

Spring 4-14-2018

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**Seasonal Shifts in C3 and C4 Resource Use by a Small  
Mammal Community Under Changing Precipitation Regimes**

**by**

**Alaina Dianne Pershall**

**Bachelor of Science, Anthropology/Biology,  
University of New Mexico, 2002**

**THESIS**

**Submitted in Partial Fulfillment of the  
Requirements for the Degree of  
Master of Science  
Biology**

**The University of New Mexico  
Albuquerque, New Mexico**

**May 2018**

## ACKNOWLEDGEMENTS

I would like to thank my thesis committee for their dedication and guidance during this project. I thank my co-authors and advisors, Dr. Blair Wolf and Dr. Seth Newsome, for the time they put into this project, the edits they provided, and the improvements they made to this project, the data analysis, and the manuscript. Without them this work would not have been possible. I would also like to thank my family for helping me take the time to complete this work and for their understanding while I spent numerous hours away from them.

This work would also not have been possible without the help of other student researchers and volunteers. I would like to thank Cindy Mathiasen for her faithful help with data collection and gentle handling of the biggest and meanest rats and squirrels, nearly every month for three years. I thank Robin Warne for his help with data collection and method development. I also thank REU students A. Washburne and V. Torres for their dependable data collection efforts; K. Wetherill, C. Hickman, and the Sevilleta LTER field crew and interns for vegetation data collection and training; S. Knapp and the Hantavirus Research Crew, and F. Gurule and R. Ricci, for blood collection training; V. Atudori and Z. Sharp for providing access and training on the UNM Earth and Planetary Sciences IRMS; and D. Lightfoot and S. Brantley from the UNM Museum of Southwestern Biology for training and assistance in arthropod collection and identification. I also thank S. L. Collins for insightful reviews of this manuscript; as well as other volunteers, including H. Lease, I. Murray, C. Gilman, T. Hyde, T. Orr, B. Zimmerman, D. Williams, K. Kouper, B. Barker, and K. Thibault.

Research support was provided by National Science Foundation grants to the Sevilleta LTER (DEB-0217774) and to B. O. Wolf (DEB-0213659 and IBN-0426764). Research support was also provided to A. D. Pershall by the Sevilleta LTER Summer Research Scholarship (DEB-0217774), UNM Biology Grove Research Scholarship, T and E Incorporated Grant for Conservation Biology Research, and UNM Graduate Resource Allocation Committee (GRAC).

**Seasonal Shifts in C<sub>3</sub> and C<sub>4</sub> Resource Use by a Small Mammal Community Under Changing Precipitation Regimes**

by

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**THESIS**

**Submitted in Partial Fulfillment of the Requirements for the Degree of  
M.S., Biology, University of New Mexico, 2018**

**ABSTRACT**

In light of climate change and projections of increasing temperatures and aridity in the North American southwest, it is essential to understand how consumer populations will respond to changes in the resource landscape. Rainfall varies in timing and intensity and therefore the timing, proportion, phenology, and abundance of C<sub>3</sub> and C<sub>4</sub> plant resources vary seasonally and annually. Here we examine rodent resource use in the Chihuahuan desert and focus on two distinct precipitation pulses in this system, where spring C<sub>3</sub> plants increase production in response to winter rains and C<sub>4</sub> plants respond to summer monsoons. We used the distinct carbon isotope ratios of the C<sub>3</sub> and C<sub>4</sub> plant photosynthetic types to quantify resource use and diet breadth by measuring  $\delta^{13}\text{C}$  in blood plasma and assessed relative trophic level by measuring  $\delta^{15}\text{N}$ . We compared resource use across three years with different precipitation regimes and C<sub>3</sub> and C<sub>4</sub> abundances. We observed a generally increasing use of C<sub>4</sub> derived carbon, as C<sub>4</sub> vegetation became more available and C<sub>3</sub> decreased. However, diets were generally

composed of a greater proportion of C<sub>3</sub> derived carbon. Heteromyid rodents exhibited a greater overall reliance on C<sub>3</sub> resources. When C<sub>3</sub> resources were not available, we observed a division of resources among heteromyids, and the cricetid rodents maintained generally greater than 50% C<sub>4</sub> use and higher peaks in C<sub>4</sub> use. We observed a community wide shift to C<sub>3</sub> resources when abundant, even in the presence of abundant C<sub>4</sub> resources. Diet breadth was most constrained and dietary overlap was greatest when C<sub>3</sub> plants were abundant and highly utilized. *Onychomys arenicola*, the most insectivorous species, showed the least variation in C<sub>3</sub>/C<sub>4</sub> usage, greater reliance on C<sub>4</sub> resources, and smallest diet breadth. In general, trophic level increases coincided with increased use of C<sub>4</sub>. Because of differences in physiology, C<sub>4</sub> plants may outcompete important C<sub>3</sub> plants under warmer drier conditions, changing the physical structure of the community and decreasing the nutritional quality and abundance of food resources. This could have a significant impact on consumer population size, species diversity, and competition in small mammals, which could have implications throughout the food chain.

## TABLE OF CONTENTS

<b>Acknowledgements .....</b>	<b>iii</b>
<b>Abstract.....</b>	<b>v</b>
<b>Introduction.....</b>	<b>1</b>
<b>Materials and Methods.....</b>	<b>6</b>
<i>Study Site.....</i>	<i>6</i>
<i>Weather and Aboveground Net Primary Production.....</i>	<i>6</i>
<i>Tissue Collection &amp; Sample Preparation for Stable Isotope Analysis. ....</i>	<i>6</i>
<i>Stable Isotope Analysis. ....</i>	<i>8</i>
<i>Estimation of C<sub>3</sub> and C<sub>4</sub> Carbon Incorporation into Rodent Blood Plasma. ....</i>	<i>8</i>
<i>Data Analysis.....</i>	<i>9</i>
<b>Results .....</b>	<b>11</b>
<i>Seasonal and Annual Shifts in Precipitation and Plant Productivity.....</i>	<i>11</i>
<i>Small Mammal Captures.....</i>	<i>12</i>
<i>Shifts in Resource Use Among Species, Seasons, and Years. ....</i>	<i>13</i>
Spring 2005- winter/spring 2005/2006. Normal precipitation followed by a failure of winter rains and C <sub>3</sub> resources.....	13
Spring 2006- summer 2006 record monsoon and increase in total ANPP. ....	14
2007 and greatest production of C <sub>3</sub> vegetation.....	15
<i>δ<sup>15</sup>N and Relative Trophic Level among Species. ....</i>	<i>17</i>
<b>Discussion.....</b>	<b>28</b>
<i>Seasonal Diet Changes in Rodents Associated with Changes in Resource Abundance.....</i>	<i>29</i>
<i>The Importance of C<sub>3</sub> Plants to Consumer Diets.....</i>	<i>31</i>
<i>C<sub>3</sub> Resource Pulses and Rodent Populations.....</i>	<i>32</i>
<i>Trophic Structure of the Rodent Community and Shifts Associated with Resource Scarcity. ....</i>	<i>33</i>
<i>What do Current Climate Projections and our Data Suggest for Desert Rodents? .....</i>	<i>34</i>
<i>Conclusions.....</i>	<i>36</i>
<b>Appendices.....</b>	<b>38</b>
<b>Appendix A. Whole plant δ<sup>15</sup>N and δ<sup>13</sup>C values.....</b>	<b>39</b>
<b>Appendix B. Supplemental Tables and Figures .....</b>	<b>41</b>
<b>References .....</b>	<b>46</b>



## TABLES

Table 1. Heteromyid Rodent Plasma $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ , % $\text{C}_4$ and SEA ( $\% ^2$ ) by Season.....	19
Table 2. Cricetid Rodent and <i>X. Spilosoma</i> Plasma $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ , % $\text{C}_4$ and SEA ( $\% ^2$ ) by Season.....	20
Table 3. Seasonal SEA ( $\% ^2$ ) Overlap Between Each Species.....	21
Table A1. Whole plant $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the 38 most abundant species of $\text{C}_3$ and $\text{C}_4$ plants at the Sevilleta Long Term Ecological Research site.....	39
Table B1. Heteromyid Tukey HSD p-values for comparisons between seasonal $\delta^{13}\text{C}$ ( $\% \text{ VPDB}$ ) of plasma indicating, for each species, significant differences in diet between seasons.....	43
Table B2. Cricetid and <i>X. spilosoma</i> Tukey HSD p-values for comparisons between seasonal $\delta^{13}\text{C}$ ( $\% \text{ VPDB}$ ) of plasma indicating, for each species, significant differences in diet between seasons.....	44
Table B3. Rodent community Tukey HSD p-values for comparisons between each species' seasonal $\delta^{13}\text{C}$ ( $\% \text{ VPDB}$ ) of plasma indicating, for each season, significant differences in diet between species.....	45

## FIGURES

Figure 1. Heteromyid $\delta^{13}\text{C}$ ( $\% \text{ VPDB}$ ) of rodent plasma and $\text{C}_4$ plant use (% total assimilated carbon) as a function of trapping month.....	22
Figure 2. Cricetid and <i>X. spilosoma</i> $\delta^{13}\text{C}$ ( $\% \text{ VPDB}$ ) of rodent plasma and $\text{C}_4$ plant use (% total assimilated carbon) as a function of trapping month.....	23
Figure 3. Standard ellipse areas ( $\% ^2$ ) for the heteromyid rodent community as a function of season and year showing seasonal diet shift.....	24
Figure 4. Standard ellipse areas ( $\% ^2$ ) for the cricetid rodents and <i>X. spilosoma</i> as a function of season and year showing seasonal diet shift.....	25
Figure 5. Standard ellipse areas ( $\% ^2$ ) for nine individual rodent species as a function of season and year showing diet overlap between species each season.....	26
Figure 6. $\delta^{15}\text{N}$ ( $\% \text{ AIR}$ ) of the rodent community pooled by species showing relative trophic position and variance within and among species.....	27
Figure B1. Heteromyid $\delta^{15}\text{N}$ ( $\% \text{ AIR}$ ) as a function of trapping month.....	41
Figure B2. Figure B2. Cricetid and <i>X. spilosoma</i> $\delta^{15}\text{N}$ ( $\% \text{ AIR}$ ) as a function of trapping month.....	42

## INTRODUCTION

In arid ecosystems, precipitation limits primary productivity and drives seasonal variation in diversity and abundance of primary producers. Therefore, the timing and intensity of precipitation is pivotal in determining resource availability to consumers (Baez et al. 2006, Fay 2009, Robertson et al. 2009, Wilcox et al. 2017). Thus, there is a critical need to understand how a rapidly warming climate will alter resource availability and associated dietary niche breadth within and among consumer populations (Brown 1984, Lawton and Pratchett 2012, Roughgarden 1972, Vandermeer 1972), which may ultimately alter the composition and structure of animal communities. In the Chihuahuan Desert of southwestern North America, it is predicted that rapid warming will be accompanied by decreased winter/spring rains (Gutzler and Robbins 2011, Seager et al. 2007, Sheppard et al. 2002), delayed monsoons (Cook and Seager 2013), and increasingly extreme precipitation events with storms of greater magnitude and severe droughts (Christensen et al. 2013, Maurer et al. 2007).

The high seasonal and inter-annual climate variability in the northern Chihuahuan Desert provides an ideal system to quantify the effects of resource quantity and quality on the ecology of a diverse small mammal community (Sala et al. 2012). Precipitation is bimodal with (on average) ~60% of annual rainfall delivered by the summer monsoon season (July-October) (Notaro et al. 2010). Monthly averages for the more unpredictable winter and spring precipitation are lower than the monsoon season, while the driest and hottest period of the year is typically May through June (Fig. 1 and 2). Another attribute of this bimodal system is variability; this high degree of variation is a common attribute of precipitation regimes in arid ecosystems, and it is one reason why such systems have

served as the backdrop for field-based experiments examining the influence of abiotic factors such as precipitation and temperature on plant (Mowll et al. 2015, Baez et al. 2013) and consumer communities (Chesson et al. 2004, Kelt 2011, Meserve et al. 2003, Thibault et al. 2004).

This bimodal precipitation regime results in seasonal separation in the production of plants that use the C<sub>3</sub> versus C<sub>4</sub> photosynthetic pathways, which have very different carbon isotope ( $\delta^{13}\text{C}$ ) values (Ehleringer and Cerling 2002), and thus can be used to quantify the transfer of nutrients into desert consumer tissues (Orr et al. 2015, Warne et al. 2010). Similarly, measurements of  $\delta^{15}\text{N}$  provide information on animal trophic levels and trophic level shifts associated with changes in resource availability (Kelly 2000, Post 2002). C<sub>3</sub> shrub/forb productivity predominates during cooler spring precipitation (Xia et al. 2010), while C<sub>4</sub> grass biomass typically dominates net primary production during the warm summer monsoon rains (Muldavin et al. 2008). The seasonal growth and nutritional character of these two plant functional groups directly affect how consumers across all trophic levels are able to assimilate and utilize available energy resources for growth and reproduction (Price and Joyner 1997). C<sub>3</sub> and C<sub>4</sub> plants vary in their nutritional quality, energy content, and persistence in the environment. The leaves of C<sub>3</sub> plants are more nutritious, with higher nitrogen and digestible carbohydrate content, than C<sub>4</sub> grasses (Barbehenn et al. 2004a, 2004b, Caswell et al. 1973, Caswell and Reed 1975, 1976). C<sub>3</sub> annuals also produce larger seeds (Davidson et al. 1985, Reichman 1975, Samson et al. 1992). In contrast, the leaves of C<sub>4</sub> grasses are harder to process and digest and are more resistant to decomposition (Vanderbilt et al. 2008), and thus previous season growth potentially serves as a fallback food for folivores during periods of resource scarcity.

Given these traits, primary productivity and the relative proportions of C<sub>3</sub> and C<sub>4</sub> functional groups within an ecosystem are not only reflective of seasonal and annual weather patterns, but can be considered direct indicators of the quality of the resources that are available to the consumer community. Lastly, climate models predict warmer temperatures and diminishing winter/spring rains, which will likely result in decreased abundance of C<sub>3</sub> perennial (e.g., shrubs) and annual (e.g., forbs) plants, and expansion of C<sub>4</sub> grasses over the next century (Cotton et al. 2016, Epstein et al. 1997, 2002, Ehleringer et al. 1997, 2002, Groisman and Knight 2008).

While much descriptive information exists on the diets of small mammals in the American Southwest (e.g., Bailey 1971, Brown et al. 1979, Homer et al. 1964, Hope and Parmenter 2007, Reichman 1975), the relative importance of winter/spring versus summer (monsoon) resource production to diet within and among species is not known. The studies that have examined intra-annual variation in rainfall (Ernest et al. 2000, Lima et al. 2008, Thibault et al. 2010) focused solely on numerical responses in small mammal abundance and did not directly examine, even at coarse resolution, inter- or intra-specific variation in diet composition. In comparison to traditional approaches that are used to study animal diets (e.g., stomach/fecal analyses), stable isotope analysis (SIA) has two primary advantages. First, SIA provides a time-integrated record of dietary inputs, depending on the type of tissue analyzed, that ranges from as short as weeks (e.g., blood plasma) to years (e.g., bone collagen) (Martinez del Rio et al. 2009). Second, many tissues used in SIA-based studies can be sampled and re-sampled non-invasively (e.g., blood components) and can be used to generate a longitudinal profile of individual diet (Hobson and Clark 1993).

How a shift in resource availability from a C<sub>3</sub> based to C<sub>4</sub> based system will impact the diet of consumer communities that live in seasonal and highly unpredictable desert ecosystems is an important question. Given the significant differences in the seasonal timing, and the quantity and quality of C<sub>3</sub> and C<sub>4</sub> resources, it is important to understand the choices individual consumers and species make to maximize their survival and fitness as the resource landscape changes to that which would be expected under the future climate change scenario of increasing temperatures and aridity. Here we used the highly unpredictable nature of seasonal and annual precipitation in the Chihuahuan Desert and the distinct  $\delta^{13}\text{C}$  values of C<sub>3</sub> and C<sub>4</sub> plants as a natural experiment to quantify the differential resource use in a diverse community of desert small mammals, including species that use different foraging strategies (folivores, granivores, omnivores) and have different life histories. We also assessed relative trophic level of individuals by measuring  $\delta^{15}\text{N}$  in tissues.

Specifically, we aimed to address the following questions: 1) Do the diets of Cricetid and Heteromyid rodents track seasonal changes in C<sub>3</sub> and C<sub>4</sub> resource availability, 2) Are more nutritious C<sub>3</sub> resources preferred by all members of the rodent community, and does diet breadth increase during periods of C<sub>3</sub> resource scarcity and 3) Does omnivory provide a buffer to plant scarcity with particular species increasing trophic level during times of decreased primary production? Small mammals are important to ecosystem processes not only to higher trophic levels, but also because they influence the composition and structure of the vegetation and arthropod communities, soils, and nutrient cycling (Davidson et al. 1984, Greene and Murphy 1932). Understanding changes in energy acquisition by consumers in response to climate change

is central to understanding the structure and dynamics of ecosystems at the individual, population, and community levels and therefore the ecological consequences of climate change.

## MATERIALS AND METHODS

**Study Site.** The study site was located on the Sevilleta National Wildlife Refuge ~100 km south of Albuquerque, New Mexico. Our trapping webs were located across a grassland-shrubland ecotone in the Chihuahuan Desert, composed of a mixture of C<sub>3</sub> plants dominated by *Larrea tridentata* (creosote) and *Gutierrezia sarothrae* (broom snakeweed), and C<sub>4</sub> grasses *Bouteloua eriopoda* (black grama) and *Sporobolus spp.* (dropseed grasses).

**Weather and Aboveground Net Primary Production.** Precipitation and aboveground net primary production (ANPP) data were collected by the Sevilleta Long Term Ecological Research (LTER) program. A LTER meteorological station located <1 km from our study site generates hourly measurements of air temperature, wind speed, solar radiation, humidity, and precipitation. ANPP was measured at sampling sites <2 km from the study site in mixed *L. tridentata* and *B. eriopoda* dominated shrub-grasslands. Each ANPP site consisted of 80 permanent quadrats (1 m<sup>2</sup>) arranged in five circular, 200 m diameter webs ~0.3 km apart. Measurements of plant height, percent cover, and number of individuals of each species per 1 m<sup>2</sup> quadrat were made two times each year during spring (May) and fall (September). Species specific linear regression models in which the volumetric data was regressed against seasonally measured dry green leaf biomass were used to calculate ANPP for each season and year. All ANPP data are available in archival dataset SEV185 (Muldavin and Moore 2016; <http://sev.lternet.edu>).

**Tissue Collection & Sample Preparation for Stable Isotope Analysis.** From May 2005 to October 2007, we collected plants for carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis; see Appendix A. During mid-summer, we collected whole plant above ground

biomass samples of five individuals from each of 38 plant species that represented >90% of the plant biomass on our study site. Material for each species was combined into a single sample and homogenized into a powder; ~1 mg of powdered plant sample was loaded into tin capsules for SIA.

Small mammals were trapped approximately monthly from April 2005 to November 2007. Two webs consisting of 148 Sherman live traps each were arrayed as described in Parmenter et al. (2003). Traps were set for 2-3 nights each month and baited with rolled oats. Beginning in the spring of 2006, traps were kept open all day and checked periodically to capture diurnal rodents (*Xerospermophilus spilosoma*). During the winter months, a small ball of cotton batting was placed in each trap to reduce cold stress; traps were checked during the night during some exceptionally cold periods. Species identification, age, sex, reproductive status, and mass ( $\pm 0.1$  g) was recorded for each individual. A blood sample was obtained by puncturing the retro-orbital sinus with a 50  $\mu$ l heparinized micro-capillary tube after the administration of anesthetic eye drops (0.5% Tetracaine Hydrochloride Ophthalmic Solution, Akorn Inc.). Animals were ear tagged at the time of capture or marked on the pelage with ink to prevent double sampling of individuals during each monthly sampling bout. Handling time was <10 min for each individual and followed the American Society of Mammalogists Guidelines (American Society of Mammalogists Animal Care and Use Committee 1998). Animals were released at the site of capture after processing. Microcapillary tubes containing blood samples were sealed with critacaps (Leica Biosystems Critocaps) and stored on ice for transport to the laboratory. Blood samples were then centrifuged for two minutes to separate plasma from red blood cells within 48 hours of sample collection.



Approximately 5-15  $\mu$ l of plasma was then pipetted into tin capsules, air-dried and folded. Capture and processing protocols were approved by the University of New Mexico (UNM) Institutional Animal Care and Use Committee (IACUC # 05MCC005).

***Stable Isotope Analysis.***  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of plant and animal tissues were measured with a Costech ECS 4010 Elemental Analyzer coupled to a Thermo Finnigan Delta Plus isotope ratio mass spectrometer at the UNM Earth and Planetary Sciences Department (Albuquerque, NM). Stable isotope values are expressed using delta ( $\delta$ ) notation in parts per thousand (‰) as  $\delta X = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000$ , where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the ratios of  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  of the sample and the reference standard, respectively. The internationally accepted reference standards for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are Vienna-Pee Dee Belemnite (VPDB) and atmospheric  $\text{N}_2$  (AIR) respectively. Within-run precision (SD) was assessed via repeated analysis of internal reference materials, and was measured to be  $\pm 0.2\text{‰}$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.

***Estimation of C<sub>3</sub> and C<sub>4</sub> Carbon Incorporation into Rodent Blood Plasma.*** We used  $\delta^{13}\text{C}$  values of plasma, a tissue that incorporates ecological information during the previous 10-14 days for an endotherm the size of the rodent species studied here (Carleton et al. 2005). We also used a single isotope system ( $\delta^{13}\text{C}$ ) and two endmember (source) mixing model to estimate the proportion of a rodent's incorporated carbon derived from each plant photosynthetic type (C<sub>4</sub> versus C<sub>3</sub>) (Martinez del Rio and Wolf 2005),

$$\delta^{13}\text{C}_{\text{plasma}} = p(\delta^{13}\text{C}_{\text{C4}}) + (1 - p)(\delta^{13}\text{C}_{\text{C3}}) + \Delta^{13}\text{C}$$

where  $p$  is the fraction of C<sub>4</sub> plant material in the diet that is incorporated into the sampled tissue and  $\Delta^{13}\text{C}$  is the trophic discrimination factor defined as the difference in

$\delta^{13}\text{C}$  value between a consumer's tissue (plasma) and its diet (Cerling and Harris 1999, DeNiro and Epstein 1978, Hobson and Clark 1992). We used a  $\Delta^{13}\text{C}$  for blood plasma of 2‰ (MacAvoy et al. 2006).

**Data Analysis.** To link temporal shifts in small mammal diet with resource abundance we used three seasonal resource use metrics: 1) percentage of total carbon that is derived from  $\text{C}_3$  or  $\text{C}_4$  biomass, 2) standard ellipse area (SEA (‰<sup>2</sup>)) estimates of the dietary breadth and overlap among species, which provides insight into resource competition, and 3) the apparent trophic level of each species based on mean blood plasma  $\delta^{15}\text{N}$  values (Kelly 2000, Post 2002). To compare seasonal variation, we separated the rodent  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data into monsoon (July-October) and non-monsoon periods. The 2005 spring period included data collected from April to May. The 2005-06 winter/spring period included data collected from November 2005 to June 2006. The 2006-07 winter/spring period included data collected from November 2006 to May 2007. The 2007 fall period included data collected in November 2007.

SAS software (SAS Institute 2008) was used to perform statistical analyses. For each species, differences between seasonal  $\delta^{13}\text{C}$  for the entire study were assessed, and for each season, differences between species seasonal  $\delta^{13}\text{C}$  were determined. These analyses were conducted using a one-way ANOVA with a post-hoc Tukey HSD test. Appendix B, Tables B1, B2 and B3 present the p-values resulting from the Tukey HSD pairwise comparisons.

To calculate dietary niche breadth and overlap, Stable Isotope Analysis in R (SIAR) package was used to calculate and compare Stable Isotope Bayesian Ellipses in R (SIBER) metrics (Jackson et al. 2011) among seasons and years for each species.  $\delta^{13}\text{C}$

versus  $\delta^{15}\text{N}$  SEAs for blood plasma provided isotopic niche width metrics at monthly resolution based upon isotopic turnover rates for plasma (half-life = 3-4 days) (Hobson and Clark 1993, Hilderbrand et al. 1996). We tested for population level differences in isotopic niche width among seasons (pre-monsoon and post-monsoon) and years, and between consecutive seasons, by generating Bayesian estimates of blood plasma isotope SEAs using 10,000 posterior draws.

## RESULTS

*Seasonal and Annual Shifts in Precipitation and Plant Productivity.* The long-term average annual precipitation for 1989-2007 across the Sevilleta LTER was  $274.1 \pm 65.1$  mm (mean  $\pm$  1 SD) and exhibited the typical bimodal pattern with about 60% of the rainfall produced during the summer monsoon season (July-October 1989-2007 =  $164.5 \pm 47.6$  mm) and 40% falling as winter snow and spring rain (November to June 1989-2007 =  $109.7 \pm 53.2$  mm).

During the winter of 2004-2005, precipitation was  $153.5 \pm 14.0$  mm, well above this long-term average and the highest recorded at the research site since precipitation was first measured in 1999. This resulted in ANPP of  $22.16 \pm 27.30$  g/m<sup>2</sup> for C<sub>3</sub> plants and only  $2.4 \pm 2.97$  g/m<sup>2</sup> for C<sub>4</sub> plants, the lowest C<sub>4</sub> abundance during this study, across the across the shrubland-grassland ecotone. Monsoon rains in 2005 were close to average at  $163.5 \pm 36.7$  mm, and C<sub>4</sub> ANPP was also average at  $62.75 \pm 42.31$  g/m<sup>2</sup>. C<sub>3</sub> production doubled from spring to  $42.47 \pm 70.48$  g/m<sup>2</sup>, the highest summer C<sub>3</sub> production observed during the study period (Fig. 1 and 2).

In contrast, the winter of 2005-2006 was the driest in recorded history at the research site, with less than half of the long-term average precipitation ( $27.5 \pm 6.4$  mm), and resulted in the lowest productivity observed during this study period. There was more than a four-fold reduction in spring C<sub>3</sub> productivity ( $4.7 \pm 21.57$  g/m<sup>2</sup>) in comparison to 2005 values, and a modest level of spring C<sub>4</sub> plant productivity ( $12.63 \pm 17.85$  g/m<sup>2</sup>). The summer monsoon of 2006 produced  $298.6 \pm 37.1$  mm of precipitation, which was the most rainfall measured at the research site. Average summer ANPP in 2006 was greater than that of 2005. C<sub>4</sub> primary production equaled  $77.52 \pm 47.21$  g/m<sup>2</sup> and C<sub>3</sub> primary

production equaled  $26.61 \pm 43.93 \text{ g/m}^2$ , the lowest monsoon C<sub>3</sub> production, but an increase in C<sub>3</sub> production from the spring of 2006 (Fig. 1 and 2).

During the winter of 2006-2007, precipitation was  $149.3 \pm 14.8 \text{ mm}$ , also above average, which resulted in C<sub>3</sub> plant production of  $49.25 \pm 88.23 \text{ g/m}^2$  and C<sub>4</sub> production of  $21.1 \pm 13.12 \text{ g/m}^2$ , which was the highest C<sub>3</sub> production of any season and the highest spring C<sub>4</sub> production observed during the study period (Fig. 1 and 2). The summer monsoon of 2007 produced  $92.1 \pm 16.5 \text{ mm}$  of rainfall, the least monsoon precipitation experienced during this study. Summer C<sub>3</sub> production was  $39.25 \pm 77.11 \text{ g/m}^2$ , and C<sub>4</sub> was  $145.89 \pm 85.58 \text{ g/m}^2$ , the highest of any seasonal C<sub>4</sub> production observed during the entire study (Fig. 1 and 2).

***Small Mammal Captures.*** The medium-sized kangaroo rats, *Dipodomys merriami* ( $41 \pm 6.9 \text{ g}$  SD N= 197) and *Dipodomys ordii* ( $53.8 \pm 22.5 \text{ g}$  SD N= 245) were the most commonly encountered heteromyid rodents in the study area. The largest kangaroo rat on the study site, *Dipodomys spectabilis*, ( $121.8 \pm 27.4 \text{ g}$  SD N= 137) was the least abundant heteromyid. The smallest member of the rodent community was the heteromyid *Perognathus flavus* ( $7.4 \pm 1.0 \text{ g}$  SD N= 238). The largest of the cricetidae rodents captured during the study was *Neotoma (albigula and micropus)*, which was also the least abundant ( $156 \pm 42.4 \text{ g}$  SD N= 50). The most common cricetid captured was *Onychomys arenicola* ( $19.6 \pm 4.0 \text{ g}$  SD N= 148), followed by *Reithrodontomys megalotis* ( $9.9 \pm 1.8 \text{ g}$  SD N= 98) and *Peromyscus (leucopus and eremicus)* ( $22.8 \pm 5.5 \text{ g}$  SD N= 66). The only Sciurid captured during the study was *Xerospermophilus spilosoma* ( $106.6 \pm 18.6 \text{ SD}$  N= 65).

**Shifts in Resource Use Among Species, Seasons, and Years.**  $\delta^{13}\text{C}$  values for  $\text{C}_3$  plants were ( $\delta^{13}\text{C}$ :  $-26.9 \pm 2.0$ ) and ( $\delta^{13}\text{C}$ :  $-14.8 \pm 0.9\text{‰}$ ) for  $\text{C}_4$  plants (Appendix A). These values were used in the mixing model to estimate the proportion of a rodent's incorporated carbon derived from each plant photosynthetic type.

**Spring 2005- winter/spring 2005/2006. Normal precipitation followed by a failure of winter rains and  $\text{C}_3$  resources.** Following the spring of 2005, most species increased  $\text{C}_4$  resource until the monsoon season of 2006. Although the use of  $\text{C}_3$  resources increased initially in the winter 2005, the lack of winter/spring precipitation lead to increasing use of  $\text{C}_4$  biomass through the spring of 2006. Heteromyids generally consumed a higher proportion of  $\text{C}_4$  resources with increased diet breadth (SEA) and overlap during the spring of 2006 compared to the spring of 2005. From the monsoon of 2005 to the spring of 2006, very limited  $\text{C}_3$  growth during the winter/spring resulted in a  $\sim 400\%$  increase in Standard Ellipse Area (SEA) of *D. merriami*, as well as SEA increases in *D. spectabilis* and *P. flavus* of 20 to 60%, except in *D. ordii* which decreased dietary breadth by  $\sim 12\%$ . *D. merriami*, *D. spectabilis*, and *P. flavus* maintained diets of  $\geq 50\%$   $\text{C}_3$ , while *D. ordii*'s diet shifted to  $\sim 60\%$   $\text{C}_4$ , which was the largest dietary shift of the season (Fig. 1 and 3 and Table 1). The greatest SEA overlap during the spring of 2005 was between *D. spectabilis* and *P. flavus*. *D. spectabilis* increased  $\text{C}_4$  use through October 2005, and then showed a strong shift to  $\text{C}_3$  (about 65%  $\text{C}_3$ ) in the spring of 2006, with an increase in diet breadth, and a decrease in overlap with the other heteromyids. *P. flavus* had the greatest dietary breadth among heteromyids, with an SEA in the spring of 2005 which was 50% greater than observed in kangaroo rats. *P. flavus* increased SEA during the spring of 2006 to  $\sim 100\text{-}300\%$  larger than most other species and increased overlap

with *D. merriami* and *D. ordii*. *D. merriami* had the smallest SEA and highest trophic level of the heteromyids, thus more dietary overlap with the cricetid species (Fig. 5 and Table 3).

From the spring to early monsoon 2005, the incorporation of C<sub>4</sub> carbon by *O. arenicola* doubled from ~35% to ~70%, and was >80% in *Neotoma spp.*, which was significantly greater C<sub>4</sub> utilization than observed in the heteromyids except *D. spectabilis* (Appendix B Table B3). Between August 2005 and January 2006, *O. arenicola*'s source of carbon shifted abruptly back to higher levels of C<sub>3</sub> use (~50-60% C<sub>4</sub>). During this time *O. arenicola* decreased diet breadth and overlap with the other cricetids and increased overlap with all heteromyid species except *D. spectabilis*. Similarly, *Neotoma spp.* also shifted to C<sub>3</sub> resources during the winter of 2006, then increased C<sub>4</sub> usage prior to the monsoon season. The omnivorous *Peromyscus spp.* had the highest peak in C<sub>4</sub> resource use, approaching ~70-90% of its assimilated carbon, which was significantly greater C<sub>4</sub> use than the other species (Appendix B Table B3). This was associated with a doubling of diet breadth during the monsoon of 2005, with a subsequent decline to about 50% C<sub>4</sub> use and decreasing diet breadth and overlap with both heteromyids and cricetids in the spring. *R. megalotis* was less variable showing 45-65% C<sub>4</sub> use, declining diet breadth, and a decrease in dietary overlap with all species except *D. spectabilis* by spring 2006 (Fig. 2, 4, and 5 and Table 2 and 3).

#### **Spring 2006- summer 2006 record monsoon and increase in total ANPP.**

Despite increases in C<sub>3</sub> and C<sub>4</sub> resources, from pre- to post-monsoon in 2006, the rodent community showed highly variable interest in C<sub>4</sub> resources. From the early spring until the beginning of the monsoon, *D. merriami* and *ordii* showed a 15-20% decrease, and *P.*

*flavus* a ~35% decrease in C<sub>4</sub> incorporation. In contrast, *D. Spectabilis* nearly doubled its use of C<sub>4</sub> resources. During the monsoon of 2006, all heteromyids increased C<sub>4</sub> resource use by 15 to 50%, which was greater utilization of C<sub>4</sub> resources than during the monsoon of 2005 (Fig. 1 and 3 and Table 1). From spring to the monsoon of 2006, changes in dietary breadth with the onset of the monsoon in 2006 varied from a decrease in *D. spectabilis*, no change in *D. merriami*, and an increase of ~37% in *D. ordii*. *P. flavus* increased diet breadth ~19% and had the largest dietary breadth among species (Fig. 3 and Table 1). Dietary overlap in 2006 increased in the heteromyids as the spring progressed into summer (Fig. 5 and Table 3).

Within cricetids, *O. arenicola* and *Neotoma spp.* increased C<sub>4</sub> use to 75% and 95%, respectively, from spring to monsoon 2006. In contrast, *Peromyscus spp.* showed a >40% reduction in C<sub>4</sub> use prior to the monsoon, while *R. megalotis* continued to use 50-60% C<sub>4</sub> resources during the spring. During the monsoon of 2006, cricetids and *X. spilosoma* decreased C<sub>4</sub> use, after an initial peak. *Peromyscus spp.* continued to reduce C<sub>4</sub> use in contrast to increasing C<sub>4</sub> use during this period in 2005 (Fig. 2 and 4 and Table 2). *O. arenicola* dietary breadth remained similar during 2006, and showed no overlap with the other cricetid species. *Neotoma spp.* and *X. spilosoma* also increased dietary breadth and overlap with all other species (Fig. 4 and 5 and Table 2 and 3).

**2007 and greatest production of C<sub>3</sub> vegetation.** The very large increase in the production of C<sub>3</sub> vegetation in the spring of 2007 produced a large shift toward C<sub>3</sub> resources by all heteromyids, with C<sub>4</sub> incorporation decreasing by at least 50% to only 15-25% of the total assimilated carbon. This was the highest use of C<sub>3</sub> resources observed, which was accompanied by the lowest apparent trophic levels observed in the



study. During the monsoon of 2007, C<sub>3</sub> resources comprised a significantly higher proportion of the diet of *D. ordii* and *P. flavus* than all preceding seasons, and for *D. spectabilis* was significantly greater than the previous monsoons. For *D. merriami*, C<sub>3</sub> utilization was significantly higher during the 2007 monsoon than any point in 2006, but was similar to utilization observed in 2005 (Appendix B Tables B1 and B2). During the monsoon of 2007, *P. flavus* utilized significantly more C<sub>3</sub> resources than the other species, except *D. ordii* (Appendix B Table B3). *D. merriami*, *D. ordii*, and *P. flavus* subsequently showed small increases in C<sub>4</sub> use into the fall of 2007. *D. spectabilis* showed a greater increase in C<sub>4</sub> use during the same period (Fig. 1 and 3 and Table 1). Heteromyids greatly decreased their diet breadth by 44-74% from the spring onward and the SEAs also contracted compared to the 2006 monsoon across most species. Heteromyid SEAs continued to decrease through the fall, except in *D. ordii*, which showed a broadening of diet and increase in trophic level. From the monsoon of 2006 to the winter/spring of 2006/2007, overlap among all the *Dipodomys* species continued to increase with C<sub>3</sub> production and use. *P. flavus* decreased dietary overlap with the *Dipodomys* species, except *D. spectabilis*, with which overlap increased four-fold, similar to the spring of 2005 (Fig. 3 and 5, and Table 1 and 3).

The mostly insectivorous *O. arenicola* exhibited diminished changes in resource use compared to species feeding at lower trophic levels. From the winter/spring of 2006/2007 to the fall of 2007, *O. arenicola* showed a pattern of resource use where C<sub>4</sub> carbon was 40-60% of its total carbon incorporation. *O. arenicola*, in general, showed peak C<sub>4</sub> use at the beginning of the monsoon which then declined throughout the monsoon to ~40% in 2007. During the monsoon of 2007 *O. arenicola* utilized more C<sub>4</sub>

resources than the heteromyids, *Neotoma spp.*, and *X. spilosoma* (Appendix B Table B3). Subsequently, *O. arenicola* utilized significantly more C<sub>3</sub> resources during the fall of 2007 than any season since the spring of 2005. During the winter/spring 2006/2007, *Neotoma spp.*, *Peromyscus spp.*, *R. megalotis*, and *X. spilosoma* increased C<sub>3</sub> resource use to ~75% of total carbon assimilation, which was a significant increase from the previous winter/spring period (Appendix B Tables B1 and B2). During the monsoon of 2007, *Neotoma spp.* and *R. megalotis* C<sub>4</sub> use was relatively unchanging, and *R. megalotis* maintained 45-50% C<sub>4</sub> use during this same period. Although *X. spilosoma* increased C<sub>4</sub> use during the monsoon, total C<sub>4</sub> use was still only 40% of carbon assimilation. (Fig. 2 and 4, and Table 2). Dietary breadth, for *O. arenicola* during this period was smaller than previous seasons and highly constrained by high levels of insectivory. *O. arenicola* and *Neotoma spp.* SEAs decreased from the monsoon of 2006 to the monsoon of 2007, but then showed a broadening diet in the fall. *R. megalotis* decreased diet breadth in the fall, and *X. spilosoma* remained essentially the same. Similar to the previous season, there was little overlap among the cricetids during the winter/spring of 2006/2007. However, there was an increase in overlap between cricetids and heteromyids than in the previous winter/spring of 2005/2006 when C<sub>3</sub> resources failed. The cricetids decreased overlap with other species through the fall of 2007 (Fig. 4 and 5, and Table 2 and 3).

***δ<sup>15</sup>N and Relative Trophic Level among Species.*** δ<sup>15</sup>N blood plasma values indicated differences in diet between species and guilds. δ<sup>15</sup>N values are enriched on average 3.2‰ for each trophic level above the base of the food web (Kelly 2000). Over the entire study period, δ<sup>15</sup>N was generally highest in the cricetid species except for *Neotoma spp.*, indicating a higher trophic level in these species and higher insect content

of their diet. *O. arenicola* was at the highest trophic level, followed by *Peromyscus spp.*, *R. megalotis*, and *Neotoma spp.* *X. spilosoma* had  $\delta^{15}\text{N}$  enrichment similar to that of the heteromyid species. Of the heteromyid species, *D. merriami* and *D. ordii* had the diet most enriched in  $\delta^{15}\text{N}$  (Fig. 6 and Table 1 and 2).

In general, trophic level increases coincided with increased use of  $\text{C}_4$  (Fig. 1 and 2, and Fig. B1 and B2 (Appendix B)). An increase in trophic level closely followed an increase in  $\text{C}_4$  use in *O. arenicola* and *Neotoma spp.*, and to a lesser extent in *D. merriami*, *D. ordii*, and *Peromyscus spp.*, which in contrast showed an inverse relationship between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  during the spring of 2005. There appeared to be an inverse relationship at times between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in *D. spectabilis*, *P. flavus*, and *R. megalotis*. Heteromyids generally exhibited higher  $\delta^{15}\text{N}$  during the winter/spring than during monsoons. Conversely, cricetid  $\delta^{15}\text{N}$  values indicated a lower trophic position during the winter/spring seasons than summers (Fig. 1 and 2, and Fig. B1 and B2 (Appendix B)).

Table 1. Heteromyid Rodent Plasma  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , % C<sub>4</sub> and SEA (‰<sup>2</sup>) by Season

Time Period	n	Plasma $\delta^{13}\text{C}$	Plasma $\delta^{15}\text{N}$	% C <sub>4</sub>	SEA (‰ <sup>2</sup> )
<b>DIME</b>					
2005 Spring	16	-21.1±1.2	10.3±0.8	32±10	2.4
2005 Monsoon	12	-20.3±0.9	9.5±0.6	38±8	1.6
2005-06 Winter/Spring	52	-19.9±2.0	10.2±1.3	41±16	7.9
2006 Monsoon	27	-19.6±1.9	9.2±1.6	44±16	7.5
2006-07 Winter/Spring	49	-19.1±2.4	8.9±0.9	48±20	6.9
2007 Monsoon	25	-22.1±1.1	8.2±0.5	23±9	3.2
2007 Fall	18	-21.1±1.2	8.9±0.7	31±10	2.6
<b>DIOR</b>					
2005 Spring	34	-21.2±1.2	8.7±1.2	31±10	4.3
2005 Monsoon	33	-19.8±1.3	9.3±1.2	42±11	4.9
2005-06 Winter/Spring	59	-17.9±1.9	10.1±0.9	57±16	4.3
2006 Monsoon	33	-19.5±1.7	8.8±1.1	45±14	5.9
2006-07 Winter/Spring	55	-19.9±2.7	8.9±0.9	41±23	7.1
2007 Monsoon	29	-23.0±0.6	7.5±1.3	15±5	3.0
2007 Fall	11	-21.7±2.9	9.1±0.9	26±24	7.3
<b>DISP</b>					
2005 Spring	12	-19.5±1.2	8.1±1.1	44±10	4.4
2005 Monsoon	16	-17.9±1.3	7.7±0.8	58±10	3.3
2005-06 Winter/Spring	34	-19.3±1.8	7.8±1.0	46±15	5.4
2006 Monsoon	19	-17.8±2.2	8.0±0.8	58±18	4.1
2006-07 Winter/Spring	34	-20.2±2.3	8.2±1.3	39±19	8.8
2007 Monsoon	15	-21.6±1.4	7.9±0.9	27±11	4.9
2007 Fall	7	-17.8±1.2	8.0±0.7	58±10	3.3*
<b>PGFV</b>					
2005 Spring	55	-19.1±1.9	7.8±1.1	48±15	6.6
2005 Monsoon	36	-18.7±2.7	8.7±0.9	51±22	8.0
2005-06 Winter/Spring	56	-19.6±2.7	9.5±1.3	44±22	9.7
2006 Monsoon	34	-20.3±3.2	9.3±1.2	38±26	11.6
2006-07 Winter/Spring	46	-18.4±2.9	7.6±0.9	54±24	8.1
2007 Monsoon	12	-23.6±0.7	8.6±1.4	11±6	2.1
2007 Fall	2	-22.2±1.3	10.1±1.6	22±11	–

\* denotes a sample size of less than 10.

Table 2. Cricetid Rodent and *X. Spilosoma* Plasma  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , %  $\text{C}_4$  and SEA ( $\text{‰}^2$ ) by Season

Time Period	n	Plasma $\delta^{13}\text{C}$	Plasma $\delta^{15}\text{N}$	% $\text{C}_4$	SEA ( $\text{‰}^2$ )
<b>ONAR</b>					
2005 Spring	27	-19.6 $\pm$ 1.8	10.6 $\pm$ 0.8	44 $\pm$ 15	4.8
2005 Monsoon	32	-16.8 $\pm$ 1.2	10.9 $\pm$ 0.7	67 $\pm$ 10	2.7
2005-06 Winter/Spring	29	-18.6 $\pm$ 1.3	10.5 $\pm$ 0.9	52 $\pm$ 10	2.3
2006 Monsoon	14	-17.8 $\pm$ 1.4	10.3 $\pm$ 0.6	58 $\pm$ 12	2.3
2006-07 Winter/Spring	26	-18.8 $\pm$ 1.0	10.1 $\pm$ 0.6	50 $\pm$ 8	1.9
2007 Monsoon	12	-18.2 $\pm$ 0.7	10.7 $\pm$ 0.3	55 $\pm$ 5	0.6
2007 Fall	14	-20.2 $\pm$ 0.7	10.8 $\pm$ 0.7	39 $\pm$ 6	1.6
<b>PM</b>					
2005 Spring	15	-20.0 $\pm$ 2.2	9.8 $\pm$ 1.3	40 $\pm$ 18	8.8
2005 Monsoon	7	-17.0 $\pm$ 3.1	10.0 $\pm$ 1.4	66 $\pm$ 25	16.1*
2005-06 Winter/Spring	26	-15.9 $\pm$ 2.2	10.3 $\pm$ 0.9	74 $\pm$ 18	6.2
2006 Monsoon	4	-17.6 $\pm$ 3.4	10.1 $\pm$ 1.1	60 $\pm$ 28	–
2006-07 Winter/Spring	15	-19.8 $\pm$ 2.6	10.1 $\pm$ 0.9	42 $\pm$ 22	7.5
2007 Monsoon	3	-20.8 $\pm$ 0.4	10.0 $\pm$ 3.1	34 $\pm$ 3	–
2007 Fall	2	-14.2 $\pm$ 0.3	10.3 $\pm$ 0.6	89 $\pm$ 3	–
<b>REMG</b>					
2005 Spring	12	-18.8 $\pm$ 2.3	9.7 $\pm$ 1.2	51 $\pm$ 19	8.6
2005 Monsoon	8	-19.3 $\pm$ 1.5	9.3 $\pm$ 1.6	46 $\pm$ 13	6.0*
2005-06 Winter/Spring	31	-18.1 $\pm$ 1.7	8.5 $\pm$ 1.2	57 $\pm$ 14	4.9
2006 Monsoon	–	–	–	–	–
2006-07 Winter/Spring	29	-19.3 $\pm$ 2.3	8.0 $\pm$ 0.7	46 $\pm$ 19	4.9
2007 Monsoon	5	-19.4 $\pm$ 1.6	8.4 $\pm$ 0.8	46 $\pm$ 13	–
2007 Fall	16	-20.1 $\pm$ 0.8	9.4 $\pm$ 1.1	39 $\pm$ 7	2.6
<b>NEOTOMA</b>					
2005 Spring	–	–	–	–	–
2005 Monsoon	5	-16.0 $\pm$ 3.1	7.9 $\pm$ 0.6	74 $\pm$ 25	–
2005-06 Winter/Spring	10	-16.6 $\pm$ 2.8	7.8 $\pm$ 1.3	68 $\pm$ 23	10.0
2006 Monsoon	7	-17.0 $\pm$ 2.8	8.6 $\pm$ 1.1	65 $\pm$ 24	11.9*
2006-07 Winter/Spring	8	-21.7 $\pm$ 2.0	8.0 $\pm$ 1.4	27 $\pm$ 17	10.2*
2007 Monsoon	13	-20.4 $\pm$ 2.0	8.5 $\pm$ 0.8	37 $\pm$ 16	5.0
2007 Fall	7	-20.0 $\pm$ 2.4	8.6 $\pm$ 1.0	40 $\pm$ 20	7.6*
<b>XESP</b>					
2005 Spring	–	–	–	–	–
2005 Monsoon	–	–	–	–	–
2005-06 Winter/Spring	24	-18.8 $\pm$ 1.4	9.0 $\pm$ 0.6	51 $\pm$ 12	2.4
2006 Monsoon	17	-19.4 $\pm$ 1.4	8.2 $\pm$ 0.7	45 $\pm$ 12	3.2
2006-07 Winter/Spring	15	-21.6 $\pm$ 1.0	8.4 $\pm$ 0.7	28 $\pm$ 8	2.3
2007 Monsoon	13	-20.6 $\pm$ 1.6	8.8 $\pm$ 0.5	36 $\pm$ 13	2.4
2007 Fall*	–	–	–	–	–

\* denotes a sample size of less than 10.

Table 3. Seasonal SEA (%<sup>2</sup>) Overlap Between Each Species

		2005 SPRING									
		DIME	DIOR	DISP	PGFV	ONAR	PM	REMG	XESP	NEO	
2005-06 WINTER/SPRING	DIME		0.4	0.0	0.0	1.1	2.1	0.9	-	-	
	DIOR	1.9		1.6	0.7	0.0	2.1	0.2	-	-	
	DISP	0.0	0.0		3.7	0.0	1.2	0.4	-	-	
	PGFV	5.1	3.3	0.9		0.0	0.5	0.8	-	-	
	ONAR	1.8	1.1	0.0	1.6		3.9	3.2	-	-	
	PM	0.1	2.1	0.0	1.2	0.0		6.1	-	-	
	REMG	0.0	0.1	2.0	1.0	0.0	0.3		-	-	
	XESP	0.6	0.5	0.3	1.9	0.0	0.0	1.3		-	
	NEO	0.0	0.0	2.3	0.0	0.0	0.0	2.2	0.1		
			2005 MONSOON								
		DIME	DIOR	DISP	PGFV	ONAR	PM	REMG	XESP	NEO	
2006 MONSOON	DIME		1.7	0.0	0.9	0.0	0.8	1.1	-	-	
	DIOR	4.9		0.0	3.2	0.0	2.7	4.0	-	-	
	DISP	2.2	1.6		1.3	0.0	0.1	0.0	-	-	
	PGFV	6.1	5.0	1.0		0.0	4.2	4.1	-	-	
	ONAR	0.1	0.1	0.0	0.8		2.6	0.1	-	-	
	PM	-	-	-	-	-		4.6	-	-	
	REMG	-	-	-	-	-	-		-	-	
	XESP	2.4	2.8	1.8	1.7	0.0	-	-		-	
	NEO	3.3	3.1	3.9	3.0	0.0	-	-	2.4		
			2007 MONSOON								
		DIME	DIOR	DISP	PGFV	ONAR	PM	REMG	XESP	NEO	
2006-07 WINTER/SPRING	DIME		0.8	1.2	0.0	0.0	-	-	1.4	2.3	
	DIOR	5.4		0.4	0.0	0.0	-	-	0.1	0.3	
	DISP	3.8	5.1		0.0	0.0	-	-	0.6	2.8	
	PGFV	1.2	1.0	4.0		0.0	-	-	0.0	0.0	
	ONAR	0.4	0.2	0.0	0.0		-	-	0.0	0.0	
	PM	1.6	1.4	0.4	0.0	2.0		-	-	-	
	REMG	1.7	1.7	4.3	4.3	0.0	0.0		-	-	
	XESP	0.6	1.9	2.4	0.2	0.0	0.0	0.7		2.4	
	NEO	1.5	3.1	5.3	1.9	0.0	0.0	2.2	2.4		
			2007 FALL								
		DIME	DIOR	DISP	PGFV	ONAR	PM	REMG	XESP	NEO	
	DIME		2.7	0.0	-	0.0	-	0.7	-	1.8	
	DIOR			0.0	-	0.0	-	1.5	-	2.5	
	DISP				-	0.0	-	0.0	-	0.6	
	PGFV						-	-	-	-	
	ONAR						-	0.3	-	0.0	
	PM							-	-	-	
	REMG								-	1.6	
	XESP									-	
	NEO										

Notes: Seasons are delineated above and below the gray boxes. Dashes represent species combinations where overlap could not be calculated due to lack of data.

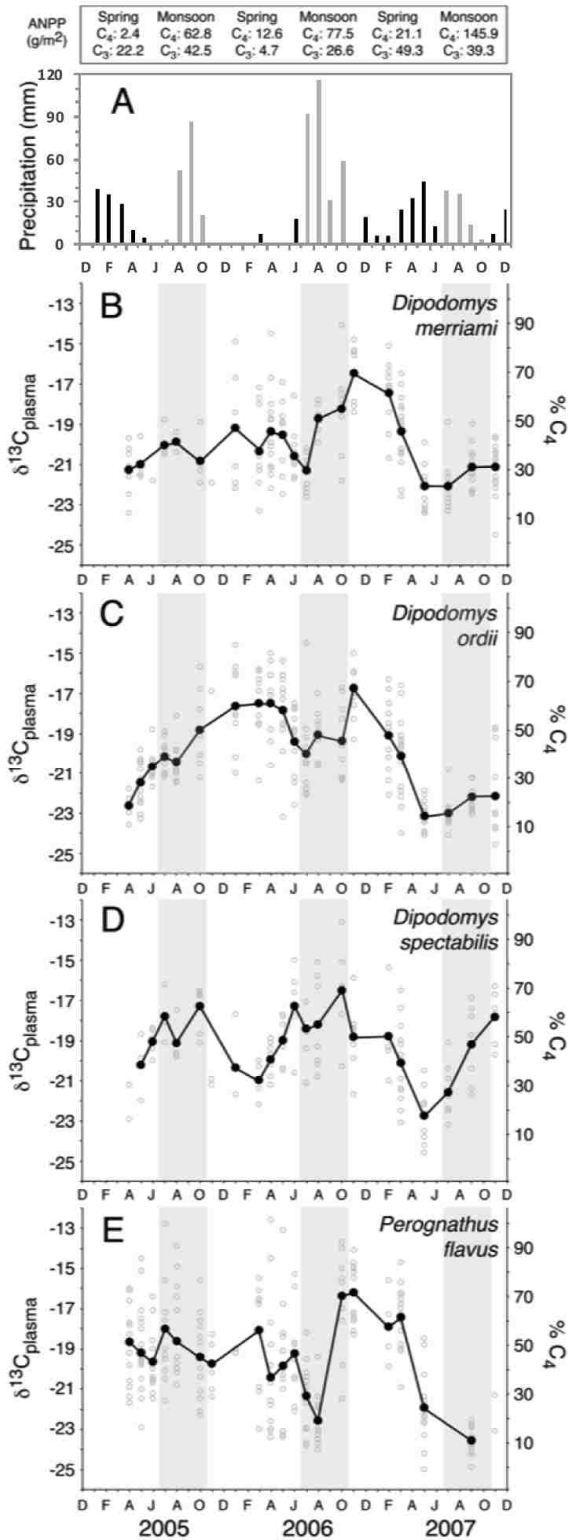


Figure 1. Heteromyid  $\delta^{13}\text{C}$  (% VPDB) of rodent plasma and  $\text{C}_4$  plant use (% total assimilated carbon) as a function of trapping month. Also presented are seasonal precipitation values and ANPP measured on nearby plots.

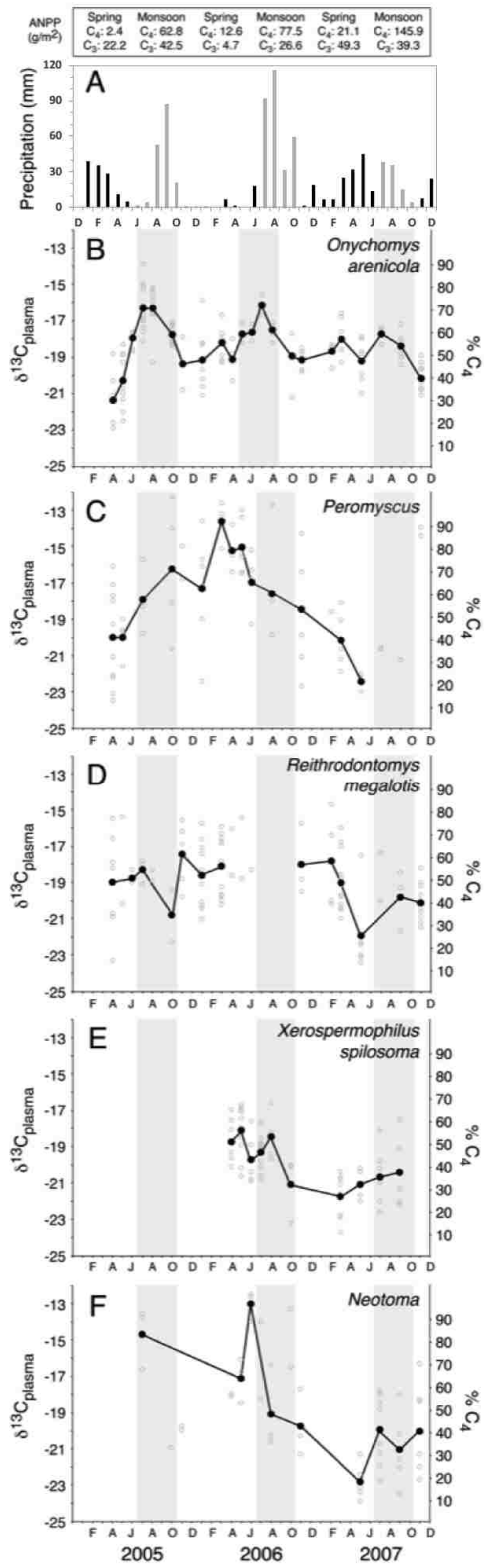


Figure 2. Cricetid and *X. spilosoma*  $\delta^{13}\text{C}$  (‰ VPDB) of rodent plasma and  $\text{C}_4$  plant use (% total assimilated carbon) as a function of trapping month.

Also presented are seasonal precipitation values and ANPP measured on nearby plots.



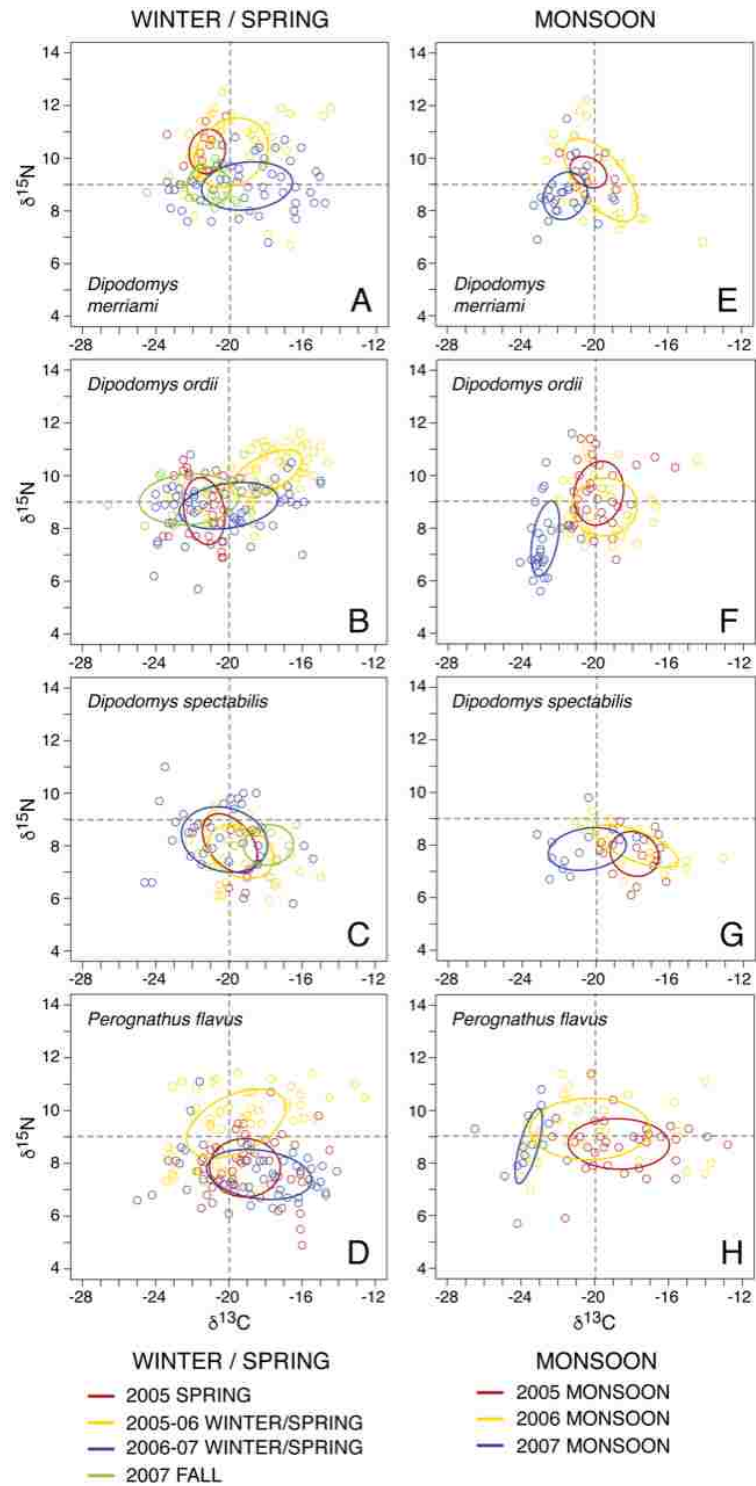


Figure 3. Standard ellipse areas (%<sup>2</sup>) for the heteromyid rodent community as a function of season and year showing seasonal diet shift.

*Notes:* The vertical dashed line represents the 50-50 line where C<sub>3</sub>-C<sub>4</sub> resource use is evenly split among compartments. Ellipses for species with less than 10 samples in a season were not plotted.

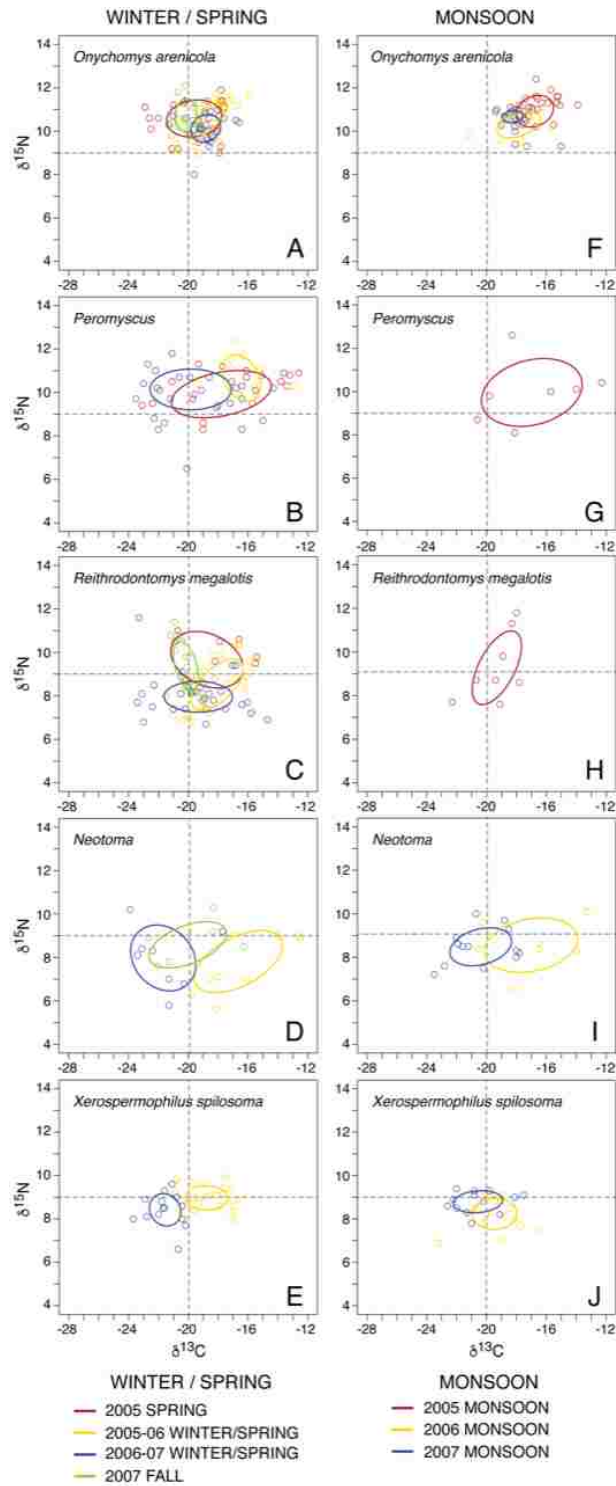


Figure 4. Standard ellipse areas (%<sup>2</sup>) for the cricetid rodents and *X. spilosoma* as a function of season and year showing seasonal diet shift.

*Notes:* The vertical dashed line represents the 50-50 line where C<sub>3</sub>-C<sub>4</sub> resource use is evenly split among compartments. Ellipses for species with less than 10 samples in a season were not plotted.

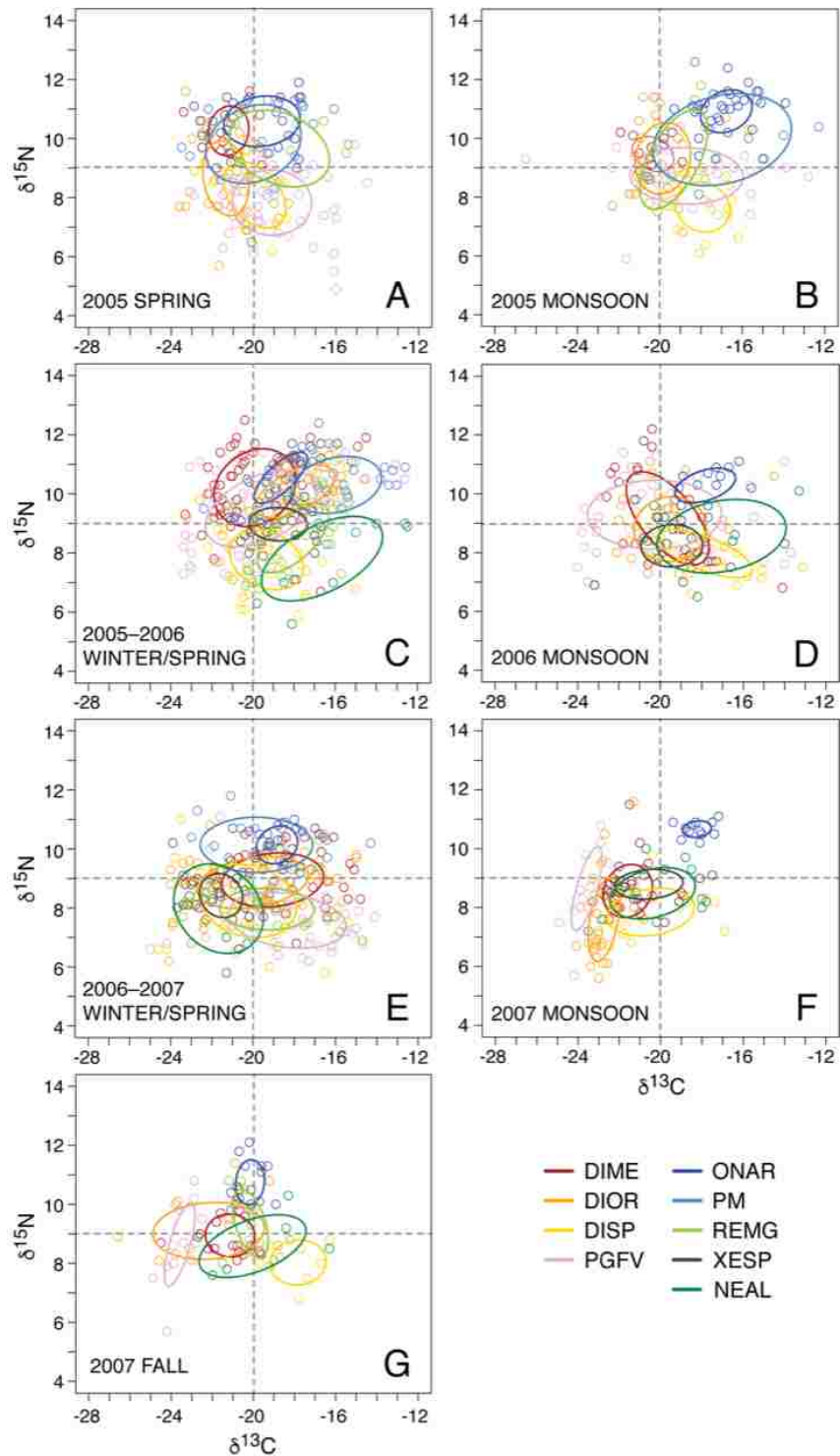


Figure 5. Standard ellipse areas ( $\%^{2}$ ) for nine individual rodent species as a function of season and year showing diet overlap between species each season.

*Notes:* The vertical dashed line represents the 50-50 line where  $C_3$ - $C_4$  resource use is evenly split among compartments. Ellipses for species with less than 10 samples in a season were not plotted.

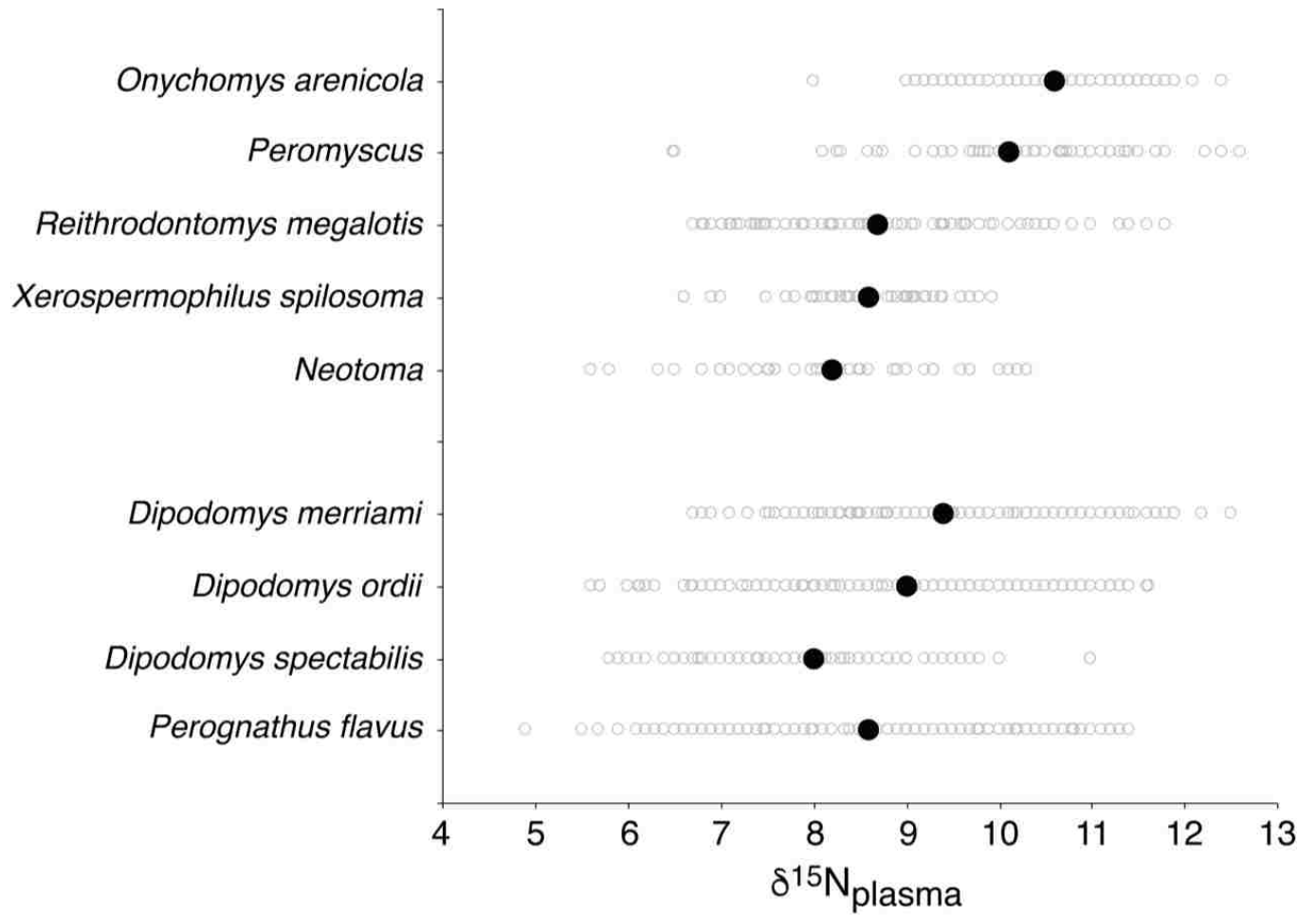


Figure 6.  $\delta^{15}\text{N}$  (‰ AIR) of the rodent community pooled by species showing relative trophic position and variance within and among species.

## DISCUSSION

Our study is one of the first to directly link small mammal community resource use to highly variable C<sub>3</sub> and C<sub>4</sub> plant production, on a seasonal and inter-annual basis, which is directly linked to climatic variation. Other studies have examined the use of C<sub>3</sub> and C<sub>4</sub> resources by consumers, but not at a community level or across trophic levels, and at a coarser time scale (Ambrose and DeNiro 1986, Kelly 2000, Magnusson et al. 1999, Stapp et al. 1999, Tieszen and Imbamba 1980). This study captured a year during which winter/spring rainfall and consequently C<sub>3</sub> resources were greatly diminished, as might be expected to occur with future climate change scenarios, which was compared to resource use during years with average and increased precipitation. This allows us to assess how consumer resource utilization might be altered in the future, as the climate becomes more arid, which we would expect to influence consumer life histories. Our results showed that: 1) Most species show significant flexibility and are able to directly or indirectly increase use of C<sub>4</sub> resources during periods of low winter/spring rainfall and scarcity of C<sub>3</sub> resources; 2) Most species rely primarily on C<sub>3</sub> resources and decrease diet breadth when C<sub>3</sub> resources are abundant, with the exception of the most insectivorous species, which appear to get more of their dietary carbon from C<sub>4</sub> derived resources; 3) Heteromyid rodents do not all appear to use stored C<sub>3</sub> resources as a buffer and make rapid shifts in dietary carbon that follow changes in resource availability, 4) In general, trophic level appears to increase in all species coincident with C<sub>3</sub> resource scarcity. In the following discussion we look at the importance of C<sub>3</sub> resources to the community, variation in trophic level, diet breadth and overlap, and the potential influence of climate

change on future resource availability for consumers in deserts in southwestern North America.

***Seasonal Diet Changes in Rodents Associated with Changes in Resource***

***Abundance.*** Given the variable resource landscape of the Chihuahuan Desert, we expect rodents to be generalists with a broad dietary niche breadth and dietary flexibility (Dennis et al. 2011, Krassen 2002). Current studies suggest that heteromyid diets reflect resource availability, can vary substantially between season and years, and that the use of forb and grass seeds change seasonally in response to the timing of seed production (Brown et al. 1979, Reichman 1975, 1977, Reichman and Van De Graaf 1973). Consistent with these observations, our study showed that both cricetid and heteromyid rodents shifted resource use with changes in resource availability. Tissue carbon isotope ratios showed that rodent diets were generally composed of >50% C<sub>3</sub> carbon, and heteromyids exhibited a greater overall reliance on C<sub>3</sub> resources than the cricetid species. C<sub>4</sub> use was highest in the cricetids where *Peromyscus spp.* and *Neotoma spp.* had peaks in C<sub>4</sub> use accounting for >90% of their assimilated carbon and *O. arenicola*, the most insectivorous species, showed a greater, continuous reliance on C<sub>4</sub> resources (Fig. 1, 2, 3, and 4, and Table 1 and 2). Across all species, there was a general increase in C<sub>4</sub> resource use as C<sub>4</sub> biomass increased and C<sub>3</sub> biomass declined.

The winter of 2005-2006 was the driest in recorded history at the research site which resulted in the lowest spring productivity observed during this study period; only 25% of the C<sub>3</sub> biomass compared to the prior year. This appeared to drive an apparent division of resources among heteromyids (Bowers 1982, Hallet 1982, Price 1978, Reichman 1975, Reichman and Price 1993). *D. spectabilis* obtained >50% of its carbon

from C<sub>3</sub> sources and *D. ordii* >50% of its carbon from C<sub>4</sub> sources, while *D. merriami* and *P. flavus* carbon sources were approximately 50:50 - C<sub>3</sub>:C<sub>4</sub>. Cricetid rodents, in contrast, generally obtained >50% of their carbon from C<sub>4</sub> and showed higher peaks in C<sub>4</sub> use (Fig. 1 and 5, and Table 1).

In contrast, during the winter of 2006-2007, precipitation was well above average, and the resulting spring C<sub>3</sub> plant productivity and the summer monsoon C<sub>3</sub> and C<sub>4</sub> production was the greatest observed during the entire study. Coincident to this boom in production was a large shift to C<sub>3</sub> resource use by the rodent community (>70% C<sub>3</sub> for all species except *O. arenicola*), even in the presence of abundant C<sub>4</sub> resources, which was the highest winter C<sub>4</sub> production observed during this study. During this period, dietary breadth was highly constrained and dietary overlap increased as the rodent community focused on abundant C<sub>3</sub> resources. (Fig. 1, 2, 3, 4, and 5, and Table 1, 2, and 3). Although *Peromyscus spp.* and *O. arenicola* fed at higher trophic levels, their peak C<sub>3</sub> use occurred in concert with the rest of the rodent community. *O. arenicola*, the most insectivorous species, however, showed only modest shifts towards C<sub>3</sub> resources, and the most constrained diet breadth compared to other rodent species, suggesting that it employed a more specialized resource acquisition strategy or that the use of insects decreased total variability (Warne et al. 2010) (Fig. 2 and 4, and Table 2).

We observed a nonlinear vegetation response to precipitation similar to that observed in other studies at the Sevilleta LTER (Muldavin et al. 2008, Wilcox et al. 2017). Increased precipitation occurred during the monsoon of 2006 and spring of 2007 and more precipitation occurred in late spring 2007. However, the largest pulse of plant production during the study period occurred during the 2007 monsoon even though

earlier monsoons had greater precipitation. This suggests that the timing and intensity of rainfall and antecedent soil moisture influences the total biomass of plant pulses (Sala et al. 2012, Petrie et al. 2018). The rodent community also showed a non-linear response to precipitation and biomass increase with a much greater shift to C<sub>3</sub> resources during the monsoon of 2007 than in 2005, despite similar C<sub>3</sub> total biomass and C<sub>4</sub> resources being more abundant, which could be attributed to differences in C<sub>3</sub> plant species composition.

***The Importance of C<sub>3</sub> Plants to Consumer Diets.*** Our study showed a strong community response to an increase in C<sub>3</sub> resources and increasing dietary overlap with this increase in C<sub>3</sub> resource use. This increase in C<sub>3</sub> resource assimilation, especially in heteromyids, occurred in the presence of abundant C<sub>4</sub> resources, indicating that C<sub>3</sub> resources are of primary importance, most likely due to their high nutritional quality. The leaves of C<sub>3</sub> plants are more nutritious, with higher nitrogen and digestible carbohydrate content, than C<sub>4</sub> grasses (Barbehenn et al. 2004a, 2004b, Caswell et al. 1973, Caswell and Reed 1975, 1976). C<sub>3</sub> annuals also produce larger seeds (Davidson et al. 1985, Reichman and Colton 1976, Samson et al. 1992) and heteromyids have been shown to prefer larger more nutritious seeds (Reichman and Price 1993) and tend to gather and ingest seeds that are higher in energy content (Reichman 1977, Reichman and Price 1993). In contrast, the leaves of C<sub>4</sub> grasses are harder to process and digest and are more resistant to decomposition (Vanderbilt et al. 2008).

Other studies have similarly noted the overall importance of the C<sub>3</sub> resources to consumers in this system. Warne et al. (2010) found that, at the Sevilleta LTER during 2005, grasshopper and lizard resource assimilation tracked the increasing abundance of C<sub>4</sub> plants, but the carbon assimilated was mostly from C<sub>3</sub> resources. The failure of winter



rains and C<sub>3</sub> resources in 2006 forced consumers to rely more strongly on recalcitrant C<sub>4</sub> resources, but C<sub>3</sub> biomass still comprised 60% of the total biomass assimilated by the lizard community, showing a strong preference for this scarce resource in the arthropod community. The preference for C<sub>3</sub> resources may be tied to the lower performance observed in arthropods fed C<sub>4</sub> plant materials; they have smaller adult body sizes, as well as lower growth rates, survival, and fecundity (Awmack and Leather 2002, Barbehenn et al. 2004a, Caswell et al. 1973).

As in this study, other researchers have remarked on the importance of C<sub>3</sub> forbs in the diets of desert rodents (Bailey 1971, Reichman 1975). Specifically, at the Sevilleta LTER, the importance of C<sub>3</sub> productivity to the rodent community was shown by dietary data collected by Hope and Parmenter (2007). They examined the stomach contents of rodents and found that, across all habitat types, rodents consumed green vegetation, grass (C<sub>4</sub> species) and forb seeds (C<sub>3</sub> species), and sometimes arthropods. Despite the variation in diets, forb seeds comprised the majority, or a significant proportion, of the seeds collected by the individual species, and were utilized more heavily during the spring and summer months, and to a lesser extent in winter.

***C<sub>3</sub> Resource Pulses and Rodent Populations.*** Many species rely on peaks of nutrient availability that resource pulses provide for reproduction (Durant et al. 2005, 2007, Hamalainen et al. 2017, Williams et al. 2017). Several studies have shown the importance of the spring pulse of vegetation to the initiation of reproduction in desert rodent communities (Beatley 1969, 1974, 1976a, 1976b, Brown and Heske 1990b, Reichman and Vandegraaf 1975, Reynolds 1960, Van de Graff and Balda 1973). Similarly, to satisfy increased water demands during lactation, *D. merriami* will increase

consumption of green vegetation and arthropods during reproduction (Bradley and Maur 1971, Nagy and Gruchacz 1994, Soholt 1977, Tracy and Walsberg 2002). Increased reproductive output was also associated with assimilation of energy from C<sub>3</sub> plants, which was ultimately constrained by rainfall, in *C. gunnisoni* (Hayes et al. 2016).

***Trophic Structure of the Rodent Community and Shifts Associated with Resource Scarcity.*** The trophic structure of this rodent community is as one would expect based on prior dietary analyses (Hope and Parmenter 2007). We found that *N. albigula*, *X. spilosoma*, and *D. spectabilis* consistently fed at the lowest trophic levels, rarely showing high tissue  $\delta^{15}\text{N}$  values ( $>10\text{‰}$ ) that would indicate omnivory. Among the cricetids, *O. arenicola* and *Peromyscus. spp.* showed mean tissue  $\delta^{15}\text{N} >10\text{‰}$ , which ranged as high as 12‰ indicating that  $>50\%$  of individuals sampled were omnivorous. Tissue  $\delta^{15}\text{N}$  values for *R. megalotis* indicated that  $\sim 25\%$  of individuals sampled were also omnivorous. Among the heteromyids, 20-30% of *D. merriami* and *D. ordii* appeared to engage in some omnivory ( $\delta^{15}\text{N} >10\text{‰}$ ). In addition, approximately 25% of the pocket mice, *P. flavus*, that were sampled showed some omnivory. In general, trophic level appeared to increase in all species coincident with increased use of C<sub>4</sub>, which may indicate increased consumption of arthropods as C<sub>3</sub> resources became less available. Periods of omnivory by heteromyids *D. merriami*, *D. ordii*, and *P. flavus* were particularly focused in the spring and summer months of 2006, following the failure of winter rains and C<sub>3</sub> plant productivity. Other studies indicate that arthropods can constitute a substantial proportion of heteromyid diets (Hope and Parmenter 2007, Nagy and Gruchacz 1994, Reichman 1975, Reichman and Price 1993, Tracy and Walsberg 2002). The high protein and water content of arthropod prey consumed during this period

could have supported reproductive activities during a period of resource scarcity. For some heteromyids, seed caching may also provide a buffer from resource scarcity, as indicated by high C<sub>3</sub> use during periods of decreased C<sub>3</sub> availability. *D. spectabilis* and *D. merriami* maintained 50% or greater C<sub>3</sub> use when C<sub>3</sub> production failed during the winter of 2005/2006. However, *D. ordii* and *P. flavus* showed resource use similar to the cricetid species *R. megalotis* and *O. arenicola*, which was close to 50% or greater C<sub>4</sub> use.

We found that heteromyid rodent  $\delta^{15}\text{N}$  values were generally higher during the winter and, conversely, cricetid  $\delta^{15}\text{N}$  values were lower during this period, suggesting a lower trophic position when arthropods are less available. We note, however, that  $\delta^{15}\text{N}$  values of blood plasma can be influenced by the variation of  $\delta^{15}\text{N}$  ratio of plants, which is attributed to differences in nitrogen fixation, moisture stress, plant parts, or other plant physiological traits which can change seasonally (Dawson et al. 2002).  $\delta^{15}\text{N}$  of nitrogen fixing plants, which are generally C<sub>3</sub> plants, is lower than non-nitrogen fixing plants (Shearer et al. 1983) and the use of these nitrogen fixing plants would somewhat decrease  $\delta^{15}\text{N}$  values of blood plasma. We found low tissue  $\delta^{15}\text{N}$  values (~6‰) in heteromyids mostly during the spring and summer, when C<sub>3</sub> utilization was also the highest, suggesting significant intake of seeds from nitrogen fixing C<sub>3</sub> plants by some individuals.

#### ***What do Current Climate Projections and our Data Suggest for Desert***

***Rodents?*** Climate projections for southwest North America suggest overall increasing temperatures and aridity, with a decrease in winter precipitation, and monsoonal precipitation arriving later in the year with less frequent and more intense events (Christensen et al. 2013, Maurer et al. 2007). In the Chihuahuan desert, the increases in aridity and temperature would lead to decreased primary production, with decreased plant

species richness and decreased production of C<sub>3</sub> forbs (Fay et al. 2003, Knapp et al. 2002, Munson et al. 2013, Caracciolo et al. 2016). Increases in nitrogen deposition could increase plant growth and quality (Throop and Lerdau 2004, Ladwig et al. 2012), but elevated atmospheric carbon dioxide concentration will decrease the nutrient density of C<sub>3</sub> plants, but not C<sub>4</sub> plants (Barbehenn et al. 2004a). Changes in rainfall patterns and increasing temperatures have also been shown to alter the phenology of plants (Badeck et al. 2004, Keeling et al. 1996) thus additionally altering the timing of resource availability.

Given the different dietary strategies of the rodents in this community we would expect the changes in the resource landscape, mainly diminished availability of C<sub>3</sub> resources, to have differential impacts across the rodent community. Heteromyids tend to avoid seeds smaller than 0.3 mg and increase consumption of seeds up to 5 mg (Reichman and Price 1993). A reduction in the abundance of forbs, which have larger seeds with higher caloric content, would increase seed foraging costs and predation risk. In addition, because of the high reliance of heteromyid rodents on C<sub>3</sub> resources during the spring, reduced rainfall may well result in decreased reproductive output. Across the whole rodent community, when C<sub>3</sub> production was absent, there was a general increase in the use of C<sub>4</sub> resources with a concomitant increase in trophic level, as well as greater dietary breadth and less dietary overlap in all species except *O. arenicola*. Increased C<sub>4</sub> use by the bulk of the arthropod community and the resulting decrease in abundance, body size, and nutritional quality could also have negative effects on higher trophic levels such as the rodent community. Climate change induced decreases in total primary productivity and highly nutritious C<sub>3</sub> resources, and potential decreases in arthropod biomass, may have effects on rodent body condition, disease and parasite susceptibility,

survival and reproductive output, which would ultimately influence population size and community structure (Bowers et al. 1987, Brown and Heske 1990a, 1990b, Brown and Lieberman 1973, Brown and Munger 1985, Brown and Zeng 1989).

**Conclusions.** Through quantification of resource availability, and more importantly quantification of resource assimilation, as provided in this study, we can begin to understand the importance of resource pulses to consumers. This study provides direct information on the utilization of distinct pulses of plant production, of greatly varying composition and quality, to consumers. This enables us to link precipitation to plant production and consumer utilization by providing data on resource use by animals as a function of photosynthetic pathway, which provides insight into how resource use may be altered by climate change. Changes in precipitation patterns and therefore resource availability, and the availability of energy for growth and reproduction, would be expected to directly influence consumer population dynamics and community composition (White et al. 2004). However, the relationship between rainfall and fluctuations in rodent populations in the northern Chihuahuan desert have been weak or non-linear. This has been attributed to the species composition of the vegetation, timing and magnitude of precipitation, as well as top down and bottom up processes (Baez et al. 2006, Ernest et al. 2000, Thibault et al. 2010). Pulses of precipitation and vegetation vary in magnitude, proportion of C<sub>3</sub> and C<sub>4</sub> vegetation, species composition, phenology and, therefore, these pulses vary in quality. Given the importance of C<sub>3</sub> resources to rodent diets and reproduction, and variability of resources pulses, rodent populations should not be expected to have a linear response to precipitation. Resource pulses, such as the pulse of C<sub>3</sub> resources in this system, illicit responses at individual level in terms of food choice,

at the population level in terms of reproductive output and timing or aggregations of animals (Yang 2008), and at the community level in terms of population densities, competition, and changes in species interactions (Brown and Munger 1985, Collins et al. 2014). The impact of the altered resource landscape in the face of climate change would therefore be expected to have a significant impact on population size, species diversity, and competition in small mammals, which would also affect ecosystem processes and have implications cascading up and down trophic levels in the ecosystem (Chesson 2004, Schmitz 2008).

## APPENDICES

**Appendix A.** Whole plant  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values

**Appendix B.** Supplemental Tables and Figures

**APPENDIX A. WHOLE PLANT  $\delta^{15}\text{N}$  AND  $\delta^{13}\text{C}$  VALUES**

Table A1. Whole plant  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for the 38 most abundant species of  $\text{C}_3$  and  $\text{C}_4$  plants at the Sevilleta Long Term Ecological Research site.

<b>Plant Species</b>	<b><math>\text{C}_3/\text{C}_4</math></b>	<b><math>\delta^{15}\text{N}</math></b>	<b>SD</b>	<b><math>\delta^{13}\text{C}</math></b>	<b>SD</b>	<b># sampled</b>
<i>Aphanostephus arizonicus</i>	$\text{C}_3$	5.8	*	-26.9	*	1
<i>Asclepias asperula</i>	$\text{C}_3$	1.6	*	-25.4	*	1
<i>Astragalus missouriensis</i>	$\text{C}_3$	0.6	*	-26.5	*	1
<i>Hoffmannseggia drepanocarpa</i>	$\text{C}_3$	1.4	1.1	-26.6	0.3	4
<i>Calycoseris wrightii</i>	$\text{C}_3$	2.2	0.1	-27.7	0.4	2
<i>Chamaesaracha coniodes</i>	$\text{C}_3$	*	*	-26.2	*	1
<i>Cryptantha crassisepala</i>	$\text{C}_3$	1.7	2.9	-27.2	0.3	3
<i>Dalea formosa</i>	$\text{C}_3$	-1.9	1.8	-25.3	0.5	2
<i>Dalea nana</i>	$\text{C}_3$	-2	*	-26.8	*	1
<i>Desucainia pinnata</i>	$\text{C}_3$	3	*	-27.9	0.7	3
<i>Sitanion hystrix</i>	$\text{C}_3$	2.6	0.8	-27.1	1.6	4
<i>Ephedra torreyana</i>	$\text{C}_3$	4.6	1	-24.1	0.3	3
<i>Eriogonum rotundifolium</i>	$\text{C}_3$	7.1	*	-27.7	*	1
<i>Evolvulus pilosus</i>	$\text{C}_3$	1.6	0.3	-26.8	0.5	2
<i>Gaillardia pinnatifida</i>	$\text{C}_3$	1.1	1.2	-27.9	1.4	2
<i>Gutierrezia sarothrae</i>	$\text{C}_3$	1.7	1.2	-27.5	0.1	2
<i>Hedyotis rubra</i>	$\text{C}_3$	1.4	0.2	-28.6	1.3	2
<i>Ipomopsis pumila</i>	$\text{C}_3$	3	2.6	-26.7	2	2
<i>Ceratoides lanata</i>	$\text{C}_3$	5.7	0.5	-26.5	1.3	3
<i>Lappula redowskii</i>	$\text{C}_3$	3.7	0.4	-27.2	1.5	4
<i>Larrea tridentata</i>	$\text{C}_3$	5.6	1.3	-25	1.3	3
<i>Lesquerella fendleri</i>	$\text{C}_3$	4.7	0.2	-25.1	1.2	4
<i>Haplopappus spinulosus</i>	$\text{C}_3$	2.2	0.9	-27.5	0.2	3
<i>Orobanche multiflora</i>	$\text{C}_3$	*	*	-28.2	*	1
<i>Phacelia integrifolia</i>	$\text{C}_3$	6.6	1.1	-28.2	1	4
<i>Plantago purshii</i>	$\text{C}_3$	2.5	0.6	-27.4	1.2	4
<i>Solanum elaeagnifolium</i>	$\text{C}_3$	3.3	1.4	-27.1	0.1	2
<i>Sphaeralcea leptophylla</i>	$\text{C}_3$	2.2	1.1	-26.1	1.2	4
<i>Sphaeralcea wrightii</i>	$\text{C}_3$	5.1	0.9	-27.2	1.4	4
<i>Townsendia annua</i>	$\text{C}_3$	2.8	*	-27.5	*	1
<b><math>\text{C}_3</math> (mean <math>\pm</math> SE)</b>		<b>2.9 <math>\pm</math> 0.4</b>		<b>-26.9 <math>\pm</math> 0.2</b>		
<i>Amaranthus graecizans</i>	$\text{C}_4$	5.9	0.9	-12.8	0.4	2
<i>Aristida purpurea</i>	$\text{C}_4$	1.1	0.6	-13.7	0.6	5
<i>Atriplex canescens</i>	$\text{C}_4$	8.4	*	-13	*	1



Table A1. (continued)

<i>Bouteloua eriopoda</i>	C <sub>4</sub>	-0.5	0.6	-14.8	0.4	2
<i>Bouteloua gracilis</i>	C <sub>4</sub>	-0.1	0.2	-14.4	0.4	3
<i>Chamaesyce albomarginata</i>	C <sub>4</sub>	1.7	0.7	-13.4	0.7	5
<i>Erioneuron pulchellum</i>	C <sub>4</sub>	1.4	0.5	-14.6	0.1	4
<i>Muhlenbergia arenicola</i>	C <sub>4</sub>	1.7	*	-14.1	*	1
<i>Muhlenbergia porteri</i>	C <sub>4</sub>	0.7	0.7	-14.5	0.7	4
<i>Scleropogon brevifolius</i>	C <sub>4</sub>	4.6	*	-14.3	*	1
<i>Sporobolus airoides</i>	C <sub>4</sub>	4.6	*	-24.7	*	1
<i>Sporobolus contractus</i>	C <sub>4</sub>	1.3	1.6	-14.7	0.7	2
<i>Sporobolus cryptandrus</i>	C <sub>4</sub>	1.4	*	-13.7	*	1
<i>Sporobolus flexuosus</i>	C <sub>4</sub>	3.3	1.2	-13.9	0.7	2
<b>C<sub>4</sub> (mean ± SE)</b>		<b>2.5 ± 0.7</b>		<b>-14.8 ± 0.9</b>		

*Notes:* Isotope values are for homogenized plant tissues from 1-5 individual plants per species. Asterisks represent missing data.

APPENDIX B. SUPPLEMENTAL TABLES AND FIGURES

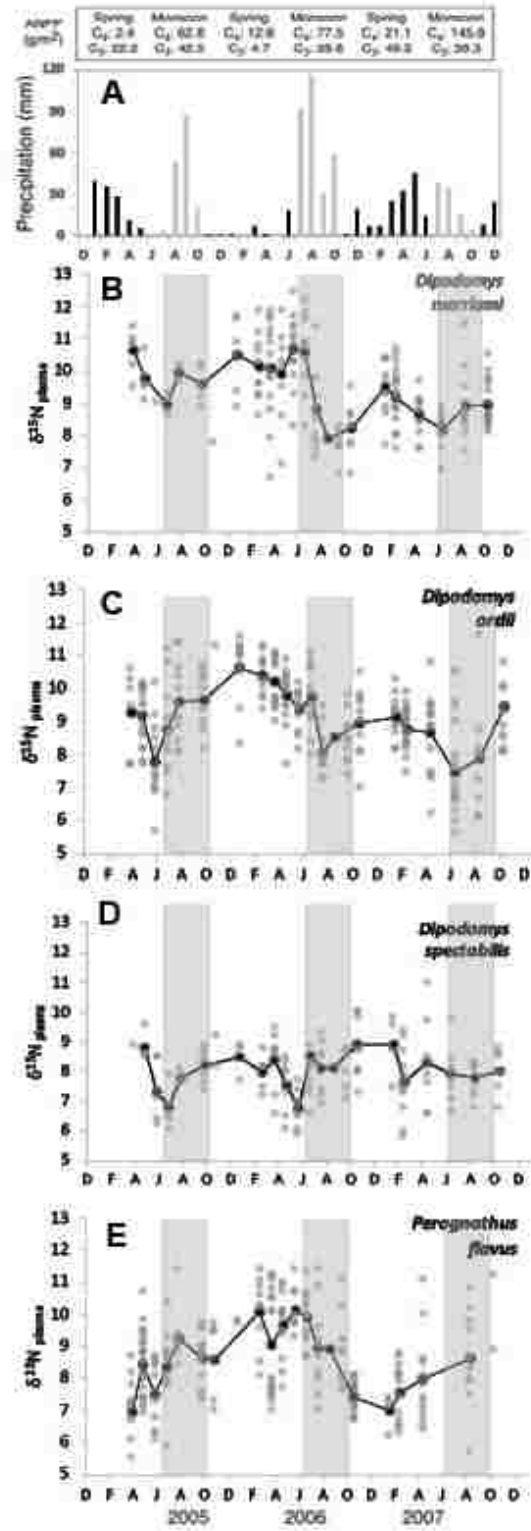


Figure B1. Heteromyid  $\delta^{15}\text{N}$  ( $\% \text{ AIR}$ ) as a function of trapping month. Also presented are seasonal precipitation values and ANPP measured on nearby plots.

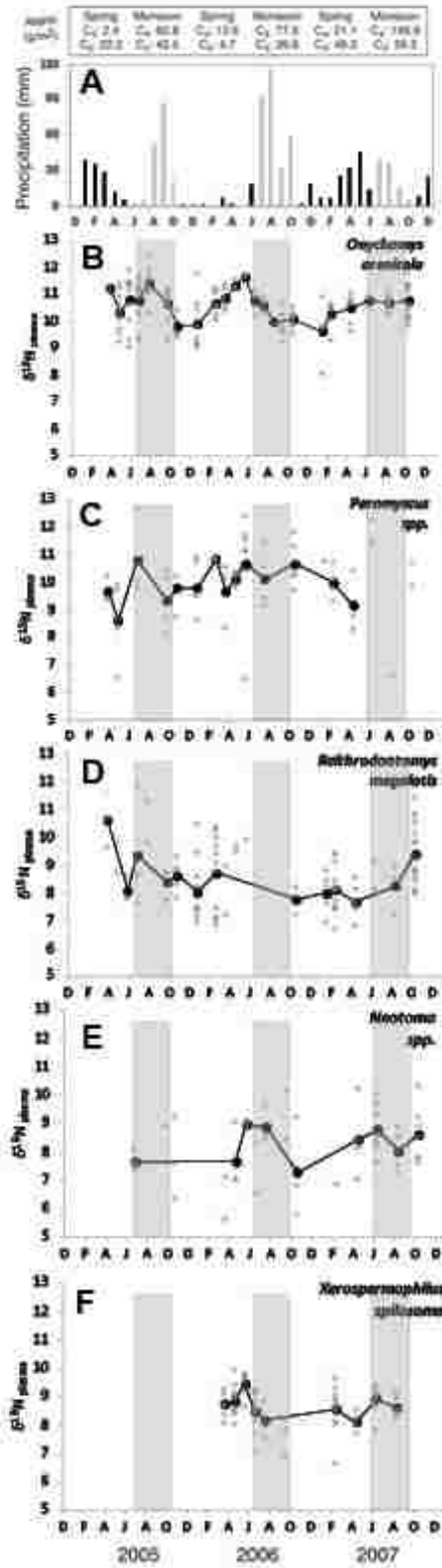


Figure B2. Cricetid and *X. spilosoma*  $\delta^{15}\text{N}$  (‰ AIR) as a function of trapping month. Also presented are seasonal precipitation values and ANPP measured on nearby plots.

Table B1. Heteromyid Tukey HSD p-values for comparisons between seasonal  $\delta^{13}\text{C}$  (‰ VPDB) of plasma indicating, for each species, significant differences in diet between seasons.

<i>D. merriami</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	0.843	0.218	0.136	<b>0.004</b>	1.000	1.000
Monsoon 2005		X	0.993	0.945	0.353	0.479	0.909
Winter/Spring 2005-2006			X	0.997	0.249	<b>0.006</b>	0.211
Monsoon 2006				X	0.836	<b>0.005</b>	0.133
Winter/Spring 2006-2007					X	<b>&lt; 0.0001</b>	<b>0.002</b>
Monsoon 2007						X	0.987
Fall 2007							X
<i>D. ordii</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	<b>0.036</b>	<b>&lt; 0.0001</b>	<b>0.004</b>	<b>0.044</b>	<b>0.042</b>	0.840
Monsoon 2005		X	<b>0.000</b>	0.992	1.000	<b>&lt; 0.0001</b>	0.007
Winter/Spring 2005-2006			X	<b>0.003</b>	<b>&lt; 0.0001</b>	<b>&lt; 0.0001</b>	<b>&lt; 0.0001</b>
Monsoon 2006				X	0.886	<b>&lt; 0.0001</b>	<b>0.001</b>
Winter/Spring 2006-2007					X	<b>&lt; 0.0001</b>	<b>0.009</b>
Monsoon 2007						X	0.961
Fall 2007							X
<i>D. spectabilis</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	0.229	0.999	0.170	0.982	0.940	0.419
Monsoon 2005		X	0.179	1.000	<b>0.002</b>	<b>0.005</b>	1.000
Winter/Spring 2005-2006			X	0.102	0.493	0.482	0.472
Monsoon 2006				X	<b>0.001</b>	<b>0.002</b>	1.000
Winter/Spring 2006-2007					X	0.999	<b>0.047</b>
Monsoon 2007						X	<b>0.046</b>
Fall 2007							X
<i>P. flavus</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	0.938	0.997	0.628	0.572	<b>&lt; 0.0001</b>	0.716
Monsoon 2005		X	0.659	0.145	0.997	<b>&lt; 0.0001</b>	0.509
Winter/Spring 2005-2006			X	0.892	0.198	<b>&lt; 0.0001</b>	0.806
Monsoon 2006				X	0.020	<b>0.004</b>	0.950
Winter/Spring 2006-2007					X	<b>&lt; 0.0001</b>	0.386
Monsoon 2007						X	0.993
Fall 2007							X

Notes: Significant differences noted in **bold** font. “-” indicates missing data.

Table B2. Cricetid and *X. spilosoma* Tukey HSD p-values for comparisons between seasonal  $\delta^{13}\text{C}$  (‰ VPDB) of plasma indicating, for each species, significant differences in diet between seasons.

<i>O. arenicola</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	< <b>0.0001</b>	0.468	<b>0.010</b>	0.844	0.197	0.371
Monsoon 2005		X	< <b>0.0001</b>	0.106	< <b>0.0001</b>	<b>0.010</b>	< <b>0.0001</b>
Winter/Spring 2005-2006			X	0.408	0.997	0.964	<b>0.004</b>
Monsoon 2006				X	0.180	0.980	< <b>0.0001</b>
Winter/Spring 2006-2007					X	0.804	<b>0.023</b>
Monsoon 2007						X	<b>0.002</b>
Fall 2007							X
<i>Peromyscus spp.</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	0.096	<b>0.001</b>	0.452	1.000	-	-
Monsoon 2005		X	0.994	1.000	0.038	-	-
Winter/Spring 2005-2006			X	0.967	<b>0.000</b>	-	-
Monsoon 2006				X	0.288	-	-
Winter/Spring 2006-2007					X	-	-
Monsoon 2007						X	-
Fall 2007							X
<i>R. megalotis</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	0.990	0.931	-	0.969	0.991	0.502
Monsoon 2005		X	0.518	-	1.000	1.000	0.901
Winter/Spring 2005-2006			X	-	0.089	0.671	<b>0.005</b>
Monsoon 2006				X	-	-	-
Winter/Spring 2006-2007					X	1.000	0.711
Monsoon 2007						X	0.964
Fall 2007							X
<i>Neotoma spp.</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	-	-	-	-	-	-
Monsoon 2005		X	0.995	0.971	<b>0.002</b>	<b>0.014</b>	0.063
Winter/Spring 2005-2006			X	0.999	<b>0.001</b>	<b>0.008</b>	0.067
Monsoon 2006				X	<b>0.007</b>	0.054	0.210
Winter/Spring 2006-2007					X	0.859	0.800
Monsoon 2007						X	1.000
Fall 2007							X
<i>X. spilosoma</i>	Spring 2005	Monsoon 2005	Winter/Spring 2005-2006	Monsoon 2006	Winter/Spring 2006-2007	Monsoon 2007	Fall 2007
Spring 2005	X	-	-	-	-	-	-
Monsoon 2005		X	-	-	-	-	-
Winter/Spring 2005-2006			X	0.424	< <b>0.0001</b>	<b>0.002</b>	-
Monsoon 2006				X	<b>0.000</b>	0.123	-
Winter/Spring 2006-2007					X	0.241	-
Monsoon 2007						X	-
Fall 2007							X

Notes: Significant differences noted in **bold** font. “-” indicates missing data.

Table B3. Rodent community Tukey HSD p-values for comparisons between each species' seasonal  $\delta^{13}\text{C}$  (‰ VPDB) of plasma indicating, for each season, significant differences in diet between species.

Spring 2005										Monsoon 2005									
	DIME	DIOR	DISP	PGFV	ONAR	PM	NEOTOMA	REMG	XESP		DIME	DIOR	DISP	PGFV	ONAR	PM	NEOTOMA	REMG	XESP
DIME	X	1.000	0.177	<b>0.003</b>	<b>0.014</b>	0.878	-	<b>0.010</b>	-	DIME	X	0.993	<b>0.018</b>	0.148	< <b>0.0001</b>	<b>0.002</b>	< <b>0.0001</b>	0.927	-
DIOR		X	0.065	< <b>0.0001</b>	<b>0.000</b>	0.813	-	<b>0.002</b>	-	DIOR		X	<b>0.019</b>	0.186	< <b>0.0001</b>	<b>0.003</b>	< <b>0.0001</b>	0.996	-
DISP			X	0.993	0.999	0.952	-	0.879	-	DISP			X	0.851	0.459	0.887	<b>0.011</b>	0.661	-
PGFV				X	1.000	0.533	-	0.972	-	PGFV				X	<b>0.001</b>	0.211	<b>0.000</b>	0.990	-
ONAR					X	0.691	-	0.960	-	ONAR					X	1.000	0.200	<b>0.015</b>	-
PM						X	-	0.368	-	PM						X	0.419	0.158	-
NEOTOMA							X	-	-	NEOTOMA							X	<b>0.000</b>	-
REMG								X	-	REMG								X	-
XESP									X	XESP									X
Winter/Spring 2005-2006										Monsoon 2006									
	DIME	DIOR	DISP	PGFV	ONAR	PM	NEOTOMA	REMG	XESP		DIME	DIOR	DISP	PGFV	ONAR	PM	NEOTOMA	REMG	XESP
DIME	X	< <b>0.0001</b>	0.953	0.998	0.777	< <b>0.0001</b>	<b>0.001</b>	<b>0.004</b>	1.000	DIME	X	1.000	0.155	0.963	0.237	0.613	0.132	-	1.000
DIOR		X	0.058	<b>0.001</b>	0.234	<b>0.002</b>	0.768	1.000	<b>0.050</b>	DIOR		X	0.191	0.875	0.288	0.676	0.161	-	1.000
DISP			X	1.000	1.000	< <b>0.0001</b>	<b>0.020</b>	0.252	0.998	DISP			X	<b>0.007</b>	1.000	1.000	0.991	-	0.444
PGFV				X	0.984	< <b>0.0001</b>	<b>0.003</b>	<b>0.031</b>	1.000	PGFV				X	<b>0.020</b>	0.243	<b>0.018</b>	-	0.919
ONAR					X	< <b>0.0001</b>	0.055	0.547	0.980	ONAR					X	1.000	0.995	-	0.518
PM						X	0.983	<b>0.006</b>	< <b>0.0001</b>	PM						X	1.000	-	0.780
NEOTOMA							X	0.747	<b>0.011</b>	NEOTOMA							X	-	0.282
REMG								X	0.150	REMG								X	-
XESP									X	XESP									X
Winter/Spring 2006-2007										Monsoon 2007									
	DIME	DIOR	DISP	PGFV	ONAR	PM	NEOTOMA	REMG	XESP		DIME	DIOR	DISP	PGFV	ONAR	PM	NEOTOMA	REMG	XESP
DIME	X	0.588	0.461	0.829	1.000	0.983	0.098	1.000	<b>0.017</b>	DIME	X	<b>0.033</b>	0.261	<b>0.001</b>	< <b>0.0001</b>	0.993	0.217	<b>0.031</b>	0.457
DIOR		X	1.000	<b>0.017</b>	0.488	1.000	0.650	0.940	0.400	DIOR		X	< <b>0.0001</b>	0.659	< <b>0.0001</b>	0.292	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>
DISP			X	<b>0.016</b>	0.371	1.000	0.843	0.846	0.695	DISP			X	< <b>0.0001</b>	<b>0.001</b>	1.000	1.000	0.806	1.000
PGFV				X	0.996	0.485	<b>0.007</b>	0.741	<b>0.000</b>	PGFV				X	< <b>0.0001</b>	<b>0.041</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>
ONAR					X	0.932	0.071	0.998	<b>0.015</b>	ONAR					X	0.072	<b>0.003</b>	0.791	<b>0.001</b>
PM						X	0.711	0.999	0.564	PM						X	1.000	0.739	1.000
NEOTOMA							X	0.235	1.000	NEOTOMA							X	0.883	1.000
REMG								X	0.083	REMG								X	-
XESP									X	XESP									X

Notes: Significant differences noted in bold font. “-“ indicates missing data

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