative to a Great Plains regional record of July Temperature Deviations (°C) derived from  $\delta^{13}\text{C}$  values from soil organic matter (Nordt et al., 2012). The AOS MAT anomalies reflect the general warming across the Pleistocene-Holocene boundary, which is important for determining that regional Great Plains climate records do reflect the overall global climate changes. While there are sharp variations in July Temperature Deviations, there is considerable spread in AOS MAT anomalies for a given time point reducing the proxy's ability to pick up rapid fluctuations in temperature discussed by Nordt et al. (2012).

The broad warming trend observed by Nordt et al. (2012) and the AOS MAT anomalies align with the NGRIP ice core dataset including cooler overall temperatures across the Great Plains during the Last Glacial Maximum followed by general warming (Figure 26C). Older Dansgaard-Oeschger events recorded in the NGRIP  $\delta^{18}\text{O}$  record do not align with any warming events recorded by AOS MAT, which may again be the result of the AOS methodology not recording rapid or short climate changes.

When extending the AOS MAT anomaly record back to the last one million years the number of localities is greatly reduced. The reduction in suitable localities containing at least three extant species with overlapping geographic ranges limits our ability to decipher long-term climate trends (Figure 26D). There are some localities that do indicate cooling troughs (e.g. at 0.55, 0.75, .02 MA) and others that indicate warming peaks (e.g. 0.4 MA and modern). Most MAT reconstructions occur during warming or cooling time periods and mostly within the last 0.4MA.

AOS MAP estimates throughout the last one million years range between 600 mm/yr and -800 mm/yr relative to modern precipitation levels in the Great Plains. Precipitation reconstructions using AOS methods do not illustrate any major changes in precipitation amounts through time (Figure 27). The Great Plains may have been drier during the Last Glacial Maximum between 22 and 25 MA prior to increased precipitation during global warming during Pleistocene-Holocene transition (Figure 27C).

The temperature and precipitation estimates for five climate intervals (Last Glacial Maximum, Oldest, Dryas, Bølling-Allerød, Younger Dryas, and the early Holocene) were binned and plotted against the climate space of Whittaker Biomes (Figure 28). Each climate interval is represented by localities distributed across similar geographic space (Figure 21) allowing for comparisons of MAT and MAP gradients (Figure 29 and Figure 30, respectively) and biomes among climate intervals.

Climate reconstructions for Last Glacial Maximum (LGM) localities indicate biomes ranging from tundra to temperate forests and shrublands. The LGM is the only interval with multiple localities in the climate envelope for tundra, which is expected given that the LGM was the coldest climate interval and had the most contracted MAT gradient across the central United States, but still resembles the latitudinal gradient of MAT today (Figure 29). Relative to modern precipitation levels, the LGM was drier and generally follows the west-east increase in MAP on the landscape today (Figure 30).

As warming began during the Oldest Dryas, only one locality plots on the boundary between tundra and boreal forest, but a number of localities are estimated to be boreal forests. OD localities were overall warmer than LGM localities and extend further into temperate forest and shrubland climate spaces (Figure 28). OD MATs are estimated to distinctly illustrate a latitudinal gradient found on the landscape today, however generally cooler during the OD (Figure 29). This follows suit with an estimation of boreal forest climate space extending as far south as the Nebraska-Kansas border. MAP during the OD did not differ much from the LGM and hold a similar spatial gradient with more MAP in the eastern to northeastern portion of the study region (Figure 30).

The Bølling-Allerød (BA) was an interval of rapid warming between the OD and Younger Dryas, and BA estimates are similar to those for the OD (Figure 28). A few localities still boast boreal forest climates, but many are estimated to have been temperate forests or shrublands with a couple as temperate grasslands. However, the overall MAT of the region is warmer and the boreal localities are farther north than those in the OD, thus extending the latitudinal temperature gradient as continental glaciers recede (Figure 29). MAP during the BA maintains a similar spatial gradient as the OD (Figure 30).

Localities during the Younger Dryas (YD), a period of cooling, occupy similar climate space as the OD and BA (Figure 28). The BA and YD include boreal forest reconstructions are for locations below 44°N (sites located in Wyoming, South Dakota, and Iowa). Modern boreal forests only extend as far south as northern Minnesota where

temperatures are cooler and wetter than modern Wyoming, South Dakota, and Iowa. This indicates that boreal climate was still farther south during the BA and YD than it is today. The YD MAT gradient deviates from the typical latitudinal gradient and depicts a more southeast to northwest pattern with boreal climate space holding on in the southwest corner of South Dakota (Figure 29). There is no definitive MAP spatial gradient during the YD with reconstruction values varying around ~500 mm/yr throughout the region (Figure 30).

Early Holocene localities yield a similar distribution of biomes to those on the landscape today. Most early Holocene localities were temperate forests that transition to woodland/shrubland mixtures and temperate grasslands (Figure 28). There are a few Holocene localities with MAT and MAP values that indicate boreal forest, which is expected provided that boreal forest only occurs in northern Minnesota and parts of Michigan. Overall, early Holocene localities indicate an increase in MAT and MAP across the region (Figures 29 and 30). The latitudinal MAT gradient re-emerges in the early Holocene as well as the increase in MAP moving west to east. The precipitation gradient is definitive in the early Holocene and most similar to the modern landscape with the only deviation being drier conditions during the early Holocene in the northern Great Plains (Figure 30).

## DISCUSSION

*Method validation.* - An area of sympatry is best constrained when using all species that may occur at one location in space and time. On the modern landscape we have the benefit of observing the geographic range of each species and can document all species present at a single location. We demonstrate that using all available extant species estimates MAT and MAP accurately and precisely (Figure 22). The AOS methodology successfully estimated MAT at locations with high/low MATs and the same was true for locations with high/low MAPs. While these AOS estimates of the modern landscape help illustrate the proof of concept, they are ideal situations that would not typically be encountered in the fossil record.

Applying our methodology to the fossil record presents some challenges because the fossil records are incomplete due to various preservation, taphonomic, and sampling biases. The species represented in the fossil record is likely not the entire list of species that were living at that location at the time of burial. The AOS methodology is also limited

to using extant species with known geographic ranges, which limits the number of species we can use from a fossil locality. As a result, the number of species varies decreases with the fauna's age, therefore older faunas have less extant species occurrences and subsequently decreases the number of geographic ranges to constrain the AOS. With these limitations, we subjected the AOS method to sensitivity tests to simulate how the number of species used effects temperature and precipitation estimates.

*Sensitivity tests.*- We performed a number of sensitivity tests to determine how accuracy and precision changes with different combinations and number of species. Calculated MAT and MAP values greatly vary when using only three or five species. We randomly sampled the species list to account for different combinations of species that would result in different AOS and potentially different estimates. The large variance when using three and five species indicates that which taxa used will influence the accuracy of an estimate. For example, rodent taxa such as *Peromyscus maniculatus* (deer mouse) or *Castor canadensis* (North American beaver) have geographic ranges that span nearly all of North America. If either of these species were included as one of the three species selected, their geographic ranges would not provide any geographic constraint (i.e. climate constraint) on the AOS. Only the geographic ranges of the other two taxa would be used to determine the AOS and subsequently the climate space, which would potentially and likely lead to inaccurate climate estimates. However, the geographic ranges of the two remaining taxa may minimally overlap and still provide a well constrained estimate of MAT and MAP. After 1,000 iterations at each using three species at each point, the standard deviation of the mean MAT ranges between 1.5 and 2.9°C. These low standard deviations, considering the number of species used, indicate that it likely that AOS method, even when using three species, accurately estimates MAT and broad changes in climate could be discerned.

MAT estimates for the northernmost points in the sensitivity tests were skewed towards underestimating the expected MAT value (Figure 23, top row). A bias towards colder temperatures may be the result of taxa with mostly northern ranging distributions being included in the AOS. The land area on the North America landmass is unequally distributed with a greater proportion of land in northern (colder) latitudes than in southern (warmer) latitudes. As a result, colder temperature have a greater probability of being included because of more area with colder temperatures that may possible be included. However, MAT estimates for the southernmost (warmer) points (81418 – 8437) are

skewed towards warmer temperatures, which is contrary to the distribution of landmass hypothesis (Figure 23, bottom row). The bias towards colder temperatures in the north and warmer temperatures in the south suggests biases are a function of the species' geographic ranges. The species lists of the northern points may be dominated by taxa at the southern end of their geographic range thus most AOS would trend northward (colder). The most southern points may be occupied mostly by species at the northern limits of their range, thus AOS would trend southward (warmer MAT). This is further supported by normally distributed temperature estimates in the mid latitude points (Points 6948 – 6963) (Figure 23, middle row). These mid latitude points may include a mixture of species occurring in their southern limit, northern limit, or central portion of their geographic ranges.

MAP estimates using three or five species are highly variable within subsamples and among points. Precipitation estimates of the driest locations (Points 6948 and 8418) have the lowest variances except for some outliers relative to the vast majority of MAP estimates close to the expected values (Figure 24). The points with the greatest variance are those with the highest expected MAP (Figure 24, points 8437, 6963, and 8427). The greatest standard deviation of 1,000 iterations for one point was  $\pm 176.9$  mm/yr (Point 8437), which may still be small enough to detect major biome shifts among deserts, grasslands, and temperate forests.

Areas of sympatry created with 10 or more species would provide extremely accurate and precise estimates of MAT and MAP based on the sensitivity tests. Differences between the upper and lower bounds greatly reduce between using five and ten species (Figure 25). Temperature and precipitation estimates could certainly indicate small shifts in biomes and capture climate transition at one location over thousands of years. Increasing the number of species to 15 does not change the estimate error greatly and 10 species is more than suitable for an accurate and precise climate estimate.

The sensitivity tests conducted here, support the potential the AOS methodology has for estimating paleoclimate using the fossil record. With at least 10 species, the AOS methodology could pick up climate changes on the scale of 1,000's of years, while reconstructions using three or more could indicate large changes in climate on the order of 10's or 100's of thousands of years. Our sensitivity tests were focused on the Great Plains and immediately surrounding regions for application to the fossil record of the same study area. If fossil localities from other biomes or climate spaces, in regards to

MAT and MAP, additional sensitivity tests would be needed across North America to take into account the climate regimes not included in this study.

*Fossil Assemblages.*- We applied the quantitative AOS method to 370 localities that contained at least three extant species that results in an AOS. The assemblages that did not result in an AOS and assemblages that only resulted in an AOS when not using all extant species in the assemblage were expected because of past research that identified disharmonious fauna (see Semken, 1966; Graham and Semken, 1987; Graham, 2005) and non-analog plant communities (e.g. Williams et al., 2013). These species were responding to climatic and environmental changes independently, at different rates, and in different ways, which resulted in faunal communities that we do not find on the landscape today. While these non-analog communities may indicate non-analog climates that boast seasonal extremes or other ecosystem controls that differ from today, paleoclimate reconstructions using the AOS method would still provide a general estimate of climate and biome type during the Pleistocene-Holocene transition.

Our faunules extend back one million years, but deciphering general climate trends are difficult over that time period because few faunules meeting our criteria. Interpretations of the temperature record over the last million years is limited by the few localities older than 100 kyr and possible mis-alignment of localities with global climate records because of the age uncertainties for the faunas. The remainder of our discussion will focus on the last 60 kyr and specifically the Pleistocene-Holocene transition.

MAT estimates for faunas in central United States reflect the global and regional warming during the Pleistocene-Holocene transition (Figure 26). There is variation in the MAT anomalies throughout the AOS temperature record, which may be derived from error in the temperature estimates based on the number of species used to determine the AOS, but the variance in anomalies may be the result of some regions undergoing different shifts in temperature. Some regions may have experienced more cooling, warming, or minimal deviations from modern temperatures. We address this possibility by interpolating MAT and MAP estimates during five climate intervals (see Figures 28 and 29). Our results indicate that there is landscape variability, which is to be expected based on previously published paleoclimate proxies indicating that some regions were different combinations of warmer/cooler and drier/wetter relative to today (see Meltzer and Holliday, 2001 and sources therein). Therefore, the variance in MAT anomalies for a

given time slice is likely due to spatial variance. The variance in MAP estimates is likely derived from the same landscape variations as temperature. Precipitation is even more spatially heterogeneous than temperature given there are global records of temperature change, but interpretations of precipitation records are limited to regional or local spatial scales. In general, our estimates of MAT and MAP using the quantitative AOS method reflects the global temperature changes over thousands of years with finer resolution of spatial temperature and precipitation gradients on the regional scale.

MAT estimates in the early Holocene reflect the warmer and near present temperatures, but does not distinctly reflect climate events occurring over 100's of years. Climate variations occurring over only a few hundred years (i.e. the Medieval Warm Period) may not be detectable by the AOS method potentially because 1) the method is not capable of resolving small deviations in temperature and precipitation, 2) species did not drastically change their geographic ranges during the Medieval Warm Period, 3) regional differences in climate during this period may have been different around the globe and the lack of general warming in the Great Plains during this time may be an accurate reconstruction. Additional localities during the Little Ice Age (LIA) would help determine if Holocene climate events could be captured by the AOS method. With ongoing global climate change, species have already shifted their geographic distributions (Chen et al., 2011) and are projected to continue to relocate as climate changes and biomes continue to relocate (Loarie et al., 2009).

*Pleistocene-Holocene Transition.* – Climate reconstructions for the LGM indicate tundra ecosystems in the continental United States, which do not occur there today. This aligns with previous biome estimates using the AOS method (Graham et al., 1987) and pollen records from the Great Lakes region indicating tundra and boreal parklands around the Great Lakes (Yu and Wright, 2001; Williams et al., 2004). Collectively, MAT estimates for LGM faunas are cooler than those during the latest Pleistocene (BA, YD faunas) and significantly cooler than the early Holocene and modern landscapes.

Warming begins during the OD and substantially during the BA and both project similar biomes on the landscape. However, localities during the BA are from more northern latitudes than those in the OD and pushes the cooler temperatures (and biomes) farther north in the BA than in the OD. Precipitation does not differ between the two climate intervals (see Figure 30) and biomes may have only migrated northward in response to the overall global warming trend. The overall warming trend does seem to



stall in the Great Plains during the YD and also the precipitation gradient on the landscape is different than all other climate intervals.

The interpretation for the YD interval was an overall global cooling centralized in the north Atlantic. Cooling spread across northeastern North America where tundra conditions persisted in southern Quebec (Yu and Wright, 2001; Meltzer and Holliday, 2010). The cooling during the YD continued across the northern United States, but dissipated moving west into the Great Lakes region. However, not all locations experienced warming during the YD, such as the southeastern United States (Yu and Wright, 2001). Moving west to the southwest (west Texas, New Mexico, Arizona), paleorecords indicate general cooling in the region and a mixture of some locations receiving more and less precipitation (Meltzer and Holliday, 2010). However, there is a large gap in paleoclimate records during the Pleistocene-Holocene transition in the central and southern Great Plains (See Figure 1 in Meltzer and Holliday, 2010). This gap is the record left researchers to hypothesize climate for the region based on evidence from the rest of North America. Yu and Wright (2001) hypothesized that the cold arctic air generating in the north Atlantic traveled to northeastern North America and reaching the Great Lakes Region and also traveled through the north Pacific down the west coast of North America and transmitted as far east as the Rocky Mountains. However, they proposed that cold air in central North America was trapped north of the Laurentide ice sheet permitting warm Caribbean air to protrude out of the Gulf of Mexico and bring warm-humid air into the Great Plains and even up the continental ice margin.

Our interpolated MAT values for the Great Plains during the YD support the hypothesis of warm Caribbean air being transmitted up the Great Plains. The gradient of MAT in the region today is a strong north-south trend and is evident during most of the climate intervals investigated here (Figure 28). The interpolated MAT values for the YD however, differs with a more southeastern to northwestern, which would support the hypothesis that cold arctic air being trapped north of the Laurentide ice sheet and warm Caribbean air setting the spatial gradient of MAT in the Great Plains. Yu and Wright (2001) further suggest that this alternative climate pattern that differs from today might explain the many non-analog plant and faunal communities described from multiple records in the Great Plains, Midwest, and Southeast.

In addition to an anomalous temperature gradient during the YD, precipitation may also have differed during this time. MAP gradients today and during most of the climate intervals vary along a west to east trend with greater precipitation in the east.

The YD interval was the only time that this precipitation gradient did not hold (Figure 30). Furthermore, there may have been a lack of any gradient between wet and dry locations throughout the southern and central Great Plains. The deviation from modern precipitation patterns and temperature spatial gradient may have created the non-analog climates that subsequently lead to the non-analog flora and fauna communities.

More detailed paleoclimate records (e.g. pollen, phytoliths, soil organic matter) from the central Great Plains are required to further our resolution of these non-analog climates and how seasonality, seasonal extremes, and other ecosystem influences (e.g. fire, aeolian processes, and biologic interactions) that culminate in the glacial and interglacial ecosystems. This region is particularly of interest because it is the transition zone between temperate forests and cooler boreal forests to the warm and dry shrublands and deserts of the North American southwest.

Finally, the Great Plains region reaches near modern temperature in the early Holocene and both temperature and precipitation distributions on the landscape greatly resemble the gradients on the landscape today. Comparing our climate reconstructions for the early Holocene climates to those for the LGM, our quantitative analysis using the AOS significantly tracks warming during deglaciation. Our results indicate warmer temperatures in the Holocene, but also significant changes in biomes from more tundra/boreal/cool-forests and shrublands to a greater proportion of temperate seasonal forests, shrublands, and temperate grasslands.

## **CONCLUSIONS**

Our study presented here has demonstrated that the AOS method can be used to quantitatively estimate MAT and MAP in the greater Great Plains region. The sensitivity tests we conducted indicate that any AOS consisting of at least three species will provide some useful estimates depending on the species used, the length of the climate interval being assessed, and the magnitude climate may have changed. We applied our quantitative assessment to faunas in the greater Great Plains region that extend back one million years. The method certainly captured the regional warming trend during the Pleistocene-Holocene and spatially interpolated MAT and MAP values for five climate intervals provide and analysis of the landscape dynamics during these intervals that support previous hypotheses of climate regimes during the Younger Dryas. These landscape are models that can be tested with additional paleoclimate proxies

(e.g. pollen, phytoliths, tooth, paleosol geochemistry) collected in the Central Great Plains and surrounding regions.



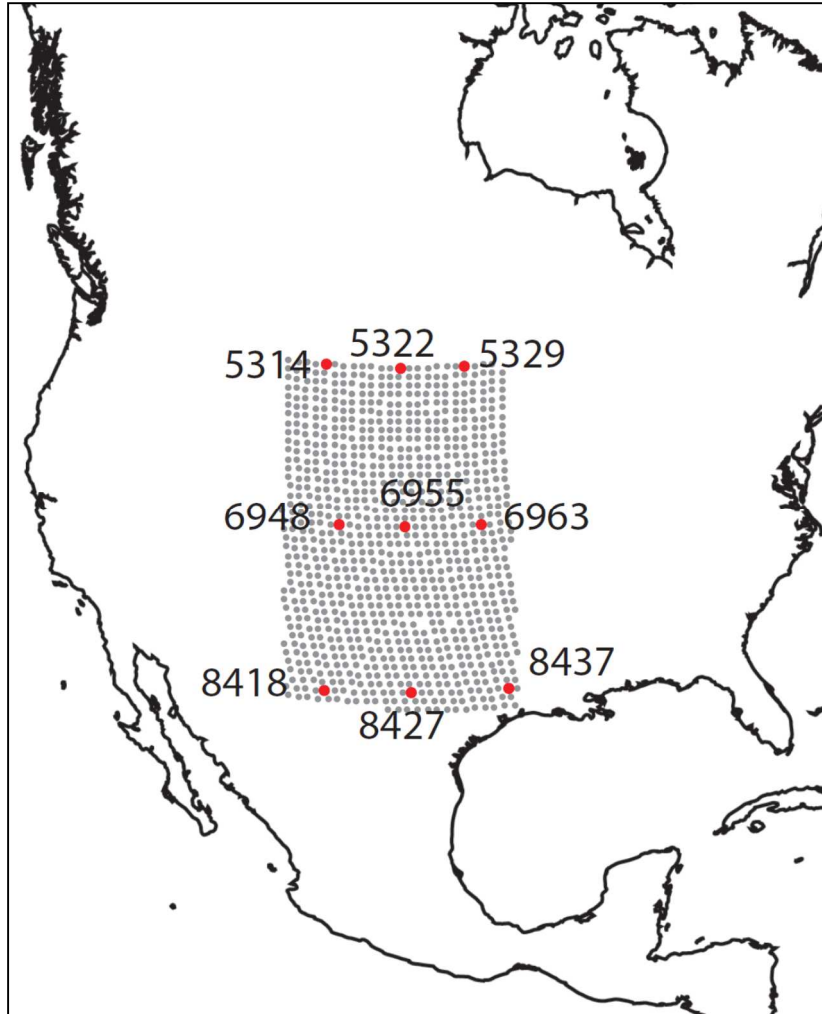


Figure 20 – Map of equidistant points for the Great Plains. Red circles with numbered labels indicate points selected for the sensitivity tests.

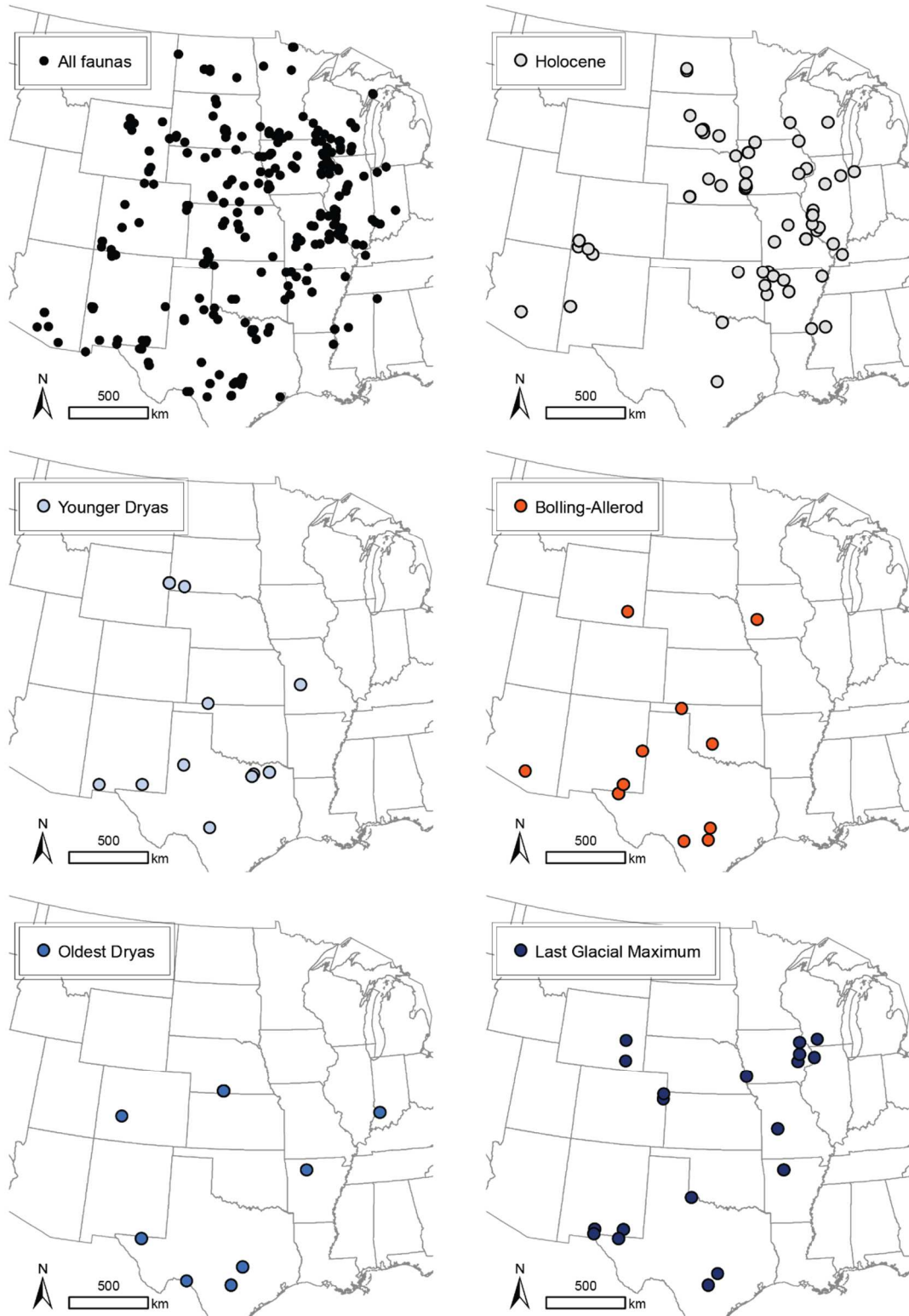


Figure 21 – Maps indicating the fauna localities used to determine AOS. The upper left panel includes all faunas used in this study and the remaining panels indicate faunas binned by climate events investigated here.

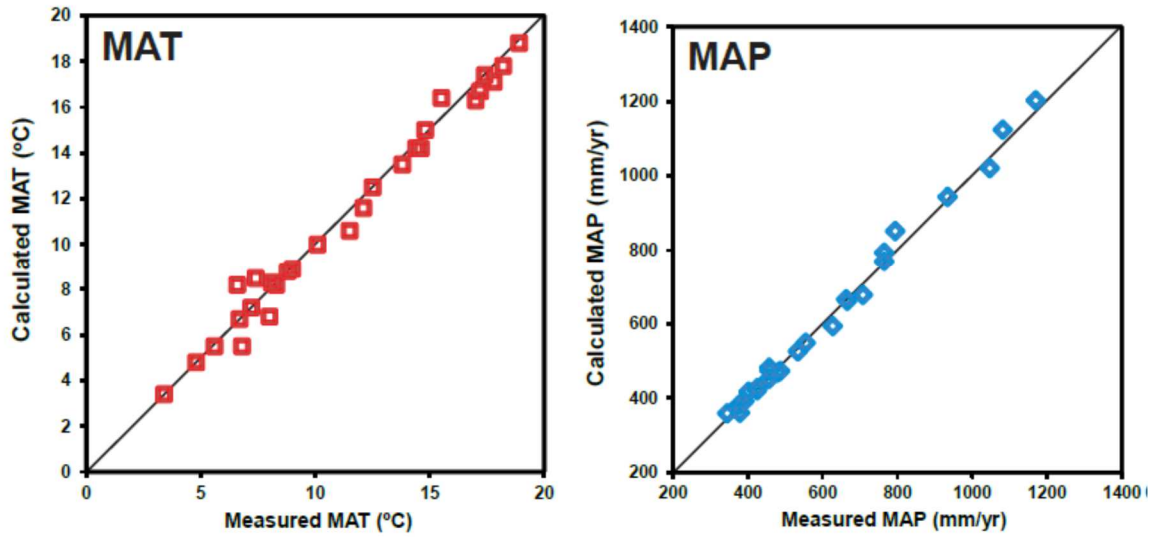


Figure 22 – Expected MAT vs calculated MAT using all species to determine AOS. B) Expected MAP vs calculated MAP using all species. Black diagonal lines are 1:1

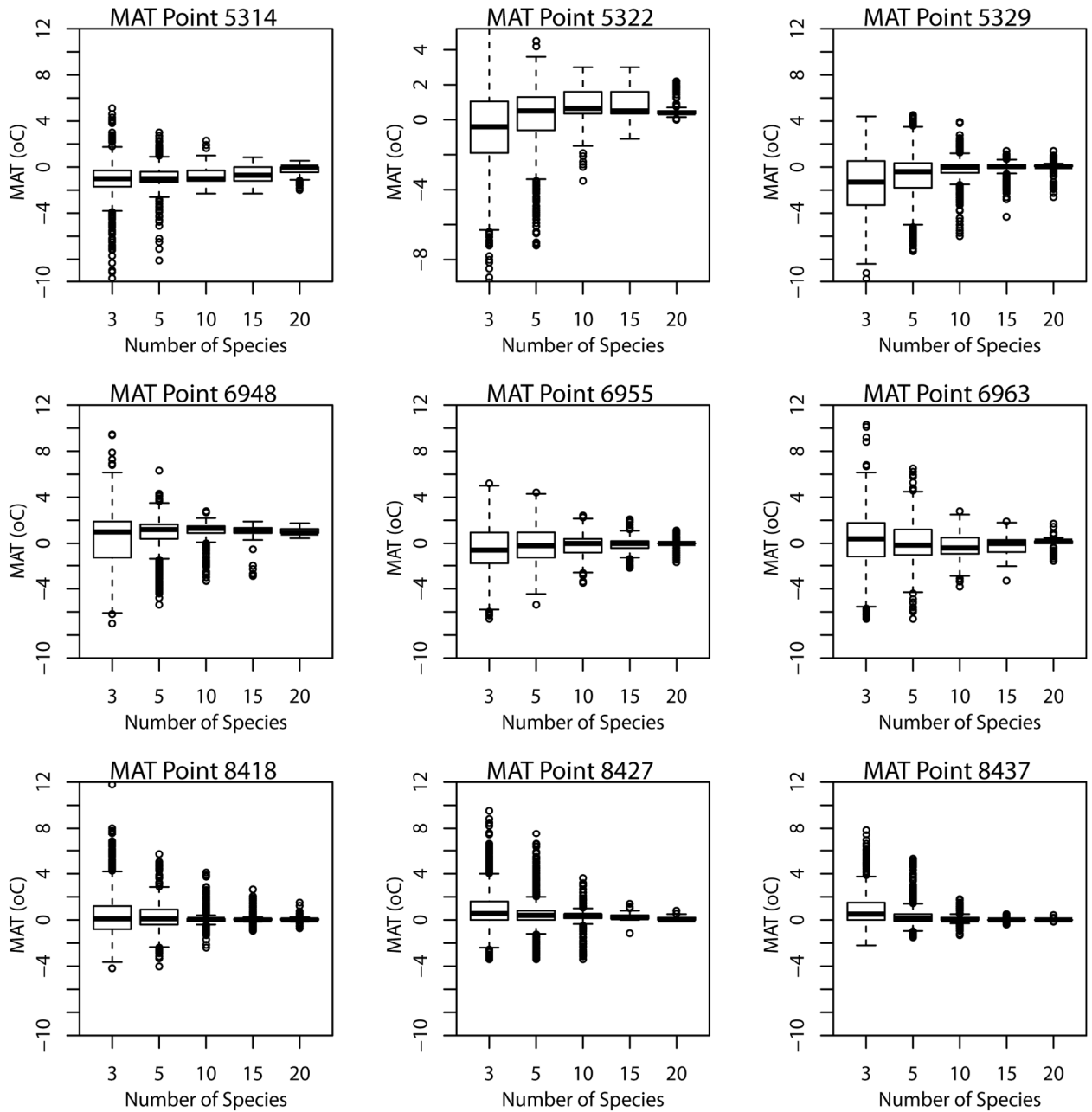


Figure 23 – Box and whisker plots of MAT estimates from sensitivity tests



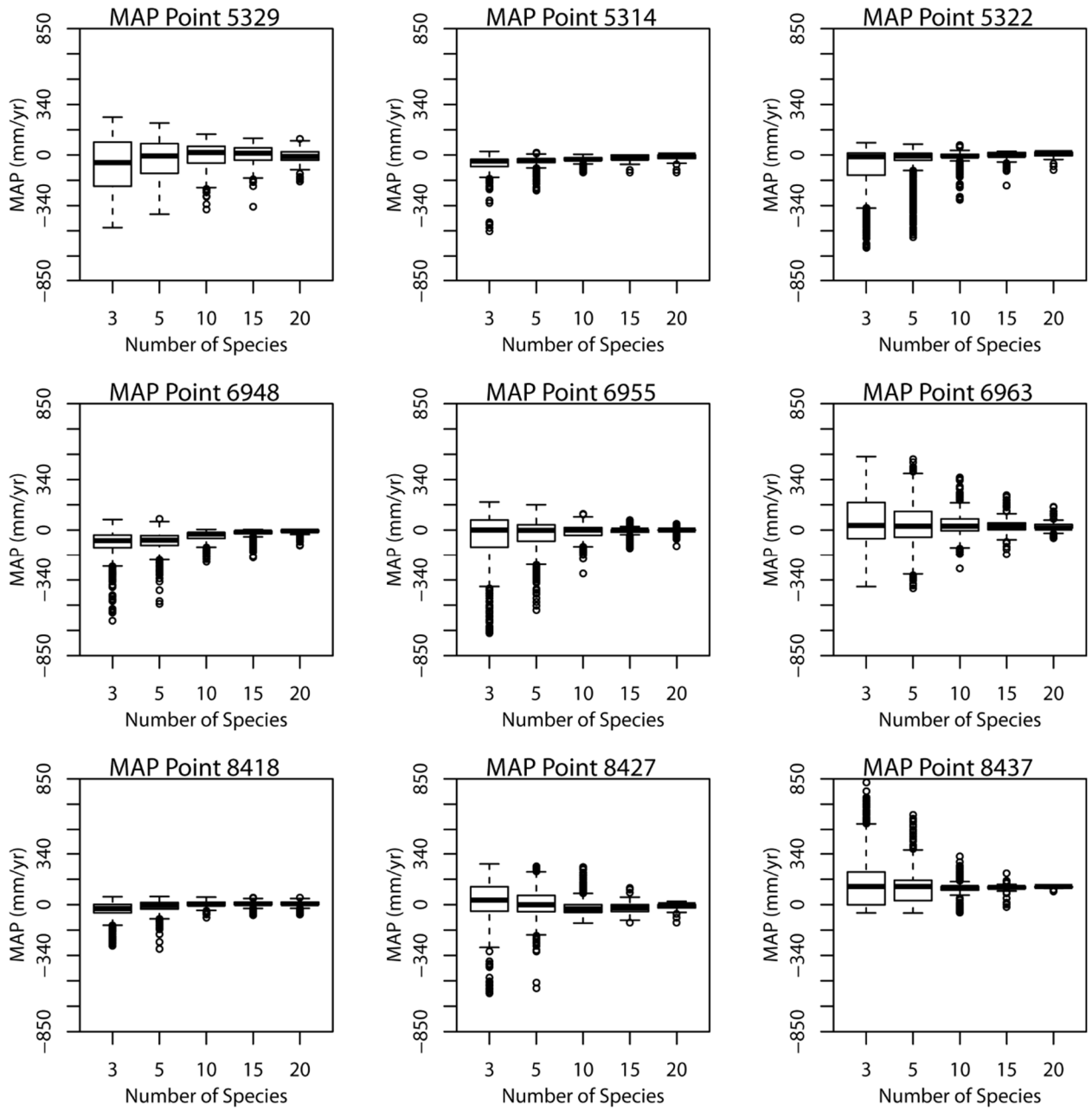


Figure 24 – Box and whisker plots of MAP estimates from sensitivity tests

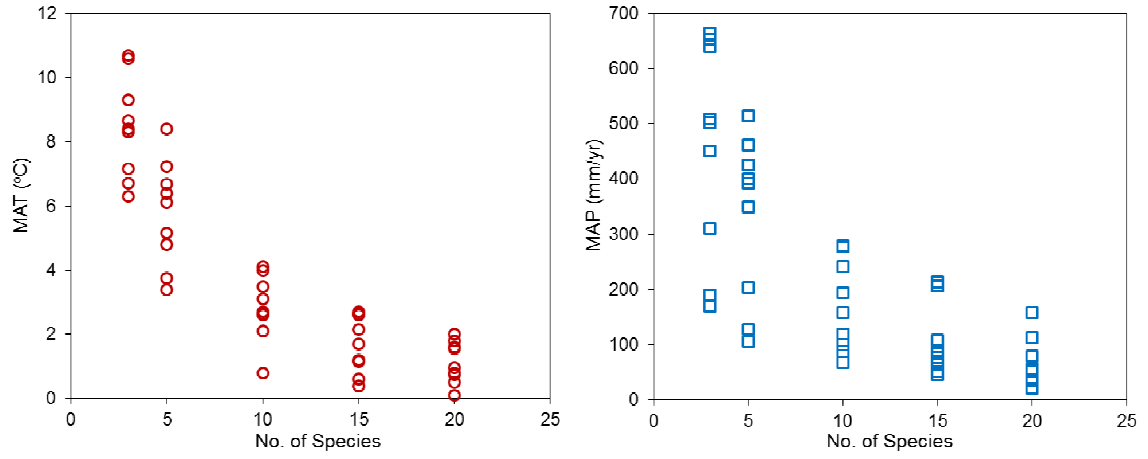


Figure 25.- Differences between the upper (97.5%) and lower (2.5%) bounds for estimates of A) MAT and B) MAP at each of the nine locations used in the sensitivity tests.

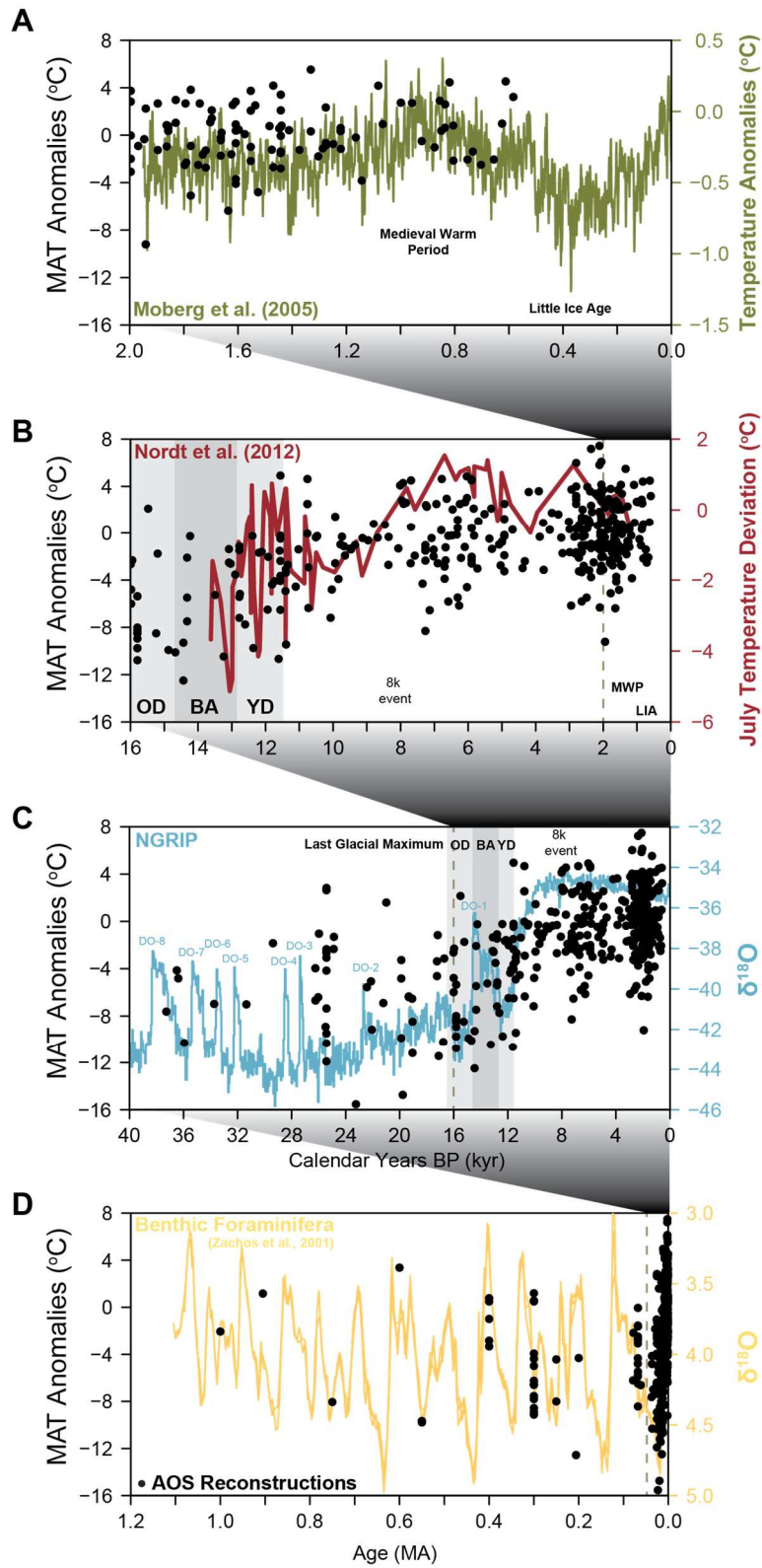


Figure 26 – Calculated MAT (mean annual temperature) values (black circles) within the AOS determined for each fauna and compared to published climate records of A) Temperature anomalies (Moberg et al., 2005); B) July temperature deviations (Nordt et al., 2012); C)  $\delta^{18}O$  from the NGRIP ice core; D)  $\delta^{18}O$  of benthic foraminifera (Zachos et al., 2001).

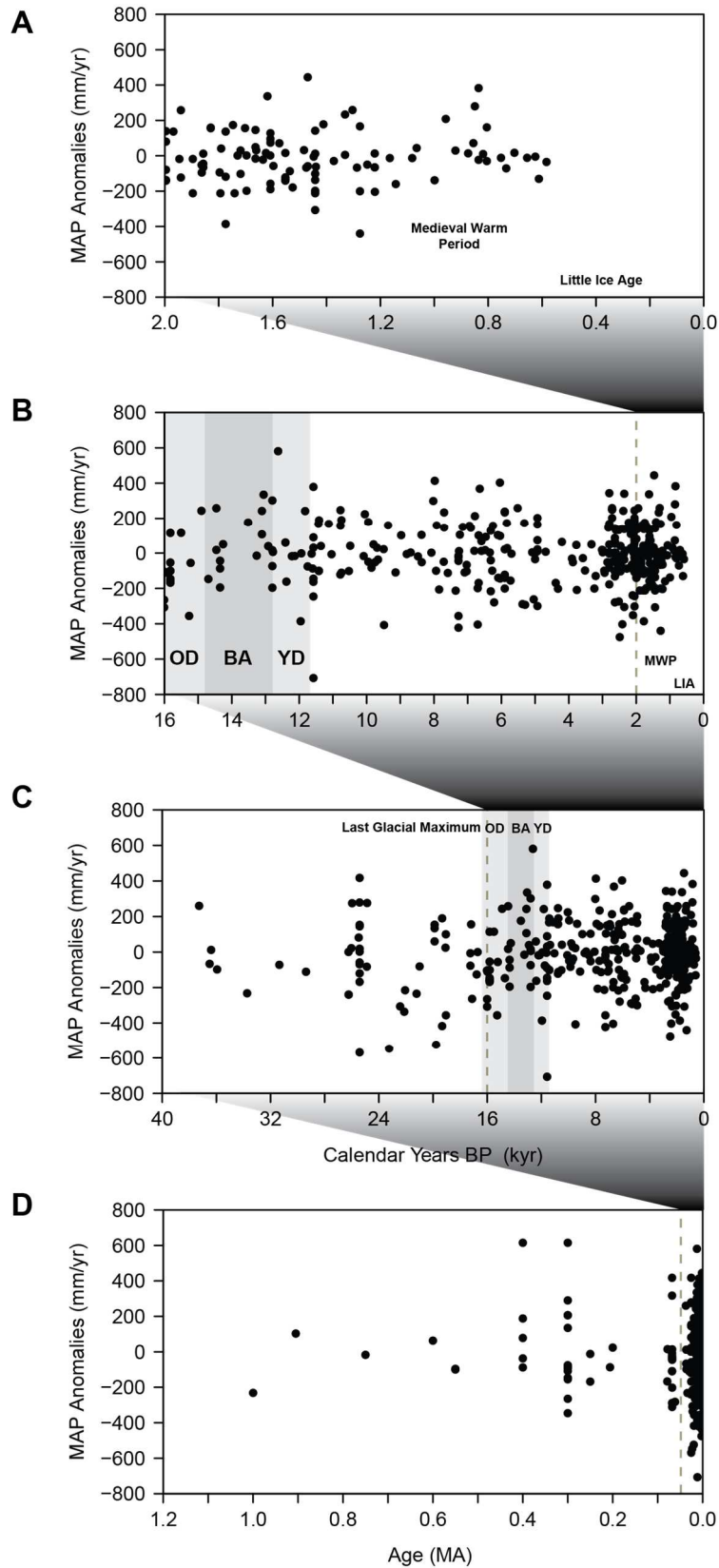


Figure 27 - Calculated MAP (mean annual precipitation) values based on the AOS determined for each fauna and panels A-D are temporally parsed the same as in Figure 26.

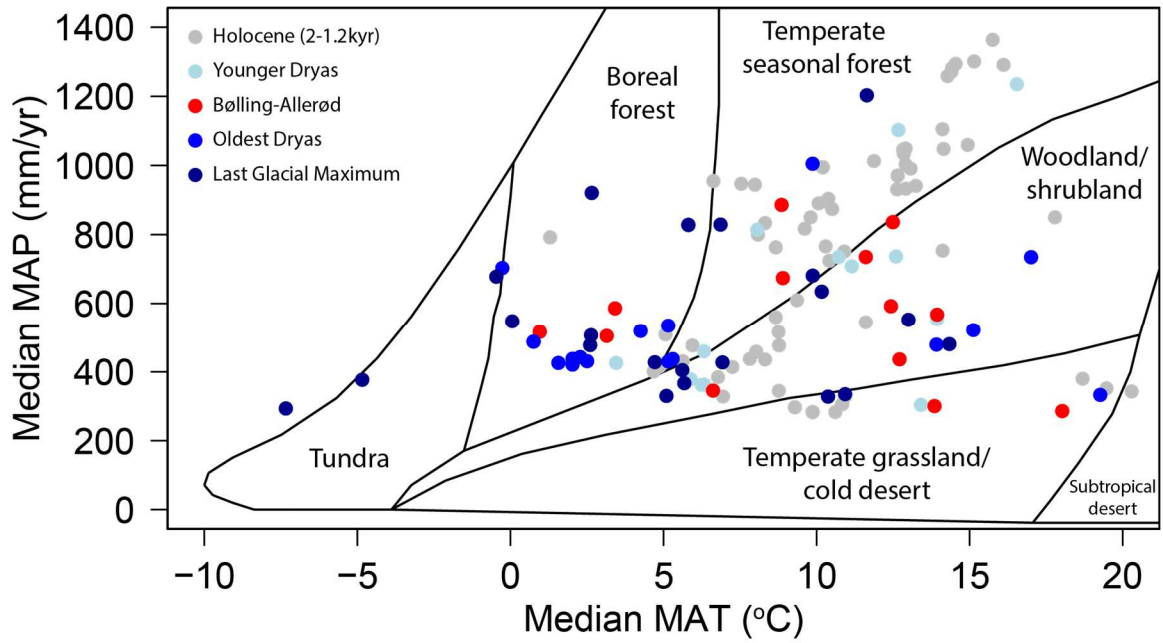


Figure 28 – Calculated MAT and MAP values grouped by climate events and plotted over Whittaker's biome classification (Whittaker, 1970)

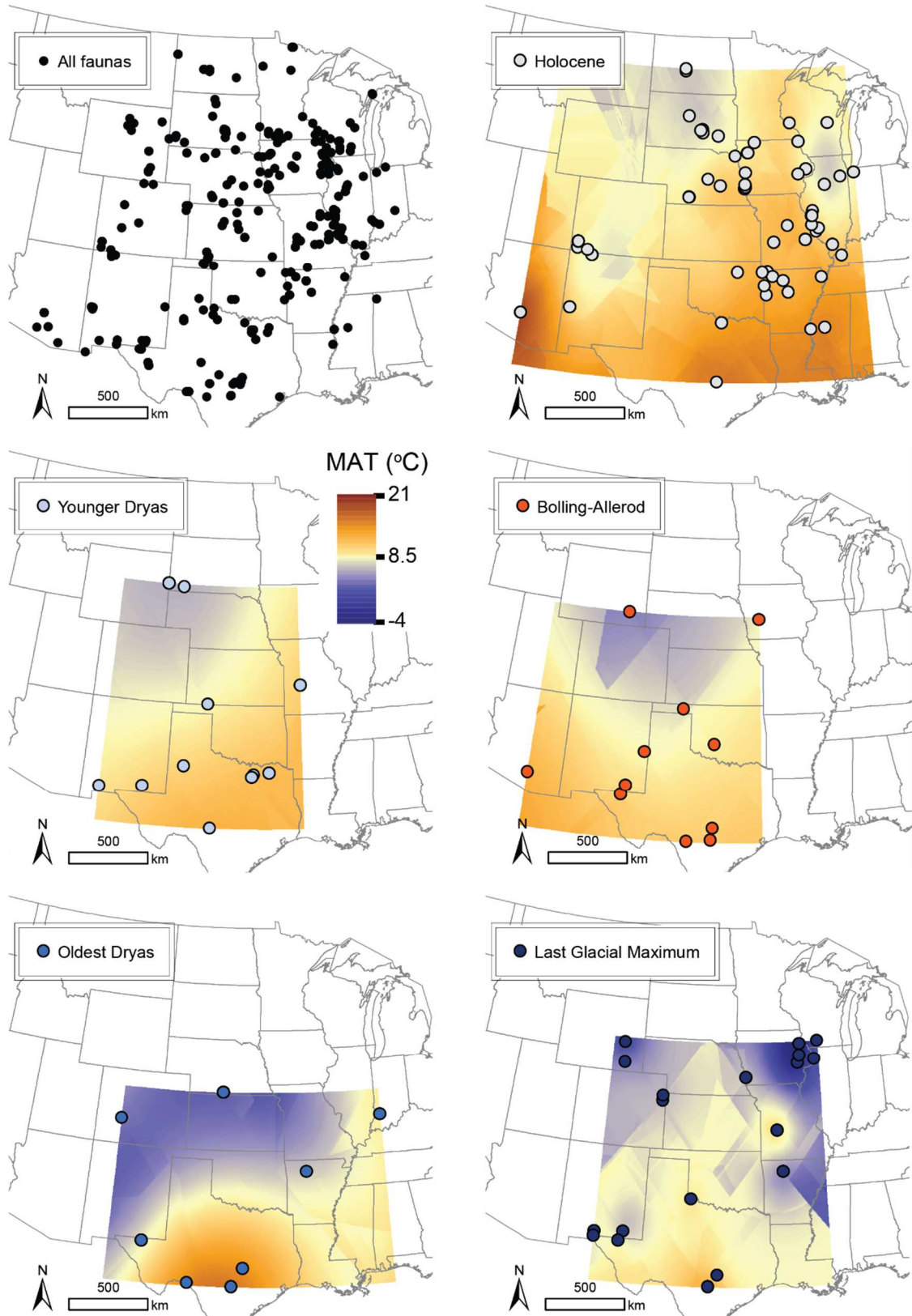


Figure 29 – Fauna localities for climate interval during the Pleistocene-Holocene transition and interpolated MAT values for each climate intervals based on calculated MAT values using the AOS methodology.

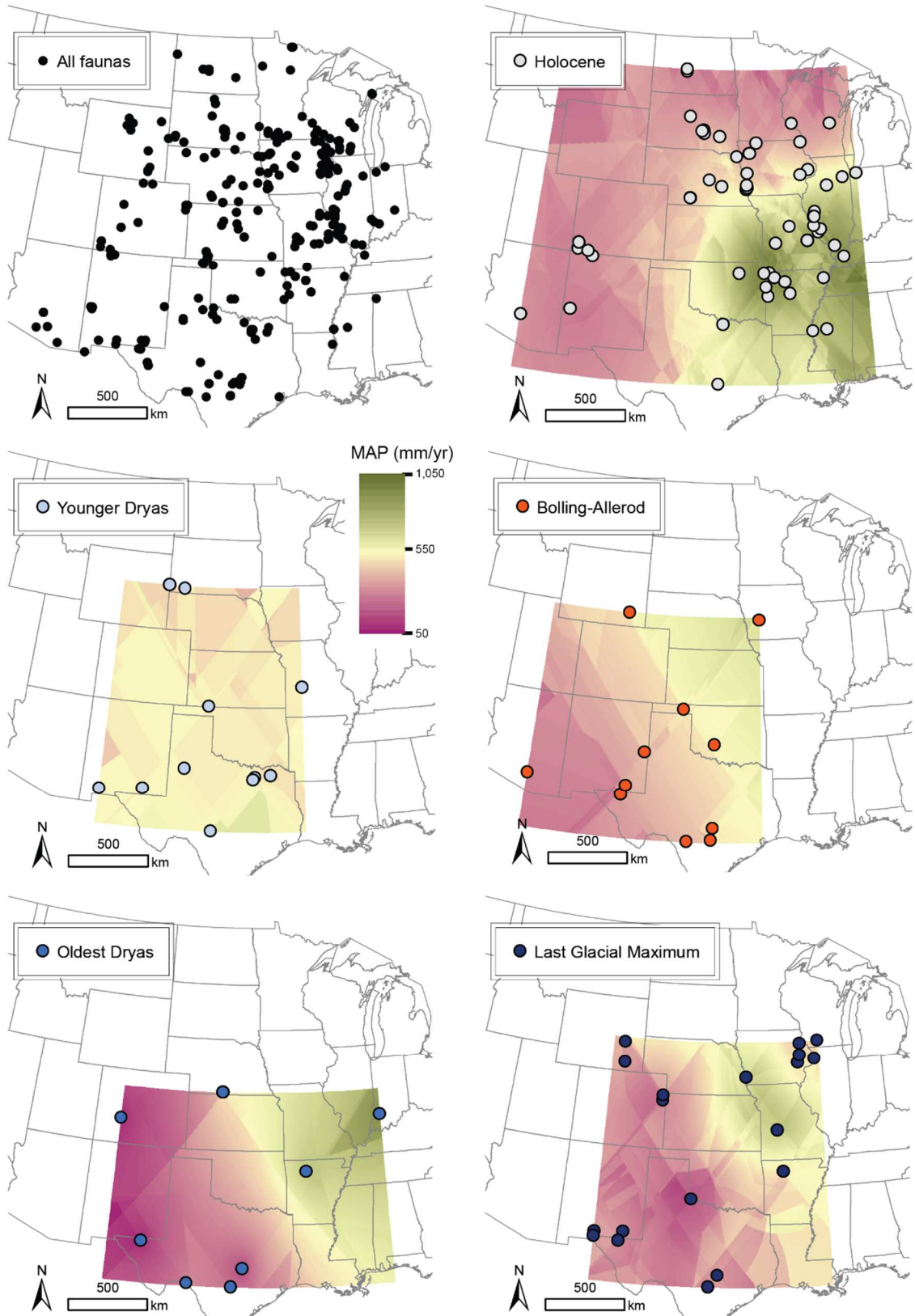


Figure 30 – Fauna localities for each climate interval during the Pleistocene-Holocene transition and interpolated MAP values for each climate interval bas on calculated MAP values using the AOS methodology.

## GENERAL CONCLUSIONS

At the beginning of this research, I proposed that the fundamental goals of paleoecologists and modern ecologists is to understand the natural world around us and determine the mechanisms that species evolve in response to biotic and abiotic factors. In this aggregation of studies, I have used small mammals to better our understanding of how small mammals partition resources on landscape using stable isotopes and have approached this at different temporal and spatial scales. Additionally, I have used small mammals as example taxa in order to further understand the environments in which they lived in the past.

In Chapter 1, I showed that three small mammals independently selected their food resources and varied their diet differently through season and during a severe drought. We can use stable isotope mixing models to estimate how plants and insects are incorporated into their diets, with some species like *Dipodomys ordii* focused on seed collection (particularly C<sub>4</sub> plant seeds), *Onychomys ochrogaster* focused on consuming invertebrates, and *Peromyscus maniculatus*, a generalist, taking advantage of whatever resources are most available. Additionally, this work was conducted with known spatial and temporal control. This allows us to interpret with confidence our stable isotope values that were recorded in hair. From this we were able to determine that intermediate  $\delta^{13}\text{C}$  values between C<sub>3</sub> and C<sub>4</sub> derived resources are most likely the result of integrating multiple resources through direct consumption, but most likely from invertivory. Therefore when interpreting  $\delta^{13}\text{C}$  values from small mammals in the fossil record, we can constrain our interpretations realizing the multiple pathways (dietary selections) that an individual can make to result in the measured  $\delta^{13}\text{C}$  value. Lastly, Chapter 1 contributes to modern ecology studies and ecosystem managers. Stable isotopes can be a useful tool to determine an individual's diet, particularly  $\delta^{15}\text{N}$  to determine trophic position. However, the results presented here further illustrate the importance of standardizing nitrogen isotopes by their respective collection locality. Nitrogen isotopes greatly vary on the landscape and the baseline  $\delta^{15}\text{N}$  value may differ from one ecosystem to the next they may immediately adjacent macrohabitats. As a result, stable isotope interpretations that include nitrogen isotopes, should either include a stable isotope mixing model normalize consumer nitrogen isotopes values using either the median values of local vegetation or the uppermost soil organic matter.



In Chapters 2 and 3, I build upon our findings of small mammals diets at the local scale and expand to the regional scale to determine how small mammals partition C<sub>3</sub> and C<sub>4</sub> resources as the proportion of C<sub>4</sub> biomass on the landscape changes. This spatial analysis is a space for time substitution. The abundance of C<sub>4</sub> plants in the Great Plains has increased during the latter part of the Cenozoic and in future research I will determine if, when, and how small mammals utilize this new food resource or ecospace. I showed that while overall, small mammals still rely on C<sub>3</sub> derived resources, there are some spatial and ecological tendencies.

Folivores typically have isotopically more negative  $\delta^{13}\text{C}_d$  values and maintain a similar diet regardless of  $\delta^{13}\text{C}_e$ , MAT, and MAP and only slightly increase in variation with the more positive  $\delta^{13}\text{C}_e$  values. Granivores incorporate generally more C<sub>4</sub> derived resources than any other dietary category and the percentage of C<sub>4</sub> derived resources increase with  $\delta^{13}\text{C}_e$ . Furthermore, the difference between median values of granivores and folivores is significant and highly correlated with soil organic matter  $\delta^{13}\text{C}$  values, which implies that the  $\Delta^{13}\text{C}_{\text{F-G}}$  value of a fossil community could be used to estimate the %C<sub>4</sub> and/or help reconstruct the associated paleoenvironment.

Climate variables did explain some variance in C<sub>4</sub> consumption for some species, while other species' diets were not explained by climate variables. Most climate variables that contributed towards species specific models best explaining  $\delta^{13}\text{C}_d$  values were generally metrics of seasonality or seasonal extremes. The seasonal aspect of this research is an area in need of future research. The seasonality of the grassland ecosystems can be a distinguishing factor that separates an area from being a grassland versus a desert or forest. The extremes and distribution of temperatures and precipitation have great influence on ecosystem formation. This arises multiple times in the above studies. *Peromyscus maniculatus* diets varied with seasons and short-term climate events, while the other species maintained relatively constant diets. Then in comparison to climate gradients, the variables that best explain  $\delta^{13}\text{C}$  variance in rodents (i.e. diet) were typically measures of seasonality. Furthermore, we demonstrated that  $\delta^{13}\text{C}$  values in rodent hairs become more positive overall during the peak summer in the central Great Plains, which aligns with peak C<sub>4</sub> growing season. These variations spatially, temporally, and climatically, are all variables that we need to characterize on the modern landscape in order to better interpret similar data from the fossil record. With the datasets presented here, we can begin to interpret small mammal paleodiets with

some confidence and my in turn be able to their paleoecology to indicate the environment around them.

The research presented here sets the groundwork for establishing an extensive database that can Specific to the Great Plains, including more individuals from the northern Great Plains that are dominated by cool-season grasses will increase the range of expected  $\delta^{13}\text{C}_e$  values, which will help put the values presented here in a greater perspective. Including a greater proportion of the landscape would subsequently include greater ranges of environmental and climatic variables that would be used to better understand the controls on rodent diets. Other variables like potential evapotranspiration, soil type, or number of frost free days, may yield an improved understanding of  $\delta^{13}\text{C}_d$  variance. Furthermore, including more biomes that occur along the boundaries of grasslands, would create a more robust gradient from closed canopy forests to deserts. Furthermore, expanding the database to be integrative with previously published diet reconstructions of modern individuals. The database would initially be three fold and build upon the datasets compiled here. Expansion of stable isotope values from small mammals would begin with compiling published values. The second expansion would be to add more museum samples that includes more species and area for large scale analyses rather than ecosystem comparisons from the local trapping efforts. The third expansion would include compiling published stomach content data that identify diet. The combination and integration of these different sources would provide a database that can be queried and parsed according to the scientific question of interest whether it be a modern ecology or paleoecological question.

As an example, fossil data can then be used to reconstruct paleoenvironments, or test hypotheses about faunal turnover such as the Red Queen (Van Valen, 1973) and Court Jester (Barnosky, 2001) models. Furthermore, an expanded database and fossil record could be used to further test the niche variation hypothesis (Van Valen, 1965) that predicts greater population variability in species with wider niches. The addition of more species and lineages could be used to address questions about niche conservatism of species and higher taxonomic levels in space and time

The last Chapter presented here uses small mammals to reconstruct temperature and precipitation during the last million years using the area of sympatry methodology. The quantitative assessment of this methodology applies temperature and precipitation values to faunas through the Pleistocene-Holocene transition and reflect the general warming during that period. Furthermore with temperature and precipitation

estimates, landscape gradients were estimated for regions (i.e. central Great Plains) that lack paleoclimate proxies. The method supports climate circulation hypotheses for the Younger Dryas and may contribute towards our understanding of no-climate climates, no-analog plant communities, and disharmonious faunas. Additional calibrations beyond mean annual temperature and mean annual precipitation may provide even more details climate parameters. Furthermore, conducting sensitivity tests for other regions of North America would be beneficial to determine if this quantitative method could be applied elsewhere in North America.

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Appendix I – Detailed summary of stomach content data for rodents compiled from the literature.  
Table 5 is a subset of this larger dataset.

Species	Plant Community	Location	N	%Animal	%Plant	%Veg	%Seed	Sampling Date	Source
D. ordii	short-grass steppe	Sevilleta NWR	5	19.0	81.0	19.0	62.0	spring	Hope and Parmenter, 2007
D. ordii	short-grass steppe	Sevilleta NWR	6	0.0	100.0	53.0	47.0	summer	Hope and Parmenter, 2007
D. ordii	short-grass steppe	Sevilleta NWR	10	3.0	97.0	27.0	70.0	winter	Hope and Parmenter, 2007
D. ordii	short-grass prairie	Pawnee National Grassland	216	3.7	91.0	13.1	77.9	May-Jun, Jul-Aug, Sept-Oct, Nov-Dec, Jan-Feb, Mar-Apr	Flake 1973
D. ordii	mesquite savanna	Sevilleta NWR	2	22.0	68.0	1.0	67.0	spring	Hope and Parmenter, 2007
D. ordii	mesquite savanna	Sevilleta NWR	6	0.0	100.0	21.0	79.0	summer	Hope and Parmenter, 2007
D. ordii	mesquite savanna	Sevilleta NWR	3	7.0	93.0	0.0	93.0	winter	Hope and Parmenter, 2007
D. ordii	mesquite grasslands	central Texas	83	18.4	79.1			spring	Alcoze and Zimmerman, 1973
D. ordii	mesquite grasslands	central Texas	57	18.6	79.4			spring	Alcoze and Zimmerman, 1973
D. ordii	mesquite grasslands	central Texas	83	8.8	83.3			winter	Alcoze and Zimmerman, 1973
D. ordii	mesquite grasslands	central Texas	57	11.3	91.1			winter	Alcoze and Zimmerman, 1973
D. ordii	desert scrubland	Sevilleta NWR	1	25.0	75.0	0.0	75.0	summer	Hope and Parmenter, 2007
I. tridactylus	short-grass prairie	Pawnee National Grassland	157	47.1	50.4	38.5	11.9	May-Jun, Jul-Aug, Sept-Oct, Mar-Apr	Flake 1973
O. leucogaster	short-grass prairie	Pawnee National Grassland	291	68.3	22.4	14.6	7.8	May-Jun, Jul-Aug, Sept-Oct, Nov-Dec, Jan-Feb, Mar-Apr	Flake 1973
O. leucogaster	mesquite savanna	Sevilleta NWR	6	66.0	34.0	0.0	34.0	spring	Hope and Parmenter, 2007
O. leucogaster	mesquite savanna	Sevilleta NWR	2	91.0	9.0	0.0	9.0	winter	Hope and Parmenter, 2007
O. leucogaster	mesquite savanna	Sevilleta NWR	5	35.0	65.0	10.0	55.0	spring	Hope and Parmenter, 2007
P. leucopus	short-grass steppe	Sevilleta NWR	1	20.0	80.0	0.0	80.0	summer	Hope and Parmenter, 2007
P. leucopus	short-grass steppe	Sevilleta NWR	1	80.0	20.0	0.0	20.0	spring	Hope and Parmenter, 2007
P. leucopus	montane piñon-juniper woodland	Sevilleta NWR	1	80.0	20.0	0.0	20.0	winter	Hope and Parmenter, 2007
P. leucopus	montane piñon-juniper woodland	Sevilleta NWR	1	17.0	83.0	17.0	66.0	spring	Hope and Parmenter, 2007
P. leucopus	mesquite savanna	Sevilleta NWR	4	73.0	27.0	7.0	20.0	summer	Hope and Parmenter, 2007
P. leucopus	mesquite savanna	Sevilleta NWR	3	46.0	54.0	8.0	46.0	winter	Hope and Parmenter, 2007
P. leucopus	mesquite savanna	Sevilleta NWR	1	50.0	50.0	0.0	50.0	spring	Hope and Parmenter, 2007
P. leucopus	juniper-oak savanna	Sevilleta NWR	13	41.0	59.0	5.0	54.0	summer	Hope and Parmenter, 2007
P. leucopus	juniper-oak savanna	Sevilleta NWR	18	40.0	60.0	13.0	47.0	winter	Hope and Parmenter, 2007
P. leucopus	juniper-oak savanna	Sevilleta NWR	39	20.0	80.0	6.0	74.0	spring	Hope and Parmenter, 2007
P. leucopus	cottonwood riparian forest	Sevilleta NWR	23	75.0	25.0	1.0	24.0	summer	Hope and Parmenter, 2007
P. leucopus	cottonwood riparian forest	Sevilleta NWR	25	54.0	46.0	0.0	46.0	winter	Hope and Parmenter, 2007
P. leucopus	cottonwood riparian forest	Sevilleta NWR	22	54.0	46.0	6.0	40.0	spring	Hope and Parmenter, 2007
P. leucopus	desert scrubland	Sevilleta NWR	2	90.0	10.0	0.0	10.0	summer	Hope and Parmenter, 2007
P. leucopus	desert scrubland	Sevilleta NWR	2	33.0	67.0	0.0	67.0	winter	Hope and Parmenter, 2007
P. leucopus	desert scrubland	Sevilleta NWR	4	19.0	81.0	5.0	76.0	summer	Hope and Parmenter, 2007
P. maniculatus	spruce-fir forest	Togwotee Pass	25	10.0	77.0	7.0	70.0	August 9 and 10 1955	Williams, 1959
P. maniculatus	short-grass prairie	Pawnee National Grassland	656	34.7	53.9	11.7	42.2	May-Jun, Jul-Aug, Sept-Oct, Nov-Dec, Jan-Feb, Mar-Apr	Flake 1973
P. maniculatus	sagebrush grassland	Jackson Hole, WY	11	69.0	69.0	0.0	69.0	first week August 1955	Williams, 1959
P. maniculatus	mostly open stand of lodgepole pine	Yellowstone Park south gate	25	15.0	84.0	51.0	33.0	August 17 to 19, 1955	Williams, 1959
P. maniculatus	pure stand of whitebark pine	Togwotee Pass	15	20.0	81.0	2.0	79.0	12-Aug	Williams, 1959
P. maniculatus	ponderosa pine community	west of Boulder, CO	6	16.0	76.0	0.0	76.0	First week of May 1956	Williams, 1959
P. maniculatus	grasses, forbs with numerous yucca	Marshall Lake	22	11.0	89.0	18.0	71.0	third week of April 1956	Williams, 1959
P. maniculatus	dense spruce-fir forest; open subalpine meadow	Jackson Hole, WY	18	20.0	80.0	14.0	66.0	6-Aug-55	Williams, 1959

Appendix II – Results of small mammal trapping and subsequent stable isotope analysis

Species	Identifier	Year	Month	Date	Macrohabitat	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	wt%C	wt%N	Trapping Grid	SubGrid
<i>Chaetodipus hispidus</i>	H019	2012	6		Sagebrush Grassland	-21.8	4.6	45.7	15.0	CT	Up
<i>Chaetodipus hispidus</i>	H008	2012	6		Tamarisk	-24.0	12.0	39.7	12.9	SC	LI
<i>Chaetodipus hispidus</i>	H010	2012	6		Tamarisk	-19.9	4.0	35.6	11.9	SC	LI
<i>Cheatodipus hispidus</i>	38	2013	6	6/15/2013	Sagebrush Grassland	-21.9	11.6			CT	
<i>Cheatodipus hispidus</i>	95	2013	10	10/8/2013	Sagebrush Grassland	-24.0	4.7	33.2	11.1	SC	Up
<i>Cheatodipus hispidus</i>	99	2013	10	10/8/2013	Sagebrush Grassland	-20.0	6.2	47.2	15.7	SC	Up
<i>Dipodomys ordii</i>	Eu8	2014	5	5/22/2014	Sagebrush Grassland	-17.3	7.7	43.3	14.7	CT	Up
<i>Dipodomys ordii</i>	Eu9	2014	5	5/22/2014	Sagebrush Grassland	-11.3	9.7	42.0	13.5	CT	Up
<i>Dipodomys ordii</i>	XIT-302	2014	5	5/20/2014	Sagebrush Grassland	-11.1	9.8	42.5	14.3	CT	Up
<i>Dipodomys ordii</i>	Cute1	2013	10	10/7/2013	Sagebrush Grassland	-13.7	6.3	44.4	15.0	Road	
<i>Dipodomys ordii</i>	Cute2	2013	10	10/7/2013	Sagebrush Grassland	-18.5	5.7	43.9	14.0	Road	
<i>Dipodomys ordii</i>	52	2013	6	6/17/2013	Sagebrush Grassland	-21.5	4.9			SB	
<i>Dipodomys ordii</i>	53	2013	6	6/18/2013	Sagebrush Grassland	-20.8	4.7			SB	
<i>Dipodomys ordii</i>	54	2013	6	6/18/2013	Sagebrush Grassland	-19.4	2.9			SB	
<i>Dipodomys ordii</i>	55	2013	6	6/18/2013	Sagebrush Grassland	-13.6	2.8			SB	
<i>Dipodomys ordii</i>	56	2013	6	6/18/2013	Sagebrush Grassland	-13.6	3.3			SB	
<i>Dipodomys ordii</i>	101	2013	10	10/9/2013	Sagebrush Grassland	-21.7	4.5	47.0	15.5	SB	
<i>Dipodomys ordii</i>	110	2013	10	10/10/2013	Sagebrush Grassland	-14.6	2.6	53.7	17.8	SB	
<i>Dipodomys ordii</i>	111	2013	10	10/10/2013	Sagebrush Grassland	-14.5	3.7	42.4	14.4	SB	
<i>Dipodomys ordii</i>	120	2013	10	10/11/2013	Sagebrush Grassland	-18.2	6.9	41.8	13.3	SB	
<i>Dipodomys ordii</i>	121	2013	10	10/11/2013	Sagebrush Grassland	-20.0	6.6	43.6	14.1	SB	
<i>Dipodomys ordii</i>	112A	2013	10	10/10/2013	Sagebrush Grassland	-14.7	3.7	48.5	16.5	SB	
<i>Dipodomys ordii</i>	SB-136	2014	5	5/25/2014	Sagebrush Grassland	-12.5	4.0	43.4	14.7	SB	
<i>Dipodomys ordii</i>	SB-137	2014	5	5/25/2014	Sagebrush Grassland	-14.2	5.6	43.5	15.1	SB	
<i>Dipodomys ordii</i>	SB-138	2014	5	5/25/2014	Sagebrush Grassland	-18.0	4.3	45.9	15.2	SB	
<i>Dipodomys ordii</i>	XIT-EU-14	2014	5	5/22/2014	Sagebrush Grassland	-14.0	3.8	24.7	8.5	SB	
<i>Dipodomys ordii</i>	XIT-EU-22	2014	5	5/22/2014	Sagebrush Grassland	-20.9	5.1	42.4	13.9	SB	
<i>Dipodomys ordii</i>	XIT-SB-122	2014	5	5/24/2014	Sagebrush Grassland	-12.8	3.9	42.4	14.4	SB	
<i>Dipodomys ordii</i>	XIT-SB-126	2014	5	5/24/2014	Sagebrush Grassland	-13.2	6.1	28.1	9.1	SB	
<i>Dipodomys ordii</i>	XIT-SB-25	2014	5	5/24/2014	Sagebrush Grassland	-12.2	3.9	38.3	13.2	SB	
<i>Dipodomys ordii</i>	XIT-SB-A	2014	5	5/24/2014	Sagebrush Grassland	-11.8	5.5	41.8	13.7	SB	
<i>Dipodomys ordii</i>	XIT-SB-B	2014	5	5/24/2014	Sagebrush Grassland	-12.5	3.9	32.7	11.2	SB	
<i>Dipodomys ordii</i>	H003	2012	6		Sagebrush Grassland	-17.1	5.1	41.1	13.6	SC	Up
<i>Dipodomys ordii</i>	H009	2012	6		Sagebrush Grassland	-14.9	3.5	36.9	12.5	SC	Up
<i>Dipodomys ordii</i>	9	2013	6	6/14/2013	Sagebrush Grassland	-18.7	7.2			SC	Up
<i>Dipodomys ordii</i>	28	2013	6	6/14/2013	Sagebrush Grassland	-21.5	10.5			SC	Up
<i>Dipodomys ordii</i>	29	2013	6	6/14/2013	Sagebrush Grassland	-13.2	3.9			SC	Up
<i>Dipodomys ordii</i>	32	2013	6	6/15/2013	Sagebrush Grassland	-15.8	7.0			SC	Up
<i>Dipodomys ordii</i>	33	2013	6	6/15/2013	Sagebrush Grassland	-14.6	5.4			SC	Up
<i>Dipodomys ordii</i>	49	2013	6	6/16/2013	Sagebrush Grassland	-20.4	8.9			SC	Up
<i>Dipodomys ordii</i>	96	2013	10	10/8/2013	Sagebrush Grassland	-12.4	3.6	47.4	15.7	SC	Up
<i>Dipodomys ordii</i>	XIT-303	2014	5	5/21/2014	Sagebrush Grassland	-13.5	5.2	41.6	14.1	SC	Up
<i>Dipodomys ordii</i>	XIT-SB-24	2014	5	5/24/2014	Sagebrush Grassland	-12.2	4.3	43.8	13.7	SC	
<i>Dipodomys ordii</i>	XIT-SC-B	2014	5	5/24/2014	Sagebrush Grassland	-16.1	5.1	40.7	12.3	SC	
<i>Dipodomys ordii</i>	XIT-SC-C	2014	5	5/24/2014	Sagebrush Grassland	-12.8	4.8	41.0	13.6	SC	
<i>Lepus californicus</i>	Jrabb	2014	5	5/27/2014	Sagebrush Grassland	-24.0	4.5	18.0	6.2	Road	
<i>Neotoma micropus</i>	H014	2012	6		Cottonwoods	-24.8	5.0	43.2	14.2	CT	Cw
<i>Neotoma micropus</i>	H119	2013	10	10/11/2013	Sagebrush Grassland	-15.4	3.3	41.7	13.5	SB	
<i>Onychomys leucogaster</i>	83	2013	10	10/8/2013	Sagebrush Grassland	-17.7	9.5	28.7	9.1	CT	Up
<i>Onychomys leucogaster</i>	94	2013	10	10/8/2013	Sagebrush Grassland	-14.8	4.8	38.8	12.3	CT	Up
<i>Onychomys leucogaster</i>	100	2013	10	10/8/2013	Sagebrush Grassland	-16.7	9.9	46.8	15.2	CT	Up
<i>Onychomys leucogaster</i>	Eu5	2014	5	5/21/2014	Sagebrush Grassland	-17.1	9.4	45.1	14.6	CT	Up
<i>Onychomys leucogaster</i>	XIT-304	2014	5	5/20/2014	Sagebrush Grassland	-22.7	12.1	40.9	12.8	CT	Up
<i>Onychomys leucogaster</i>	Stink	2013	10	10/9/2013	Sagebrush Grassland	-21.4	8.8	46.9	15.2	Road	
<i>Onychomys leucogaster</i>	51	2013	6	6/17/2013	Sagebrush Grassland	-22.3	8.6			SB	
<i>Onychomys leucogaster</i>	57	2013	6	6/18/2013	Sagebrush Grassland	-18.3	6.5			SB	

Appendix II.- continued...

Species	Identifier	Year	Month	Date	Macrohabitat	δ <sup>13</sup> C	δ <sup>15</sup> N	wt%C	wt%N	Trapping Grid	SubGrid
<i>Onychomys leucogaster</i>	58	2013	6	6/18/2013	Sagebrush Grassland	-21.0	6.8			SB	
<i>Onychomys leucogaster</i>	60	2013	6	6/19/2013	Sagebrush Grassland	-22.5	9.8			SB	
<i>Onychomys leucogaster</i>	61	2013	6	6/19/2013	Sagebrush Grassland	-21.2	8.3			SB	
<i>Onychomys leucogaster</i>	62	2013	6	6/19/2013	Sagebrush Grassland	-21.5	8.5			SB	
<i>Onychomys leucogaster</i>	104	2013	10	10/9/2013	Sagebrush Grassland	-16.7	5.3	44.7	14.7	SB	
<i>Onychomys leucogaster</i>	105	2013	10	10/9/2013	Sagebrush Grassland	-19.8	5.8	46.4	14.9	SB	
<i>Onychomys leucogaster</i>	106	2013	10	10/9/2013	Sagebrush Grassland	-19.1	6.1	50.6	16.2	SB	
<i>Onychomys leucogaster</i>	107	2013	10	10/9/2013	Sagebrush Grassland	-19.6	5.9	47.7	15.5	SB	
<i>Onychomys leucogaster</i>	108	2013	10	10/9/2013	Sagebrush Grassland	-19.8	6.3	48.3	15.7	SB	
<i>Onychomys leucogaster</i>	113	2013	10	10/10/2013	Sagebrush Grassland	-16.3	5.0	62.0	20.0	SB	
<i>Onychomys leucogaster</i>	114	2013	10	10/10/2013	Sagebrush Grassland	-18.0	5.9	46.9	15.0	SB	
<i>Onychomys leucogaster</i>	115	2013	10	10/10/2013	Sagebrush Grassland	-19.8	7.2	61.0	19.8	SB	
<i>Onychomys leucogaster</i>	H102	2013	10	10/9/2013	Sagebrush Grassland	-18.0	5.9	50.6	16.4	SB	
<i>Onychomys leucogaster</i>	SB-135	2014	5	5/25/2014	Sagebrush Grassland	-18.2	7.0	44.9	15.1	SB	
<i>Onychomys leucogaster</i>	SB-139	2014	5	5/25/2014	Sagebrush Grassland	-19.5	8.2	30.2	10.0	SB	
<i>Onychomys leucogaster</i>	XI-EU-12	2014	5	5/22/2014	Sagebrush Grassland	-17.4	6.3	37.3	12.2	SB	
<i>Onychomys leucogaster</i>	XI-EU-13	2014	5	5/22/2014	Sagebrush Grassland	-21.9	7.7	32.0	10.5	SB	
<i>Onychomys leucogaster</i>	XI-EU-15	2014	5	5/22/2014	Sagebrush Grassland	-17.5	6.1	31.7	10.0	SB	
<i>Onychomys leucogaster</i>	XI-EU-16	2014	5	5/22/2014	Sagebrush Grassland	-18.7	6.7	45.6	14.7	SB	
<i>Onychomys leucogaster</i>	XI-EU-17	2014	5	5/22/2014	Sagebrush Grassland	-20.5	8.3	38.2	12.9	SB	
<i>Onychomys leucogaster</i>	XI-EU-18	2014	5	5/22/2014	Sagebrush Grassland	-22.4	8.2	39.7	13.1	SB	
<i>Onychomys leucogaster</i>	XI-EU-19	2014	5	5/22/2014	Sagebrush Grassland	-13.5	9.5	36.1	11.7	SB	
<i>Onychomys leucogaster</i>	XI-EU-20	2014	5	5/22/2014	Sagebrush Grassland	-13.8	5.8	40.4	13.3	SB	
<i>Onychomys leucogaster</i>	XI-SB-123	2014	5	5/24/2014	Sagebrush Grassland	-19.0	6.0	44.0	14.3	SB	
<i>Onychomys leucogaster</i>	XI-SB-124	2014	5	5/24/2014	Sagebrush Grassland	-21.0	8.7	42.5	13.6	SB	
<i>Onychomys leucogaster</i>	XI-SB-C	2014	5	5/24/2014	Sagebrush Grassland	-21.3	7.1	28.1	9.0	SB	
<i>Onychomys leucogaster</i>	H004	2012	6		Sagebrush Grassland	-23.1	7.6	41.2	13.5	SC	Up
<i>Onychomys leucogaster</i>	H011	2012	6		Sagebrush Grassland	-19.3	8.2	34.7	11.4	SC	Up
<i>Onychomys leucogaster</i>	H012	2012	6		Sagebrush Grassland	-19.6	8.6	45.1	14.7	SC	Up
<i>Onychomys leucogaster</i>	H013	2012	6		Sagebrush Grassland	-17.5	6.0	40.9	13.5	SC	Up
<i>Onychomys leucogaster</i>	50	2013	6	6/16/2013	Sagebrush Grassland	-20.5	6.4			SC	Up
<i>Onychomys leucogaster</i>	50	2013	10	10/8/2013	Sagebrush Grassland	-16.6	7.7	45.4	14.8	SC	Up
<i>Onychomys leucogaster</i>	77	2013	10	10/6/2013	Sagebrush Grassland	-16.3	8.8	47.7	15.2	SC	Up
<i>Onychomys leucogaster</i>	78	2013	10	10/6/2013	Sagebrush Grassland	-19.0	6.9	49.1	16.0	SC	Up
<i>Onychomys leucogaster</i>	84	2013	10	10/7/2013	Sagebrush Grassland	-17.6	6.8	46.6	15.2	SC	Up
<i>Onychomys leucogaster</i>	85	2013	10	10/7/2013	Sagebrush Grassland	-17.3	8.1	49.2	16.2	SC	Up
<i>Onychomys leucogaster</i>	86	2013	10	10/7/2013	Sagebrush Grassland	-18.3	7.0	50.9	16.2	SC	Up
<i>Onychomys leucogaster</i>	97	2013	10	10/8/2013	Sagebrush Grassland	-15.6	7.8	42.1	13.6	SC	Up
<i>Onychomys leucogaster</i>	77	2014	5	5/20/2014	Sagebrush Grassland	-16.8	8.5	43.1	13.9	SC	Up
<i>Onychomys leucogaster</i>	77	2014	5	5/21/2014	Sagebrush Grassland	-16.9	8.2	46.8	15.7	SC	Up
<i>Onychomys leucogaster</i>	XI-EU-21	2014	5	5/22/2014	Sagebrush Grassland	-17.3	7.3	44.3	14.3	SC	Up
<i>Onychomys leucogaster</i>	XI-SC-A	2014	5	5/24/2014	Sagebrush Grassland	-17.6	8.0	35.3	11.9	SC	
<i>Peromyscus maniculatus</i>	H015	2012	6		Cottonwoods	-23.2	8.6	49.4	15.8	CT	Cw
<i>Peromyscus maniculatus</i>	H016	2012	6		Cottonwoods	-23.1	8.7	49.1	15.9	CT	Cw
<i>Peromyscus maniculatus</i>	H017	2012	6		Cottonwoods	-21.5	8.2	51.2	16.3	CT	Cw
<i>Peromyscus maniculatus</i>	H018	2012	6		Cottonwoods	-22.5	8.9	42.7	13.9	CT	Cw
<i>Peromyscus maniculatus</i>	H020	2012	6		Cottonwoods	-18.8	8.1	51.1	16.5	CT	Cw
<i>Peromyscus maniculatus</i>	H021	2012	6		Cottonwoods	-22.9	9.5	48.6	15.5	CT	Cw
<i>Peromyscus maniculatus</i>	H022	2012	6		Cottonwoods	-22.9	7.7	47.1	15.3	CT	Cw
<i>Peromyscus maniculatus</i>	H023	2012	6		Cottonwoods	-17.1	8.7	44.9	14.6	CT	Cw
<i>Peromyscus maniculatus</i>	H024	2012	6		Cottonwoods	-22.0	8.6	43.3	14.0	CT	Cw
<i>Peromyscus maniculatus</i>	H025	2012	6		Cottonwoods	-21.2	10.2	50.6	16.5	CT	Cw
<i>Peromyscus maniculatus</i>	H026	2012	6		Cottonwoods	-19.9	10.5	44.9	14.4	CT	Cw
<i>Peromyscus maniculatus</i>	H027	2012	6		Cottonwoods	-22.6	8.5	57.4	18.6	CT	Cw
<i>Peromyscus maniculatus</i>	16	2013	6	6/14/2013	Cottonwoods	-17.0	9.3			CT	Cw
<i>Peromyscus maniculatus</i>	30	2013	6	6/14/2013	Cottonwoods	-11.8	11.4			CT	
<i>Peromyscus maniculatus</i>	31	2013	6	6/14/2013	Cottonwoods	-18.2	9.8			CT	
<i>Peromyscus maniculatus</i>	34	2013	6	6/15/2013	Cottonwoods	-19.0	11.5			CT	

Appendix II.- continued

Species	Identifier	Year	Month	Date	Macrohabitat	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	wt%C	wt%N	Trapping Grid	SubGrid
<i>Peromyscus maniculatus</i>	36	2013	6	6/15/2013	Cottonwoods	-19.3	10.7			CT	
<i>Peromyscus maniculatus</i>	37	2013	6	6/15/2013	Cottonwoods	-15.8	9.7			CT	
<i>Peromyscus maniculatus</i>	39	2013	6	6/16/2013	Cottonwoods	-22.1	12.9			CT	
<i>Peromyscus maniculatus</i>	41	2013	6	6/16/2013	Cottonwoods	-18.7	8.5			CT	
<i>Peromyscus maniculatus</i>	42	2013	6	6/16/2013	Cottonwoods	-12.1	12.0			CT	
<i>Peromyscus maniculatus</i>	43	2013	6	6/16/2013	Cottonwoods	-15.7	10.2			CT	
<i>Peromyscus maniculatus</i>	44	2013	6	6/16/2013	Cottonwoods	-13.4	11.7			CT	
<i>Peromyscus maniculatus</i>	45	2013	6	6/16/2013	Cottonwoods	-12.4	10.2			CT	
<i>Peromyscus maniculatus</i>	46	2013	6	6/16/2013	Cottonwoods	-18.3	10.2			CT	
<i>Peromyscus maniculatus</i>	47	2013	6	6/16/2013	Cottonwoods	-16.2	10.5			CT	
<i>Peromyscus maniculatus</i>	48	2013	6	6/16/2013	Cottonwoods	-17.5	10.7			CT	
<i>Peromyscus maniculatus</i>	41	2013	10	10/8/2013	Cottonwoods	-22.2	7.9	53.3	17.2	CT	Cw
<i>Peromyscus maniculatus</i>	42	2013	10	10/6/2013	Cottonwoods	-18.9	11.4	46.3	15.1	CT	Cw
<i>Peromyscus maniculatus</i>	44	2013	10	10/6/2013	Cottonwoods	-17.2	11.4	44.9	14.6	CT	Cw
<i>Peromyscus maniculatus</i>	63	2013	10	10/6/2013	Cottonwoods	-19.2	9.5	52.1	16.7	CT	Cw
<i>Peromyscus maniculatus</i>	64	2013	10	10/6/2013	Cottonwoods	-20.0	9.6	50.7	16.5	CT	Cw
<i>Peromyscus maniculatus</i>	65	2013	10	10/6/2013	Cottonwoods	-17.6	10.5	50.0	16.2	CT	Cw
<i>Peromyscus maniculatus</i>	66	2013	10	10/6/2013	Cottonwoods	-19.1	8.6	47.3	15.2	CT	Cw
<i>Peromyscus maniculatus</i>	68	2013	10	10/5/2013	Cottonwoods	-17.3	10.2	48.9	15.7	CT	Cw
<i>Peromyscus maniculatus</i>	69	2013	10	10/6/2013	Cottonwoods	-20.5	9.8	58.4	18.6	CT	Cw
<i>Peromyscus maniculatus</i>	70	2013	10	10/6/2013	Cottonwoods	-18.3	10.6	50.0	16.1	CT	Cw
<i>Peromyscus maniculatus</i>	72	2013	10	10/8/2013	Cottonwoods	-20.0	9.5	48.0	15.4	CT	Cw
<i>Peromyscus maniculatus</i>	79	2013	10	10/8/2013	Cottonwoods	-21.3	8.6	48.7	15.4	CT	Cw
<i>Peromyscus maniculatus</i>	80	2013	10	10/8/2013	Cottonwoods	-21.3	7.9	50.3	16.1	CT	Cw
<i>Peromyscus maniculatus</i>	88	2013	10	10/8/2013	Cottonwoods	-19.5	10.0	36.4	11.9	CT	Cw
<i>Peromyscus maniculatus</i>	90	2013	10	10/8/2013	Cottonwoods	-21.4	9.9	51.3	16.4	CT	Cw
<i>Peromyscus maniculatus</i>	91	2013	10	10/8/2013	Cottonwoods	-21.2	8.9	44.1	14.1	CT	Cw
<i>Peromyscus maniculatus</i>	76a	2013	10	10/5/2013	Cottonwoods	-16.5	12.5	55.5	17.6	CT	Cw
<i>Peromyscus maniculatus</i>	87?	2013	10	10/8/2013	Cottonwoods	-18.6	10.9	43.6	13.9	CT	Cw
<i>Peromyscus maniculatus</i>	76	2013	10	10/5/2013	Cottonwoods	-22.5	8.9	50.4	15.9	CT	Up
<i>Peromyscus maniculatus</i>	Eu10	2014	5	5/22/2014	Cottonwoods	-22.2	4.9	36.7	11.9	CT	Cw
<i>Peromyscus maniculatus</i>	Eu11	2014	5	5/22/2014	Cottonwoods	-11.9	5.9	41.5	13.0	CT	Cw
<i>Peromyscus maniculatus</i>	Eu3	2014	5	5/21/2014	Cottonwoods	-16.9	9.6	44.5	14.4	CT	Cw
<i>Peromyscus maniculatus</i>	Eu6	2014	5	5/22/2014	Cottonwoods	-14.7	10.5	42.5	13.5	CT	Cw
<i>Peromyscus maniculatus</i>	Eu7	2014	5	5/22/2014	Cottonwoods	-16.4	9.1	47.4	15.8	CT	Cw
<i>Peromyscus maniculatus</i>	XT-105	2014	5	5/22/2014	Cottonwoods	-14.0	3.2	30.8	10.3	CT	Cw
<i>Peromyscus maniculatus</i>	XT-301	2014	5	5/20/2014	Cottonwoods	-13.4	8.2	67.8	22.6	CT	Cw
<i>Peromyscus maniculatus</i>	XT-65	2014	5	5/20/2014	Cottonwoods	-14.2	8.8	34.3	11.1	CT	Cw
<i>Peromyscus maniculatus</i>	XT-Eu4	2014	5	5/21/2014	Cottonwoods	-11.8	9.6	44.2	14.0	CT	Cw
<i>Peromyscus maniculatus</i>	117	2013	10	10/10/2013	Riparian Grassland	-18.8	8.7	50.6	16.2	RP	
<i>Peromyscus maniculatus</i>	H001	2012	6		Riparian Grassland	-22.9	7.3	48.4	16.0	RT	II
<i>Peromyscus maniculatus</i>	H002	2012	6		Riparian Grassland	-23.5	10.5	36.5	11.7	RT	II
<i>Peromyscus maniculatus</i>	16	2013	10	10/8/2013	Sagebrush Grassland	-21.0	9.6	42.5	13.6	CT	Up
<i>Peromyscus maniculatus</i>	67	2013	10	10/5/2013	Sagebrush Grassland	-16.6	6.3	47.8	15.2	CT	Up
<i>Peromyscus maniculatus</i>	75	2013	10	10/5/2013	Sagebrush Grassland	-23.2	10.3	45.5	14.3	CT	Up
<i>Peromyscus maniculatus</i>	81	2013	10	10/8/2013	Sagebrush Grassland	-18.6	9.2	54.8	17.4	CT	Up
<i>Peromyscus maniculatus</i>	89	2013	10	10/8/2013	Sagebrush Grassland	-22.3	9.5	51.1	16.1	CT	Up
<i>Peromyscus maniculatus</i>	92	2013	10	10/8/2013	Sagebrush Grassland	-19.5	9.5	47.1	15.0	CT	Up
<i>Peromyscus maniculatus</i>	93	2013	10	10/8/2013	Sagebrush Grassland	-22.1	10.1	48.8	15.4	CT	Up
<i>Peromyscus maniculatus</i>	118	2013	10	10/11/2013	Sagebrush Grassland	-20.6	4.2	41.4	13.2	SB	
<i>Peromyscus maniculatus</i>	SB-140	2014	5	5/25/2014	Sagebrush Grassland	-15.5	6.9	35.5	11.8	SB	
<i>Peromyscus maniculatus</i>	XT-SB-125	2014	5	5/24/2014	Sagebrush Grassland	-13.2	8.1	30.5	10.1	SB	
<i>Peromyscus maniculatus</i>	XT-Eu-1	2014	5	5/21/2014	Sagebrush Grassland	-18.6	6.2	44.9	14.1	SC	
<i>Peromyscus maniculatus</i>	XT-SB-26	2014	5	5/24/2014	Sagebrush Grassland	-15.5	6.3	49.7	14.6	SC	
<i>Peromyscus maniculatus</i>	H005	2012	6		Tamarisk	-22.0	7.2	56.5	18.1	SC	LI
<i>Peromyscus maniculatus</i>	H006	2012	6		Tamarisk	-22.1	7.9	36.1	11.5	SC	LI
<i>Reithrodontomys megalotis</i>	59	2013	6	6/18/2013	Riparian Grassland	-21.6	5.0			RP	
<i>Xerospermophilus spilosoma</i>	103	2013	10	10/9/2013	Sagebrush Grassland	-17.9	4.4	48.0	16.2	SB	



Species	Identifier	Year	Month	Date	Macrohabitat	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	wt%C	wt%N	Trapping Grid	SubGrid
<i>Peromyscus maniculatus</i>	31	2013	6	6/14/2013	Cottonwoods	-18.2	9.8			CT	
<i>Peromyscus maniculatus</i>	34	2013	6	6/15/2013	Cottonwoods	-19.0	11.5			CT	
<i>Peromyscus maniculatus</i>	36	2013	6	6/15/2013	Cottonwoods	-19.3	10.7			CT	
<i>Peromyscus maniculatus</i>	37	2013	6	6/15/2013	Cottonwoods	-15.8	9.7			CT	
<i>Peromyscus maniculatus</i>	39	2013	6	6/16/2013	Cottonwoods	-22.1	12.9			CT	
<i>Peromyscus maniculatus</i>	41	2013	6	6/16/2013	Cottonwoods	-18.7	8.5			CT	
<i>Peromyscus maniculatus</i>	42	2013	6	6/16/2013	Cottonwoods	-12.1	12.0			CT	
<i>Peromyscus maniculatus</i>	43	2013	6	6/16/2013	Cottonwoods	-15.7	10.2			CT	
<i>Peromyscus maniculatus</i>	44	2013	6	6/16/2013	Cottonwoods	-13.4	11.7			CT	
<i>Peromyscus maniculatus</i>	45	2013	6	6/16/2013	Cottonwoods	-12.4	10.2			CT	
<i>Peromyscus maniculatus</i>	46	2013	6	6/16/2013	Cottonwoods	-18.3	10.2			CT	
<i>Peromyscus maniculatus</i>	47	2013	6	6/16/2013	Cottonwoods	-16.2	10.5			CT	
<i>Peromyscus maniculatus</i>	48	2013	6	6/16/2013	Cottonwoods	-17.5	10.7			CT	
<i>Peromyscus maniculatus</i>	41	2013	10	10/8/2013	Cottonwoods	-22.2	7.9	53.3	17.2	CT	Cw
<i>Peromyscus maniculatus</i>	42	2013	10	10/6/2013	Cottonwoods	-18.9	11.4	46.3	15.1	CT	Cw
<i>Peromyscus maniculatus</i>	44	2013	10	10/6/2013	Cottonwoods	-17.2	11.4	44.9	14.6	CT	Cw
<i>Peromyscus maniculatus</i>	63	2013	10	10/6/2013	Cottonwoods	-19.2	9.5	52.1	16.7	CT	Cw
<i>Peromyscus maniculatus</i>	64	2013	10	10/6/2013	Cottonwoods	-20.0	9.6	50.7	16.5	CT	Cw
<i>Peromyscus maniculatus</i>	65	2013	10	10/6/2013	Cottonwoods	-17.6	10.5	50.0	16.2	CT	Cw
<i>Peromyscus maniculatus</i>	66	2013	10	10/6/2013	Cottonwoods	-19.1	8.6	47.3	15.2	CT	Cw
<i>Peromyscus maniculatus</i>	68	2013	10	10/5/2013	Cottonwoods	-17.3	10.2	48.9	15.7	CT	Cw
<i>Peromyscus maniculatus</i>	69	2013	10	10/6/2013	Cottonwoods	-20.5	9.8	58.4	18.6	CT	Cw
<i>Peromyscus maniculatus</i>	70	2013	10	10/6/2013	Cottonwoods	-18.3	10.6	50.0	16.1	CT	Cw
<i>Peromyscus maniculatus</i>	72	2013	10	10/8/2013	Cottonwoods	-20.0	9.5	48.0	15.4	CT	Cw
<i>Peromyscus maniculatus</i>	79	2013	10	10/8/2013	Cottonwoods	-21.3	8.6	48.7	15.4	CT	Cw
<i>Peromyscus maniculatus</i>	80	2013	10	10/8/2013	Cottonwoods	-21.3	7.9	50.3	16.1	CT	Cw
<i>Peromyscus maniculatus</i>	88	2013	10	10/8/2013	Cottonwoods	-19.5	10.0	36.4	11.9	CT	Cw
<i>Peromyscus maniculatus</i>	90	2013	10	10/8/2013	Cottonwoods	-21.4	9.9	51.3	16.4	CT	Cw
<i>Peromyscus maniculatus</i>	91	2013	10	10/8/2013	Cottonwoods	-21.2	8.9	44.1	14.1	CT	Cw
<i>Peromyscus maniculatus</i>	76a	2013	10	10/5/2013	Cottonwoods	-16.5	12.5	55.5	17.6	CT	Cw
<i>Peromyscus maniculatus</i>	87?	2013	10	10/8/2013	Cottonwoods	-18.6	10.9	43.6	13.9	CT	Cw
<i>Peromyscus maniculatus</i>	76	2013	10	10/5/2013	Cottonwoods	-22.5	8.9	50.4	15.9	CT	Up
<i>Peromyscus maniculatus</i>	Eu10	2014	5	5/22/2014	Cottonwoods	-22.2	4.9	36.7	11.9	CT	Cw
<i>Peromyscus maniculatus</i>	Eu11	2014	5	5/22/2014	Cottonwoods	-11.9	5.9	41.5	13.0	CT	Cw
<i>Peromyscus maniculatus</i>	Eu3	2014	5	5/21/2014	Cottonwoods	-16.9	9.6	44.5	14.4	CT	Cw
<i>Peromyscus maniculatus</i>	Eu6	2014	5	5/22/2014	Cottonwoods	-14.7	10.5	42.5	13.5	CT	Cw
<i>Peromyscus maniculatus</i>	Eu7	2014	5	5/22/2014	Cottonwoods	-16.4	9.1	47.4	15.8	CT	Cw
<i>Peromyscus maniculatus</i>	XIT-105	2014	5	5/22/2014	Cottonwoods	-14.0	3.2	30.8	10.3	CT	Cw
<i>Peromyscus maniculatus</i>	XIT-301	2014	5	5/20/2014	Cottonwoods	-13.4	8.2	67.8	22.6	CT	Cw
<i>Peromyscus maniculatus</i>	XIT-65	2014	5	5/20/2014	Cottonwoods	-14.2	8.8	34.3	11.1	CT	Cw
<i>Peromyscus maniculatus</i>	XIT-Eu4	2014	5	5/21/2014	Cottonwoods	-11.8	9.6	44.2	14.0	CT	Cw
<i>Peromyscus maniculatus</i>	117	2013	10	10/10/2013	Riparian Grassland	-18.8	8.7	50.6	16.2	RP	
<i>Peromyscus maniculatus</i>	H001	2012	6		Riparian Grassland	-22.9	7.3	48.4	16.0	RT	II
<i>Peromyscus maniculatus</i>	H002	2012	6		Riparian Grassland	-23.5	10.5	36.5	11.7	RT	II
<i>Peromyscus maniculatus</i>	16	2013	10	10/8/2013	Sagebrush Grassland	-21.0	9.6	42.5	13.6	CT	Up
<i>Peromyscus maniculatus</i>	67	2013	10	10/5/2013	Sagebrush Grassland	-16.6	6.3	47.8	15.2	CT	Up
<i>Peromyscus maniculatus</i>	75	2013	10	10/5/2013	Sagebrush Grassland	-23.2	10.3	45.5	14.3	CT	Up
<i>Peromyscus maniculatus</i>	81	2013	10	10/8/2013	Sagebrush Grassland	-18.6	9.2	54.8	17.4	CT	Up
<i>Peromyscus maniculatus</i>	89	2013	10	10/8/2013	Sagebrush Grassland	-22.3	9.5	51.1	16.1	CT	Up
<i>Peromyscus maniculatus</i>	92	2013	10	10/8/2013	Sagebrush Grassland	-19.5	9.5	47.1	15.0	CT	Up
<i>Peromyscus maniculatus</i>	93	2013	10	10/8/2013	Sagebrush Grassland	-22.1	10.1	48.8	15.4	CT	Up
<i>Peromyscus maniculatus</i>	118	2013	10	10/11/2013	Sagebrush Grassland	-20.6	4.2	41.4	13.2	SB	
<i>Peromyscus maniculatus</i>	SB-140	2014	5	5/25/2014	Sagebrush Grassland	-15.5	6.9	35.5	11.8	SB	
<i>Peromyscus maniculatus</i>	XIT-SB-125	2014	5	5/24/2014	Sagebrush Grassland	-13.2	8.1	30.5	10.1	SB	
<i>Peromyscus maniculatus</i>	XIT-Eu-1	2014	5	5/21/2014	Sagebrush Grassland	-18.6	6.2	44.9	14.1	SC	
<i>Peromyscus maniculatus</i>	XIT-SB-26	2014	5	5/24/2014	Sagebrush Grassland	-15.5	6.3	49.7	14.6	SC	
<i>Peromyscus maniculatus</i>	H005	2012	6		Tamarisk	-22.0	7.2	56.5	18.1	SC	LI
<i>Peromyscus maniculatus</i>	H006	2012	6		Tamarisk	-22.1	7.9	36.1	11.5	SC	LI
<i>Reithrodontomys megalotis</i>	59	2013	6	6/18/2013	Riparian Grassland	-21.6	5.0			RP	
<i>Xerospemophilus spilosoma</i>	103	2013	10	10/9/2013	Sagebrush Grassland	-17.9	4.4	48.0	16.2	SB	

Appendix III -  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , Wt% C, and Wt% N of plants collected in southwestern Kansas.

Field_ID	Year	Month	Season	TrappingGrid	Habitat	FG	Growth_Habit	Family	Genus	Species.binomial	CommonName	C3_C4	Plant Part	$\delta^{13}\text{C}$	Wt %C	$\delta^{15}\text{N}$	Wt %N
2014.5.AH.CN.4	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Hordeum	Hordeum jubatum	Foxtail barley	C3	Seeds	-25.5	44.0	-0.3	2.0
2014.5.AH.CN.4	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Hordeum	Hordeum jubatum	Foxtail barley	C3	Leaf	-27.6	44.8	-0.5	2.2
2014.5.AH.CN.5	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Seeds	-22.4	39.6	4.9	2.6
2014.5.AH.CN.5	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Leaf	-27.0	46.0	2.8	2.9
CT.W10.00.07	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Leaf	-29.0	38.6	5.6	3.4
CT.W11.00.08	2012	6	2012Su	CT	Cottonwood Riparian	Grass		Poaceae				C3	Leaf	-22.6	37.8	3.9	1.3
CT.W13.01.04	2012	6	2012Su	CT	Cottonwood Riparian							C3	Leaf	-27.2	38.7	3.1	2.0
CT.W13.01.24	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-27.7	38.3	5.5	2.8
CT.W13.01.24	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Flower	-27.3	33.9	5.1	3.3
CT.W13.02.04	2012	6	2012Su	CT	Cottonwood Riparian	Forb	No ID					C3	Leaf	-25.4	39.7	2.2	2.5
CT.W16.00.13	2012	6	2012Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	Leaf	-13.8	35.0	6.4	3.6
CT.W16.00.13	2012	6	2012Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	Leaf	-14.2	38.9	7.1	4.2
CT.X17.00.04	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Polygonaceae	Eriogonum	Eriogonum annuum	Annual Eriogonum	C4	Stems/Leaf	-13.8	39.6	9.0	2.2
CT.Y11.00.03	2012	6	2012Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Grass	-27.9	35.4	4.0	0.8
CT.Y11.00.03	2012	6	2012Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Seeds	-27.5	39.0	2.2	2.3
CT.Y11.00.05	2012	6	2012Su	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-28.3	43.5	2.5	2.0
CT.Y14.00.08	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Stems/Leaf	-27.9	38.3	3.3	1.8
CT.Y14.00.08	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Leaf	-29.6	39.2	3.5	2.5
CT.Y15.00.09	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-27.8	41.3	6.7	5.9
CT.Y15.00.10	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Solidago	Solidago missouriensis	Missouri goldenrod	C3	Leaf	-26.6	32.6	7.1	3.3
CT.Y15.00.10	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Solidago	Solidago missouriensis	Missouri goldenrod	C3	Seeds	-26.9	36.4	4.8	3.6
CT.Y19.00.15	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Stems/Leaf	-28.4	41.4	3.9	1.2
CT.Y19.00.15	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Leaf	-28.8	43.5	4.0	1.8
CT.Y19.00.15	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Seeds	-29.0	47.3	5.3	2.7
CT.Z10.00.02	2012	6	2012Su	CT	Cottonwood Riparian							C4	Leaf	-14.9	39.4	2.1	1.1
CT.Z13.00.07	2012	6	2012Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C4	Leaf	-14.4	40.7	2.9	1.6
CT.Z13.02.20	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Stems/Leaf	-26.1	34.7	4.1	3.0
CT.Z13.02.20	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-26.7	37.5	3.8	4.0
CT.Z13.02.25	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-28.9	37.3	4.5	4.6
CT.Z14.02.04	2012	6	2012Su	CT	Cottonwood Riparian	Grass		Poaceae				C4	All	-14.8	40.2	2.9	1.5
2013.6.CT.A.1	2013	6	2013Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Chamaesaracha	Chamaesaracha conioides	Ground saracha	C3	Leaf	-29.1	44.2	6.4	3.2
2013.6.CT.A.2	2013	6	2013Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	All	-26.7	44.1	2.4	2.0
2013.6.CT.A.3	2013	6	2013Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Asteraceae	Cirsium	Cirsium altissimum	Tall thistle	C3	Seeds	-27.9	45.0	4.5	3.4
2013.6.CT.A.5	2013	6	2013Su	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Lipcarpha	Lipcarpha micrantha	Small flower dwarf bulrush	C4	All	-13.6	41.8	0.5	3.3
2013.6.CT.A.6	2013	6	2013Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Psilostrophe	Psilostrophe villosa	Paper flower	C3	All	-29.2	39.2	1.3	3.3
2013.6.CT.A.7	2013	6	2013Su	CT	Cottonwood Riparian	Grass		Poaceae				C4	Leaf	-13.7	42.6	-0.5	3.4
2013.6.CT.A.9	2013	6	2013Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	Seeds	-29.4	30.8	2.4	1.7
2013.6.CT.A.9	2013	6	2013Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	Leaf	-29.9	41.5	2.7	2.2
2013.6.CT.AH.10	2013	6	2013Su	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Bulbostylis	Bulbostylis capillaris	Hair sedge	C4	All	-14.7	33.7	4.7	3.7
2013.6.CT.AH.4	2013	6	2013Su	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Bulbostylis	Bulbostylis capillaris	Hair sedge	C4	Leaf	-13.7	41.5	1.0	2.7
2013.6.CT.P.8	2013	6	2013Su	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-28.8	46.4	3.3	3.0
2013.10.AH.CT.10	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Leaf	-14.4	39.9	2.5	1.8
2013.10.AH.CT.10	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Seed	-14.1	43.8	0.9	3.3
2013.10.AH.CT.11	2013	10	2013F	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Flower	-29.5	52.0	3.9	1.0
2013.10.AH.CT.11	2013	10	2013F	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-28.2	44.7	2.4	1.7
2013.10.AH.CT.13	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Leaf	-13.8	42.0	3.6	1.4
2013.10.AH.CT.13	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Seed	-12.8	42.4	5.6	2.0
2013.10.AH.CT.14	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Stalk	-13.4	42.6	-0.2	0.5
2013.10.AH.CT.14	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Seed	-12.8	43.2	1.2	1.7

Appendix III continued...

Field_ID	Year	Month	Season	TrappingGrid	Habitat	FG	Growth_Habit	Family	Genus	Species.binomial	CommonName	C3_C4	Plant Part	$\delta^{13}C$	Wt %C	$\delta^{15}N$	Wt %N
2014.5.AH.CN.4	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Hordeum	Hordeum jubatum	Foxtail barley	C3	Seeds	-25.5	44.0	-0.3	2.0
2014.5.AH.CN.4	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Hordeum	Hordeum jubatum	Foxtail barley	C3	Leaf	-27.6	44.8	-0.5	2.2
2014.5.AH.CN.5	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Seeds	-22.4	39.6	4.9	2.6
2014.5.AH.CN.5	2014	5	2014Sp	CH		Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Leaf	-27.0	46.0	2.8	2.9
CT.W10.00.07	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Leaf	-29.0	38.6	5.6	3.4
CT.W11.00.08	2012	6	2012Su	CT	Cottonwood Riparian	Grass		Poaceae				C3	Leaf	-22.6	37.8	3.9	1.3
CT.W13.01.04	2012	6	2012Su	CT	Cottonwood Riparian							C3	Leaf	-27.2	38.7	3.1	2.0
CT.W13.01.24	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-27.7	38.3	5.5	2.8
CT.W13.01.24	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Flower	-27.3	33.9	5.1	3.3
CT.W13.02.04	2012	6	2012Su	CT	Cottonwood Riparian	Forb	No ID					C3	Leaf	-25.4	39.7	2.2	2.5
CT.W16.00.13	2012	6	2012Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	Leaf	-13.8	35.0	6.4	3.6
CT.W16.00.13	2012	6	2012Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	Leaf	-14.2	38.9	7.1	4.2
CT.X17.00.04	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Polygonaceae	Eriogonum	Eriogonum annuum	Annual Eriogonum	C4	Stems/Leaf	-13.8	39.6	9.0	2.2
CT.Y11.00.03	2012	6	2012Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Grass	-27.9	35.4	4.0	0.8
CT.Y11.00.03	2012	6	2012Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	Seeds	-27.5	39.0	2.2	2.3
CT.Y11.00.05	2012	6	2012Su	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-28.3	43.5	2.5	2.0
CT.Y14.00.08	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Stems/Leaf	-27.9	38.3	3.3	1.8
CT.Y14.00.08	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Leaf	-29.6	39.2	3.5	2.5
CT.Y15.00.09	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-27.8	41.3	6.7	5.9
CT.Y15.00.10	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Solidago	Solidago missouriensis	Missouri goldenrod	C3	Leaf	-26.6	32.6	7.1	3.3
CT.Y15.00.10	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Solidago	Solidago missouriensis	Missouri goldenrod	C3	Seeds	-26.9	36.4	4.8	3.6
CT.Y19.00.15	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Stems/Leaf	-28.4	41.4	3.9	1.2
CT.Y19.00.15	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Leaf	-28.8	43.5	4.0	1.8
CT.Y19.00.15	2012	6	2012Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Seeds	-29.0	47.3	5.3	2.7
CT.Z10.00.02	2012	6	2012Su	CT	Cottonwood Riparian							C4	Leaf	-14.9	39.4	2.1	1.1
CT.Z13.00.07	2012	6	2012Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C4	Leaf	-14.4	40.7	2.9	1.6
CT.Z13.02.20	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Stems/Leaf	-26.1	34.7	4.1	3.0
CT.Z13.02.20	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-26.7	37.5	3.8	4.0
CT.Z13.02.25	2012	6	2012Su	CT	Cottonwood Riparian	Forb						C3	Leaf	-28.9	37.3	4.5	4.6
CT.Z14.02.04	2012	6	2012Su	CT	Cottonwood Riparian	Grass		Poaceae				C4	All	-14.8	40.2	2.9	1.5
2013.6.CT.A.1	2013	6	2013Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Chamaesaracha	Chamaesaracha conioides	Ground saracha	C3	Leaf	-29.1	44.2	6.4	3.2
2013.6.CT.A.2	2013	6	2013Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	All	-26.7	44.1	2.4	2.0
2013.6.CT.A.3	2013	6	2013Su	CT	Cottonwood Riparian	Shrub	Forb/Herb	Asteraceae	Cirsium	Cirsium altissimum	Tall thistle	C3	Seeds	-27.9	45.0	4.5	3.4
2013.6.CT.A.5	2013	6	2013Su	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Lipcarpha	Lipcarpha micrantha	Small flower dwarf bulrush	C4	All	-13.6	41.8	0.5	3.3
2013.6.CT.A.6	2013	6	2013Su	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Psilostrophe	Psilostrophe villosa	Paper flower	C3	All	-29.2	39.2	1.3	3.3
2013.6.CT.A.7	2013	6	2013Su	CT	Cottonwood Riparian	Grass		Poaceae				C4	Leaf	-13.7	42.6	-0.5	3.4
2013.6.CT.A.9	2013	6	2013Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	Seeds	-29.4	30.8	2.4	1.7
2013.6.CT.A.9	2013	6	2013Su	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	Leaf	-29.9	41.5	2.7	2.2
2013.6.CT.AH.10	2013	6	2013Su	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Bulbostylis	Bulbostylis capillaris	Hair sedge	C4	All	-14.7	33.7	4.7	3.7
2013.6.CT.AH.4	2013	6	2013Su	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Bulbostylis	Bulbostylis capillaris	Hair sedge	C4	Leaf	-13.7	41.5	1.0	2.7
2013.6.CT.P.8	2013	6	2013Su	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-28.8	46.4	3.3	3.0
2013.10.AH.CT.10	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Leaf	-14.4	39.9	2.5	1.8
2013.10.AH.CT.10	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Seed	-14.1	43.8	0.9	3.3
2013.10.AH.CT.11	2013	10	2013F	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Flower	-29.5	52.0	3.9	1.0
2013.10.AH.CT.11	2013	10	2013F	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-28.2	44.7	2.4	1.7
2013.10.AH.CT.13	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Leaf	-13.8	42.0	3.6	1.4
2013.10.AH.CT.13	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Seed	-12.8	42.4	5.6	2.0
2013.10.AH.CT.14	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Stalk	-13.4	42.6	-0.2	0.5
2013.10.AH.CT.14	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Seed	-12.8	43.2	1.2	1.7

## Appendix III continued...

Field_ID	Year	Month	Season	TrappingGrid	Habitat	FG	Growth_Habit	Family	Genus	Species.binomial	CommonName	C3_C4	Plant Part	δ <sup>13</sup> C	Wt %C	δ <sup>15</sup> N	Wt %N
2013.10.AH.CT.18	2013	10	2013F	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Lipcarpha	Lipocarpha micrantha	Small flower dwarf bulrush	C4	Leaf	-14.2	42.2	0.2	0.7
2013.10.AH.CT.19	2013	10	2013F	CT	Cottonwood Riparian	Sedge/Rush	Forb/Herb	Equisetaceae	Equistum	Equisetum hyemale	Horsetail	C3	All	-27.6	34.6	10.9	1.8
2013.10.AH.CT.2	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Leaf	-14.3	41.3	3.2	1.7
2013.10.AH.CT.6	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Heterotheca	Heterotheca subaxillaris	Camphor weed	C3	All	-27.7	44.5	3.4	1.4
2013.10.AH.CT.6	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Heterotheca	Heterotheca subaxillaris	Camphor weed	C3	Leaf	-31.3	42.3	2.3	2.5
2013.10.AH.CT.8	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Fruit	-26.3	51.9	3.1	2.5
2013.10.AH.CT.8	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Leaf	-28.0	43.5	4.5	3.0
2013.10.AH.CT.9	2013	10	2013F	CT	Cottonwood Riparian	Shrub	Forb/Herb	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	All	-13.9	39.0	4.7	3.3
2013.10.ND.CT.1	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Seed	-27.6	47.2	5.5	2.2
2013.10.ND.CT.10	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Apocynaceae	Asclepias	Asclepias sp.	Milkweed	C3	Leaf	-29.3	38.1	5.1	2.2
2013.10.ND.CT.13	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Setaria	Setaria pumila	Yellow foxtail	C4	Seed	-13.0	42.5	0.4	0.9
2013.10.ND.CT.13	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Setaria	Setaria pumila	Yellow foxtail	C4	Leaf	-12.9	36.8	0.4	1.2
2013.10.ND.CT.2	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Loasaceae	Mentzelia	Mentzelia nuda	Sand lily	C3	Seed	-28.5	46.1	8.3	2.6
2013.10.ND.CT.4	2013	10	2013F	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	Leaf	-14.2	41.6	1.7	1.9
2013.10.ND.CT.6	2013	10	2013F	CT	Cottonwood Riparian	Cactus	Shrub	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	CAM	Flesh	-13.0	33.0	5.2	1.6
2013.10.ND.CT.6	2013	10	2013F	CT	Cottonwood Riparian	Cactus	Shrub	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	CAM	Seed	-12.7	54.1	5.4	3.1
2013.10.ND.CT.7	2013	10	2013F	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Psilostrophe	Psilostrophe villosa	Paper flower	C3	All	-30.9	39.9	3.0	2.6
2014.5.AH.CT.1	2014	5	2014Sp	CT	Cottonwood Riparian	Shrub	Forb/Herb	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	All	-27.5	49.0	3.4	2.4
2014.5.AH.CT.10	2014	5	2014Sp	CT	Cottonwood Riparian	Sedge/Rush	Graminoid	Cyperaceae	Lipcarpha	Lipocarpha micrantha	Small flower dwarf bulrush		Leaf	-19.9	42.7	2.6	2.2
2014.5.AH.CT.11	2014	5	2014Sp	CT	Cottonwood Riparian	Sedge/Rush						C3	Leaf	-24.2	34.5	6.2	3.9
2014.5.AH.CT.12	2014	5	2014Sp	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-28.6	45.9	1.9	2.4
2014.5.AH.CT.12	2014	5	2014Sp	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Seeds	-27.6	48.6	2.6	4.7
2014.5.AH.CT.13	2014	5	2014Sp	CT	Cottonwood Riparian	Forb	Forb/Herb	Apocynaceae	Asclepias	Asclepias purpurascens	Purple milkweed	C3	All	-27.2	42.3	4.9	5.6
2014.5.AH.CT.15	2014	5	2014Sp	CT	Cottonwood Riparian							C3	All	-27.3	39.9	3.7	2.9
2014.5.AH.CT.15	2014	5	2014Sp	CT	Cottonwood Riparian							C3	All	-27.4	40.0	3.8	2.9
2014.5.AH.CT.3	2014	5	2014Sp	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Psilostrophe	Psilostrophe villosa	Paper flower	C3	Flower/Leaf	-26.4	41.7	4.3	2.7
2014.5.AH.CT.4	2014	5	2014Sp	CT	Cottonwood Riparian	Legume	Forb/Herb	Fabaceae	Astragalus	Astragalus crassicaerpus	Ground-plum milk vetch	C3	Seeds	-25.5	42.3	5.6	2.7
2014.5.AH.CT.4	2014	5	2014Sp	CT	Cottonwood Riparian	Legume	Forb/Herb	Fabaceae	Astragalus	Astragalus crassicaerpus	Ground-plum milk vetch	C3	Leaf	-27.8	46.5	2.7	4.0
2014.5.AH.CT.5	2014	5	2014Sp	CT	Cottonwood Riparian	Forb	Forb/Herb	Solanaceae	Chamaesaracha	Chamaesaracha coniodes	Ground saracha	C3	All	-25.8	40.6	4.6	4.7
2014.5.AH.CT.7	2014	5	2014Sp	CT	Cottonwood Riparian	Cactus	Shrub	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	CAM	All	-13.1	39.7	7.2	2.0
2014.5.AH.CT.8	2014	5	2014Sp	CT	Cottonwood Riparian							C4	All	-14.2	35.4	8.7	3.3
2014.5.AH.CT.9	2014	5	2014Sp	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	Seeds	-23.6	44.4	3.9	2.7
2014.5.KFD.CT.1	2014	5	2014Sp	CT	Cottonwood Riparian	Tree	Tree	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	Leaf	-26.7	47.1	5.5	2.1
2014.5.KFD.CT.10	2014	5	2014Sp	CT	Cottonwood Riparian	Shrub	Forb/Herb	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	All	-14.0	35.6	6.4	3.7
2014.5.KFD.CT.14	2014	5	2014Sp	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	Dead Material	-15.0	39.7	2.2	0.8
2014.5.KFD.CT.15	2014	5	2014Sp	CT	Cottonwood Riparian	Shrub	Shrub	Agavaceae	Yucca	Yucca glauca	Yucca	C3	Flower	-22.6	42.3	1.4	3.4
2014.5.KFD.CT.3	2014	5	2014Sp	CT	Cottonwood Riparian	Forb						C3	All	-25.3	34.4	6.5	4.2
2014.5.KFD.CT.4	2014	5	2014Sp	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	Seeds	-24.5	43.4	4.5	2.2
2014.5.KFD.CT.4	2014	5	2014Sp	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	Leaf	-28.9	42.3	3.4	2.8
2014.5.KFD.CT.6	2014	5	2014Sp	CT	Cottonwood Riparian	Forb	Forb/Herb	Asteraceae	Heterotheca	Heterotheca canescens	Hairy golden aster	C3	All	-27.2	45.0	5.0	2.5
2014.5.KFD.CT.7	2014	5	2014Sp	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	Seeds	-25.5	43.8	3.2	1.9
2014.5.KFD.CT.9	2014	5	2014Sp	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	All	-13.0	44.8	6.8	2.4
2014.5.KFD.CT.9	2014	5	2014Sp	CT	Cottonwood Riparian	Grass	Graminoid	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	Leaf	-15.3	41.9	5.7	2.4
2013.10.AH.SB.11	2013	10	2013F	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Schizachyrium	Schizachyrium scoparium	Little bluestem	C4	Flower	-14.3	41.7	0.5	1.0

Appendix III continued...

Field_ID	Year	Month	Season	TrappingGrid	Habitat	FG	Growth_Habit	Family	Genus	Species.binomial	CommonName	C3_C4	Plant Part	$\delta^{13}\text{C}$	Wt %C	$\delta^{15}\text{N}$	Wt %N
2013.10.AH.SB.11	2013	10	2013F	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Schizachyrium	Schizachyrium scoparium	Little bluestem	C4	Stalk	-14.1	41.2	2.0	1.0
2013.10.AH.SB.13b	2013	10	2013F	SB	Sagebrush Grassland	Shrub	Forb/Herb	Pedaliaceae	Proboscidea	Proboscidea louisianica	Devil's claw	C3	Seed	-23.0	42.9	0.2	3.3
2013.10.AH.SB.14	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Capparaceae	Cleome	Cleome serrulata	Rocky Mountain bee plant	C3	Bean Seeds	-26.2	44.6	2.3	3.9
2013.10.AH.SB.15	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Polygonaceae	Eriogonum	Eriogonum annuum	Annual Eriogonum	C3	Leaf	-30.8	39.6	1.4	2.0
2013.10.AH.SB.8	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Polygonaceae	Eriogonum	Eriogonum annuum	Annual Eriogonum	C3	Seed	-28.7	45.2	1.8	2.3
2013.10.AH.SB.4	2013	10	2013F	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Eragrostis	Eragrostis cilianensis	Stink grass	C4	Seed	-13.2	38.4	2.5	1.5
2013.10.AH.SB.6	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Heterotheca	Heterotheca subaxillaris	Camphor weed	C3	All	-25.9	43.5	2.2	2.3
2013.10.AH.SB.8	2013	10	2013F	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Chloris	Chloris verticillata	Windmill grass	C4	Stalk	-13.2	42.7	3.8	1.0
2013.10.AH.SB.8	2013	10	2013F	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Chloris	Chloris verticillata	Windmill grass	C4	Seed	-14.0	43.9	-0.8	1.3
2013.10.ND.SB.1	2013	10	2013F	SB	Sagebrush Grassland	Shrub	Forb/Herb	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	All	-26.9	47.6	0.8	1.5
2013.10.ND.SB.13	2013	10	2013F	SB	Sagebrush Grassland	Cactus	Shrub	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	CAM	Seed	-12.1	49.8	0.1	1.0
2013.10.ND.SB.15	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Flower	-26.0	42.4	3.4	2.4
2013.10.ND.SB.15	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Leaf	-28.2	44.7	3.0	3.4
2013.10.ND.SB.16	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Hymenoxys	Hymenoxys odorata	Bitterweed	C3	All	-28.6	43.4	1.7	2.1
2013.10.ND.SB.4	2013	10	2013F	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	Seed	-14.3	42.9	-0.5	1.9
2013.10.ND.SB.5	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Seed	-27.9	45.1	4.6	1.9
2013.10.ND.SB.5	2013	10	2013F	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	Leaf	-28.0	42.7	4.8	3.0
2013.10.ND.SB.8	2013	10	2013F	SB	Sagebrush Grassland	Shrub	Shrub	Rosaceae	Prunus	Prunus americana	Wild plum	C3	Leaf	-28.0	49.1	-0.6	1.9
2013.6.SB.A.3	2013	6	2013Su	SB	Sagebrush Grassland	Sedge/Rush	Graminoid	Cyperaceae	Carex	Carex gravida	Heavy sedge	C3	Leaf	-27.8	40.1	-0.1	3.9
2013.6.SB.A.4	2013	6	2013Su	SB	Sagebrush Grassland	Legume	Forb/Herb	Fabaceae	Dalea	Dalea leporina	Foxtail Dalea	C3	All	-29.4	44.4	-4.0	4.6
2013.6.SB.A.5	2013	6	2013Su	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Erigeron	Erigeron strigosus	Daisy fleabane	C3	Leaf/Flower	-28.8	42.9	-1.1	2.5
2013.6.SB.A.6	2013	6	2013Su	SB	Sagebrush Grassland	Forb	Forb/Herb	Loasaceae	Mentzelia	Mentzelia nuda	Sand lily	C3	Leaf	-27.5	39.5	0.3	3.5
2013.6.SB.P.7	2013	6	2013Su	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	Stalks	-28.5	44.5	0.4	1.8
2013.6.SB.P.7	2013	6	2013Su	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	Seeds	-28.7	44.5	-0.2	3.1
2014.5.AH.SB.10	2014	5	2014Sp	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Hordeum	Hordeum jubatum	Foxtail barley	C3	Seeds	-25.0	44.1	-1.1	2.1
2014.5.AH.SB.11	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	Leaf	-27.9	43.4	2.2	3.6
2014.5.AH.SB.2	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Gaillardia	Gaillardia pulchella	Indian blanket flower	C3	Leaf	-27.3	39.9	-0.2	4.3
2014.5.AH.SB.3	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Gaillardia	Gaillardia pulchella	Indian blanket flower	C3	Flower Heads	-26.0	38.1	-0.3	2.0
2014.5.AH.SB.4	2014	5	2014Sp	SB	Sagebrush Grassland	Legume	Forb/Herb	Fabaceae	Vicia	Vicia		C3	Flower/Leaf	-27.2	45.2	-2.3	4.5
2014.5.AH.SB.7	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae				C3	Leaf	-28.3	40.1	-0.6	3.0
2014.5.AH.SB.9	2014	5	2014Sp	SB	Sagebrush Grassland	Shrub	Forb/Herb	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	All	-25.5	47.8	-0.1	2.4
2014.5.KCP.SB.1	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Brassicaceae	Lesquerella	Lesquerella gordonii	Mustard	C3	All	-24.9	42.2	1.1	2.6
2014.5.KCP.SB.1	2014	5	2014Sp	SB	Sagebrush Grassland	Legume	Forb/Herb	Fabaceae	Vicia	Vicia		C3	All	-24.9	42.2	1.1	2.6
2014.5.KCP.SB.1	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Brassicaceae	Lesquerella	Lesquerella gordonii	Mustard	C3	Leaf	-28.9	44.7	-1.7	4.1
2014.5.KCP.SB.1	2014	5	2014Sp	SB	Sagebrush Grassland	Legume	Forb/Herb	Fabaceae	Vicia	Vicia		C3	Leaf	-28.9	44.7	-1.7	4.1
2014.5.KCP.SB.10	2014	5	2014Sp	SB	Sagebrush Grassland	Shrub	Forb/Herb	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	All	-25.5	47.8	-0.1	2.4
2014.5.KCP.SB.12	2014	5	2014Sp	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Bromus	Bromus		C3	Seeds	-24.1	41.1	1.4	1.9
2014.5.KCP.SB.13	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Helianthus	Helianthus annuus	Common sunflower	C3	Flower/Leaf	-28.1	44.2	1.1	2.5
2014.5.KCP.SB.13	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Helianthus	Helianthus annuus	Common sunflower	C3	Leaf	-26.7	36.5	1.3	3.9
2014.5.KCP.SB.3	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Malvaceae	Callirhoe	Callirhoe involucrata	Purple mallow	C3	Leaf	-28.0	39.2	0.6	3.0
2014.5.KCP.SB.4	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Gaillardia	Gaillardia pulchella	Indian blanket flower	C3	Flower Heads	-27.9	36.7	2.4	1.7
2014.5.KCP.SB.4	2014	5	2014Sp	SB	Sagebrush Grassland	Forb	Forb/Herb	Asteraceae	Gaillardia	Gaillardia pulchella	Indian blanket flower	C3	Leaf	-29.9	39.0	1.8	2.1
2014.5.KCP.SB.5	2014	5	2014Sp	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	Seeds	-14.7	36.4	-3.1	1.0
2014.5.KCP.SB.5	2014	5	2014Sp	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	Leaf	-15.1	42.3	-2.5	2.3
2014.5.KCP.SB.7	2014	5	2014Sp	SB	Sagebrush Grassland	Grass	Graminoid	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	Seeds	-24.3	42.2	-0.3	1.7
2014.5.KCP.SB.8	2014	5	2014Sp	SB	Sagebrush Grassland							C3	Leaf	-27.5	39.1	1.2	3.6
2014.5.KCP.SB.9	2014	5	2014Sp	SB	Sagebrush Grassland							C3	Leaf	-25.2	39.4	2.7	4.1



Appendix IV –  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , Wt% C, and Wt% N values of plants collected in southwestern Kansas. The values of plant specimens with multiple plant parts analyzed were averaged to generate one value per specimen that were then used to calculate the means and standard deviations for food resources used in the mixing models.

Plant Identifier	FG_1	Growth_Habit	GH_code	Family	Genus	Species#binomial	CommonName	C3_C4	Time	Year	Month	Grid	N	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		wt% C		wt% N	
														$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$
CT.W10.00.07	Forb	Forb/Herb	1	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	1	2012	6	CT	1	-29.0	-	5.6	-	38.6	-	3.4	-
CT.Y14.00.08	Forb	Forb/Herb	1	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	1	2012	6	CT	2	-28.8	1.2	3.4	0.1	38.8	0.6	2.2	0.5
CT.Y15.00.10	Forb	Forb/Herb	1	Asteraceae	Solidago	Solidago missouriensis	Missouri goldenrod	C3	1	2012	6	CT	2	-26.8	0.2	6.0	1.6	34.5	2.7	3.5	0.2
CT.W16.00.13	Shrub	Forb/Herb	1	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	1	2012	6	CT	2	-14.0	0.3	6.8	0.5	37.0	2.8	3.9	0.4
CT.Y11.00.03	Grass	Graminoid	2	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	1	2012	6	CT	2	-27.7	0.3	3.1	1.3	37.2	2.5	1.6	1.1
CT.Z13.00.07	Grass	Graminoid	3	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C4	1	2012	6	CT	1	-14.4	-	2.9	-	40.7	-	1.6	-
CT.W11.00.08	Grass	Graminoid	2	Poaceae				C3	1	2012	6	CT	1	-22.6	-	3.9	-	37.8	-	1.3	-
CT.Z14.02.04	Grass	Graminoid	3	Poaceae				C4	1	2012	6	CT	1	-14.8	-	2.9	-	40.2	-	1.5	-
CT.X17.00.04	Forb	Forb/Herb	1	Polygonaceae	Eriogonum	Eriogonum annuum	Annual Eriogonum	C4	1	2012	6	CT	1	-13.8	-	9.0	-	39.6	-	2.2	-
CT.Y11.00.05	Tree	Tree	1	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	1	2012	6	CT	1	-28.3	-	2.5	-	43.5	-	2.0	-
CT.Y19.00.15	Forb	Forb/Herb	1	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	1	2012	6	CT	3	-28.7	0.3	4.4	0.8	44.1	3.0	1.9	0.8
CT.W13.01.04								C3	1	2012	6	CT	1	-27.2	-	3.1	-	38.7	-	2.0	-
CT.W13.01.24	Forb	Forb/Herb	1					C3	1	2012	6	CT	2	-27.5	0.3	5.3	0.3	36.1	3.1	3.1	0.4
CT.W13.02.04	Forb	Forb/Herb	1					C3	1	2012	6	CT	1	-25.4	-	2.2	-	39.7	-	2.5	-
CT.Y15.00.09	Forb	Forb/Herb	1					C3	1	2012	6	CT	1	-27.8	-	6.7	-	41.3	-	5.9	N
CT.Z10.00.02								C4	1	2012	6	CT	1	-14.9	-	2.1	-	39.4	-	1.1	-
CT.Z13.02.20	Forb	Forb/Herb	1					C3	1	2012	6	CT	2	-26.4	0.4	4.0	0.2	36.1	2.0	3.5	0.7
CT.Z13.02.25	Forb	Forb/Herb	1					C3	1	2012	6	CT	1	-28.9	-	4.5	-	37.3	-	4.6	-
2013.6.CT.A.2	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	2	2013	6	CT	1	-26.7	-	2.4	-	44.1	-	2.0	-
2013.6.CT.A.3	Shrub	Forb/Herb	1	Asteraceae	Cirsium	Cirsium altissimum	Tall thistle	C3	2	2013	6	CT	1	-27.9	-	4.5	-	45.0	-	3.4	-
2013.6.CT.A.6	Forb	Forb/Herb	1	Asteraceae	Psilostrophe	Psilostrophe villosa	Paper flower	C3	2	2013	6	CT	1	-29.2	-	1.3	-	39.2	-	3.3	-
2013.6.CT.AH.10	Sedge/Rush	Graminoid	3	Cyperaceae	Bulbostylis	Bulbostylis capillaris	Hair sedge	C4	2	2013	6	CT	1	-14.7	-	4.7	-	33.7	-	3.7	-
2013.6.CT.AH.4	Sedge/Rush	Graminoid	3	Cyperaceae	Bulbostylis	Bulbostylis capillaris	Hair sedge	C4	2	2013	6	CT	1	-13.7	-	1.0	-	41.5	-	2.7	-
2013.6.CT.A.5	Sedge/Rush	Graminoid	3	Cyperaceae	Lipcarpha	Lipocarpha micrantha	Small flower dwarf bulrush	C4	2	2013	6	CT	1	-13.6	-	0.5	-	41.8	-	3.3	-
2013.6.CT.A.9	Grass	Graminoid	2	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	2	2013	6	CT	2	-29.7	0.4	2.6	0.2	36.2	7.6	2.0	0.4
2013.6.CT.A.7	Grass	Graminoid	3	Poaceae				C4	2	2013	6	CT	1	-13.7	-	-0.5	-	42.6	-	3.4	-
2013.6.CT.P.8	Tree	Tree	1	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	2	2013	6	CT	1	-28.8	-	3.3	-	46.4	-	3.0	-
2013.6.CT.A.1	Forb	Forb/Herb	1	Solanaceae	Chamaesaracha	Chamaesaracha coniodes	Ground saracha	C3	2	2013	6	CT	1	-29.1	-	6.4	-	44.2	-	3.2	-
2013.10.ND.CT.10	Forb	Forb/Herb	1	Apocynaceae	Asclepias	Asclepias sp.	Milkweed	C3	3	2013	10	CT	1	-29.3	-	5.1	-	38.1	-	2.2	-
2013.10.ND.CT.1	Forb	Forb/Herb	1	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	3	2013	10	CT	1	-27.6	-	5.5	-	47.2	-	2.2	-
2013.10.AH.CT.6	Forb	Forb/Herb	1	Asteraceae	Heterotheca	Heterotheca subaxillaris	Camphor weed	C3	3	2013	10	CT	2	-29.5	2.5	2.9	0.8	43.4	1.6	2.0	0.8
2013.10.ND.CT.7	Forb	Forb/Herb	1	Asteraceae	Psilostrophe	Psilostrophe villosa	Paper flower	C3	3	2013	10	CT	1	-30.9	-	3.0	-	39.9	-	2.6	-
2013.10.ND.CT.6	Cactus	Shrub	4	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	CAM	3	2013	10	CT	2	-12.9	0.2	5.3	0.1	43.6	14.9	2.4	1.1
2013.10.AH.CT.9	Shrub	Forb/Herb	1	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	3	2013	10	CT	1	-13.9	-	4.7	-	39.0	-	3.3	-
2013.10.AH.CT.18	Sedge/Rush	Graminoid	3	Cyperaceae	Lipcarpha	Lipocarpha micrantha	Small flower dwarf bulrush	C4	3	2013	10	CT	1	-14.2	-	0.2	-	42.2	-	0.7	-
2013.10.AH.CT.19	Sedge/Rush	Forb/Herb	1	Equisetaceae	Equisetum	Equisetum hyemale	Horsetail	C3	3	2013	10	CT	1	-27.6	-	10.9	-	34.6	-	1.8	-
2013.10.ND.CT.2	Forb	Forb/Herb	1	Loasaceae	Mentzelia	Mentzelia nuda	Sand lily	C3	3	2013	10	CT	1	-28.5	-	8.3	-	46.1	-	2.6	-
2013.10.ND.CT.4	Grass	Graminoid	3	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	3	2013	10	CT	1	-14.2	-	1.7	-	41.6	-	1.9	-
2013.10.AH.CT.10	Grass	Graminoid	3	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	3	2013	10	CT	2	-14.3	0.2	1.7	1.1	41.9	2.8	2.6	1.1
2013.10.AH.CT.13	Grass	Graminoid	3	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	3	2013	10	CT	2	-13.3	0.7	4.6	1.4	42.2	0.3	1.7	0.4
2013.10.AH.CT.14	Grass	Graminoid	3	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	3	2013	10	CT	2	-13.1	0.4	0.5	1.0	42.9	0.4	1.1	0.8
2013.10.AH.CT.2	Grass	Graminoid	3	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	3	2013	10	CT	1	-14.3	-	3.2	-	41.3	-	1.7	-
2013.10.ND.CT.13	Grass	Graminoid	3	Poaceae	Setaria	Setaria pumila	Yellow foxtail	C4	3	2013	10	CT	2	-13.0	0.1	0.4	0.0	39.7	4.0	1.1	0.2

Appendix IV continued...

Plant Identifier	FG_1	Growth_Habit	GH_code	Family	Genus	Species#binomial	CommonName	C3	C4	Time	Year	Month	Grid	N	d	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		wt% C		wt% N	
																$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$
2013.10.AH.CT.11	Tree	Tree	1	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	3	2013	10	CT	2			-28.9	0.9	3.2	1.1	48.4	5.2	1.4	0.5
2013.10.AH.CT.8	Forb	Forb/Herb	1	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	3	2013	10	CT	2			-27.2	1.2	3.8	1.0	47.7	5.9	2.8	0.4
2014.5.KFD.CT.15	Shrub	Shrub	1	Agavaceae	Yucca	Yucca glauca	Yucca	C3	4	2014	6	CT	1			-22.6	-	1.4	-	42.3	-	3.4	-
2014.5.AH.CT.13	Forb	Forb/Herb	1	Apocynaceae	Asclepias	Asclepias purpurascens	Purple milkweed	C3	4	2014	6	CT	1			-27.2	-	4.9	-	42.3	-	5.6	-
2014.5.AH.CT.1	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	4	2014	6	CT	1			-27.5	-	3.4	-	49.0	-	2.4	-
2014.5.KFD.CT.6	Forb	Forb/Herb	1	Asteraceae	Heterotheca	Heterotheca canescens	Hairy golden aster	C3	4	2014	6	CT	1			-27.2	-	5.0	-	45.0	-	2.5	-
2014.5.AH.CT.3	Forb	Forb/Herb	1	Asteraceae	Psilostrophe	Psilostrophe villosa	Paper flower	C3	4	2014	6	CT	1			-26.4	-	4.3	-	41.7	-	2.7	-
2014.5.AH.CT.7	Cactus	Shrub	4	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	CAM	4	2014	6	CT	1			-13.1	-	7.2	-	39.7	-	2.0	-
2014.5.KFD.CT.10	Shrub	Forb/Herb	1	Chenopodiaceae	Salsola	Salsola tragus	Russian thistle	C4	4	2014	6	CT	1			-14.0	-	6.4	-	35.6	-	3.7	-
2014.5.AH.CT.10	Sedge/Rush	Graminoid	2	Cyperaceae	Lipcarpha	Lipcarpha micrantha	Small flower dwarf bulrush		4	2014	6	CT	1			-19.9	-	2.6	-	42.7	-	2.2	-
2014.5.AH.CT.4	Legume	Forb/Herb	1	Fabaceae	Atragalus	Astragalus crassicus	Ground-plum milk vetch	C3	4	2014	6	CT	2			-26.7	1.6	4.2	2.1	44.4	3.0	3.4	0.9
2014.5.KFD.CT.14	Grass	Graminoid	3	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	4	2014	6	CT	1			-15.0	-	2.2	-	39.7	-	0.8	-
2014.5.AH.CT.9	Grass	Graminoid	2	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	4	2014	6	CT	1			-23.6	-	3.9	-	44.4	-	2.7	-
2014.5.KFD.CT.4	Grass	Graminoid	2	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	4	2014	6	CT	2			-26.7	3.1	4.0	0.8	42.9	0.8	2.5	0.4
2014.5.KFD.CT.7	Grass	Graminoid	2	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	4	2014	6	CT	1			-25.5	-	3.2	-	43.8	-	1.9	-
2014.5.KFD.CT.9	Grass	Graminoid	3	Poaceae	Panicum	Panicum virgatum	Switchgrass	C4	4	2014	6	CT	2			-14.2	1.6	6.3	0.8	43.4	2.1	2.4	0.0
2014.5.AH.CT.12	Tree	Tree	1	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	4	2014	6	CT	1			-28.1	0.7	2.3	0.5	47.3	1.9	3.6	1.6
2014.5.KFD.CT.1	Tree	Tree	1	Salicaceae	Populus	Populus deltoides	Cottonwood	C3	4	2014	6	CT	1			-26.7	-	5.5	-	47.1	-	2.1	-
2014.5.AH.CT.5	Forb	Forb/Herb	1	Solanaceae	Chamaesaracha	Chamaesaracha coniodes	Ground saracha	C3	4	2014	6	CT	1			-25.8	-	4.6	-	40.6	-	4.7	-
2014.5.AH.CT.11	Sedge/Rush	Graminoid	2					C3	4	2014	6	CT	1			-24.2	-	6.2	-	34.5	-	3.9	-
2014.5.AH.CT.15								C3	4	2014	6	CT	2			-27.4	0.1	3.8	0.1	40.0	0.1	2.9	0.0
2014.5.AH.CT.8								C4	4	2014	6	CT	1			-14.2	-	8.7	-	35.4	-	3.3	-
2014.5.KFD.CT.3	Forb	Forb/Herb	1					C3	4	2014	6	CT	1			-25.3	-	6.5	-	34.4	-	4.2	-
2013.6.SB.A.5	Forb	Forb/Herb	1	Asteraceae	Erigeron	Erigeron strigosus	Daisy fleabane	C3	2	2013	6	SB	1			-28.8	-	-1.1	-	42.9	-	2.5	-
2013.6.SB.A.3	Sedge/Rush	Graminoid	2	Cyperaceae	Carex	Carex gravida	Heavy sedge	C3	2	2013	6	SB	1			-27.8	-	-0.1	-	40.1	-	3.9	-
2013.6.SB.A.4	Legume	Forb/Herb	1	Fabaceae	Dalea	Dalea leporina	Foxtail Dalea	C3	2	2013	6	SB	1			-29.4	-	-4.0	-	44.4	-	4.6	-
2013.6.SB.A.6	Forb	Forb/Herb	1	Loasaceae	Mentzelia	Mentzelia nuda	Sand lily	C3	2	2013	6	SB	1			-27.5	-	0.3	-	39.5	-	3.5	-
2013.6.SB.P.7	Grass	Graminoid	2	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C3	2	2013	6	SB	2			-28.6	0.1	0.1	0.4	44.5	0.0	2.5	0.9
2013.10.ND.SB.15	Forb	Forb/Herb	1	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	3	2013	10	SB	2			-27.1	1.6	3.2	0.3	43.6	1.6	2.9	0.7
2013.10.ND.SB.5	Forb	Forb/Herb	1	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	3	2013	10	SB	2			-28.0	0.1	4.7	0.1	43.9	1.7	2.5	0.8
2013.10.ND.SB.1	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	3	2013	10	SB	1			-26.9	-	0.8	-	47.6	-	1.5	-
2013.10.AH.SB.6	Forb	Forb/Herb	1	Asteraceae	Heterotheca	Heterotheca subaxillaris	Camphor weed	C3	3	2013	10	SB	1			-25.9	-	2.2	-	43.5	-	2.3	-
2013.10.ND.SB.16	Forb	Forb/Herb	1	Asteraceae	Hymenoxys	Hymenoxys odorata	Bitterweed	C3	3	2013	10	SB	1			-28.6	-	1.7	-	43.4	-	2.1	-
2013.10.ND.SB.13	Cactus	Shrub	4	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	CAM	3	2013	10	SB	1			-12.1	-	0.1	-	49.8	-	1.0	-
2013.10.AH.SB.14	Forb	Forb/Herb	1	Capparaceae	Cleome	Cleome serrulata	Rocky Mountain bee plant	C3	3	2013	10	SB	1			-26.2	-	2.3	-	44.6	-	3.9	-
2013.10.AH.SB.13b	Shrub	Forb/Herb	1	Pedaliaceae	Proboscidea	Proboscidea louisianica	Devil's claw	C3	3	2013	10	SB	1			-23.0	-	0.2	-	42.9	-	3.3	-
2013.10.ND.SB.4	Grass	Graminoid	3	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	3	2013	10	SB	1			-14.3	-	-0.5	-	42.9	-	1.9	-
2013.10.AH.SB.8	Grass	Graminoid	3	Poaceae	Chloris	Chloris verticillata	Windmill grass	C4	3	2013	10	SB	2			-13.6	0.6	1.5	3.3	43.3	0.8	1.2	0.2
2013.10.AH.SB.4	Grass	Graminoid	3	Poaceae	Eragrostis	Eragrostis cilianensis	Stink grass	C4	3	2013	10	SB	1			-13.2	-	2.5	-	38.4	-	1.5	-



Appendix IV continued...

Plant Identifier	FG_1	Growth_Habit	GH_code	Family	Genus	Species#binomial	CommonName	C3	C4	Time	Year	Month	Grid	N	d	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		wt% C		wt% N	
																$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$
2013.10.AH.SB.11	Grass	Graminoid	3	Poaceae	Schizachyrium	Schizachyrium scoparium	Little bluestem	C4	3	2013	10	SB	2			-14.2	0.1	1.3	1.1	41.5	0.4	1.0	0.0
2013.10.AH.SB.15	Forb	Forb/Herb	1	Polygonaceae	Eriogonum	Eriogonum annuum	Annual Eriogonum	C3	3	2013	10	SB	2			-29.8	1.5	1.6	0.3	42.4	4.0	2.2	0.2
2013.10.ND.SB.8	Shrub	Shrub	1	Rosaceae	Prunus	Prunus americana	Wild plum	C3	3	2013	10	SB	1			-28.0	-	-0.6	-	49.1	-	1.9	-
2014.5.KCP.SB.10	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	4	2014	6	SB	1			-25.5	-	-0.1	-	47.8	-	2.4	-
2014.5.AH.SB.3	Forb	Forb/Herb	1	Asteraceae	Gaillardia	Gaillardia pulchella	Indian blanket flower	C3	4	2014	6	SB	1			-26.0	-	-0.3	-	38.1	-	2.0	-
2014.5.KCP.SB.4	Forb	Forb/Herb	1	Asteraceae	Gaillardia	Gaillardia pulchella	Indian blanket flower	C3	4	2014	6	SB	2			-28.9	1.4	2.1	0.4	37.9	1.6	1.9	0.3
2014.5.KCP.SB.13	Forb	Forb/Herb	1	Asteraceae	Helianthus	Helianthus annuus	Common sunflower	C3	4	2014	6	SB	2			-27.4	1.0	1.2	0.1	40.4	5.4	3.2	1.0
2014.5.AH.SB.7	Forb	Forb/Herb	1	Asteraceae				C3	4	2014	6	SB	1			-28.3	-	-0.6	-	40.1	-	3.0	-
2014.5.KCP.SB.1	Forb	Forb/Herb	1	Brassicaceae	Lesquerella	Lesquerella gordonii	Mustard	C3	4	2014	6	SB	4			-26.9	2.3	-0.3	1.6	43.5	1.4	3.4	0.9
2014.5.AH.SB.4	Legume	Forb/Herb	1	Fabaceae				C3	4	2014	6	SB	1			-27.2	-	-2.3	-	45.2	-	4.5	-
2014.5.KCP.SB.3	Forb	Forb/Herb	1	Malvaceae	Callirhoe	Callirhoe involucrata	Purple mallow	C3	4	2014	6	SB	1			-28.0	-	0.6	-	39.2	-	3.0	-
2014.5.KCP.SB.5	Grass	Graminoid	3	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	4	2014	6	SB	2			-14.9	0.3	-2.8	0.4	39.4	4.2	1.7	0.9
2014.5.KCP.SB.12	Grass	Graminoid	2	Poaceae	Bromus			C3	4	2014	6	SB	1			-24.1	-	1.4	-	41.1	-	1.9	-
2014.5.AH.SB.10	Grass	Graminoid	2	Poaceae	Hordeum	Hordeum jubatum	Foxtail barley	C3	4	2014	6	SB	1			-25.0	-	-1.1	-	44.1	-	2.1	-
2014.5.KCP.SB.7	Grass	Graminoid	2	Poaceae	Hordeum	Hordeum pusillum	Little barley	C3	4	2014	6	SB	1			-24.3	-	-0.3	-	42.2	-	1.7	-
2014.5.AH.SB.11	Forb	Forb/Herb	1	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	4	2014	6	SB	1			-27.9	-	2.2	-	43.4	-	3.6	-
2014.5.AH.SB.2								C3	4	2014	6	SB	1			-27.3	-	-0.2	-	39.9	-	4.3	-
2014.5.AH.SB.9								C3	4	2014	6	SB	1			-24.3	-	-1.2	-	45.2	-	2.1	-
2014.5.KCP.SB.8								C3	4	2014	6	SB	1			-27.5	-	1.2	-	39.1	-	3.6	-
2014.5.KCP.SB.9								C3	4	2014	6	SB	1			-25.2	-	2.7	-	39.4	-	4.1	-
SC.A10.00.05	Shrub	Shrub	1	Agavaceae	Yucca	Yucca glauca	Yucca	C3	1	2012	6	SC	1			-23.0	-	0.6	-	43.1	-	0.8	-
SC.E7.01.06	Forb	Forb/Herb	1	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	1	2012	6	SC	1			-27.1	-	5.4	-	40.4	-	3.0	-
SC.F7.00.12	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	1	2012	6	SC	1			-25.7	-	3.7	-	50.4	-	1.1	-
SC.J7.02.02	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	1	2012	6	SC	2			-24.0	0.1	3.5	0.0	45.6	1.6	1.3	0.2
SC.C10.00.06	Forb	Forb/Herb	1	Asteraceae	Haplopappus	Haplopappus spinulosus	Cutleaf ironplant	C3	1	2012	6	SC	2			-25.9	0.8	4.7	0.8	41.9	3.0	1.8	0.3
SC.A1.02.18	Sedge/Rush	Graminoid	3	Cyperaceae	Bulbostylis	Bulbostylis capillaris	Hair sedge	C4	1	2012	6	SC	1			-16.2	-	-1.5	-	39.8	-	1.0	-
SC.D9.00.07	Forb	Forb/Herb	1	Loasaceae	Mentzelia	Mentzelia nuda	Sand lily	C3	1	2012	6	SC	1			-25.2	-	3.8	-	36.7	-	1.8	-
SC.E4.00.09	Grass	Graminoid	2	Poaceae	Elymus	Elymus canadensis	Canada wild rye	C3	1	2012	6	SC	2			-28.8	1.1	0.4	0.1	39.0	2.5	1.8	1.0
SC.E4.00.10	Grass	Graminoid	2	Poaceae	Hordeum	Hordeum jubatum	Foxtail barley	C3	1	2012	6	SC	2			-28.3	0.9	4.4	2.8	38.7	3.3	1.0	0.3
SC.E7.01.04	Grass	Graminoid	3	Poaceae	Pascopyrum	Pascopyrum smithii	Western wheatgrass	C4	1	2012	6	SC	1			-13.8	-	-1.0	-	39.9	-	2.6	-
SC.J1.01.12	Grass	Graminoid	3	Poaceae				C4	1	2012	6	SC	1			-15.7	-	-1.8	-	39.8	-	1.4	-
SC.J10.2.4	Forb	Forb/Herb	1	Polygonaceae	Eriogonum	Eriogonum annuum	Annual Eriogonum	C3	1	2012	6	SC	2			-26.1	1.2	3.2	0.2	45.5	0.3	2.0	0.1
SC.J10.00.13	Forb	Forb/Herb	1	Solanaceae	Quincula	Quincula lobata	Chinese lantern	C3	1	2012	6	SC	2			-25.6	2.4	2.7	2.7	39.9	0.1	2.5	1.0
SC.F9.00.08	Forb	Forb/Herb	1	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	1	2012	6	SC	2			-26.8	0.1	6.5	0.6	44.2	0.7	3.2	0.2
SC.J10.1.2	Forb	Forb/Herb	1	Solanaceae	Solanum	Solanum elaeagnifolium	Silver-leaf nightshade	C3	1	2012	6	SC	2			-26.6	1.0	1.3	0.1	43.9	1.3	1.9	0.6
SC.E1.00.12	Tree	Tree	1	Tamaricaceae	Tamarix	Tamarix chinensis	Tamarisk	C3	1	2012	6	SC	2			-28.5	0.8	-0.7	0.4	43.7	6.6	1.0	0.2
SC.C8.00.02	Cactus	Shrub	4					CAM	1	2012	6	SC	2			-13.5	0.0	2.1	0.0	36.4	0.0	0.6	0.0
SC.E10.01.04								C4	1	2012	6	SC	1			-15.2	-	2.4	-	37.8	-	1.6	-

Appendix IV continued...

Plant Identifier	FG 1	Growth Habit	GH code	Family	Genus	Species#binomial	CommonName	C3	C4	Time	Year	Month	Grid	N	d	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		wt% C		wt% N	
																$\bar{x}$	$\sigma$	d	$\bar{x}$	$\sigma$	d	$\bar{x}$	$\sigma$
SC.E10.01.04								C4	1	2012	6	SC	1			-15.2	-	2.4	-	37.8	-	1.6	-
SC.E8.00.09	Forb	Forb/Herb	1					C3	1	2012	6	SC	2			-25.9	0.6	5.5	0.3	40.0	1.3	4.6	0.1
SC.E9.00.06	Forb	Forb/Herb	1					C3	1	2012	6	SC	1			-26.0	-	1.8	-	42.8	-	1.8	-
2013.6.SC.A.2	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	2	2013	6	SC	1			-27.1	-	3.9	-	48.6	-	1.7	-
2013.6.SC.A.7	Forb	Forb/Herb	1	Asteraceae	Erigeron	Erigeron strigosus	Daisy fleabane	C3	2	2013	6	SC	1			-28.2	-	2.2	-	43.4	-	2.8	-
2013.6.SC.A.1	Forb	Forb/Herb	1	Asteraceae	Gaillardia	Gaillardia pulchella	Indian blanket flower	C3	2	2013	6	SC	1			-27.6	-	2.2	-	41.2	-	2.9	-
2013.6.SC.A.5	Forb	Forb/Herb	1	Convolvulaceae	Evolvulus	Evolvulus nuttallianus	Shaggy dwarf morning glory	C3	2	2013	6	SC	1			-27.0	-	0.4	-	43.1	-	2.9	-
2013.6.SC.A.4	Sedge/Rush	Graminoid	3	Cyperaceae	Lipcarpha	Lipocarpha micrantha	Small flower dwarf bulrush	C4	2	2013	6	SC	2			-14.2	0.0	-0.7	0.0	40.8	0.0	2.8	0.0
2013.6.SC.A.10	Grass	Graminoid	3	Poaceae	Chloris	Chloris verticillata	Windmill grass	C4	2	2013	6	SC	1			-13.8	-	0.5	-	42.3	-	3.4	-
2013.6.SC.A.3	Forb	Forb/Herb	1	Solanaceae	Chamaesaracha	Chamaesaracha coniodes	Ground saracha	C3	2	2013	6	SC	1			-27.1	-	1.9	-	43.3	-	4.2	-
2013.10.ND.SC.1	Forb	Forb/Herb	1	Asteraceae	Ambrosia	Ambrosia artemisiifolia	Pale ragweed	C3	3	2013	10	SC	2			-27.2	0.4	5.1	0.4	40.0	2.4	2.5	0.6
2013.10.ND.SC.3	Shrub	Forb/Herb	1	Asteraceae	Artemisia	Artemisia filifolia	Sagebrush	C3	3	2013	10	SC	1			-27.5	-	2.5	-	49.8	-	1.3	-
2013.10.ND.SC.10	Cactus	Shrub	1	Cactaceae	Opuntia	Opuntia macrorhiza	Plains prickly pear	C4	3	2013	10	SC	1			-12.6	-	2.5	-	51.0	-	1.2	-
2013.10.AH.SC.5	Forb	Forb/Herb	1	Geraniaceae	Geranium	Geranium pusillum	Small Crane's Bill	C3	3	2013	10	SC	1			-27.6	-	1.7	-	37.8	-	3.7	-
2013.10.AH.SC.2	Forb	Forb/Herb	1	Loasaceae	Mentzelia	Mentzelia nuda	Sand lily	C3	3	2013	10	SC	2			-27.0	0.4	3.9	0.2	40.3	5.2	1.9	0.6
2013.10.ND.SC.5	Grass	Graminoid	3	Poaceae	Bouteloua	Bouteloua gracilis	Blue grama	C4	3	2013	10	SC	1			-13.4	-	-0.3	-	43.6	-	0.7	-
2013.10.AH.SC.8	Grass	Graminoid	3	Poaceae	Chloris	Chloris verticillata	Windmill grass	C4	3	2013	10	SC	2			-14.4	0.1	3.6	1.6	41.3	0.5	2.1	0.0
2013.10.AH.SC.10	Grass	Graminoid	3	Poaceae	Panicum	Panicum obtusum	Vine-Mesquite	C4	3	2013	10	SC	2			-13.8	0.4	1.4	0.4	42.9	1.6	2.0	0.4
2013.10.ND.SC.4	Forb	Forb/Herb	1	Solanaceae	Datura	Datura stramonium	Jimsonweed	C3	3	2013	10	SC	1			-29.6	-	3.1	-	43.6	-	1.5	-

Appendix V -  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , Wt% C, and Wt% N values of invertebrate specimens collected in southwestern Kansas.

All Grids and Seasons	Diet Category	N	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		wt% C		wt% N		
			$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	$\bar{x}$	$\sigma$	
<b>ORDER: ARANEAE</b>											
Family: Lycosidae											
	<i>Hogna carolinensis</i>	P	1	-21.3	-	9.3	-	47.2	-	14.6	-
<b>CLEOPTERA</b>											
Carabidae											
	<i>Pasimachus depressus</i>		1	-22.1	-	6.1	-	46.1	-	13.8	-
Scarabaeidae											
	<i>Canthon chalcites</i>	C	3	-15.4	0.9	7.3	4.1	50.3	2.3	13.6	0.6
	<i>Euphoria kernii</i>	N	1	-18.9	-	8.5	-	31.3	-	9.4	-
Tenebrionidae											
	<i>Eleodes acutus</i>	Ph (D)	2	-19.8	5.2	4.7	0.8	45.0	5.2	10.6	2.9
<b>HEMIPTERA</b>											
Cicadidae											
	<i>Tibicen superbus</i>	Ph	1	-26.5	-	7.8	-	44.2	-	12.1	-
<b>HYMENOPTERA</b>											
Formicidae											
			1	-22.5		3.3		47.9		12.6	
<b>LEPIDOPTERA</b>											
Pieridae											
	<i>Pontia protodice</i>	N	1	-27.7	-	10.2	-	50.5	-	14.8	-
<b>ONDONATA</b>											
	indet.	P	1	-21.1		6.2		53.5		10.4	
<b>ORTHOPTERA</b>											
Acrididae											
	<i>Acrolophus hirtipes</i>	Py (Fo)	1	-25.0	-	2.3	-	49.4	-	15.7	-
	<i>Ageneotettix deorum</i>	G	6	-20.9	3.0	6.2	1.8	45.7	8.4	14.1	2.6
	<i>Arphia simplex</i>	G	2	-19.5	6.4	1.9	0.6	44.0	6.9	13.5	3.9
	<i>Aulocara ellioti</i>	G	2	-16.0	0.4	5.6	3.4	47.6	2.3	15.1	1.0
	<i>Aulocara femoratum</i>	G	4	-15.5	2.1	3.4	2.1	45.7	4.4	14.5	2.2
	<i>Boopedon gracile</i>	G	1	-15.6	-	5.8	-	39.1	-	11.3	N
	<i>Encoptolophus costalis</i>	G	1	-14.4	-	1.3	-	48.7	-	15.9	-
	<i>Hippiscus ocelote</i>	G	3	-20.3	3.6	2.4	1.0	45.3	4.1	13.6	2.3
	<i>Melanoplus bowditchi</i>	Sa	4	-24.2	0.6	4.4	1.7	45.4	5.9	13.6	2.6
	<i>Melanoplus gladstoni</i>	Py	1	-22.7	-	5.0	-	48.3	-	15.6	-
	<i>Melanoplus lakinus</i>	Ch	5	-25.2	1.8	6.9	3.2	44.8	3.9	13.3	1.8
	<i>Melanoplus sanguinipes</i>	Py	2	-22.8	1.6	6.3	4.1	44.8	6.6	13.2	2.9
	<i>Merminia bivittata</i>	G	5	-16.9	3.4	3.4	2.2	43.7	2.6	13.5	1.5
	<i>Spharagemon collare</i>	Py	4	-21.0	2.1	3.4	1.3	42.3	6.7	13.1	2.8
	<i>Stenopelmatus fuscus</i>	Py (Tu)	2	-22.8	1.8	4.1	1.4	44.5	6.4	13.1	2.8
	indet.		3	-20.6	5.9	5.3	1.7	44.3	2.6	13.0	2.0
Gryllidae											
	<i>Gryllus pennsylvanicus</i>	Py	2	-21.7	0.4	5.1	0.8	48.0	2.3	15.3	0.8
Romaleidae											
	<i>Brachystola magna</i>	Py	6	-23.9	0.6	3.5	0.9	42.8	5.5	12.6	2.3
Tettigoniidae											
	<i>Anabrus simplex</i>	Py	1	-23.1	-	3.7	-	43.2	-	11.7	-

Appendix VI – Results of SIAR mixing models for orthopterans in southwest Kansas. Upper and lower bounds of credible intervals depicted in Figure 4.

SIAR Mixing Results

<b>Orthoptera</b>		<b>SC + SB</b>				<b>CT</b>			
<b>Diet Source</b>	<b>Intervals</b>	<b>Polyphagous</b>		<b>Graminivorous</b>		<b>Polyphagous</b>		<b>Graminivorous</b>	
		<b>lower</b>	<b>upper</b>	<b>lower</b>	<b>upper</b>	<b>lower</b>	<b>upper</b>	<b>lower</b>	<b>upper</b>
<b>FTS</b>	95%	0.13	0.47	0.035	0.44	0.16	0.74	0.007	0.44
	75%	0.22	0.4	0.13	0.37	0.29	0.61	0.085	0.38
	50%	0.26	0.37	0.19	0.33	0.36	0.54	0.16	0.33
<b>C<sub>3</sub> gram</b>	95%	0.16	0.52	0.091	0.52	0.07	0.71	0.03	0.54
	75%	0.24	0.43	0.19	0.43	0.22	0.58	0.14	0.46
	50%	0.28	0.39	0.25	0.38	0.31	0.51	0.21	0.39
<b>C<sub>4</sub> gram</b>	95%	0.0094	0.37	0.014	0.44	0	0.19	0.13	0.52
	75%	0.076	0.32	0.11	0.38	0	0.1	0.24	0.46
	50%	0.14	0.29	0.18	0.34	0.004	0.062	0.28	0.41
<b>CAM</b>	95%	0	0.32	0.000	0.38	0	0.2	0	0.29
	75%	0.015	0.24	0.05	0.32	0.000	0.11	0.009	0.2
	50%	0.05	0.19	0.11	0.28	0.005	0.071	0.03	0.15

Appendix VII – Results of SIAR mixing models for *Peromyscus maniculatus* in the cottonwood riparian macrohabitat found in southwest Kansas. Upper and lower bounds of credible intervals depicted in Figures 6 and 7.

*P. maniculatus* + Cottonwoods macrohabitat

Diet Source	Interval	2012 Su		2013 Su		2013 F		2014 Sp	
		lower	upper	lower	upper	lower	upper	lower	upper
FTS	95%	0.03	0.34	0	0.14	0	0.22	0	0.22
	75%	0.11	0.29	0	0.072	0.006	0.16	0	0.13
	50%	0.15	0.25	0.002	0.042	0.014	0.11	0.003	0.073
C <sub>3</sub> gram	95%	0.012	0.33	0	0.15	0	0.23	0	0.24
	75%	0.09	0.28	0	0.077	0.005	0.16	0	0.14
	50%	0.14	0.25	0.002	0.045	0.012	0.11	0.003	0.082
C <sub>4</sub> gram	95%	0	0.21	0	0.32	0.000	0.26	0.015	0.47
	75%	0.005	0.15	0.009	0.23	0.027	0.21	0.11	0.37
	50%	0.011	0.1	0.017	0.16	0.07	0.18	0.16	0.31
CAM	95%	0	0.2	0.140	0.58	0.042	0.33	0.022	0.46
	75%	0.003	0.13	0.22	0.5	0.11	0.28	0.12	0.37
	50%	0.008	0.087	0.26	0.44	0.14	0.24	0.17	0.31
Oi	95%	0.036	0.28	0.041	0.35	0.089	0.33	0	0.17
	75%	0.085	0.23	0.12	0.3	0.14	0.28	0	0.009
	50%	0.12	0.2	0.17	0.27	0.17	0.25	0.002	0.051
Gg	95%	0.005	0.26	0	0.18	0	0.23	0	0.36
	75%	0.044	0.21	0	0.084	0.007	0.16	0.028	0.27
	50%	0.074	0.18	0.002	0.046	0.022	0.11	0.098	0.25
Pg	95%	0.008	0.26	0	0.27	0.017	0.28	0	0.22
	75%	0.052	0.21	0.005	0.18	0.073	0.24	0	0.12
	50%	0.085	0.18	0.013	0.12	0.12	0.21	0.003	0.068

Appendix VIII – Results of SIAR mixing models for *Onychomys leucogaster* in the cottonwood riparian macrohabitat found in southwest Kansas. Upper and lower bounds of credible intervals depicted in Figures 6 and 7.

***O. leucogaster* + Sagebrush grassland macrohabitat**

Diet Source	Interval	2012 Su		2013 Su		2013 F		2014 Sp	
		lower	upper	lower	upper	lower	upper	lower	upper
<b>FTS</b>	95%	0.002	0.29	0.018	0.35	0	0.22	0	0.26
	75%	0.05	0.25	0.096	0.3	0.007	0.16	0.009	0.19
	50%	0.11	0.22	0.15	0.26	17	0.11	0.023	0.14
<b>C<sub>3</sub> gram</b>	95%	0.001	0.029	0.01	0.34	0	0.22	0	0.25
	75%	0.044	0.24	0.09	0.29	0.006	0.15	0.006	0.18
	50%	0.1	0.22	0.14	0.260	0.015	0.11	0.014	0.12
<b>C<sub>4</sub> gram</b>	95%	0	0.25	0	0.2	0.003	0.29	0	0.27
	75%	0.009	0.18	0.000	0.120	0.052	0.24	0.008	0.19
	50%	0.017	0.13	0.005	0.077	0.11	0.22	0.023	0.14
<b>CAM</b>	95%	0	0.25	0	0.180	0.014	0.3	0.001	0.27
	75%	0.007	0.18	0.001	0.11	0.084	0.26	0.039	0.23
	50%	0.021	0.13	0.006	0.071	0.13	0.23	0.091	0.21
<b>Oi</b>	95%	0.036	0.32	0.076	0.34	0.11	0.29	0.16	0.39
	75%	0.11	0.27	0.14	0.28	0.15	0.25	0.19	0.320
	50%	0.14	0.23	0.16	0.25	0.17	0.23	0.210	0.29
<b>Gg</b>	95%	0.000	0.25	0	0.19	0.0012	0.24	0	0.19
	75%	0.006	0.18	0	0.11	0.028	0.19	0.000	0.11
	50%	0.013	0.12	0.004	0.065	0.057	0.16	0.005	0.07
<b>Pg</b>	95%	0.001	0.29	0.0031	0.33	0.0036	0.29	0.00069	0.3
	75%	0.045	0.24	0.055	0.270	0.048	0.23	0.032	0.23
	50%	0.1	0.22	0.11	0.24	0.089	0.2	0.073	0.19

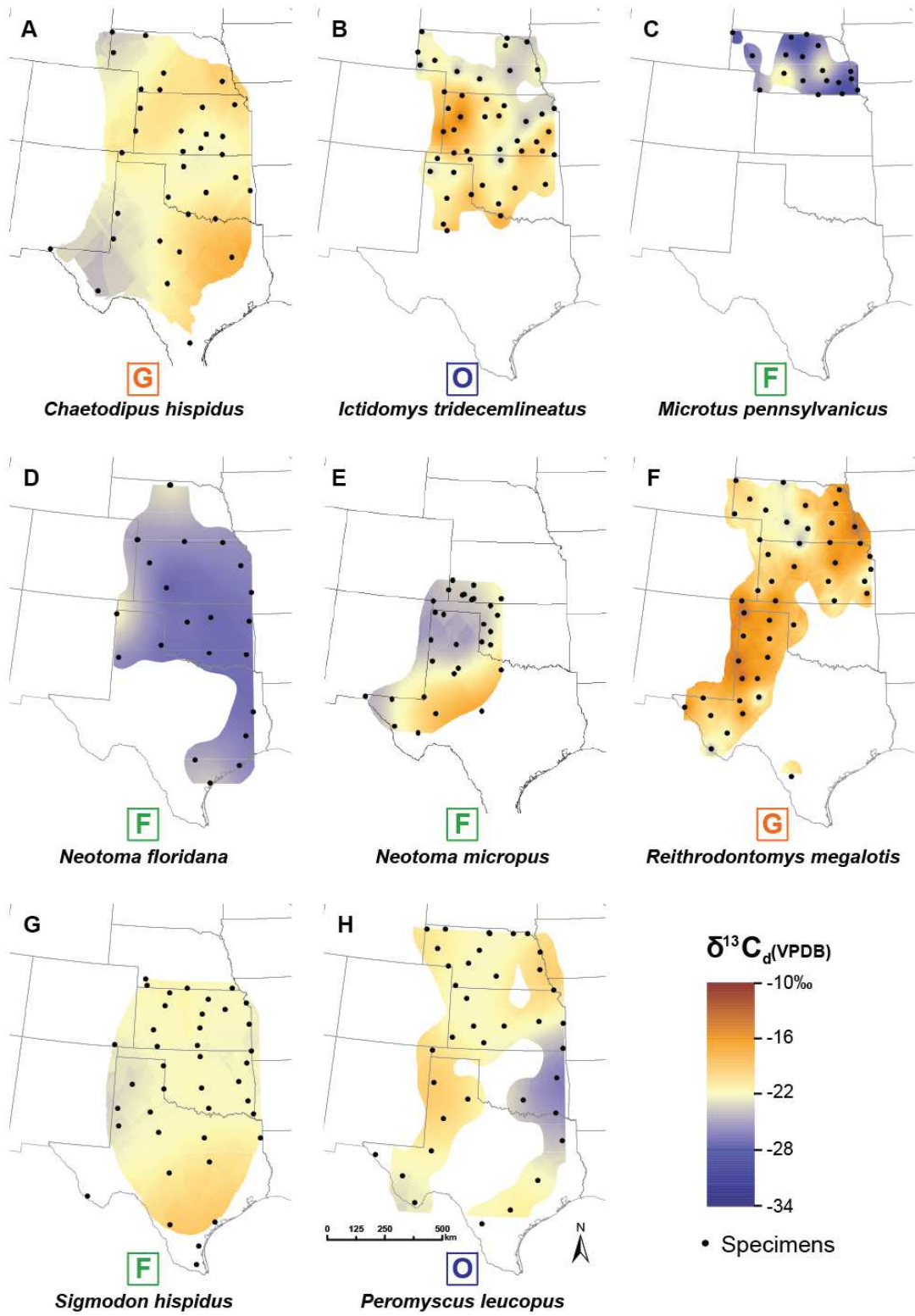
Appendix IX – Results of SIAR mixing models for *Dipodomys ordii* in the cottonwood riparian macrohabitat found in southwest Kansas. Upper and lower bounds of credible intervals depicted in Figures 6 and 7.

<i>D. ordii</i> + Sagebrush grassland macrohabitat									
Diet Source	Interval	2012 Su		2013 Su		2013 F		2014 Sp	
		lower	upper	lower	upper	lower	upper	lower	upper
FTS	95%	0	0.27	0	0.25	0	0.25	0	0.14
	75%	0.008	0.19	0.010	0.18	0.002	0.16	0.000	0.084
	50%	0.014	0.14	0.018	0.13	0.007	0.1	0.004	0.053
C <sub>3</sub> gram	95%	0	0.27	0	0.25	0	0.25	0	0.16
	75%	0.008	0.2	0.009	0.18	0.003	0.17	0.001	0.094
	50%	0.016	0.14	0.928	0.14	0.009	0.11	0.004	0.049
C <sub>4</sub> gram	95%	0	0.31	0.003	0.31	0.006	0.37	0.033	0.58
	75%	0.051	0.26	0.062	0.26	0.081	0.31	0.14	0.47
	50%	0.11	0.24	0.12	0.24	0.14	0.27	0.2	0.4
CAM	95%	0.001	0.32	0.006	0.31	0.011	0.37	0.11	0.69
	75%	0.051	0.26	0.068	0.26	0.093	0.31	0.23	0.58
	50%	0.120	0.24	0.12	0.23	0.15	0.27	0.29	0.5
Oi	95%	0	0.26	0	0.24	0	0.15	0	0.052
	75%	0.003	0.18	0.016	0.18	0	0.078	0.002	0.031
	50%	0.007	0.12	0.041	0.14	0.004	0.048	0.005	0.022
Gg	95%	0.001	0.31	0.005	0.32	0.012	0.38	0	0.23
	75%	0.049	0.25	0.074	0.27	0.095	0.31	0.005	0.12
	50%	0.11	0.23	0.130	0.24	0.15	0.27	0.017	0.083
Pg	95%	0.000	0.27	0	0.27	0	0.26	0	0.13
	75%	0.011	0.2	0.012	0.2	0.003	0.17	0.006	0.082
	50%	0.042	0.17	0.034	0.18	0.008	0.11	0.017	0.062

Appendix X – Summary table of inputs for stable isotope mixing models to estimate diet of rodent and orthopterans captured in Meade, Kansas.

Model	Taxa/Taxon	Macrohabitat	Season(s)	Dietary Sources
A	<i>P. maniculatus</i> , <i>O. leucogaster</i> , <i>D. ordii</i>	All	Combined	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM, Oi, Gh, Ph
B-1	<i>P. maniculatus</i>	CT	Combined	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM, Oi, Gh, Ph
B-2	<i>O. leucogaster</i>	SB	Combined	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM, Oi, Gh, Ph
B-3	<i>D. ordii</i>	SB	Combined	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM, Oi, Gh, Ph
C-1	<i>P. maniculatus</i>	CT	2012S, 2013S, 2013F, 2014 Sp	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM, Oi, Gh, Ph
C-2	<i>O. leucogaster</i>	SB	2012S, 2013S, 2013F, 2014 Sp	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM, Oi, Gh, Ph
C-3	<i>D. ordii</i>	SB	2012S, 2013S, 2013F, 2014 Sp	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM, Oi, Gh, Ph
D-1	Graminivorous and Polyphagous orthopterans	CT	Combined	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM
D-2	Graminivorous and Polyphagous orthopterans	SB	Combined	FTS, C <sub>3</sub> -gram, C <sub>4</sub> -gram, CAM





Appendix XI – Isoscapes of  $\delta^{13}\text{C}_d$  values of hair collected from rodents across the southern Great Plains. A) *C. hispidus*; B) *I. tridecemlineatus*; C) *M. pennsylvanicus*; D) *N. floridana*; E) *N. micropus*; F) *R. megalotis*; G) *S. hispidus*; and H) *P. maniculatus*.