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Forage selection and habitat architecture as drivers of small mammal community dynamics in an arid, nutrient limited, highly stochastic ecosystem

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DISSERTATION

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ABSTRACT

In the Northern Chihuahuan desert, grassland and shrubland co-occur as separate stable states under similar climatic conditions. In this bottom up (resource driven) system, the magnitude and timing of precipitation events drives primary production which varies from year to year and season to season. Climate change is predicted to alter precipitation regimes, and increase aridity, facilitating shrub encroachment which results in increased landscape heterogeneity and a decrease in plant biodiversity. These changes will likely result in a restructuring of small mammal communities.

We used long-term data on precipitation, primary production, and abundances of small mammals in adjacent grassland and shrubland stable states and across an ecotone between grassland and shrubland to characterize foraging patterns in heteromyids, food-caching granivores, and cricetids, omnivores that do not cache and rely on body fat for short term energy reserves. To accomplish this, we trapped 7,063 mice across a grassland/shrubland ecotone which resulted in 3,560 mouse plasma isotope analyses from 1,533 individually marked mice. By comparing raw isotopic values of δ^{13}C and δ^{15}N in mouse plasma to plant values, we can track community wide foraging patterns. Using a subset of 1,406 plasma samples from one species (*Perognathus flavus*) we were able to document the development of individualized foraging strategies to alleviate intra-specific competition during a population explosion.

The grassland supports a lower density subset of rodent species found in shrubland. Using a 25 year small mammal trapping dataset, there was no indication of directional change in species composition in either stable state, just a temporal reordering of species dominance. Consumer diets track nitrogen on the landscape, with cricetids foraging at a higher trophic level than heteromyids during resource abundance, diets converge and broaden as resources decline. A population boom in *Perognathus flavus* increased intraspecific competition causing some individuals to specialize on either C_3 or C_4 resources, while 60% of the population remained generalist foragers. Mice in this community exhibit a high degree of dietary plasticity to survive high stochasticity in resource quantity and quality. This study uses a unique suite of tools to examine the interface of precipitation, primary production, and small mammal foraging characteristics.

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Chapter 1: Introduction

Arid and semiarid lands cover approximately 41% of the terrestrial surface of the earth and are expected to cover an additional 11 to 23% by the end of this century (Maestre et al. 2016). Many arid lands that were historically covered with vast expanses of C_4 grasslands are experiencing encroachment of C_3 shrubs, dramatically altering the landscape. Shrub encroachment has many effects on ecosystem function, including changes in plant community composition, altered temperature and nutrient cycling, and increased landscape heterogeneity (Van Auken 2000 and 2009, Cabral et al. 2003, Throop et al. 2007, Collins et al. 2014). The consequences of these changes on the diverse and abundant small mammal community supported by these highly stochastic systems is currently unknown. Small mammals are primary consumers supporting multiple trophic levels, their health is vital for ecosystem function. The goal of my dissertation research is to quantify small mammal community dynamics in the Chihuahuan desert and to delineate the relationships among resource availability, and foraging characteristics accross a grassland-shrubland ecotone.

At the northern end of the Chihuahuan Desert in the Sevilleta National Wildlife Refuge (Sevilleta), creosote (*Larrea tridentata)* dominated shrubland co-occurs with black grama (*Bouteloa eriopoda)* dominated grassland as alternative stable states. However, climate models predict a ~10–20% decrease in winter precipitation in the Southwest region over the next century (Gutzler et al. 2007, Seager et al. 2007) which is expected to alter the boundary between these two stable states. An increase in aridity, combined with changing precipitation patterns is expected to favor the expansion of woody shrubs (Baez et al. 2013). As shrubs encroach into grasslands, there is an initial increase in plant biodiversity due to increasing habitat heterogeneity, however, as shrubs become dominant there are distinct changes in these two habitats. Shrublands tend to have increased temperatures due to an increase in bare ground and there is an overall loss of plant biodiversity (Baez et al. 2008, D'Odorico et al. 2010) when compared with grasslands. Resource availability, habitat heterogeneity, and seasonality all coalesce to define the density and composition of consumer communities (Pärtel et al. 2007). Relating changes in consumer communities to the availability of specific plant resources within three vegetation zones, grassland, shrubland, and across a grass-shrub ecotone will improve our understanding of ecosystem function in these highly stochastic regions.

Currently, much of the American Southwest experiences a bimodal precipitation pattern (Notaro et al. 2010) that results in two seasonal pulses of net primary production dominated by plants that use either the C_3 or C_4 photosynthetic pathway. The growth of plants in this system depends on the amount of precipitation received and the air temperatures that coincide with that precipitation (Ehleringer et al. 1977and 1991, Muldavin et al. 2008, Sala et al. 2012). Cooler temperatures and winter/spring rains favor the production of C_3 forbs with mean $\delta^{13}C$ (the isotopic ratio of ^{13}C to ^{12}C) values of -26.5‰, while the summer monsoon and warmer temperatures fuel production of C_4 grasses with mean $\delta^{13}C$ values of -14.7‰ (Xia et al. 2010). In addition to having different $\delta^{13}C$ values (Craig 1953, Farquhar et al. 1982), C_3 and C_4 plants also differ in their nutritional quality. C_3 plants are more nutritious with a higher nitrogen content, a common proxy for forage quality, in both leaf and seeds, when compared to C_4 plants (Guo et al. 2000 and 2003, Hope et al. 2007, Orr et al. 2015). Thus, primary consumers in these ecosystems must choose between a low quality and consistently abundant resource

(C_4 grasses) versus a higher quality less reliable resource (C_3 forbs). Since forb abundance is strongly correlated with seasonal rainfall (Xia et al. 2010, Mulhouse et al. 2016), climate change will likely decrease the biomass of C_3 forbs, reducing the availability of this high quality forage.

Consumer life histories are intimately tied to the quality, quantity, and timing of primary production which in turn influences community dynamics. The composition of the small mammal community at Sevilleta is especially interesting from a resource dynamics perspective because there are two families of mice, ranging in size from 5-150g with differing life histories and energy requirements. Heteromyids are food-caching granivores, caching either underground (larder hoarders) or on the surface (scatter hoarders), with constrained litter sizes and a high-energy diet (Ernest et al. 2000, Brown et al. 1989, Kelt et al. 1999, 2011). Cricetids forage at multiple trophic levels and can be generalist herbivores, omnivores, or carnivores. Unlike heteromyids, cricetids do not cache food and must rely on their body fat stores as energy reserves during times of resource scarcity. Cricetids have higher reproductive potential with generally larger litter sizes than the heteromyids. Long-term studies conducted in Portal, Arizona have shown that changing precipitation regimes, increasing frequency of extreme climatic events and shrub encroachment have caused a restructuring of small mammal communities (Thibault et al. 2010). It is currently unknown if these same conditions will result in a similar restructuring of the small mammal community at Sevilleta. To determine this, it is imperative to understand current small mammal community dynamics.

Questions: In Chapter 2 of my dissertation: **Long-term small mammal community dynamics in northern Chihuahuan Desert grassland and shrubland**

vegetation, I used datasets generated by the Sevilleta Long Term Ecological Research (LTER) program to answer the following questions (1) Does the abundance and diversity of small mammals increase with shrub encroachment? (2) Is the community composition of heteromyids and cricetids different within and between stable states? (3) Does the small mammal community exhibit long-term directional change in either stable state, or are changes in these communities a result of temporal reordering of dominant species?(4) Is there a significant effect of precipitation on primary production and small mammal community dynamics?

Analysis of these long term data sets showed clear temporal differences in small mammal community composition between both stable states and foraging guild. However, it did not address consumer adaptations to high stochasticity in forage quantity and quality. One possibility is resource partitioning which can allow several species with similar habitat and nutritional requirements to co-exist in a nutrient limited ecosystem (Kartzinel et al. 2015). This partitioning occurs either spatially, by foraging in different parts of the landscape (MacArthur 1958), or temporally, by foraging at different times (Gordon et al. 2010, Houadria et al. 2015, Atwood et al. 2011). In chapter 3 of my dissertation: **Rodent response to changes in landscape architecture**, I used raw isotopic values, forage availability indices, and an analysis of seed characteristics to quantify resource use among species. Plasma δ^{13}C values provide a measure of dietary width and δ^{15}N values a measure of dietary breadth (trophic level).

Questions: By comparing δ^{13}C and δ^{15}N isotopic values from 3,560 rodent plasma samples representing 1,533 unique individuals comprising eight dominant mice species, and comparing it to isotopic values for 698 plant samples, I answered the following questions: (1) Do rodent populations partition the landscape of available resources, or do they primarily consume the highest quality forage? (2) Do rodents maintain consistent diets, or do their diets reflect seasonally variable primary production?

The mark-recapture aspect of my data, and a population explosion of *Perognathus flavus* in 2014 provided the perfect opportunity to study the development of individual foraging strategies. Chapter 4 of my dissertation: **Climate mediated changes in foraging strategies of the silky pocket mouse (*Perognathus flavus)*** utilizes a variety of tools to quantify foraging strategies. Individuals within a population vary their forage choices in response to four major drivers: resource availability (Bolnick et al. 2003, Van Valen 1965, 1970), inter- and intraspecific competition (Araujo et al. 2008, 2011, Bolnick et al. 2007, 2010, 2011,), predation (Bolnick et al. 2003), and physiological variation (Roughgarden 1972). We measured stable isotope composition of 1,406 plasma samples from silky pocket mice (*Perognathus flavus*) to quantify the dietary contributions of C_3 (high quality) versus C_4 (low quality) primary production. Of these samples, 695 were from 173 individual mice captured three or more times over the course of two years providing a temporal record of dietary composition.

Questions: Using data generated from $\delta^{13}C$ and $\delta^{15}N$ isotope analysis of *Perognathus flavus* plasma and long-term metrics of primary production, I was able to address the following questions: Does the foraging breadth of the *P. flavus* population exhibit temporal change reflecting the landscape of available resources? Do foraging strategies vary among co-occurring individuals? And, do most individuals preferentially forage on the most energetically optimal resources (C_3 vs. C_4)?

All trapping for this research occurred within the Sevilleta National Wildlife Refuge (SNWR), located in central New Mexico at the confluence of four major ecological zones: short grass steppe, Chihuahuan Desert grassland/shrubland, juniper savannah, and pinyon-juniper woodlands. My research occurred in core sites that have been extensively monitored, desert grassland, desert shrubland, and across an ecotone between these two stable states. The SNWR is home to the National Science Foundation's Sevilleta Long-Term Ecological Research Program (LTER). In addition to three years of data collection on the Sevilleta LTER, this research utilized long-term trapping data (1989 to present), plant cover and biomass (1999 to present), plant phenology (2000 to present) and meteorological data (1999 to present), all data can be found on the Sevilleta LTER data portal (http://sev.lternet.edu).

Chapter 2: Long-term small mammal community dynamics in northern Chihuahuan Desert grassland and shrubland vegetation

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Abstract:

Shrub encroachment is a widespread global phenomenon. Although the causes of shrub encroachment vary regionally, the consequences are not well understood, particularly for consumer communities that depend on plant community composition and structure for food and habitat. We used long-term data on seasonal precipitation, percent cover of primary producers, and abundance of small mammals in adjacent grassland and shrubland habitats to determine the impacts of shrub encroachment on the dynamics of small mammal community composition in the northern Chihuahuan Desert. We found that two behaviorally distinct families of small mammals, heteromyids and cricetids, utilize these two habitats differently. The grassland tends to have a smaller subset of the species found in the shrubland, and there are significant differences between the abundances of heteromyids and cricetids in each habitat, likely reflecting differences in vegetation architecture which results in increased heterogeneity in the shrubland. The ability to forage on multiple trophic levels may reduce cricetid dependence on primary production in comparison to the heteromyid granivores. Although considerable temporal variation occurred in both grassland and shrubland habitats, neither small mammal community exhibited directional change in species composition over time. Instead, variability reflected temporal reordering of the dominant species as populations' fluctuated in response to changes in resource availability. Thus, despite large changes in

vegetation structure, shrub encroachment does not adversely affect the small mammal community. On the contrary, shrub encroachment results in increased small mammal abundances, and greater numbers of species. Heteromyids are significantly affected by the abundances of plant functional types in both grassland and shrubland while the cricetid population remains consistent despite changes in resource availability.

Introduction:

The composition and dynamics of ecological communities are driven by interactions between environmental presses and pulses (Collins et al. 2011). Pulse events, such as fires, floods, or severe storms, can rapidly alter the structure and dynamics of ecological communities. Environmental presses, on the other hand, are more subtle, but persistent, leading to slow directional change. Theory predicts that ecological communities will exhibit non-linear responses to environmental presses (Smith et al. 2009, Bestelmeyer et al. 2011) such as increasing temperatures or changing precipitation regimes. Communities respond to presses through a hierarchy of mechanisms including physiological plasticity, reordering among dominant species, and ultimately turnover in species composition. As global environmental change continues and ecological presses intensify, ecological communities may reach tipping points leading to catastrophic shifts from one alternative stable state to another (Scheffer et al. 2001).

Arid and semiarid lands represent approximately 45% of terrestrial ecosystems (Safriel and Adeel 2005) and are expected to expand by an additional 11 to 23% by the end of this century in response to global environmental change (Huang et al. 2016, Maestre et al. 2016). Over the past 150 years in the Southwestern US, nearly 20 million hectares of C_4-dominated grassland have been replaced by C_3-dominated shrubland (Van

Auken 2000, 2009), a phenomenon characterized by alternative stable state theory (D’Odorico et al. 2012). Climate models predict warmer temperatures, decreasing and more variable precipitation, and increasing aridity in this region (Gutzler and Robbins 2011, Cook et al. 2015), likely favoring the continued expansion of woody shrubs into grassland (Baez et al. 2013, Caracciolo et al. 2016, He et al. 2015). As shrubs encroach species diversity increases initially due to increased habitat heterogeneity. However, as shrubs begin to dominate there is a loss of plant biodiversity due to a decline in herbaceous biomass and decreased species diversity when compared with adjacent grasslands (Baez et al. 2008, Cabral et al. 2003, D’Odorico et al. 2010). In addition, shrublands are characterized by lower total plant cover, lower net ecosystem production and warmer winter nighttime temperatures, (Pockman and Small 2010, D’Odorico et al. 2010, Petrie et al. 2014), all of which can promote further shrub encroachment (He et al. 2015). The causes of shrub encroachment; changing land use, herbivory, fire management, and environmental presses vary regionally (Van Auken 2000 and 2009, Cabral et al. 2003, Throop et al. 2007). However, the consequences of this encroachment for consumer communities in aridland ecosystems; increased habitat heterogeneity, loss of plant biodiversity, and changes in the timing, quantity and quality of primary productivity (Pärtel et al. 2007), are poorly understood (Noy-Meir 1979, McCluney et al. 2012).

Small mammals are key consumers in arid land ecosystems (Kelt et al. 1999, Madrigal et al. 2011) and they fulfill many important ecological roles, such as a prey base for higher trophic levels (Ernest et al. 2000, Habtamu et al. 2012). In these ecosystems, small mammals are hypothesized to be resource-limited (bottom-up) and not predator controlled “top-down”, strengthening the correlation between resource fluctuations and consumer population dynamics (Slobodkin et al. 1967, Brown et al. 2002). The dynamics of these small mammal communities are linked to the quality, quantity, and timing of primary production (Thibault et al. 2010). Arid lands are characterized by a highly stochastic precipitation regime that results in variable periods of resource abundance and limitation. As a consequence, populations of small mammals fluctuate temporally, persisting at low densities during times of resource scarcity and increasing rapidly when precipitation results in higher net primary production (Holmgren et al. 2006, Letnic et al. 2010, Thibault et al. 2010, Dickman et al. 2011, Meserve et al. 2011).

In the southwestern US, arid land ecosystems are dominated by two families of small mammals that differ in life histories and energy requirements. Heteromyids are food-caching granivores, with constrained litter sizes and a high-energy diet (Ernest et al. 2000, Brown et al. 1989, Kelt et al. 1999, 2011). They are more prevalent in grasslands and rely on annual seed production for their survival (Lightfoot et al. 2012). In contrast, Cricetids forage at multiple trophic levels decoupling their dependence on primary production. As a consequence, they can be generalist herbivores, omnivores, or carnivores depending on resource availability. Unlike heteromyids, cricetids do not cache food and must rely on body fat stores as short-term energy reserves during times of resource scarcity. Cricetids have higher reproductive potential with generally larger litter sizes than the heteromyids. Differential reproductive rates among small mammal species following precipitation events can cause population boom and bust cycles, which can quickly alter the small mammal community structure (Abramsky 1988, Dickman et al. 1999, Letnic et al. 2010).

Changing precipitation regimes, increasing frequency of extreme climatic events and shrub encroachment have been shown to restructure both plant and small mammal communities (Thibault et al. 2010, Collins and Xia 2015). We used long-term data on precipitation, plant community composition, and abundances of small mammals to characterize rodent populations and community dynamics in a region of the northern Chihuahuan Desert where shrub encroachment is currently occurring. Utilizing an array of community dynamics metrics, we were able to answer the following questions (1) Does the abundance and diversity of small mammals increase with shrub encroachment? (2) Is the community composition of heteromyids and cricetids different within and between stable states? (3) Does the small mammal community exhibit long-term directional change in either stable state, or are changes in these communities a result of temporal reordering of dominant species?(4) Is there a significant effect of precipitation on primary production and small mammal community dynamics?

Methods:

Our study was conducted in the Sevilleta National Wildlife Refuge (SNWR: 34°20′N, 106°43′W), Socorro County, New Mexico, USA. Average annual precipitation is ~250 mm, more than half (~150 mm) of which occurs via convective storms which create intense but highly localized rain events during the summer monsoon, July through early September (Pennington & Collins 2007, Notaro et al. 2010, Petrie et al. 2014). Winter and spring precipitation typically occurs as a mixture of snow and light rain (Gosz et al. 1995, Pockman & Small, 2010). Our study site within SNWR incorporates a C_4-dominated black grama (*Bouteloua eriopoda)* grassland and a C_3-dominated creosote bush (*Larrea tridentata)* shrubland. Seasonal precipitation patterns directly influence the ratio of plant functional groups comprising primary production (Muldavin et al. 2008, Xia et al. 2010). Values for seasonal precipitation, plant cover, and long term small mammal trapping data are available from the Sevilleta Long-term Ecological Research (LTER) website (http://sev.lternet.edu).

Abundances of small mammals in creosote bush shrubland and black grama grassland were quantified in April/May and September/October of each year (1989 to present). These two sites are located approximately 1.5 km apart. During each sampling period, 148 traps were set on each of three trapping webs for three consecutive nights. This trapping regime coincides with vegetation sampling around the trapping webs (see below). Sherman live traps were baited with rolled oats, traps were checked at dawn each day, closed during the day, and reset just before dusk. All animals trapped were processed in accordance with approval by University of New Mexico (UNM) Institutional Animal Care and Use Committee (IACUC permit #13-100970-MC). Habitat, trap number, species, sex, age (adult or juvenile), mass, body measurements (total length, tail length, hind foot length, ear length), and reproductive condition (males: scrotal or non-scrotal; females: lactating, vaginal or pregnant) were recorded for each initial capture of an individual. Each animal was marked on the belly with a permanent ink felt pen in order to distinguish it from other individuals during the same trapping bout. Animals were then released at their original trapping locations. Each web has the same number of traps which allowed us to calculate small mammal abundance by summing the total small mammals trapped by species and dividing by the number of nights and webs set for each trapping bout. This allowed us to accurately compare across trapping bouts despite fluctuations in the number of nights trapped or quantity of webs baited. Abundances are expressed as species “n” per trap-night. We removed all Scurids and Leporids from the data-set. These are diurnal species with a trapping bias in terms of the time of day that the traps are set which results in highly variable data for these species.

Primary production was quantified from 1999 to 2004, on four permanently marked 1-m^2 vegetation monitoring plots located 10 meters from the ends of the three small mammal trapping webs in the four cardinal directions (N=80 1-m^2 plots). Monitoring plots were sampled for percent cover bi-annually by visual estimation of all species rooted in each quadrat in April/May and again in September/October, coinciding with small mammal trapping. From 2004 to present, the number of vegetation monitoring plots was reduced to 40. For details on vegetation sampling see Muldavin et al. (2008). Plant species were divided into the following functional groups for analysis; C_3 forb, C_3 grass, C_3 shrub/subshrub, C_4 forb, C_4 grass, or CAM. Meteorological data were derived from the closest weather station located ~0.5 km from the long-term small mammal trapping webs. Missing data was backfilled from a weather station approximately 3.0 kilometers away. Precipitation data were divided into two times frames, monsoon season from July 1st through October 31st, and non-monsoon season from November 1st through June 30th. This yields two measurements of seasonal precipitation per year that coincide with the semiannual measurements of primary production (Muldavin et al. 2008).

We used Non-metric Multidimensional Scaling ordination based on Bray-Curtis distances to determine if small mammal communities differed between foraging guild and grassland versus shrubland. To calculate community composition metrics, the CoDyn package in R uses richness, turnover, mean rank shift, and time lag analysis to determine if grassland and/or shrubland small mammal community dynamics result from species appearances and disappearances, reordering of dominant species or directional change. Turnover is calculated as the appearances and disappearances of species over time. Mean rank shift is the degree of species reordering between two time points based on species abundance. Time lag analysis measures community wide directional change based on Euclidean distances between pair-wise measurements (Collins et al. 2000, 2008). In addition, community metrics; stability, variance, and synchrony (Hallett et al. 2015) capture temporal changes in small mammal community dynamics. The more asynchrony within a community, the more stable it is. The variance ratio measures co-variance within species within a community, if species positively co-vary, the community will be more susceptible to a change in community composition in response to continued environmental presses. The SIMPER analysis from the vegan package in R determines the average contribution of each species to the overall dissimilarity of the community composition between grassland and shrubland. We ran linear models in R based on small mammal response to precipitation and primary production to look for significant correlations in the heteromyid and cricetid communities in both the shrubland and grassland.

Results:

We found that the shrubland supported both more species and a higher population density of small mammals than the grassland. Over 25 years of trapping data, total species richness ranged from 4 to 13 species in shrubland and from 3 to 11 species in grassland, with a shrubland average of 8 mice species per trapping bout versus 6.5 species in the grassland. Of these, Dipodomys merriami is the most abundant shrubland heteromyid and Perognathus flavus is the most abundant grassland heteromyid. Onychomys arenicola is the most abundant cricetid in both shrubland and grassland. Total numbers of heteromyids summed across all years ranged from 4,382 in grassland to 7,814 in shrubland and numbers of cricetids ranged from 529 in the grassland to 1,310 in the shrubland. The shrubland has 61.5% of the cricetids and 72.2% of the heteromyids averaged across all sampling periods. Results indicate that monsoon rains are important drivers of primary production which statistically correlate with heteromyid abundance. In the shrubland, when average monsoon rains (~150 mm) were exceeded in 2002, -06, -08, and -13, there was a significant increase in both C_3 and C_4 forb production with consequent increases in heteromyid and cricetid populations when lagged by a season. In fall of 2013 there was a 275% increase in C_3 forbs, and a 311% increase in C_4 forbs from the previous year, followed by a 900% increase in cricetids and a 270% increase in heteromyids in the fall of 2014 (Figure 2.1). Average winter precipitation of ~100 mm was exceeded in years 2001, -04, -05, -07, -10, and -15, this caused an increase in C_3 forb production, but there is not a concurrent increase in small mammal population numbers, either within the same year, or lagged by a season. In the grassland there was a 665% increase in C_3 forbs and a 2,193% increase in C_4 forbs from fall of 2012 to fall of 2013. Small mammals were not trapped in the fall of 2013, however, there was a 333% increase in cricetids and a 177% increase in heteromyids from fall of 2006 to fall of 2007 after monsoon rains in 2006 that were 19% above average. Winter rains cause an increase in C_3 forb production, but there is not a concurrent increase in the small mammal population numbers, either within the same year, or lagged by a season.

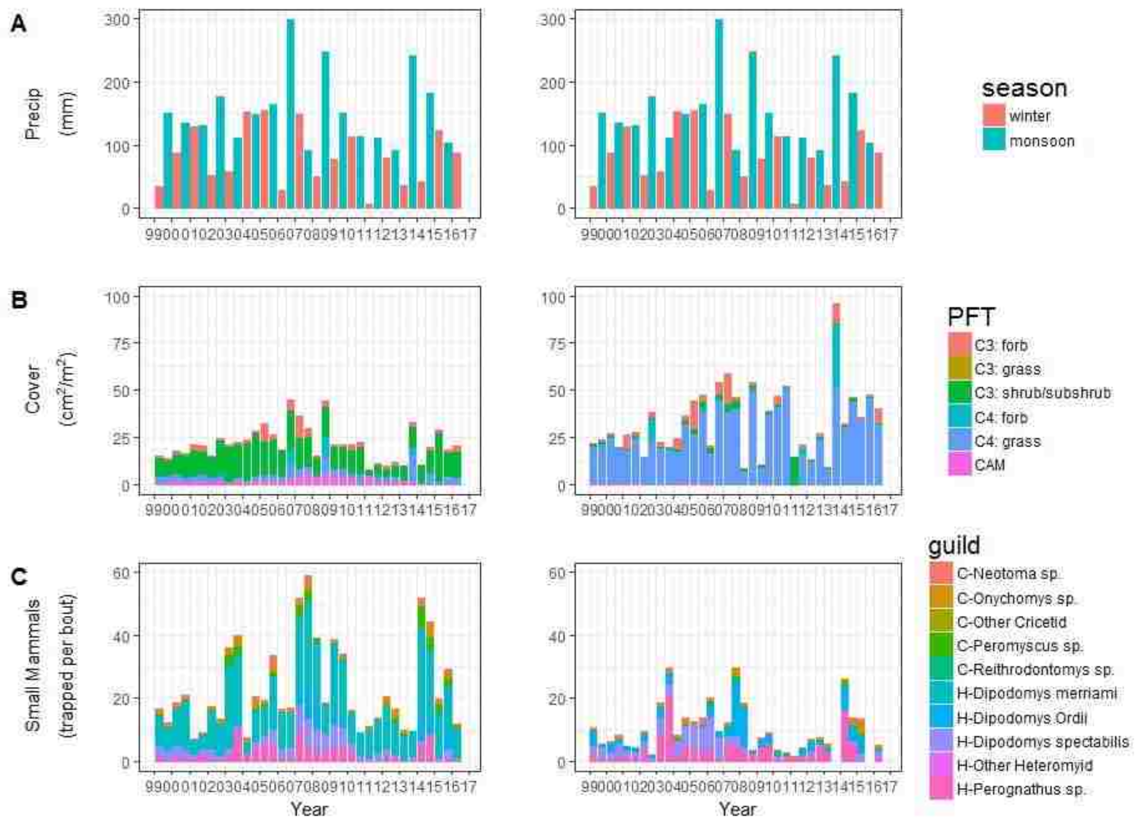

Figure 2.1: Shrubland (left) versus grassland (right). A: meteorological data from tower 49 on the Sevilleta LTER, missing data was backfilled from the next closest met station. Winter is November 1 through June 30, monsoon is July 1 through October 31. B: percent cover by plant functional type. C: small mammal abundances based on long-term trapping data, C-, and H- represent the Cricetid, and Heteromyid community respectively.

Heteromyid and cricetid community composition varied between grassland and shrubland. Bray-Curtis ordination (Figure 2.2), showed clear differences in heteromyid and cricetid communities in the shrubland versus grassland. Omnivorous cricetid community composition was similar in both ecosystems as indicated by a near complete overlap of data points in the ordination, whereas granivorous heteromyid communities vary between these ecosystems (Figure 2.2). Based on SIMPER analysis eight species explain 90% of the dissimilarity between the two sites – 4 heteromyids (70%) and 4 cricetids (20%) (Table 2.1). Small mammal communities in both grassland and shrubland are stable over the long-term (Table 2.2), however the communities are highly variable

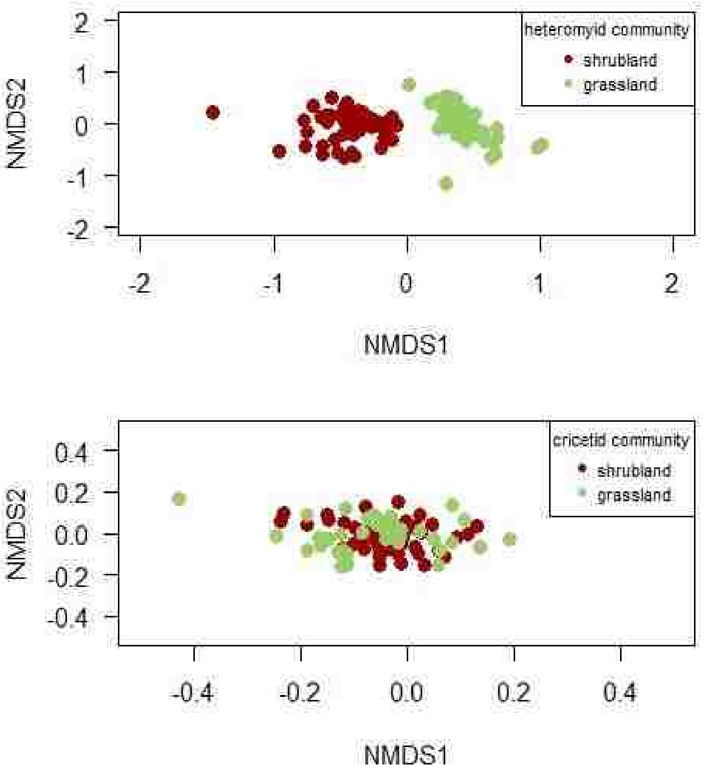

Figure 2.2: Non-metric Multidimensional Scaling (NMDS) shows temporal variation in small mammal community dynamics in shrubland (red) and grassland (green). Heteromyids (top) show variation between community composition in each of the stable states versus cricetids (bottom) whom appear to have a similar composition in each stable state. Each dot represents the community composition of small mammals for one year (1989-2016).

over short time frames with the differences primarily attributed to a continual reordering of species dominance as populations boom and bust. Community stability metrics show that shrubland small mammal communities have greater synchrony and more positive covariance than in the grassland. This explains why the following community metrics are more variable in the shrubland than the grassland, as species co-vary, they are more vulnerable to a boom or bust in response to an environmental shift that species that vary in opposition to one another (Table 2.2).

Richness, the number of species present at any given time, is highly variable in both shrubland and grassland communities, however the shrubland community has a consistently higher number of species than the grassland (Figure 2.3). Turnover is high

species	Average contribution	cumulative contribution
dime	0.27	0.31
pgfv	0.13	0.46
disp	0.12	0.60
dior	0.10	0.70
onar	0.10	0.80
pmer	0.04	0.85
nemi	0.02	0.88
neal	0.02	0.90

Table 2.1: SIMPER (similarity percentage) results, or the contribution of each species' explanatory power in describing the dissimilarities in community composition between shrubland and grassland. Average contribution is a mean of each species contribution to dissimilarity while cumulative contribution is the summed contribution of that species toward the overall dissimilarity between the two stable states across time (1989 to present).

Table 2.2: Community Stability metrics

	Shrubland	**Grassland**
Community Stability	1.67	1.67
Synchrony – Loreau	0.50	0.32
Synchrony – Goss	0.32	0.10
Variance	2.79	1.59

in both grassland and shrubland, with turnover higher in the shrubland in comparison to the grassland. Mean Rank Shift indicates near continual reordering in the dominant species in both ecosystems (Figure 2.3), however reordering is greater in the grassland than shrubland, due to a lower level of covariance among species. There is no directional change over the long-term (temporal change, Figure 2.3). There are significant differences between community composition of small mammals in grassland versus shrubland (p value = 0.001) with the heteromyids being more variable within each state than the cricetids. Using ANOVA, there is a significant difference between the community composition of cricetids (p value = 0.001) and heteromyids (p value = 0.000) within both grassland and shrubland.

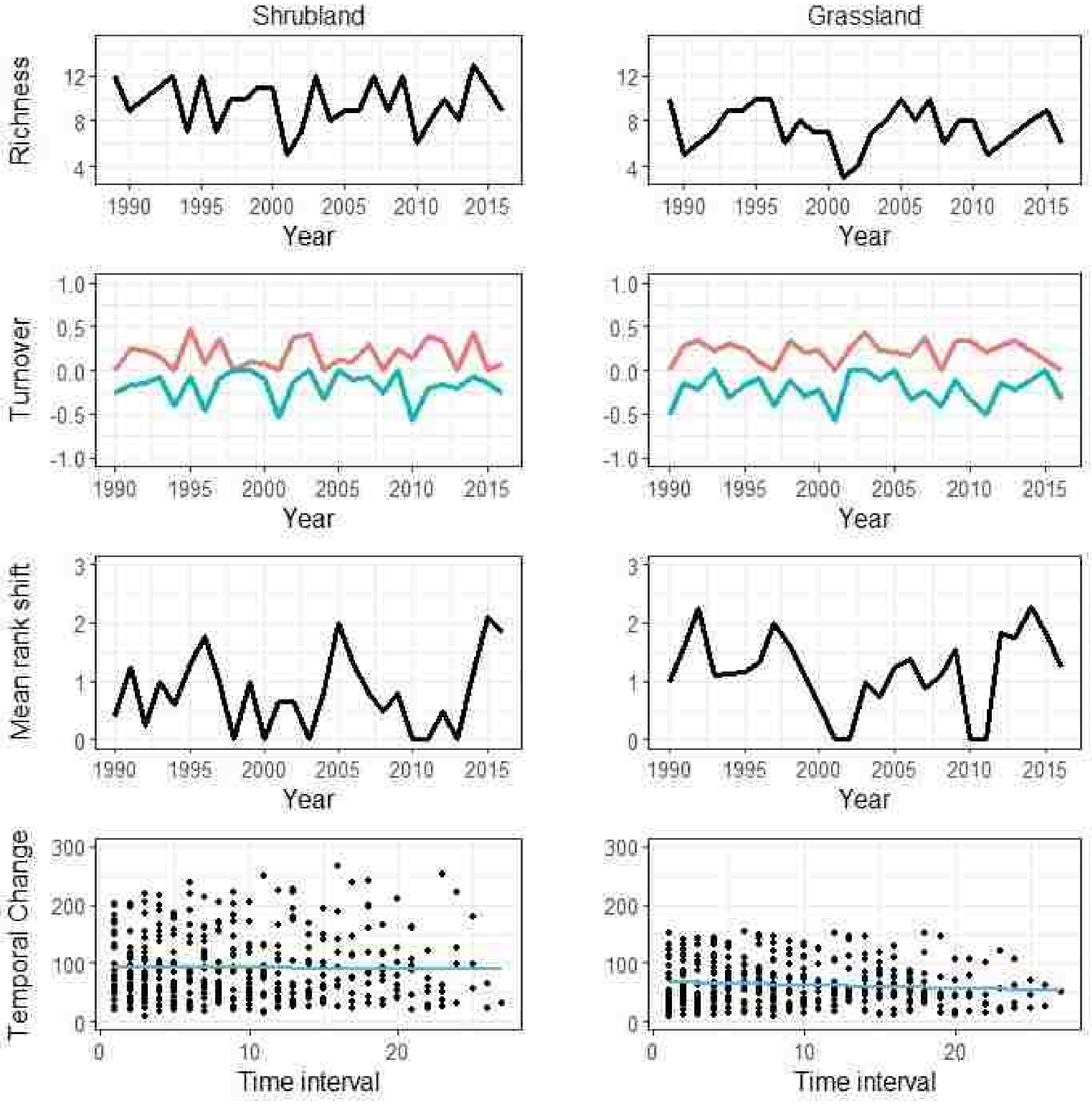

Figure 2.3: Temporal community dynamics between the shrubland (left) and grassland (right). Richness is a measure of presence/absence of species in the community per year. Turnover is annual appearances and disappearances of species. Mean rank shift indicates the degree of species reordering within each site. Temporal change utilizes annual pair-wise comparisons to determine directional change in community composition through time (1989-2016).

Heteromyid populations respond to changes in precipitation and primary production. In the shrubland, precipitation is a significant driver of C_3 forb, C_4 grass, and C_4 forb production. In the grassland precipitation is a significant predictor of C_3 forb production. Temperature does not significantly affect primary production in either stable state. Using cross correlations, both heteromyid and cricetid populations lag behind precipitation and primary production by a season. Once lagged, linear modeling indicated that heteromyids but not cricetids responded to precipitation and primary production by functional group (C_3 forb, C_3 shrub/subshrub, C_4 forb, C_4 grass). There was a significant relationship between C_3 and C_4 forb production and heteromyid populations in the shrubland (p=0.002 and 0.04, respectively). In the grassland, heteromyid populations have a significant correlation with C_3 shrub/subshrub (p=0.01) and C_4 forbs (p=0.0045).

Discussion:

We found that shrublands support a more specious and populous community than grasslands. We hypothesize that this occurs because of greater landscape and resource heterogeneity. This arid, bottom-up ecosystem, constrained by resource availability rather than predation, is in a continual state of low primary productivity (Baez et al. 2006, Turkington et al. 2009), that experiences large temporal and spatial variability in primary producer species composition, soil seed banks, and seed production (Cleland et al. 2013, Guo et al. 2000, Maron et al. 2012, Mulhouse et al. 2016). Shrublands are characterized by resource patches (Letnic et al. 2010) with bare ground between patches while cover in grasslands is more homogeneous. Using percent cover as a proxy for ecosystem structure and resource availability, we found that large precipitation events cause rapid growth in short lived C_3 and C_4 annuals producing a large quantity of food on the landscape, altering resource availability quickly and dramatically (Figure 2.1) (Aarssen et al. 2001, Smiley et al. 2015, Xia et al. 2010, McCluney et al. 2012, Meserve et al. 2003, Mulhouse et al. 2016). This causes small mammal populations to fluctuate, persisting at low densities during drought and periodically erupting following high seasonal precipitation

(Figure 2.1). Boom-bust cycles are characteristic of arid lands throughout the world and have been documented in Australia (Dickman et al. 2011, Letnic et al. 2010), Chile (Meserve et al. 2011, Holmgren et al. 2006), and in other areas of the Southwestern United States (Thibault et al. 2010). These cycles drive small mammal population variability in heteromyids, a functional group more reliant on primary production, to a greater degree than the cricetids.

Heteromyid community composition varies both within, and between grassland and shrubland ecosystems with 3.5 times the variability of cricetids (Table 2.2). The heteromyid community composition showed wider variance within each ecosystem and a different composition between ecosystems than cricetid community composition. This may be due to significant differences in primary production and landscape architecture between grassland and shrubland (Muldavin, 2008). Changes in primary production in response to precipitation constrain the composition of the heteromyid community to a greater degree than the cricetid community as indicated by the significant values detected with linear modeling. Cricetids forage on multiple trophic levels, reducing their dependence on primary production as they supplement their diet with a wide array of food. Neither stable state is undergoing long-term directional change in small mammal communities over this 26 year time frame. However, there is a high degree of short term variability as indicated by species richness, turnover, and mean rank shift. It appears that differences between the small mammal communities are primarily a product of changing population densities and a reordering of species dominance from year to year in response to a highly variable landscape of primary production (Figure 2.3).

In summary, arid lands are characterized by a variable precipitation regime that results in alternating periods of resource abundance and limitation. These resource pulses create spatial and temporal heterogeneity in primary production which increases the variability between shrubland and grassland (Epstein et al. 2002, Ernest et al. 2000, Rosenblatt et al. 2015). To survive in this highly stochastic landscape, small mammals have developed mechanisms such as internal fat stores, short periods of torpor, or seed caches (Holt 2008) to adapt to extreme variability in resources and large increases in inter- and intraspecific competition associated with population boom-bust cycles (Sala et al. 2012, Owen-Smith et al. 2010). Long-term environmental presses such as increasing CO_2 and temperatures combined with a changing precipitation cycle will change primary production, and landscape architecture likely changing the consumer community within each landscape. Persistent changes in resource availability or changes in the timing of resource production will alter consumer biomass and diversity, ultimately changing community structure and ecosystem function (Warne et al. 2010, Hanya et al. 2013). While it is anticipated that long term environmental presses will lead to catastrophic shifts in community composition, we did not find evidence of this in our study (Scheffer et al. 2001). As shrublands encroach into grasslands, the small mammal community structure will change to reflect changes in available resources, resulting in a more abundant, more specious community that is able to exploit the increased landscape heterogeneity and resource patches associated with shrublands. It is unknown if increased aridity and periods of drought will significantly impact this small mammal community. Further study could potentially illuminate a combination of abiotic factors which could cause changes in community composition in response to long-term environmental presses, however current data provides evidence of a stable and plastic small mammal community that will boom and bust in response to resource availability without directional change

Chapter 3: Rodent response to changes in landscape architecture

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Abstract:

Consumer foraging strategies depend to some extent on resource quality, quantity and predictability. In many bottom-up (resource constrained) arid ecosystems, primary production varies substantially both within and between years in response to highly variable seasonal and inter-annual climate regimes. As a consequence, consumer populations must rely on resources that vary over relatively short spatial and temporal scales. Resource variability is predicted to increase in the future while predictability across space and time is anticipated to decrease according to recent models of climate change.

We quantified resource availability and use by a diverse community of arid land rodents in a strongly bottom-up system in the northern Chihuahuan Desert to determine if these consumers foraged selectively on the highest quality resources, partitioned resources, or used resources indiscriminately in proportion to their changing abundance on the landscape. Our study site spans a shrubland/grassland ecotone that harbors a numerous and diverse rodent community comprised of seed caching heteromyids that coexist with generalist cricetids consuming seeds, foliage, and insects.

We trapped 7,063 rodents over a three year period from which we obtained 3,560 blood plasma samples from 1,533 unique individuals to conduct δ^{13}C and δ^{15}N isotopic analysis to quantify resource use by these consumers. We calculated resource availability using monthly leaf and seed phenology data, along with δ^{13}C isotopic analysis of 698 plant leaf and seed samples to determine photosynthetic pathway (C_3/C_4). We generated

an estimate of forage quality based on plant leaf and seed $\delta^{15}N$ to determine dietary breadth or trophic level. In addition, we measured average seed size and mass for the 45 most common plant species at our study site. By comparing raw mouse plasma $\delta^{13}C$ and $\delta^{15}N$ values to hypothetical diets constructed using plant $\delta^{13}C$ and $\delta^{15}N$ values, long-term phenology data, and seed characteristics, we constructed models of resource use to determine if these rodents foraged selectively or if they used resources in proportion to their availability in the landscape.

Overall, we found high resource overlap among species. Rodent diets mirror nitrogen availability on the landscape, with cricetids foraging at a higher trophic level than heteromyids when resources were abundant. When resource availability was low, both heteromyid and cricetid resource breadth converged and broadened, suggesting that all species consumed a wider array of resources to satisfy nutritional requirements. Together, these results indicate that this community of arid land rodents uses resources in proportion to their abundance on the landscape, consuming forage of the highest quality available at a given time. Understanding how primary production influences foraging will improve our ability to predict how climate change will alter resource availability and drive consumer dynamics in the future.

Introduction:

Arid bottom-up ecosystems are resource-limited more so than predator controlled, experiencing high temporal and spatial variability in primary producer species composition, soil seed banks, and seed production (Cleland et al. 2013, Guo et al. 2000, Maron et al. 2012, Mulhouse et al. 2016). In these systems consumer populations are constrained by primary productivity that is in turn limited by environmental factors such as soil nutrients, temperature, and precipitation (Meserve et al. 2003, Hunter et al. 1992) Arid lands typically support a numerous and diverse small mammal community persisting on a common suite of resources. This strengthens the correlation between resource fluctuations and consumer population dynamics (Slobodkin et al. 1967, Brown et al. 2002). In order to survive in a near continual state of low and variable primary productivity, these consumers have developed mechanisms such as internal fat stores or seed caches as well as the potential to undergo population boom and bust cycles as resources wax and wane (Baez et al. 2006, Turkington et al. 2009, Holt 2008, Gese et. al. 1996). Historically competitive coexistence has been attributed to niche partitioning, where consumers partition the landscape spatially, by foraging in different areas (MacArthur 1958), or temporally, by foraging at different times to allow a diverse assemblage of species with overlapping habitat and resource requirements to coexist (Kartzinel et. al. 2015). There are many examples of niche partitioning in arid, resource limited ecosystems across the globe. These include lizards partitioning resources temporally by varying their periods of activity throughout the day (Gordon et. al. 2006), tropical ants occupying different temporal (diurnal versus nocturnal) and dietary niches (Houadria et. al. 2015), and desert carnivores partitioning water resources both spatially and temporally to limit interaction with one another (Atwood et. al. 2011). It is currently unknown if desert rodents, key consumers in these resource constrained ecosystems, selectively forage as a mechanism to partition limited resources between and within species, or if there is a large degree of dietary overlap among consumers as they track temporally variable resources.

Ambient temperatures and varying magnitude and frequency of precipitation events, dictate both the type and abundance of primary production in arid lands (Sala et al. 2012, Aarssen et al. 2001, Smiley et al. 2015, Xia et al. 2010, McCluney et al. 2012, Meserve et al. 2003). Changes in precipitation regimes will increase variability in primary production both from season to season and year to year (Lehman et al. 2015) with the timing of precipitation events dictating the relative seasonal abundance of grasses, annual or perennial forbs, or woody shrubs (Sala et al. 2012). Winter and spring rains, paired with cooler temperatures from November to July, cause an increase in C_3 forbs and shrubs while monsoon rains and warmer temperatures in July through October, increase production of C_4 forbs and grasses (Muldavin et al. 2008, Xia et al. 2010). Spatiotemporal changes in abundance of C_3 versus C_4 primary production creates landscape heterogeneity requiring rodents to have a high degree of dietary plasticity (Thibault et al. 2010).

In arid lands nitrogen is a limiting resource for both producers and consumers. As nutritious forage (high nitrogen content) becomes scarce, consumers may expand their foraging breadth, compromising quality for quantity in accordance with the Optimal Foraging Theory (Roughgarden 1972, Thompson et al. 1990). Many consumers can switch resources according to their energetic demands, phenology, or in response to changes in resource quantity or quality. This dietary plasticity has been well documented in dingoes (Corbett et al. 1987), coyotes (Gese et al. 1996), elephant seals (Bradshaw et al. 2003), eagles (Thompson et al. 2005), pygmy possums (Morrant et al. 2012), and elk (Conard et al. 2012). An areas distinct composition of primary producers dictated by precipitation and soil type, and a consumer’s ability to adapt foraging strategies to match forage quality and quantity interact to create unique and predictable consumer community assemblages (Stephens et al. 2014, Fitzherbert et al. 2007, Ecke et al. 2002, Klimstra et al. 2015, Coppeto et al. 2006). Future climate predictions (a decrease in winter precipitation, more extreme rain events and an increase in overall aridity) will change the landscape of primary production (Gutzler and Robbins 2011, Seager et al. 2007) with unknown consequences for consumers. Knowledge of current foraging patterns will improve our ability to forecast how aridland consumers may adapt to increased resource variability under a changing climate (Barraquand et al. 2017).

Carbon isotopic values, $\delta^{13}C$ (a ratio of ^{13}C to ^{12}C), of primary producers are consistent within a photosynthetic pathway, C_3 = -26.4 +/- 2.0‰, $C_{4,}$ = -14.6 +/- 1.4‰, and CAM = -12.5 +/- 0.7‰ and can be utilized to track dietary assimilation by plant functional type (Craig et al. 1953, Farquhar 1989). The more efficient C_4 photosynthetic pathway results in high C and N use efficiency (Westoby et al. 2002) whereas C_3 plants require greater enzymatic mediation (rubisco) resulting in higher nitrogen levels in leaf and seed tissues (Lambers et al. 2008). This disparity in nitrogen and a high C to N ratio makes C_4 plants a relatively poor source of nutrition (Waller and Lewis 1979, Warne et al. 2010) in comparison to more palatable and nutritious C_3 plants (Guo et al. 2000, Hope and Parmenter 2007, Orr et al. 2015). Nitrogen content in forage is often used as a proxy for forage quality due to its limited availability. Nitrogen isotopic values $\delta^{15}N$ (a ratio of ^{15}N to ^{14}N), of primary producers fluctuate within species by season and plant tissue and between different functional groups within a site due to seasonality and soil resource availability. $\delta^{15}N$ positively co-varies with nitrogen concentration by weight in plants (Handley et al. 1999, Lehmann et al. 2015, Kartzinel et al. 2015), justifying its general utility as a measure of forage quality. New growth has the highest nitrogen concentrations with plants reallocating nitrogen to seeds and roots as they senesce (Chapin, 1980). Annuals contain higher nitrogen concentrations, allocating high amounts to reproductive structures to facilitate a short life cycle, whereas perennials typically contain less nitrogen, allocating nitrogen to rooting structures as nutrient availability declines (Vitousek, 1982). $\delta^{15}N$ values in small mammal plasma reflect the variable levels of nitrogen in primary producers offset by a predictable trophic discrimination factor. This provides a landscape level tool for studying foraging characteristics.

The small mammal community in the Northern Chihuahuan desert represents an ideal study system from a resource dynamics perspective because it encompasses two rodent families with differing life histories and energetic requirements. Heteromyid rodents are food-caching granivores comprised of both larder hoarders (caching food reserves underground) and scatter hoarders (caching on the surface) (Ernest et. al. 2000, Brown et. al. 1989, Kelt et. al. 1999). Cricetids forage at multiple trophic levels, do not cache, and must rely on body fat stores as short term energy reserves. Cricetids may have an advantage in this environment due to their ability to forage at multiple trophic levels while heteromyids rely on primary production to meet their nutritional needs. We used plasma $\delta^{13}C$ values from rodents to track consumption by plant functional type (dietary width), and $\delta^{15}N$ values were used to track consumption of plants of different nutritional content or incorporation of higher trophic levels (dietary breadth) (Kartzinel et al. 2015). Long term phenology data were used to construct a time series of leaf and seed availability over the growing season. We then used isotopic values, C:N ratios, and seed characteristics to provide a rough estimate of the quality and quantity of available forage.

By combining data on primary production, and nitrogen content, with small mammal diets, we answered the following questions: (1) Do rodent populations partition the landscape of available resources, or do they primarily consume the highest quality forage? (2) Do rodents maintain consistent diets, or do their diets reflect seasonally variable primary production?

Methods:

Our study was conducted in the Sevilleta National Wildlife Refuge (SNWR: 34°20′N, 106°43′W), Socorro County, New Mexico, USA. Average annual precipitation is ~250 mm, more than half (~150 mm) of which occurs via convective storms which create intense but highly localized rain events during the summer monsoon, July through early September (Pennington & Collins 2007, Notaro et al. 2010, Petrie et al. 2014). Winter and spring precipitation typically occurs as a mixture of snow and light rain (Gosz et al. 1995, Pockman & Small, 2010). Our study site within SNWR crosses an ecotone between two different stable states, a C_4-dominated black grama (*Bouteloua eriopoda)* grassland and a C_3-dominated creosotebush (*Larrea tridentata)* shrubland. Seasonal precipitation patterns directly influence the abundance of plant functional types comprising primary production (Muldavin et al. 2008, Xia et al. 2010).

Rodents were trapped monthly from July, 2013 to May, 2016 excluding months with nighttime temperatures below freezing. Traps were set over three consecutive nights on the weekend closest to the new moon when rodents are most active. Two permanent trapping webs were established that cross a creosote shrubland to black grama grassland ecotone. Webs were designed with 145 traps distributed on 12 equally spaced spokes containing 12 traps apiece that radiate out from a central stake where a single trap is placed (Parmenter et al. 2003). During each trapping bout, Sherman live traps were baited with rolled oats, peanut butter, and heat-treated millet. Traps were checked at dawn each day, closed during the day, and reset just before dusk. Upon capture, each mouse was fitted with a unique identifier in the form of an electronic pit-tag or ear-tag to associate with a temporal record of diet. Species, sex, age, mass, and reproductive condition were recorded (Appendix 3.1: All Small Mammal Trapping Data). During processing, a 50 μL blood sample was obtained by slipping a heparinized micro capillary tube behind the eye to puncture the pre- (Cricetids) or retro-orbital (Heteromyids) sinus. Capillary tubes were capped, labeled, and placed on ice for transport to the lab. Within ten hours, blood samples were centrifuged to separate red blood cells from plasma. Plasma was pipetted into pre-weighed tin capsules for isotopic analysis of δ^{13}C and δ^{15}N (Appendix 3.2: All Small Mammal Isotope Data). Plasma δ^{13}C turnover in rodents has a half-life of approximately 3-5 days, so monthly sampling provides a near continuous dietary record during the growing season (MacAvoy et al. 2005, Tsahar et al 2008, Parnell et al 2010). All animals were released at their original trapping location in accordance with animal trapping and processing protocols approved by the UNM Institutional Animal Care and Use Committee (IACUC #A4023-01).

Primary producers were sampled by species throughout the year, at green up (March, May, and September), when flowering (May and September/October), and when going to seed (May/June and September/October). A minimum of ten samples from each functional type were collected from both trapping webs, along four spokes in the cardinal directions. Samples were placed in coin envelopes in the field and then placed in a 40ºC drying oven for 48 hours in the laboratory. We collected leaves and seeds for δ^{13}C and

$\delta^{15}N$ isotopic analysis as well as percent carbon and nitrogen by weight and C:N ratios to establish a baseline of variation in nitrogen between tissue types and across time for comparison with plasma values (Appendix 3.3: All Plant Isotopes). Plant species with high relative abundance were selected for analysis (http://sev.lternet.edu/data/sev-129). Less abundant species that were not directly sampled were assumed to have isotopic and seed weight values equal to the median (n) values within their plant functional group (C_3 forb, C_3 grass, C_3 shrub/subshrub, C_4 forb, C_4 grass, and CAM).

For isotopic analysis, approximately 8 μl of plasma are pipetted into pre-weighed 5 x 3.5 mm tin capsules and placed in a drying oven overnight. Capsules are weighed again to calculate the weight of the dried plasma sample. After drying, ~3–5 mg of seed or leaf material are loaded into tin capsules for isotope analysis. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were measured using a Costech 4010 Elemental Analyzer (Costech Analytical Technologies, Valencia, CA) coupled to a Thermo Finnigan Delta V continuous flow mass spectrometer (Waltham, MA) in the UNM Center for Stable Isotopes (Albuquerque, NM). Stable isotope values are reported using delta (δ) notation in parts per thousand or per mil (‰) as: $\delta = (R\ sample/R\ standard) \times 1000$. R_{sample} and $R_{standard}$ are the relative ratios of the heavy and light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) in a sample and standard, respectively. Isotope values are referenced against international standards of Vienna Pee-Dee Belemnite (VPDB) for carbon and Air for nitrogen. Measured isotope values were calibrated against international standards using internal reference materials analyzed alongside plasma and plant material samples to correct for within-run instrument drift. Repeated within-run measurement of these reference materials yielded an analytical precision (SD) of 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. We selected a trophic discrimination factor ($\delta^{13}C$ tissue-$\delta^{13}C$ diet) for carbon of 1.0‰ and assumed variance (SD) of 0.25‰. The trophic discrimination factor for $\delta^{15}N$ is 4.4 ‰ with an assumed variance (SD) of 0.25. These trophic discrimination factors are based on average values from the literature for a wide range of organisms (Bearhop et al. 2004, Caut et al. 2009, DeNiro et al. 1978, Kurle et al. 2013). Nitrogen limitation in rodents has been shown to slow tissue turnover rates (Miller et. al. 2011) with a trophic discrimination for juvenile rodents smaller than the predicted 3 ‰ offset, however it is very difficult to tell the difference between a large juvenile and a small adult, so we elected to use a higher 4.4 ‰ discrimination factor for each trophic level regardless of the age of the mouse. This higher value is based on discrimination factors for a controlled experiment in our lab (Rodriguez-Curras, unpublished) and on Caut et al. 2010 meta-analysis which highlighted an inverse relationship between diet quality and $\delta^{15}N$. The poorer quality the diet (lower N), the larger the trophic discrimination factor (Caut et al. 2008, 2010, DeNiro et al. 1981).

Vegetative and reproductive phenology of all species was observed monthly (February through October) across four replicate 200 m transects in shrubland and grassland, for a total of eight transects (http://sev.lternet.edu/data/sev-137). Phenological status of leaves was recorded as new, old, brown or absent and reproductive status was recorded as buds present, flowers present, seeds present, seeds and flowers present or no sign of reproductive structures for ten individuals of each species per transect. For each month corresponding with trapping data, we calculated the proportion of individuals of each species recorded as having seed, or seed and flowers present. For clarity, we present a summed fruit (seed) availability index (FAI) for each plant functional group: C_3 forb,

C_3 grass, C_3 shrub/subshrub, C_4 forb, C_4 shrub/subshrub, or CAM (Figure 3.1). The FAI quantifies both the diversity of species producing seed at each sampling period and the proportion of plants by functional type with seeds.

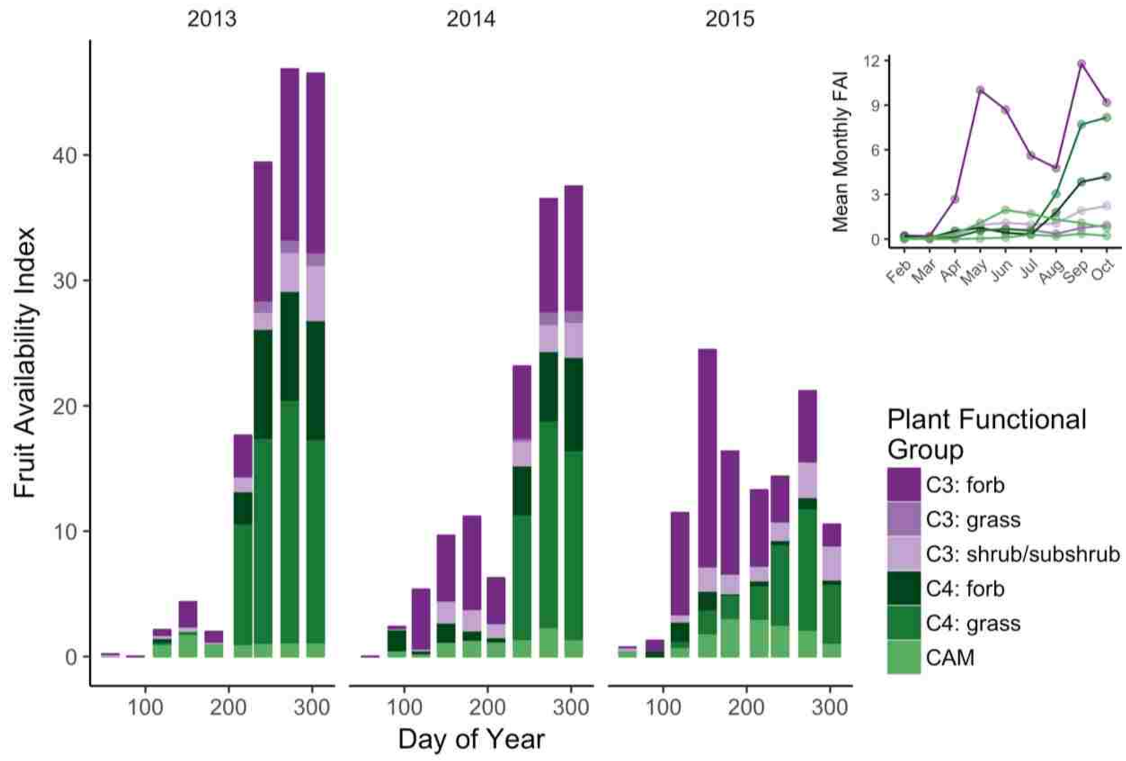

Figure 3.1: Fruit Availability Index (FAI) across two sites (shrubland and grassland) over three years that coincide with small mammal trapping. FAI, the summed proportion (values range from 0 to 1) of individuals seeding within each species (max sample size = 80 individuals/species/month), is a proxy for seed availability. This combines both seed abundance (the amount of seed) and seed diversity (the number of different species in seed). Inset: Long-term (2000-2016) mean monthly FAI. C_3 forbs, on average, have a bimodal seeding pulse. C_3 forbs consistently have a higher proportion of individuals and a greater diversity of species in seed than other plant functional groups. C_4 grasses, C_4 forbs, and C_3 grasses seed later in the year after monsoon rainfall.

In addition, we calculated the proportion of individuals of each species recorded as having old or new leaves which we present as a summed leaf availability index (LAI) (Figure 3.2). These indices are not a measure of biomass or percent cover, they are simply a metric of the status of the plants on the landscape, and are created as a surrogate for resource availability to compensate for the fact that we do not have any direct measure of seed biomass. In a highly variable landscape, plants may grow large without generating reproductive structures, or a large biomass of foliage as grass blades may have a small biomass of seed due to their small size (Appendix 3.4: Seed Attributes).

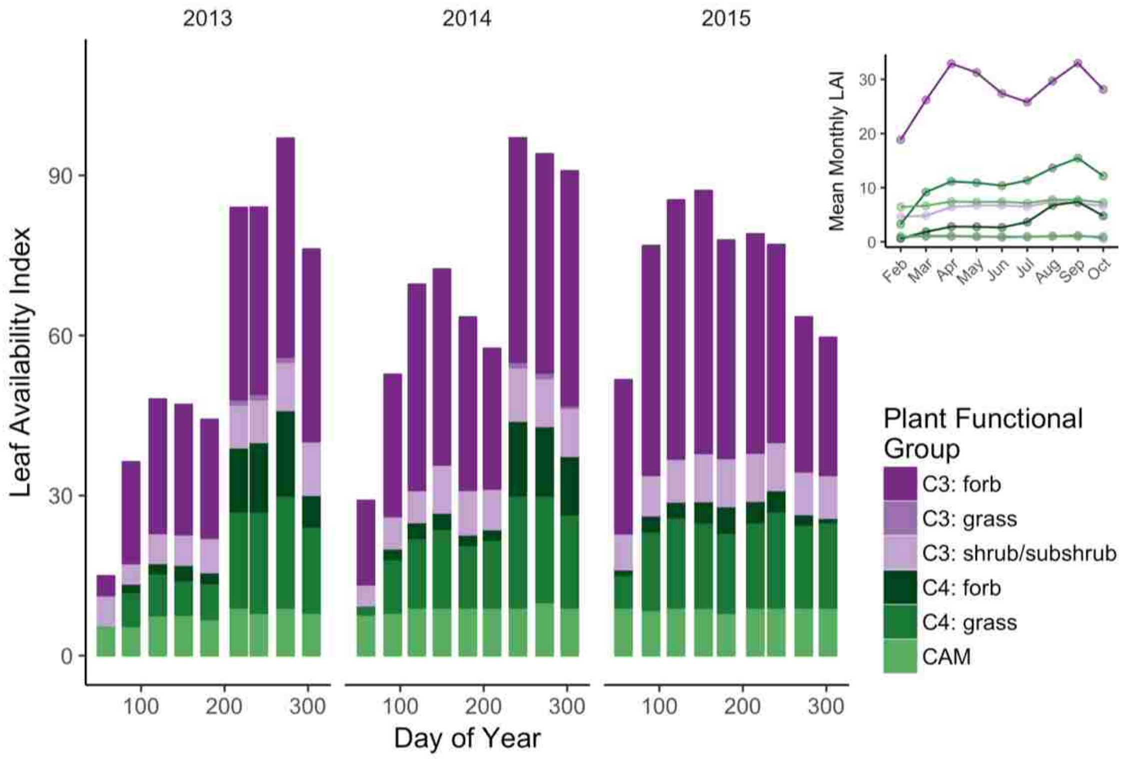

Figure 3.2 – Leaf Availability Index (LAI) across two sites (shrubland and grassland) over three years that coincide with small mammal trapping. LAI, the summed proportion (values range from 0 to 1) of individuals with new or old leaves within each species. The maximum sample size = 80 individuals per species per month, if the values are over 80, it indicates multiple species have leaves. There are many more leaves than seed, and many species maintain leaves year round. This is a proxy for foliage availability on the landscape. Inset: Long-term (2000-2016) mean monthly LAI. C_3 forbs, typically follow a bimodal pattern as seen in 2014. C_3 forbs consistently have a higher proportion of individuals and a greater diversity of species than other plant functional groups. CAM and C_3 shrub/subshrubs are relatively constant year round. The variability in forbs, and grasses likely reflects annuals appearing and disappearing on the landscape.

Using mean $\delta^{13}C$ and $\delta^{15}N$ values of seed and leaves, seed characteristics, and the proportional availability of seeds (fruit) and leaves calculated by the FAI and LAI respectively, we developed hypothetical diets which we compared to the monthly $\delta^{13}C$

and $\delta^{15}N$ values in rodent plasma. For each hypothetical diet, we created biologically informed multipliers which were applied to all plant carbon and nitrogen values. Hypothetical diets (Figure 3.3): big seed – a multiplier was created by dividing individual species seed weight by the mean weight of all seeds. Carnivore – a multiplier was created that included two trophic discrimination factors, and a weighting that assumed insects were eating a diet composed of 75% C_4 and 25% C_3 seed and leaves combined. We removed 2.5% of the data values on either end to account for outliers within one standard deviation of the mean. High C_3 - a mouse is twice as likely to eat a C_3 plant as a C_4. Highforb – a mouse is 75% more likely to forage on C_3 or C_4 forbs than other plants, values known to be reasonable in *Perognathus flavus* individuals at this site (Noble, prior research). High N – we created a multiplier which was the mean of all nitrogen values for the seeds of a plant species to the mean of nitrogen values for all seeds. Mixed – a combination of all diets. Random.leaf – rodents forage in proportion to leaf availability on the landscape as measured by the LAI and offset by one trophic discrimination factor. Random – rodents forage in proportion to seed availability on the landscape as measured by the FAI and offset by one trophic discrimination factor. Tasty or palatability – we divided 20 by the C:N ratio of all seed to create a multiplier, this gives a higher multiplier to quality seed (low C:N). Tastyleaf – we divided 20 by the C:N ratio of all leaves to create a multiplier, this gives a higher multiplier to quality leaves, this diet assumes rodents are eating foliage and not seed. Informedcarni – this diet proposed that rodents were eating 50 percent insects (Carnivore diet) 5% leaves (tastyleaf diet) and 45% seed (tasty diet). Informedveg – this diet proposed that rodents were eating 80% quality seed based on a low seed C:N ratio (tasty diet) and 20% high quality leaf (tastyleaf diet). After

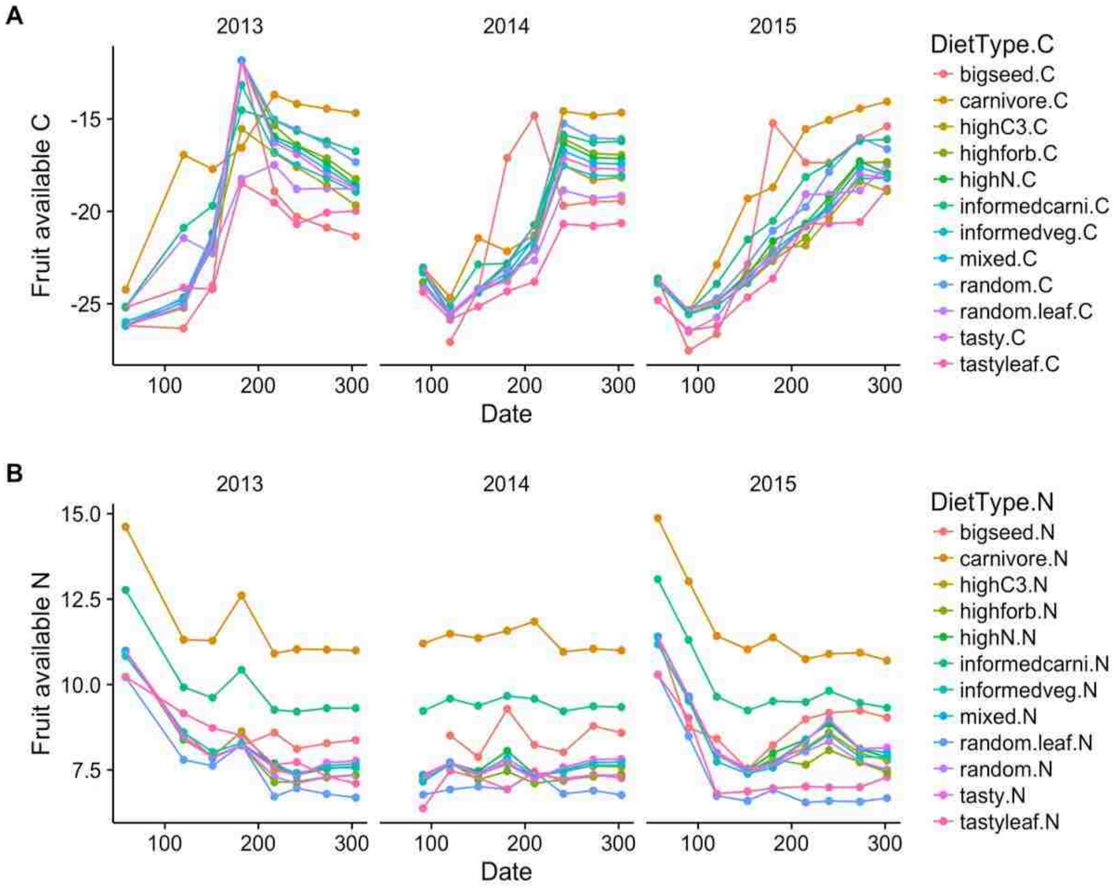

Figure 3.3: The Carbon (top) and Nitrogen (bottom) values for all hypothetical diets created for comparison to mouse plasma. Big seed – a multiplier was created by dividing individual species seed weight by the mean of all seed. Carnivore – a multiplier was created that included two trophic discrimination factors, and a weighting that assumed insects were eating a diet composed of 75% C_4 and 25% C_3 seed and leaves combined. We removed 2.5% of the data values on either end to account for outliers within one standard deviation of the mean. High C_3 - a mouse is twice as likely to eat a C_3 plant as a C_4. Highforb – a mouse is 75% more likely to forage on C_3 or C_4 forbs than other plants. High N – we created a multiplier which was the mean of all nitrogen values for the seed of a plant to the mean of all seed. Mixed – a combination of all diets. Random.leaf – rodents forage in proportion to leaf availability on the landscape as measured by the LAI and offset by one trophic discrimination factor. Random – rodents forage in proportion to seed availability on the landscape as measured by the FAI and offset by one trophic discrimination factor. Tasty or palatability – we divided 20 by the C:N ratio of all seed to create a multiplier, this gives a higher multiplier to quality seed (low C:N). Tastyleaf – we divided 20 by the C:N ratio of all leaves to create a multiplier, this gives a higher multiplier to quality leaves, this diet assumes rodents are eating foliage and not seed. Informedcarni – this diet proposed that rodents were eating 50 percent insects (Carnivore diet) 5% leaves (tastyleaf diet) and 45% seed (tasty diet). Informedveg – this diet proposed that rodents were eating 80% quality seed based on a low seed C:N ratio (tasty diet) and 20% high quality leaf (tastyleaf diet).

comparing all of these diets to the plasma values for our mouse community we elected four diets with the best fit: (1) Random diet: rodents randomly forage on all available seed on the landscape, the probability of selecting a seed from a plant species is equal to that species' FAI value. (2) Random leaf: rodents randomly forage on all available foliage on the landscape, the probability of selecting a leaf from a plant species is equal to the species' LAI value. (3) Informedveg diet: Rodents will forage on preferred seed with low C:N ratios 80% of the time and preferred leaves with low C:N ratios 20% of the time. (4) Informedcarni: Rodents choose to supplement forage with 50% arthropods that are consuming 75% C_4 forage and 25% C_3. These values are based on Allyson Richins' grasshopper data from the same study site (unpublished) which had a majority of grasshopper C_4 specialists and relative values for all arthropods in Warne et al. 2010 paper (Table 1) which indicates a 50/50 C_3: C_4 arthropod diet. We assumed rodents were eating 5% foliage based on the tastyleaf diet, and 45% seed based on the tasty diet. We choose these numbers based on the results from Hope and Parmenters' 2007 gut content analysis on rodents in our study area (Table 3.2). As noted

Table 3.1: Average δ^{13}C, δ^{15}N, and %C_4 values from Warne et al. 2010

Order	**Common Name**	**Average δ^{15}N**	**Average δ^{13}C**	**% C_4 in diet**
Araneae	Ground spiders	8.3	-18.1	63.9
Coleoptera	Beetles	6.8	-21.6	36.7
Hymenoptera	Ants	7.4	-19.7	51.3
Lepidoptera	Caterpillar	5.3	-29.4	0
Orthoptera	Grasshoppers	5.3	-20.1	48.3
Scorpionids	Scorpions	8.5	-19.0	56.8
Solifagae	Web Spiders	8.0	-18.6	60.3

above, for all diet scenarios, a $\delta^{13}C$ trophic discrimination factor ($\delta^{13}C$ tissue-$\delta^{13}C$ diet) of 1.0‰ and a $\delta^{15}N$ value of 4.4‰ were added to plant isotopic values.

Table 3.2: Summary of Hope and Parmenters' 2007 gut content analysis of rodents in our study area. All numbers reflect rodents trapped in desert shrubland. H and C indicate heteromyid versus cricetid. Shrub, Grass, and Forb are the types of seeds that comprise percent seed found in stomach contents.

Species	**Season**	**"N"**	**Seed (% diet)**	**Plant (% diet)**	**Arthropod (% diet)**	**Shrub Seed**	**Grass Seed**	**Forb Seed**
PGFV - H	Spring	15	89	0	11	0	10	90
PGFV - H	Summer	1	100	0	0	33	67	0
DIME - H	Spring	4	40	15	45	0	37	63
DIME - H	Summer	2	66	17	17	0	67	33
DIME - H	Winter	1	100	0	0	0	100	0
DIOR - H	Summer	1	75	0	25	0	100	0
DISP - H	Summer	3	7	60	3	0	73	27
REMG - C	Winter	1	100	0	0	33	33	33
PMLE - C	Spring	2	10	0	90	0	0	100
PMLE - C	Summer	2	67	0	33	25	0	75
PMLE - C	Winter	4	76	5	19	18	46	36
PMTR - C	Spring	1	60	20	20	0	0	100
PMTR - C	Summer	1	25	0	75	0	0	100
ONAR - C	Spring	2	10	0	90	0	0	100
ONAR - C	Summer	7	6	0	94	0	50	50
ONAR - C	Winter	5	26	0	74	0	29	71

Results:

The mean summed monthly Fruit Availability Index (FAI) per plant functional group quantifies the diversity of species seeding at each sampling period and the proportion of plants seeding on the landscape (Figure 3.1, inset). There is a bimodal pattern in the timing of C_3 forb seed production, with a seeding pulse occurring in spring and again during the monsoon season. C_4 grass seed production increases in response to monsoon rains; and there is typically a late season pulse of C_4 forb seed production. In 2013, there was very little seed available in the spring or summer, however, in September and October there was twice the average proportion of species seeding including a large contribution from C_3 forbs, C_4 forbs and C_4 grass in response to above-average monsoon rainfall (Figure 3.1). In 2014, there was a bimodal pulse of C_3 forbs seeding in both spring and fall. C_4 grasses and forbs responded to late fall monsoon rains, with higher than average numbers of species seeding in the fall. 2015 was a low resource year. Resources peaked in May with higher than average C_3 forb seed production. Maximum seed availability on the landscape declined over the course of this three year study, however the FAI remained above the long-term (2000-2016) summed monthly average. LAI wa s similar to FAI and shows the same general patterns, with a much higher diversity and an inset representing the mean values across all years (Figure 3.2).

We found a significant positive linear relationship between $\delta^{15}N$ and percent N in plant material ($r^2 = 0.14$, $p = 0.001$, slope = 0.75, Figure 3.4). This relationship justifies using raw $\delta^{15}N$ values in both plants and rodents as an indicator of forage selection for high quality (high N) versus a mixing model, which would not be effective due to the high variability in baseline $\delta^{15}N$ values in plants. There were clear endpoints between mean $\delta^{13}C$ values of plants by functional type (C_3 = -26.6 +/- 1.8‰, C_4 = -14.4 +/- 0.8‰, and CAM = = -12.5 +/- 0.7‰). Rodent $\delta^{13}C$ in plasma fell along a continuum implying that their diet is comprised of a combination of plant functional types offset by a trophic discrimination factor (Figure 3.5-A). Given the large $\delta^{13}C$ difference (12–14‰) between

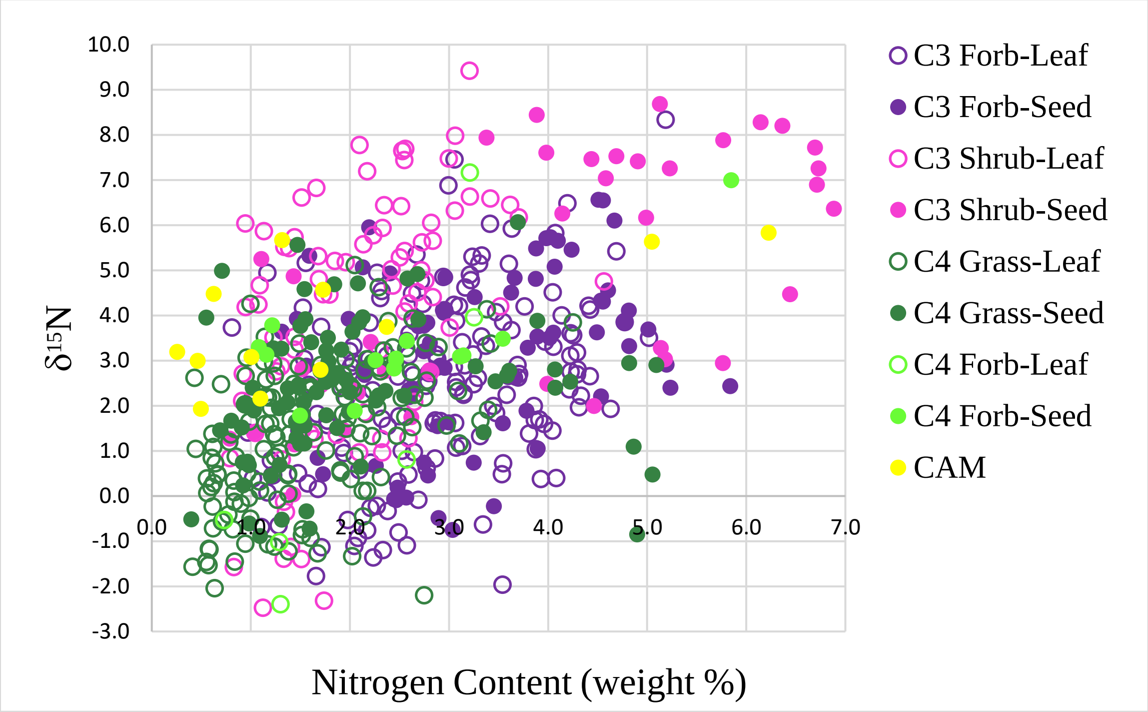

Figure 3.4: The isotopic value $\delta^{15}N$ has a positive linear correlation with nitrogen content by weight [N]. Different plant tissues and plant functional groups have different nitrogen signatures. This linear correlation validates the use of raw $\delta^{15}N$ values as a proxy for forage quality in this system. Each dot represents a unique sample color coded by functional type, seeds are closed circles and leaves are open. The R^2 for this data is low (0.14) due to scatter, however the slope of the line is 0.75 which implies that for every 0.75 increase in $\delta^{15}N$ there is a 1% increase in nitrogen content by weight. This is a significant relationship (p. value = 0.001)

C_3 and C_4 plants in this ecosystem, and the range of $\delta^{15}N$ values in primary producers, subtle variation in trophic discrimination will not greatly influence results.

Four biologically informed diets that best represented natural diets were used to determine if rodents selectively forage on higher quality items, if they maintain consistent diets throughout the year, or if their diets reflect seasonally variable primary production (Figures 3.5, 3.6). We found that rodents selectively consume plant or prey items with high nitrogen content when available (Figure 3.5-B). The middle 45 % of the rodents in each foraging guild track the N content of forage on the landscape, represented by simulated diets created using FAI (Figure 3.1), LAI (Figure 3.2) and plant isotope values. Diet 1, the random seed diet (FAI values plus a trophic discrimination factor) consistently underestimates plasma $\delta^{15}N$, indicating that rodents exhibit some degree of forage choice and choose higher quality forage, when available. This diet consistently underestimates (spring) and overestimates (fall) carbon values in rodent plasma. Diet 2, the random leaf diet (LAI values plus a trophic discrimination factor) is a better match for carbon values in rodent diets, particularly in the fall. This implies that as seed availability declines on the landscape, rodents are potentially consuming more leaf material. In nitrogen values, this diet underestimates nitrogen in years of resource abundance when rodents are foraging on higher quality seed, however in 2015 as resources declined, this diet more closely matches, presumably because rodents are incorporating more leafy material into their diets. Diet 3, the informedcarni diet is comprised of 50% arthropods that forage on 75% C_4 and 25% C_3 foliage and seed. The remaining 50% of the diet is comprised of 5% high quality foliage and 45% high quality seed determined by a low C:N ratio. This diet also overestimates and underestimates carbon rodent plasma values across the year, but to a lesser extent than the random seed diet. Nitrogen values are consistently high for heteromyids, but this diet closely resembles the mean cricetid values for nitrogen in 2014, a year of high resource abundance. The informedveg diet assumes rodents are consuming 80% high quality seed based on low C:N ratios, and 20% high quality foliage. This diet is the best fit for carbon, matching small mammal plasma in the fall as they strive to meet their nutritional needs but underestimating values in the spring. This diet closely matches heteromyid nitrogen values, implying a consistent level of folivary among species. This diet most closely mimics rodent community values as they converge in 2015 as resources decline. This implies that seed and insects are being supplemented with leaves. In addition, foraging breadth widens in 2015 implying a high degree of dietary variation as rodents strive to meet their nutritional requirements (Figure 3.5 A and B).

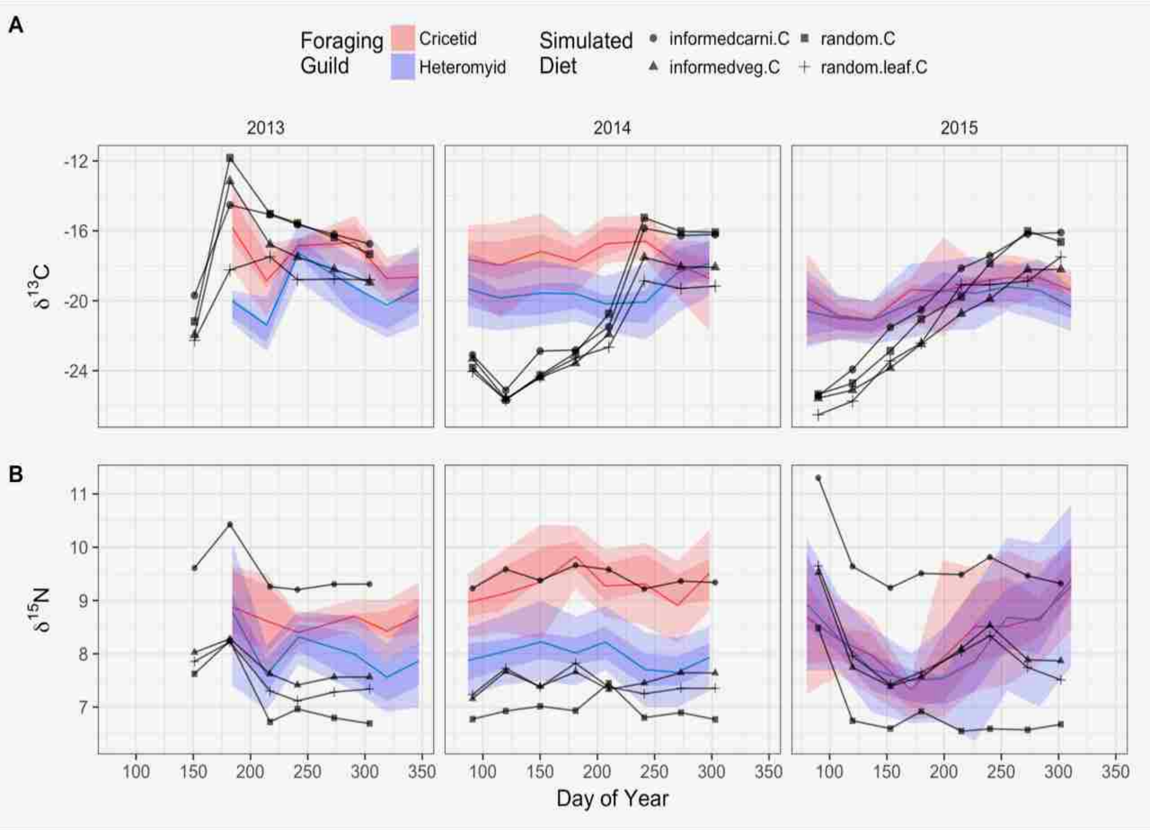

Figure 3.5: Carbon (A) and nitrogen (B) isotopic values of rodent plasma over the study period. Mean values per trapping bout of each feeding guild are shown with a solid line and the middle 30% of all individual observations are shown with the darkly shaded band with an additional 15% on either side in the lightly shaded band. Bands overlap in times of diet convergence when resources are limited (2015). Bands diverge in times of high resource availability indicating some degree of niche partitioning (2014). Black points represent simulated diets (Informedcarni, Informedveg, Random (seed), and Random.leaf). We created a null model using simulated diets offset by the trophic discrimination factors (1.0 per mil for Carbon and 4.4 per mil for Nitrogen). Rodents do not selectively forage as evidenced by the fact that there is no overlap between rodents and simulated diets as they mirror a large increase in C3 plant functional types on the landscape. Rodents to appear to track nitrogen on the landscape as evidenced by the mean d15N values tracking the simulated diets. As cricetids diverge from heteromyids (2014), their diets still mirror the nitrogen values in plants implying that any arthropods incorporated into their diet were likely obtaining their nitrogen from recent foliage. When resources are limited, diets converge and widen (2015) as rodents generalize to meet their nutritional requirements.

Mouse diets converge at the beginning of our trapping program due to poor resource availability (Figures 3.1, 3.2, 3.5, and 3.6). A strong monsoon in 2013 resulted in a large amount of late season C_4 forb production reflected in low $\delta^{13}C$ values in mouse plasma across all species. In 2014, a year with abundant resources, mouse diets diverged. The cricetids have both high $\delta^{13}C$ and high $\delta^{15}N$ isotopic values suggesting they feed at a higher trophic level (Table 3.1, Figure 3.5). The heteromyid diets are consistent in 2014 as they mirror nitrogen levels of the available resources. In 2015, a poor resource year, all diets converge with near complete overlap in $\delta^{13}C$ values. Nitrogen values also converge, and broaden suggesting that the animals are foraging widely to meet nutritional requirements. When resources decline in 2015 (Figures 3.1, 3.2), and diets converge (Figures 3.5, 3.6), cricetids are incorporating more C_3 resources into their diets (Table 3.2), and potentially eating at a lower trophic level as arthropod populations and primary production decline across the landscape. Heteromyids depend on primary production, their $\delta^{13}C$ and $\delta^{15}N$ values are less variable than the cricetids, however as resources decline in 2015, their foraging breadth expands, potentially incorporating arthropods into their diet as evidenced by a late season increase in $\delta^{15}N$ values (Figure 3.5).

At the species level, *Onychomys arincola* (ONAR) is typically the highest in $\delta^{15}N$ and median in $\delta^{13}C$, reflecting a highly carnivorous diet. *Perognathus flavus* (PGFV) is the closest to a C_3 specialist on the landscape, exhibiting consistently low $\delta^{13}C$ and $\delta^{15}N$ plasma values. Most other species appear to be eating a mix of C_3/C_4 as indicated by the overlapping $\delta^{13}C$ values. *Dipodomys spectabilis* (DISP) has low $\delta^{15}N$ values, because they selectively forage on carbohydrates over proteins due to the metabolic water released during catabolism (Hope and Parmenter, 2007, Leaver L., 2004) (Figure 3.6).

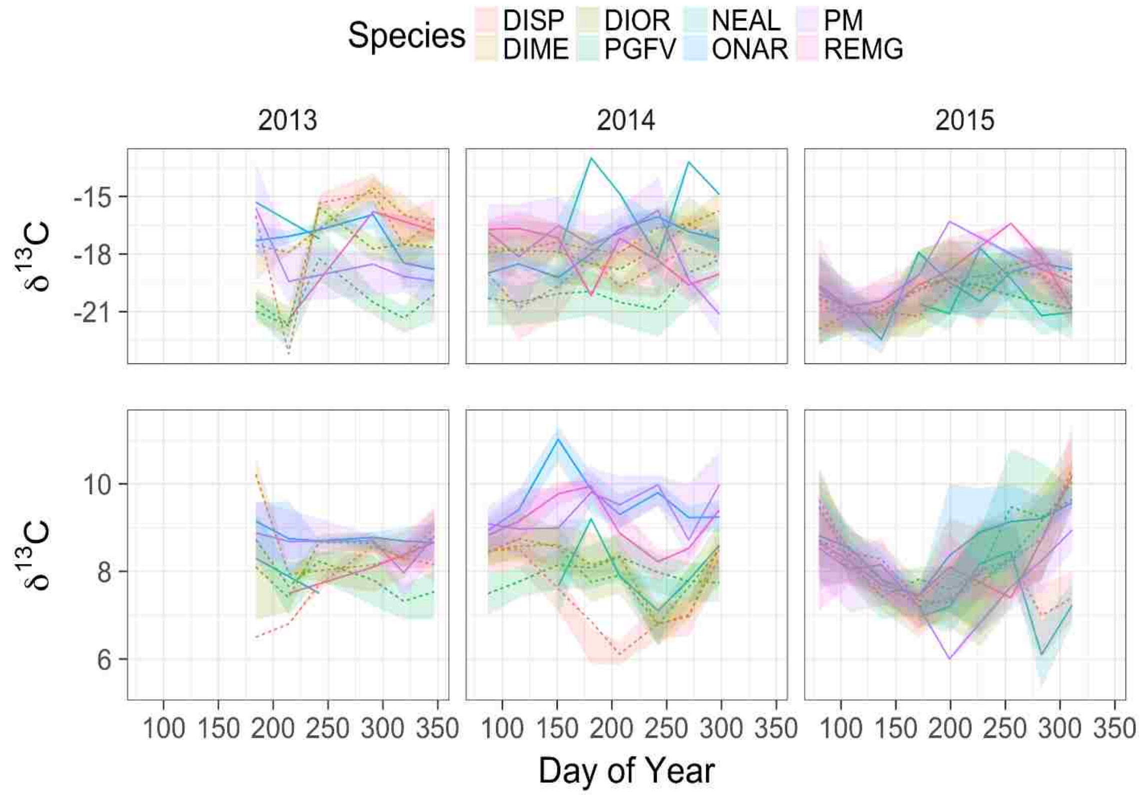

Figure 3.6: Carbon (top) and nitrogen (bottom) isotopic values of rodent plasma over the study period. Mean values per trapping bout of each feeding guild are shown with a solid line for cricetids and a dashed line for heteromyids. The colored band represents the middle 50% of all individual observations. Bands overlap in times of diet convergence in early spring. Bands diverge in times of high resource availability indicating some degree of niche partitioning (2014).

Discussion:

Coexisting species that share limiting resources theoretically compete for those resources (Atwood et al. 2011). Alternatively, like rodents in arid ecosystems, competitors may partition resources when they are abundant, and share when they are not. The sun bear and the black bear coexist in a stochastic dynamic equilibrium with extensive niche overlap, often consuming the same seed species. Niche breadths of the bears widens during periods of seed scarcity with the sun bears consuming proportionately more insects than black bears at this time (Steinmetz et al. 2013).

Rodents follow a similar pattern with near complete dietary overlap when resources are limited, and a partitioning of resources when they are abundant (Figures 3.1, 3.2, and 3.5). Fluctuating resources permit competitive coexistence on a suite of resources.

Of the several explanations for coexistence of ecologically similar rodents, capable of reducing interspecific competition while maintaining species and/or individual fitness (Kinahan et al. 2008), we propose that dietary partitioning is of primary importance (Kotler and Brown 1988, Price and Heinz 1984, Kartzinel et al. 2015). Our findings indicate that rodent diets reflect a consistent mix of plant functional types as indicated by their consistent plasma $\delta^{13}C$ values, which do not track a C_3 signature in the spring or climb toward C_4 values in the fall (Figure 3.5). There is evidence for both folivary, as supported by Kinahan et al. 2008 which found a gradation in gut modification in six species of rodents, and insectivory (Hope and Parmenter 2007) with rodents incorporating a high percentage of arthropods (high $\delta^{15}N$) into their diet when resources are abundant (Figure 3.5). Rodent $\delta^{15}N$ plasma levels indicate incorporation of high quality forage with rodent diets consistently more enriched in nitrogen than either leaf or seeds. When resources decline, diets converge and rodent populations become generalists, subsisting on a common set of resources. When this occurs, their diets most closely match the informedveg and random leaf diets, implying that they consume high quality foliage in the absence of seeds.

Rodents serve as an ideal study organism for population wide foraging strategies in a highly stochastic ecosystem. They are a specious and abundant primary consumer, often serving as prey for higher trophic levels, and they respond quickly to environmental changes (Habtamu et al. 2012). Populations of rodents fluctuate in arid environments, persisting at low densities when resources are scarce and rapidly increasing in abundance in response to increased primary production (Dickman et al. 2011). Resources in many arid environments experience spatiotemporal stochasticity in quality and quantity, requiring rodents to exhibit a high degree of dietary plasticity, a trait supported by our data. In addition, rodents have fat stores or caches, and/or use physiological mechanisms such as torpor to conserve energy and water, or burrows to buffer climactic extremes (Gese et al. 1996, Murray et al. 2006). These mechanisms serve to complicate foraging strategies, with coexistence of multiple species on a shared resource supported by heterogeneity among species in seed-caching behavior (Price et al. 2000).

Different types of caching such as scatter hoards versus larder hoards, and the location of caches could be a way to partition available resources, permitting a high degree of dietary overlap among multiple rodent species. The amount of seeds cached and the degree of scatter hoarding increases with rodent body mass (Price et al. 2000). In addition, caching increases environmental heterogeneity of resources in two phases, first when the seeds are dropped and secondly as caches are utilized and/or pilfered. This heterogeneity promotes coexistence. Larger species maintain a greater number of larger caches, possibly functioning as resource concentrators which facilitates foraging by smaller species (Price et al. 2000, Murray et al. 2006) and limits resource availability to competitors (birds and ants). Most species both scatter hoard and larder hoard with larger species potentially better equipped to defend a larder (Leaver, L. A. 2004). Heteromyids prefer seeds that are relatively high in carbohydrate and low in protein due to metabolic water accrued through catabolism (Schmidt-Nielsen, 1964). Perhaps this is why rodent plasma $\delta^{13}C$ values do not track C_3 vegetation on the landscape but instead incorporate more C_4 plants into their diet to adapt to resource limitations.

Consumers mediate foraging choices by diet switching to maximize energetics budgets, water budgets, and resource quality in response to highly stochastic resource availability (Gese et al. 1996). Spatiotemporal changes in resource availability affect foraging choices at both the individual and community level. For example, Banks et al. (2000) supplemented winter food resources to determine if a shortage of food in the winter was affecting breeding, resulting in lower summer population densities of rodents. Winter food supplementation increased body mass, and reproductive preparedness resulting in high spring fecundity. Birds in the tropics responded to changes in habitat structure and resource availability by restricting fecundity or migrating locally. Bird biomass tracked resources, for example frugivores increased when seed was prevalent and omnivores became frugivores during the dry season and insectivores during the wet season (Borghesio et al. 2004). This rodent community maintains a consistent diet, foraging on the highest quality items available, a strategy common in other species. In a community dominated by warm-season C_4 vegetation, elk preferentially grazed on C_3 vegetation as detected by stable isotope analysis (Conard et al. 2012).

Past research has focused on interspecific variation in the ability to exploit resource heterogeneity as a mechanism in support of a high diversity of co-occuring species (Price et al. 2000). Competition is secondary in this ecosystem due to high temporal variation in resource availability which is mediated differently by different populations of rodents (Wiens, J. A. 1976). Populations with shorter or longer life cycles than the periodicity of resource availability are generally more stable than those with a generation length corresponding to the temporal periodicity of the environment. In arid environments, small variations in soil, topography, and microclimate create especially well-defined vegetation patterns affecting both the floristic composition and the spatial structure of the plant community through their effects upon water availability in combination with allelopathy and herbivory (Wiens, J. A. 1976). This variability creates ecosystem stresses which do not support the basic conditions for competition versus resource controlled systems. For competition to constrain populations, the environment is considered to be in equilibrium, resources are constantly limiting with no temporary relaxation of selection pressures such as a resource abundant year, and all niches are saturated. In arid habitats, none of these parameters are supported. The environment is in continual flux, with high and low resource years supporting high and low population densities which increase and decrease the levels of inter and intra-specific competition. This results in an opportunistic approach to habitat use with relatively close tracking of variations in resources by consumers, supporting our results. As resources decline, and or population density increases, poorer quality food becomes just as valuable as higher quality forage. At this point population level use of the habitat expands as poorer quality resources are needed for survival (Wiens J. A. 1976). If resources are perfectly substitutable species diets will diverge during a resource abundant year (2014), however if a mixture of resources is required like carbohydrates and proteins, then diets converge (2015), this can be calculated as a function or a weighted sum of the intake of resources necessary for survival, similar to our leaf and fruit availability indices (Abrams, P. A. 1987).

Stable isotope analysis, fruit and leaf availability, and seed characteristics allowed us to explore possible diet scenarios for a specious desert rodent community. Stable isotope values provide a broad scale or coarse grained approach to dietary reconstruction. For them to be effective, you must have clear differences in your isotopic baseline as we do in our plant functional types for Carbon. Nitrogen has more variability and nitrogen values should be used with caution, potentially requiring different discrimination factors for each plant part and functional type (Caut et al. 2008). However isotopes are limited to plant functional type, to further compliment this study, we should conduct DNA metabarcoding to compare feces to plant genus to develop a fine grained resolution of diet preferences.

Life in the Northern Chihuahuan desert is characterized by nutrient and precipitation limitation combined with resource pulses of differing biomass and forage quality. Temperature and precipitation are the primary drivers of productivity in bottom up systems where high stochasticity affects forage quantity and quality (Fitzherbert et al. 2007, Ecke et al. 2002, Klimstra et al. 2015, Coppeto et al. 2006). Resource pulses are dramatic examples of temporal variation where species composition changes continuously in space and time (forb dominant versus grass dominant). Consumers that persist in these environments have mechanisms for tolerating or avoiding the negative effects of these pulses, an increase in density, time-lagged increases in predation, and potential increases in competition (Holt, 2008). Incorporating storage mechanisms like fat stores and/or caching into food web dynamics further complicates interpreting patterns (Gese et. al. 1996). The majority of species in these ecosystems are adapted to a stochastic environment with rodent dietary choices both responding to and reflecting a changing landscape of primary production. Rodents consume the most nutritious food available while maintaining a high level of dietary plasticity in both foraging width and breadth as dictated by resource availability. Coexistence is a balance between equalizing mechanisms which prevent a single species from having a large fitness advantage, and stabilizing mechanisms which permit growth for all species. These communities contain a mix of species with different adaptations for coping with spatiotemporal variation in resource quantity and quality which in turn drives consumer community architecture.

Chapter 4: Climate mediated changes in foraging strategies of the silky pocket mouse (*Perognathus flavus)*

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Abstract:

Aridland ecosystems are characterized by high stochasticity in temperature and precipitation resulting in low and variable primary production. Organisms that survive in these environments must engage in a variety of foraging strategies to compensate for fluctuating resource quality and quantity. Optimal Foraging Theory predicts that organisms will specialize on the highest quality resources, generalizing when preferred resources become scarce. The Niche Variation Hypothesis predicts that individuals will specialize on a subset of available resources when resources are abundant and competition is high. Appropriate tests of these theories require detailed data on individual foraging strategies and resource availability. We measured stable isotope composition in 1,406 plasma samples from silky pocket mice (*Perognathus flavus*) to quantify the dietary contributions of C_3 (high quality) versus C_4 (low quality) primary production. Of these samples, 695 were from 173 individual mice captured three or more times. During a population boom, the number of *P. flavus* individuals nearly doubled from the prior year while populations of other co-occurring small mammal species remained stable. As a consequence, intraspecific competition increased causing some individuals to specialize on either C_3 or C_4 resources, while 60% of the population remained generalist foragers. During the population boom *P. flavus* expanded its foraging breadth ($\delta^{13}C$) from spring to fall, generally tracking resource availability. In the following year, however, individuals of *P. flavus* expanded their trophic breadth ($\delta^{15}N$) to compensate for lower resource quality and quantity. Our results demonstrate that this population is comprised of mice that exhibit a high degree of intra-individual variability in foraging strategies. This dietary plasticity likely alleviates increased intraspecific competition when population numbers are high. Our results demonstrate that when analyzed at the individual level both Optimal Foraging Theory and the Niche Variation Hypothesis may apply to the foraging dynamics of small mammals in ecosystems where resources are chronically low and highly variable.

Introduction:

Desert ecosystems are characterized by temperature and precipitation extremes resulting in low and unpredictable primary productivity of variable quality (Sala et al. 2012, Collins et al. 2014). In these highly stochastic environments, consumers have developed a variety of foraging strategies to acquire resources that vary in space and time (Gordon et al. 2010, Houadria et al. 2015, Atwood et al. 2011). Individuals within a population vary their forage selection in response to four major drivers: resource quality and quantity (Bolnick et al. 2003, Van Valen 1965), inter- and intraspecific competition (Araujo et al. 2008, 2009, 2011, Agashe et al. 2010), predation risk (Bolnick et al. 2003, Kotler et al. 1994), and phenotypic variation (Agashe et al. 2010, Roughgarden 1972). The Niche Variation Hypothesis proposes that foraging specialization depends on population density. When organisms are numerous and/or niche width is narrow, individuals will specialize to reduce intraspecific competition (Van Valen 1965). In contrast, Optimal Foraging Theory proposes that individuals will preferentially forage on the most energetically valuable resources to meet their nutritional demands. When these resources decline, individuals will expand their dietary niche and "generalize"

(Roughgarden 1972, Bolnick et al. 2007). The development of specialized foraging strategies is well documented in mammals (Estes et al. 2003, Tinker et al. 2008, Robertson et al. 2014), amphibians (Araujo et al. 2009, Bolnick et al. 2007), birds (Catry et al. 2014, Martinez del Rio et al. 2009, Woo et al. 2008), fish (Frederich et al. 2010, Matich et al. 2011, Garduno-Paz et al. 2010), reptiles (Warne et al. 2010) and insects (Fontaine et al. 2008, Hagbery et al. 2012). We lack empirical data linking the development of specialized foraging strategies to population densities, especially within populations that fluctuate in response to highly stochastic resource availability (Sala et al. 2012, McCluney et al. 2012, Meserve et al. 2011, Letnic et al. 2010).

Over the past 150 years in the Southwestern US, nearly 20 million hectares of C_4-dominated grassland have been replaced by C_3-dominated shrubland (Van Auken 2000, 2009). Climate models predict a ~10–20% decrease in winter precipitation, more variable precipitation events, and increasing aridity in these regions (Gutzler and Robbins 2011, Cook et al. 2015), favoring the continued expansion of woody shrubs into grassland (Baez et al. 2013, Caracciolo et al. 2016, He et al. 2015). Shrub encroachment results in increased winter nighttime temperatures, and an overall decline in herbaceous plant biomass and diversity (Baez and Collins 2008, Cabral et al. 2003, D'Odorico et al. 2010) when compared with adjacent grasslands. The northern range boundary of creosotebush (*Larrea tridentata)* shrubland co-occurs with black grama (*Bouteloua eriopoda)* grassland creating a dynamic ecotone between desert grassland and shrubland ecosystems. This transition zone provides an ideal natural laboratory to study the development of individual foraging strategies to alleviate increased intraspecific competition during a small mammal population boom-bust cycle.

Much of the American Southwest experiences annual bimodal precipitation (Notaro et al. 2010) resulting in two seasonal pulses of net primary production that use either the C_3 or C_4 photosynthetic pathway. Cooler temperatures and winter/spring rains favor the production of C_3 plants (Xia et al. 2010) while higher temperatures and monsoon rains fuel a second pulse of production dominated by C_4 grasses (Muldavin et al. 2008). C_3 and C_4 plants differ in both isotopic signatures (Craig 1953, Farquhar et al. 1982), and nutritional quality. C_3 plants are more nutritious with greater seed mass and a higher nitrogen content in both leaves and seeds than C_4 plants (Guo et al. 2000, 2003, Hope et al. 2007, Orr et al. 2015, Amiri et al. 2012, Caswell et al. 1973). Due to their ability to tolerate high temperatures and poor quality soils, C_4 grasses have a survival advantage over herbaceous C_3 forbs under future climate scenarios (Ehleringer and Bjorkman 1977, Gibbens et al. 1996, Williams and Markley 1973, Petrie et al. 2014). Since herbaceous forb abundance is strongly correlated with seasonal rainfall (Xia et al. 2010, Mulhouse et al. 2016), climate change will likely decrease the biomass of select C_3 forbs, reducing the availability of this high quality resource. Thus, understanding how consumers utilize both high and low quality resources in this highly variable dryland ecosystem will provide valuable insight regarding how these consumer populations will respond to projected increases in climate variability.

The northern Chihuahuan Desert harbors a diverse assemblage of small mammal species (Ernest et al. 2000, Fox 2011, Kelt 2011) with a wide range of life-history strategies in terms of reproduction, foraging behavior, and fitness requirements. Abundance of small mammals has been shown to fluctuate in response to previous season precipitation and net primary production (Thibault et al. 2010). Two primary taxonomic families of rodents occur in this region: Cricetids, opportunistic omnivores, and Heteromyids, food-caching granivores. The silky pocket mouse, (Heteromyidae: *Perognathus flavus)* is a small (6-12g), abundant, larder hoarder that forages throughout the year excluding short, weather-induced periods of torpor (<72 hours) (Rymer et al. 2016, MacMillan et al. 1983). In 2014, *Perognathus flavus* experienced a population explosion at our study site, which provided an ideal opportunity to analyze the development of specialist or generalist foraging strategies in individual mice. Small mammal population explosions in response to resource abundance are well known, however strategies adopted by individuals during rapid changes in resource availability are not well documented (Dickman et al. 2011, Letnic et al. 2010, Meserve et al. 2011, Thibault et al. 2010).

In this study, we utilized carbon and nitrogen isotopic data from *P. flavus* plasma to examine the development and dynamics of individual foraging strategies within the population during a boom-bust cycle (Matthews et al. 2004). At the population level, we quantified foraging breadth in relation to resource availability. At the individual level, we delineated individual foraging strategies (e.g., C3 vs. C4 specialists) as a potential mechanism to reduce intraspecific competition. We used a temporal record of individual dietary choices combined with long-term datasets on resource availability to examine whether small mammal foraging strategies are best explained by either Optimal Foraging Theory or the Niche Variation Hypothesis. We addressed the following questions: Does the foraging breadth of the *P. flavus* population exhibit temporal change reflecting the landscape of available resources? Do foraging strategies vary among co-occurring individuals? And, do most individuals preferentially forage on the most energetically optimal resources (C_3 vs. C_4)?

Methods:

Our study was conducted in the Sevilleta National Wildlife Refuge (SNWR: 34°20′N, 106°43′W), Socorro County, New Mexico, USA. Mean annual precipitation at this site is ~250 mm, more than half (~150 mm) of which occurs via convective storms which create intense but highly localized rain events during the summer monsoon, July through early September (Notaro et al. 2010, Petrie et al. 2014). Winter and spring precipitation typically occurs as a mixture of snow and light rain (Gosz et al. 1995, Pockman & Small, 2010). This site crosses an ecotone that grades from C_4-dominated black grama (*Bouteloua eriopoda)* grassland to C_3-dominated creosotebush (*Larrea tridentata)* shrubland. Seasonal precipitation patterns directly influence the abundance and production of C_3 and C_4 functional groups (Muldavin et al. 2008, Xia et al. 2010). Values for seasonal precipitation, plant standing biomass, and seasonal net primary production (NPP) were calculated using data sets from the Sevilleta Long-term Ecological Research Program (http://sev.lternet.edu/data/sev-182, sev-51, sev-129). Biomass and NPP values were used as proxies for C_3 and C_4 resource availability (seeds) at our study site, based on the documented positive relationship between size and fecundity in herbaceous plants (Aarssen and Taylor 1992, Meserve et al. 2003).

Small mammals were trapped monthly from March to October 2014 and March to November 2015 over three consecutive nights on the weekend closest to the new moon when mice were most active (Kotler et al. 1994). A total of 290 Sherman live traps were baited with rolled oats, peanut butter and heat treated millet and set on two permanent trapping webs (see Parmenter et al. 2003 for web design). Trapped mice were identified to species, and their sex, age, mass, and reproductive condition were recorded. An electronic pit-tag was inserted subcutaneously in each mouse to enable tracking of individuals through time. All animal trapping and processing protocols were approval by the UNM Institutional Animal Care and Use Committee (IACUC #13-100970-MC).

Proportional consumption of C_3 and C_4 functional groups can be differentiated by the $\delta^{13}C$ isotopic values of plants (Craig 1953, Farquhar et al. 1982), which are mirrored in the plasma of consumers that utilize these resources. To quantify isotopic signatures, a 50 μL blood sample was obtained from each mouse by slipping a heparinized micro capillary tube behind the eye to puncture the retro-orbital sinus. Micro capillary tubes of blood were placed on ice for transport to the lab where they were centrifuged to separate plasma from red blood cells. A total of 14,210 trap nights (the sum of the number of traps set per night per month) resulted in 1,406 plasma samples from 733 individual *P. flavus* which were analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios. Of these, 173 individuals were processed during three or more monthly trapping bouts, providing a temporal profile of individual dietary choice. Since the isotopic value of blood plasma reflects the isotopic values of food eaten (with a consistent offset or trophic discrimination factor) and *P. flavus* plasma turns over approximately every three weeks (half-life is ~5 days), monthly sampling provides a near continuous record of diet in this species (Tsahar et al. 2008, Parnell et al. 2010). Data from another long-term trapping record (1989 – present; http://sev.lternet.edu/data/sev-008) using a similar web design located a kilometer from our study site were used to quantify long-term population dynamics of *P. flavus* and other small mammal species at this site.

Plants with high relative abundance and biomass were collected from each trapping web throughout the year. Plant samples were placed in coin envelopes in the field and then dried in a 40ºC oven for 48 hours. Both leaves and seeds were collected for isotopic analysis to establish a temporal baseline of $\delta^{13}C$ and $\delta^{15}N$ values for comparison with plasma values. Plasma and plant tissues were prepared for carbon and nitrogen stable isotope analysis at the University of New Mexico's Center for Stable Isotopes (CSI). Approximately 0.5–0.6 mg of plasma and 3–5 mg of plant material were sealed in tin capsules and $\delta^{13}C$ and $\delta^{15}N$ values were measured with a Costech ECS 4010 Elemental Analyzer (Costech Analytical Technologies, Valencia, CA) coupled to a Thermo Scientific Delta V mass spectrometer (Bremen, Germany). Isotope values were referenced against international standards of Vienna Pee-Dee Belemnite (VPDB) for carbon and atmospheric air for nitrogen. Measured isotope values were calibrated against international standards using internal reference materials run alongside plasma and plant material samples to correct for instrument drift. Repeated within-run measurement of these reference materials yielded an analytical precision (SD) of ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Isotope values are reported in delta (δ) notation as parts per mil (‰): $\delta = (R_{sample}/R_{standard}) \times 1000$, where R_{sample} and $R_{standard}$ are the relative ratios of the heavy and light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) in a sample and standard, respectively.

Using the spatial metric SIBER (Stable Isotope Bayesian Ellipses in R in the SIAR package, Jackson et al. 2011) we quantified standard ellipse areas in bivariate plots based on $\delta^{13}C$ and $\delta^{15}N$ plasma values for each sample period to examine changes in the foraging breadth of the population as a whole across the growing season. Changes in the length of an ellipse along the $\delta^{13}C$ axis over time indicate changes in dietary breadth in terms of carbon source (C_3 versus C_4). An expansion of an ellipse along the $\delta^{15}N$ axis infers incorporation of plants with a higher nitrogen content such as nitrogen fixers or C_3 forbs, and/or the addition of trophic levels, such as incorporating arthropods. Standard ellipse areas in 2015 were corrected for small sample size (Syvaranta et al. 2013). Using a two source; mean $\delta^{13}C$ values of plants sampled at the SNWR ($C_{3,}$ -26.6 +/- 1.8‰ and $C_{4,}$ -14.4 +/- 0.8‰), and one isotope; $\delta^{13}C$ of plasma Bayesian mixing model we estimated the proportion of assimilated carbon in *P. flavus* plasma that was derived from C_3 versus C_4 resources (Caut et al. 2009). A $\delta^{13}C$ trophic discrimination factor ($\delta^{13}C$ tissue-$\delta^{13}C$ diet) of 1.0‰ and assumed variance (SD) of 0.25‰ was selected based on average values from the literature for a wide range of organisms (Bearhop et al. 2004, Caut et al. 2009, DeNiro et al. 1978, Kurle et al. 2013). Given the large $\delta^{13}C$ difference (12–14‰) between C_3 and C_4 plants in this ecosystem, subtle variation in trophic discrimination will not greatly influence results.

Individual dietary specialization was determined using the average percentage of C_3 plant material found in individual mouse diets. Percent C_3 was determined using SIAR, a Bayesian mixing model (Parnell et al. 2010) for the 173 plasma samples collected from mice processed three or more times in 2014 and 2015. Percent C_3 values were corrected by trap month and web to reduce temporal and spatial autocorrelation caused by systematic seasonal and site differences in forage availability (Zuur 2009, Appendix 4.1). We calculated the average within-individual standard deviation in dietary percent C_3 to define an expected maximum niche width. Individuals with mean diets more than one standard deviation away from the population mean percent C_3 were determined to be C_3 or C_4 specialists and those within one standard deviation of the population mean percent C_3 were considered generalists.

Results:

At the SNWR, long-term mammal trapping data show that *P. flavus* has exhibited three population boom and bust cycles since 1989. These boom-bust cycles correspond to peaks in seasonal rainfall and subsequent pulses in NPP (Figure 4.1). The largest *P. flavus* population boom occurred in 2014. This boom was documented in the long-term trapping web data (Figure 4.1-D) as well as in our short-term trapping data set (Figure 4.1-D inset). At our site, abundance of *P. flavus* in March 2014 was 95% higher than in March 2015. During this time period abundances of cricetids were relatively constant while all other heteromyids exhibited smaller fluctuations in population size (Figure 4.1-D). The 2014 population spike, like a similar spike in 2007, occurred after a monsoon season that was 162% (243 mm) above average following a dry spring that was 72.7% below average (Figure 4.1-A). In response to abundant summer rains, forb production increased from 10.8 g m^{-2} in the spring of 2013 to 115.4 g m^{-2} in the fall of 2013 (Figure 4.1-C). This included a large increase in fall C_4 forbs. In addition to an increase in primary production, there was abundant standing biomass at the end of 2013 (Figure 4.1-B). Precipitation in 2014 was 60% below average with a dry winter/spring (40.6 mm) followed by an average monsoon (168 mm). In 2014 spring NPP was low, followed by average fall growth, however there was a large residual standing biomass from 2013. In 2015, precipitation was once again below average resulting in even lower primary production and standing biomass (Figure 4.1-B and C).

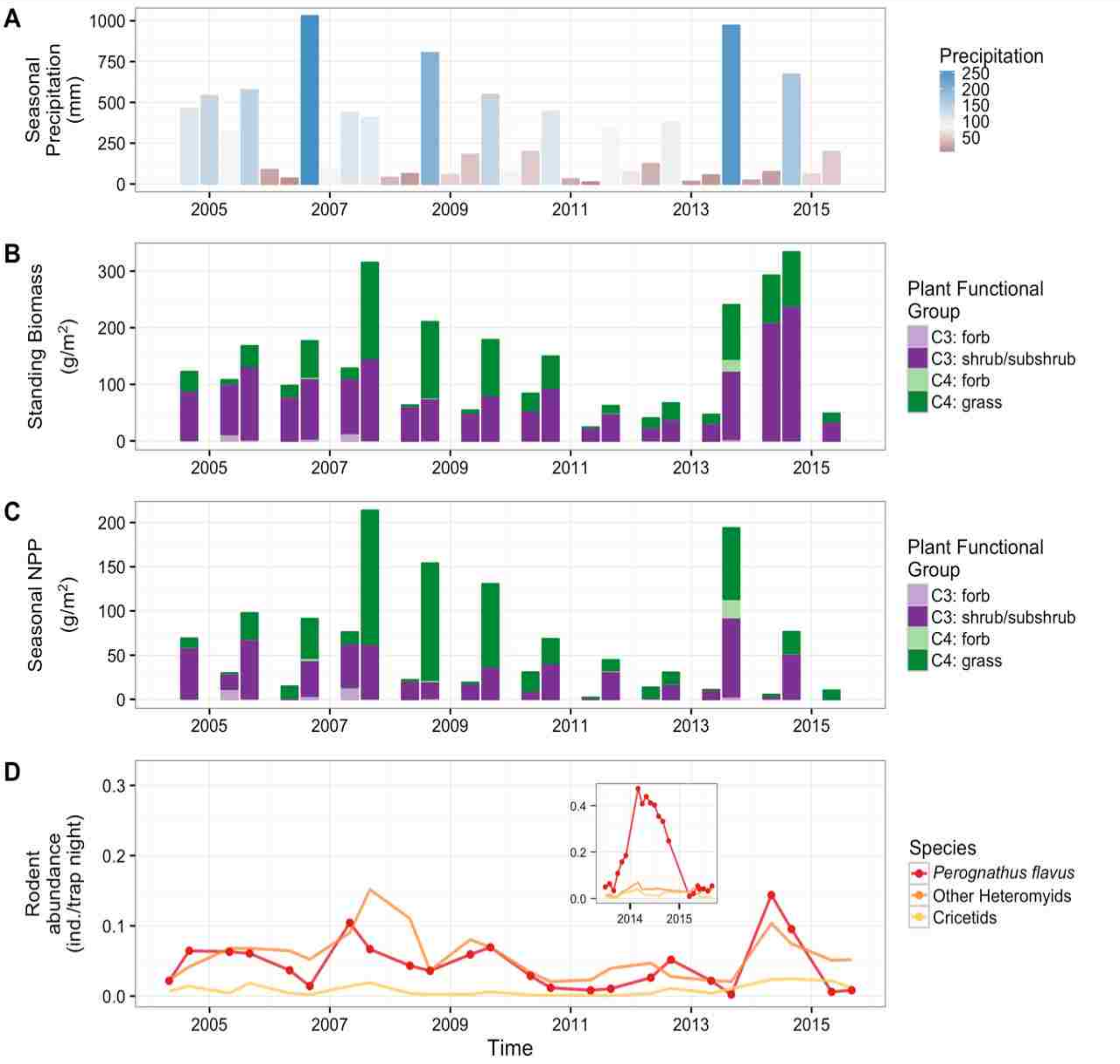


Figure 4.1: A, precipitation in mm summed every four months, data is collected from station #49 located within a km of our trapping webs. B, standing biomass calculated from volumetric measurements and destructive biomass sampling on a mixed shrub site within 0.25 km of our trapping webs. C, seasonal net primary production calculated using species specific regressions generated from destructive biomass sampling on a mixed shrub site within 0.25 km of our trapping webs. Growth from prior season is subtracted so this represents semi-annual measurements of growth in each of the plant functional types. D, rodent abundance calculated from LTER long-term data, species trapped were summed and then divided by trap night for each trapping bout. Other heteromyids and cricetids were averaged to illustrate population trends. D-inset, rodent abundance per trap night from our trapping webs which are located within a kilometer of the Sevilleta LTER trapping webs.

In spring of 2013 there was only one herbaceous forb, *Hoffmannseggia drepanocarpa*, present at the time of sampling at our site. However after the abundant monsoon rains C_4 herbaceous forb biomass increased 300%, primarily *Chamaesyce spp.*, along with a slight increase in C_3 forbs, *Chamaesaracha coniodes, Euphorbia exctipulata* and *Solanum elaeagnifolium* (Figure 4.1 B-C). C_3 woody shrubs *Larrea tridentata, Krascheninnikovia lanata*, and *Ephedra torreyana* as well as the three most common C_4 grasses *Bouteloua eriopoda, Sporobolus spp*. and *Pleuraphis jamesii* experienced moderate late season growth. In 2014 there was a 98% increase in spring C_3 forbs over the previous year with the most abundant being *C. coniodes, H. drepanocarpa,* and *Machaeranthera pinnatifida* and a decline in fall C_4 forbs (1.5% of fall 2013 biomass).

Based on tissue samples from a total of 335 plants collected on the trapping webs, the amount of nitrogen, a proxy for nutritional quality was significantly higher in C_3 plants compared to C_4 plants (mean 2.5 and 1.5% N by weight, respectively). C_3 shrubs, C_4 grasses and C_4 forbs had significantly higher N levels in their seeds than in their leaves. C_3 forbs had high levels of nitrogen in both their leaves and seeds with no significant difference between the two tissues. C_3 plants had significantly lower C:N ratios in their tissues than C_4 plants (23 versus 35 respectively) (t-statistic, p-value <0.001) (Appendix 3.3).

Isotopic analysis of C and N leaf and seed tissue from 16 C_3 forb, 5 C_3 shrub/subshrub, 7 C_4 forb and 9 C_4 grass species resulted in strong discrimination between C_3 and C_4 plants providing well separated endpoints for robust estimates of resource use by individual mice. *Perognathus flavus*, a generalist granivore, exhibited population wide shifts in foraging breadth over two years that differed in resource quality and quantity. In 2014 the foraging niche breadth (δ^{13}C), as measured by standard ellipse areas, increased from 3.3‰ pre-monsoon to 4.4‰ post monsoon (Figure 4.2-A). In 2015 there was an increase in standard ellipse areas from 8.2‰ (June) to 14.0‰ (August) and

Figure 2(A): 2014

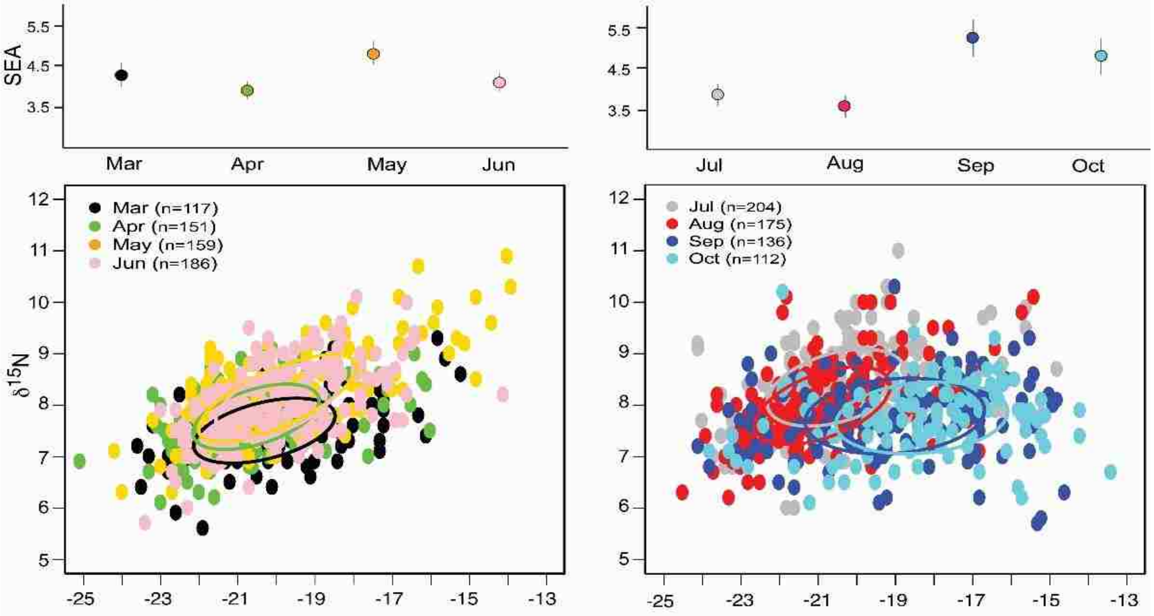


Figure 2(B): 2015

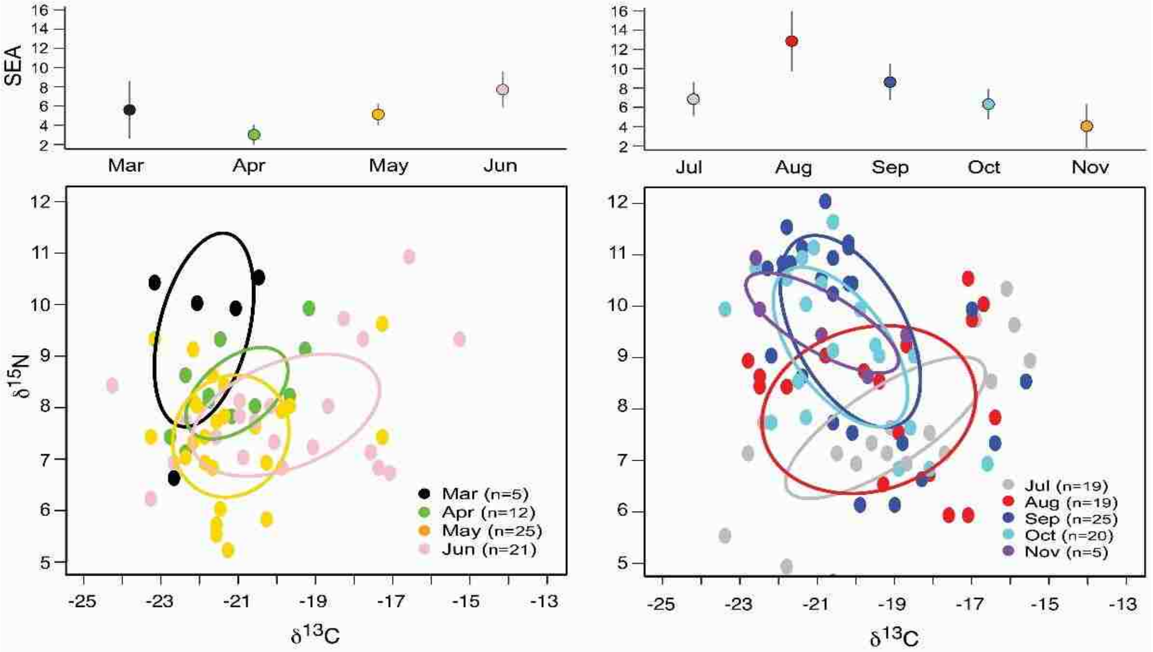


Figure 4.2 “A” 2014 standard ellipse areas. The expansion of the foraging breadth across the growing season is a result of increased intra-individual variation in foraging strategies to further partition the available resources to relieve intra-specific competition. “B” 2015 standard ellipse areas. The increase in ellipse areas are the result of a generalist foraging strategy in response to a decrease in resource quantity and quality. The increase in trophic breadth is a possible consequence of incorporating arthropods into diet to meet nutritional demands. Standard ellipse areas, are a spatial metric used to visualize dietary breadth on a monthly basis “n” for each month is indicated in parenthesis. This is a $\delta^{13}C/\delta^{15}N$ bivariate plot with $\delta^{15}N$ on the Y axis representing trophic level and $\delta^{13}C$ on the X axis illustrating forage breadth across the C_3/C_4 landscape (Jackson et al. 2011).

a shift toward higher $\delta^{15}N$ values (Figure 4.2-B). In 2014, a year with average rain providing consistent forage quality and quantity, the population wide foraging niche of *P. flavus* expanded along the C_3-C_4 axis tracking vegetative growth in response to changes in seasonal productivity. In 2015, resource quantity and quality were limited by below average precipitation. As a consequence the *P. flavus* population declined precipitously resulting in fewer mice foraging on a broader resource base, in some cases expanding their foraging breadth along the $\delta^{15}N$ axis.

Individuals displayed greater diet specialization in 2014, the year with highest resource availability and intraspecific competition (Figure 4.3). During this population boom the average *P. flavus* diet consisted of 54.2 $\pm$ 9.5% (s.d.) C_3 resources. Based on variability, 60% of individuals were generalists, 32% were C_3 specialists and 8% were C_4 specialists. In 2015 the average *P. flavus* diet consisted of 57.6 $\pm$ 13.2% (s.d.) C_3 resources, illustrating greater variability in diets of individual mice than the previous year, 16% were C_4 specialists, 84% were generalists, and there were no C_3 specialists. Specialists on high quality C_3 forage had lower standard deviations than either generalists or C_4 specialists implying that those mice consistently relied on C_3 resources. C_4 specialists had the highest standard deviation in resource use (Figure 4.3 inset) implying that specializing on a low quality forage requires mice to be less discriminating. In 2014, the year when resources were abundant, C_3 specialists were more numerous (n = 41) than C_4 specialists (n = 14).

To assess the relative importance of inter- vs intraspecific competition on foraging strategies during the boom-bust cycle, we examined the change in population mass (g) between 2014 and 2015 with and without *P. flavus* to determine if interspecific

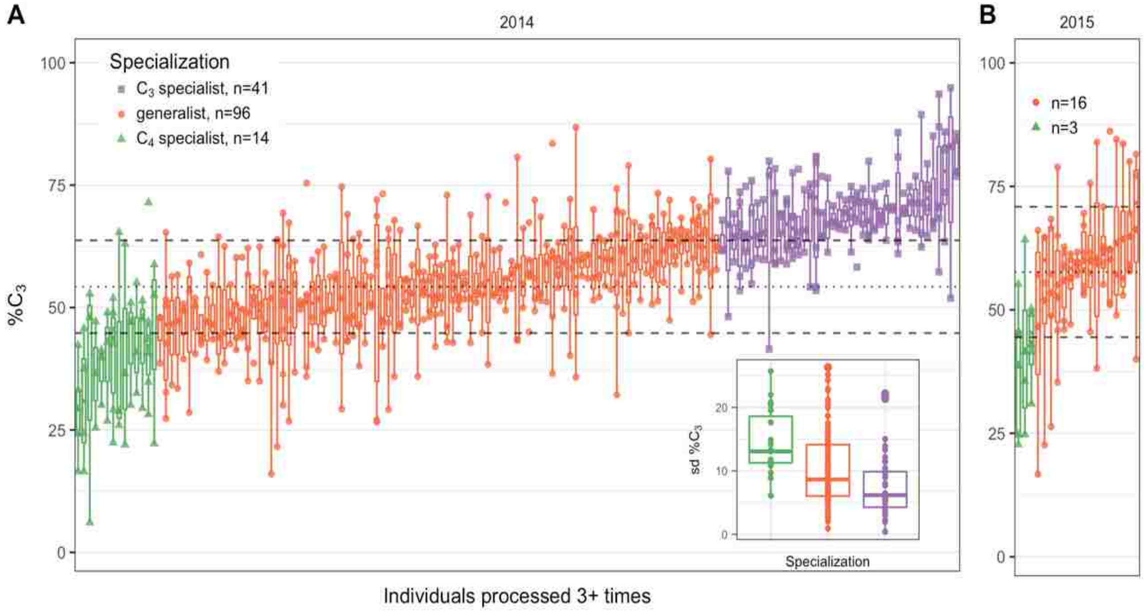


Figure 4.3: A-2014, the black dashed lines indicate one standard deviation from a mean dietary %C_3 for all mice (dotted line). Each box plot is an individual mouse that has been sampled three or more times. Generalists fall within one standard deviation of the mean, while specialist fall one standard deviation above or below a mean dietary %C_3. The inset shows a correlation between specialization and standard deviation in %C_3. C_3 specialists have a low standard deviation, consistently specializing. C_4 specialists have a high standard deviation, foraging widely to compensate for a poor quality diet. B-2015, an increased standard deviation implies more variability within individuals and a reduction in specialized foraging strategies as resource quality and quantity declines.

competition also increased temporally. We found no significant difference in the combined mass of the small mammal community between 2014 and 2015 when *P. flavus* were excluded, however there was a significant difference in total community mass (21% higher) with *P. flavus* included (Table 4.1). This implies that interspecific competition likely remained consistent throughout the two years and was likely not a factor in the development of specialized foraging strategies over the boom-bust cycle.

Mass (grams)	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**
2014 – PGFV	4912.9	4304.4	3542.2	3123.6	3283.9	3861.6	4162.1	3462.6
2015 – PGFV	3044.9	3722.0	3773.5	3166.3	4016.5	4055.8	4106.9	3817.6
	P-value = 0.687							
2014 + PGFV	5872.9	5640.4	5162.8	4766.1	4810.4	5189.3	5279.0	4294.8
2015 + PGFV	3093.2	3812.0	3960.7	3317.5	4164.5	4207.8	4286.9	3977.2
	P-value = 0.002							

Table 4.1: The average mass (g) of the entire community was summed monthly. When the mass of *P.* flavus was excluded, there was not a significant difference between 2014 and 2015, implying a constant level of interspecific competition. When *P. flavus* were included there was a significant difference between 2014 and 2015 due to the *P. flavus* population boom which resulted in increased intraspecific competition, a potential mechanism for the development of individualized foraging strategies.

Discussion:

The heteromyid rodent, *P. flavus,* experienced a population boom-bust cycle in 2014 while the abundances of co-occurring small mammal species remained constant. The increase in density likely resulted in a significant increase in intra- relative to inter-specific competition since biomass of all other species combined remain constant. This indicates that there was constant herbivory pressure on the landscape until the population boom of *P. flavus,* which increased herbivory to support a 21% increase in community wide mass during 2014. As predicted by the Niche Variation Hypothesis, individuals specialized on a subset of available resources to alleviate intraspecific competition (Figure 4.3). There was a reduction in resources concurrent with a population declined in 2015. Though intraspecific competition declined, resource scarcity due to lower than average precipitation caused individuals to forage widely across vegetation functional groups and potentially across trophic levels (Figure 4.2). This strategy supports Optimal Foraging Theory, which predicts that organisms will expand their dietary niche and generalize to meet their nutritional requirements under limited resources. Most individuals exhibited plasticity in foraging strategies, in response to changes in the quantity and quality of available resources; specializing when high quality resources were abundant and population density high, and generalizing when resources were limited and population density low.

Arid lands are characterized by a variable precipitation regime that results in alternating periods of resource abundance and limitation. These resource pulses create spatial and temporal heterogeneity in primary production (Epstein et al. 2002, Ernest et al. 2000, Rosenblatt et al. 2015). In addition, populations of small mammals fluctuate, persisting at low densities during drought and periodically erupting in association with environmental drivers, such as high seasonal precipitation as evidenced by boom-bust cycle in *P. flavus* at our study site (Figure 4.1-D). Boom-bust cycles have been observed in Australia (Dickman et al. 2011, Letnic et al. 2010), Chile (Meserve et al. 2011, Holmgren et al. 2006), and in other areas of the Southwestern United States (Thibault et al. 2010). Small mammals have developed mechanisms such as internal fat stores, short periods of torpor, or seed caches (Holt 2008) for surviving extreme variability in resources and large increases in inter- and intraspecific competition associated with population boom-bust cycles (Sala et al. 2012, Owen-Smith et al. 2010). These mechanisms complicate our understanding of foraging dynamics (Gese et al. 1996) because resource reserves like caching or standing biomass can stabilize a community in the short term. For example, Warne et al. (2010) reported that after a failure of winter rains and declining C_3 production, consumers relied on standing biomass, highlighting the importance of legacy effects from prior year production and the advantages of diet plasticity. Persistent declines in resource availability will decrease consumer biomass and diversity, ultimately changing community structure and ecosystem function (Warne et al. 2010, Hanya et al. 2013).

Bottom up ecosystems, driven by resource availability, are in a continual state of low primary productivity that constrains the abundance of consumers (Baez et al. 2006, Turkington et al. 2009). They experience large temporal and spatial variability in primary producer species composition, soil seed banks, and seed production (Cleland et al. 2013, Guo et al. 2000, Maron et al. 2012, Mulhouse et al. 2016). We used standing biomass and seasonal primary production as proxies for seed availability (Aarssen et al. 2001, Meserve et al. 2003, Smiley et al. 2015, Lehmann et al. 2015). Although C_3 shrubs and subshrubs, such as creosotebush (*Larrea tridentata)*, winter fat (*Krascheninnikovia lanata*), and snakeweed (*Gutierrezia sarothrae*), can account for a large portion of primary production and standing biomass (Figure 4.1-B and C), it is unclear if these species are important food sources for *P. flavus* (Hope and Parmenter 2007). These plants have high levels of secondary metabolites which may cause diuresis when consumed, negatively affecting water balance in desert herbivores (Dearing et al. 2002). Most likely, individuals of *P. flavus* rely on the highly nutritious seeds from several small herbaceous forbs that are a less reliable component of the ecosystem (Mulhouse et al. 2016).

Temperature, precipitation and nitrogen concentration affect forage quality, driving foraging choices at both the individual and population level (Kieft et al. 1998, White et al. 2004, Smiley et al. 2015, Brown and Lieberman 1973, Sala et al. 2012). The population boom *P. flavus* experienced in 2014 was likely precipitated by record setting late season rains in 2013 that caused a 300% increase in C_4 forb biomass. Winter/spring rains in 2013/2014 resulted in a 98% increase in spring C_3 forbs at the start of the *P. flavus* population boom. We found that both leaves and seeds of C_3 and C_4 forbs have a higher nitrogen content than C_4 grasses causing forbs to have a disproportionate effect on consumer populations (Thibault et al. 2010). In 2015, both NPP and standing biomass declined leading to an expansion in generalist foraging behavior both in dietary width and breadth in accordance with the optimal foraging theory. The high levels of nitrogen in mice plasma in 2015 (Figure 4.2 B) indicates that mice are foraging on additional trophic levels, likely incorporating arthropods into their diet (Arajou et al. 2011, Svanback 2007, Hope and Parmenter 2007).

According to Bolnick et al. (2003, 2007) generalist populations like *P. flavus* tend to expand their total niche breadth via increased intra-individual specialization on a portion of the niche. The relative foraging niche width for each individual stays constant but there is a greater number of individual niches as individuals' further partition their resources to cope with an increase in intraspecific competition. Niche expansion varies temporally as competition declines and resource quality and quantity change (Agashe et al. 2010, Araujo et al. 2008, Bison et al. 2015, Bolnick et al. 2010, Costa 2008). The 2014 expansion in foraging breadth in the SNWR (Figure 4.2-A) is likely due to an increase in resource availability (Figure 4.1) that led to an increase in population density intensifying intra-specific competition and precipitating the development of intra-individual foraging strategies (Figure 4.3). This supports predictions from the Niche Variation Hypothesis that when organisms are numerous and/or niche width is narrow, individuals will specialize to reduce intraspecific competition (Van Valen 1965).

Stable isotopes are a powerful integrative tool to measure foraging preferences in a system with large and consistent differences in the isotopic values of resources. In our case we were able to monitor the ratios of C_3 and C_4 resources consumed by individual mice through time (Mathews et al. 2004, Bearhop et al. 2004, Perkins et al. 2014). Some individuals within this generalist population were consistently selecting a specific subset of resources within the range of available resources (Figure 4.3) (Kelt et al. 2004, 2011, Bolnick et al. 2007). In accordance with the Optimal Foraging Theory, the majority of specialists selected higher quality C_3 forage (32%) compared to 8% that specialized on C_4 forage. Those mice that specialized on C_3 resources had lower standard deviations implying a more consistent diet. C_4 specialists had a high standard deviation implying that they had to forage more widely to meet their nutritional requirements on this poor quality resource. Foraging on a highly nutritious subset of resources available to a population has been demonstrated to improve fitness within populations of raptors (Terraube et al. 2014), sea otters (Tinker et al. 2007, 2008), and penguins (Lescreol et al. 2010). Dietary plasticity is a successful strategy for population persistence in highly variable environments because segments of the population will experience reproductive success under all resource scenarios (Woo et al. 2008).

Understanding the mechanisms driving foraging choices as they relate to resource quality and quantity will help to predict how small mammal communities will respond as the landscape of primary production changes in response to climate (Cook et al. 2015). Historically, Optimal Foraging Theory and the Niche Variation Hypothesis have been treated as alternative models, however, our data suggest that each hypothesis is supported under different resource and population density scenarios. Increased intra-individual specialization and population wide expansion in niche width caused by increased intraspecific competition is consistent with the Niche Variation Hypothesis. Increase in trophic breadth and individual dietary niche width as forage quantity and quality decline is consistent with Optimal Foraging Theory. Thus, both models accurately predict small mammal foraging behavior across time in highly variable environments such as aridland ecosystems. Understanding the high degree of individual variation within generalist populations is essential to predict the fate of populations in these highly variable environments as they are subjected to increasing stress under future climate change scenarios.

Chapter 5: Conclusion

By the end of 2100 44 to 62% of the earth's terrestrial surface is expected to be comprised of arid lands (Maestre et al 2016, Huang 2016). Models indicate that climate change will reduce winter precipitation, increase ariditiy, and increase the incidence of extreme weather events (Cook et al. 2015, Gutzler et al 2007). Globally, grasslands are experiencing wide scale shrub encroachment and consequent changes in plant community assembly (Baez et al 2008) with unknown consequences for consumer populations. This research makes a significant contribution to the scientific community, both in the unique suite of tools (isotopic analysis, forge availability indices, seed attributes, and long-term data) and the creative utilization of these tools. Using long-term data on primary production, precipitation, and small mammal trapping in concert with three years of mark recapture data collected across a shrubland/grassland ecotone, I have been able to characterize foraging strategies of a small mammal community. Understanding how small mammals utilize resources now will improve our understanding of the impact of a changing resource base on these important primary consumers and the additional trophic levels that they support.

We found that despite a decline in plant biodiversity, and an increase in bare ground, the increased heterogeneity of the shrubland supports both a more specious and more populous rodent community than the grassland. Heteromyids have a different community composition in each of the stable states (grassland and shrubland) while cricetid community composition is similar in each stable state. Despite a high degree of short term variation in species richness, mean rank shift, and turnover, this rodent community is not experiencing long-term directional change in either stable state. Short term variability is the result of changes in species dominance. This reordering is primarily the result of shifts in heteromyid populations as they boom and bust in response to precipitation driven increases in primary production.

Results from isotopic analysis of rodent plasma (3,560 samples from 1,533 individuals) and plants (698 samples) over a three year period indicate a high degree of dietary plasticity. Rodent populations appear to track nitrogen availability, a limiting resource, on the landscape. Rodents consume the highest quality forage available, supplementing their diet with foliage or arthropods when necessary. We utilized weighted forage availability indices by functional type created from monthly phenology data, combined with primary producer nutritional quality determined via measured seed characteristics and nutrient concentrations to quantify resource quality and quantity on the landscape. Rodent diets diverge by both species and foraging guild when resources are abundant and converge when they are limited indicating species coexistence on a common suite of resources. Diets in small mammals track seasonally variable primary production with a preference for higher quality forage when it is abundant.

A population explosion of *P. flavus* in 2014 provided a natural laboratory to study the development of specialized foraging strategies to relieve an increase in intra-specific competition. At the population level, foraging width increased across the growing season as mice incoroporated more C_4 forage into their diets in response to monsoon rains. We found that once we adjusted mouse plasma values to account for variation in primary productivity, we saw in increase in specialized foraging strategies in a resource abundant year (2014) to reduce intra-specific competition. As resources declined, so did the number of specialists. As forage availability declined, populations converged with rodent diets overlapping as mice foraged widely to meet their nutritional requirements. We did not find mice consistently foraging on the highest quality recources, on the contrary, most individuals are generalists, there were more C_3 specialists than C_4 specialists when resources were abundant indicating a preference for higher quality forage. C_4 specialists have a higher standard deviation in their diet selection, implying a higher variability in forage selection for those mice specializing on a poorer quality forage.

My dissertation work serves as a model study to characterize primary consumers foraging strategies in a nutrient limited, highly stochastic ecosystem. The techniques implemented here could be used to conduct similar studies in arid lands all over the world. Small mammals are ubiquitous on earth and often serve as indicator species signifying the health of a community. Knowing how these primary consumers utilize their landscape will provide valuable insight into ecosystem function. This work could be improved by incorporating DNA meta-barcoding, this technique will allow finer resolution of resource utilization from the current level of plant functional type to plant genus (Soininen et al. 2009, 2014, 2015). In arid lands, there is a well-documented relationship between precipitation, primary production, and small mammal populations (Ernest et al 2000, Thibault et al 2010, Brown et al 1989), despite this, we do not know the importance of specific plant species to the continued success of these small mammal communities. In this highly stochastic resource landscape (Collins et al 2015, Mulhouse et al 2016), DNA metabarcoding is an important next step, and something I hope to do in the future.

Appendices

Appendix 3.1: All Small Mammal Trapping Data

This data will be available on the Sevilleta LTER data portal as data set 314 (http://sev.lternet.edu/data/sev-314). There are 7,063 small mammal trapping records from July 2013 through May 2016. I am including the metadata here for reference purposes.

1] Data Set Code: 314

2] Data Set Title: Five Points Small Mammal Trapping (2013-2016)

3] Abstract: There has been little comprehensive research undertaken to quantify resource use by small mammal communities in a nutrient limited, highly stochastic ecosystem. The most abundant small mammals in this ecosystem are Heteromyids, food-caching granivores, and Cricetids, omnivores that must utilize on board fat stores as energy reserves. Heteromyid populations co-vary with primary production whereas the cricetids can forage at multiple trophic levels reducing their dependence on primary productivity. This data includes all mice trapped as part of a large study on foraging characteristics of small mammals using isotopes.

4] When the samples/data were collected:
Date Range: Begin Date: **07/03/2013** End Date: **07/06/2013**
Date Range: Begin Date: **08/02/2013** End Date: **08/05/2013**
Date Range: Begin Date: **08/30/2013** End Date: **09/02/2013**
Date Range: Begin Date: **10/18/2013** End Date: **10/21/2013**
Date Range: Begin Date: **11/15/2013** End Date: **11/18/2013**
Date Range: Begin Date: **12/13/2013** End Date: **12/16/2013**
Date Range: Begin Date: **03/28/2014** End Date: **03/31/2014**
Date Range: Begin Date: **04/25/2014** End Date: **04/27/2014**
Date Range: Begin Date: **05/31/2014** End Date: **06/02/2014**
Date Range: Begin Date: **06/28/2014** End Date: **06/30/2014**
Date Range: Begin Date: **07/26/2014** End Date: **07/28/2014**
Date Range: Begin Date: **08/23/2014** End Date: **08/25/2014**
Date Range: Begin Date: **03/20/2015** End Date: **03/23/2015**
Date Range: Begin Date: **04/17/2015** End Date: **04/20/2015**
Date Range: Begin Date: **05/15/2015** End Date: **05/18/2015**
Date Range: Begin Date: **06/19/2015** End Date: **06/22/2015**
Date Range: Begin Date: **07/17/2015** End Date: **07/20/2015**
Date Range: Begin Date: **08/14/2015** End Date: **08/17/2015**
Date Range: Begin Date: **09/11/2015** End Date: **09/14/2015**
Date Range: Begin Date: **10/09/2015** End Date: **10/12/2015**
Date Range: Begin Date: **11/06/2015** End Date: **11/09/2015**
Date Range: Begin Date: **03/10/2016** End Date: **03/13/2016**
Date Range: Begin Date: **04/07/2016** End Date: **04/10/2016**
Date Range: Begin Date: **05/05/2016** End Date: **05/08/2016**

5] Who is Involved with the Samples/Data: Noble, Jenny; Richins, Allyson; Wilson, Nick; Rodriquez Curras, Mauriel; Lujan, Sarah; Newsome, Seth; Volunteers as Needed.

Principle Investigator(s): Jennifer Noble

Field Crew: Jenny Noble, Allyson Richins, Nick Wilson, Emma Elliot Smith, Laura Pages, Ilyssa Nelson, Mauriel Rodriquez, Sarah Lujan, and Catalina Tome.

Data Manager: Jennifer Noble

Contact: Jennifer Noble; j1noble@yahoo.com, 505-917-3206

6] Where the Data were Collected:

Sites: Two trapping webs established by Blair Wolf in 2005/2006. These are located slightly southeast of the Five Points junction.

6a] Additional Geographic Metadata:
Study Area 1:
*Study Area Name: Web 1
*Study Area Location: Southeast of five points
*Study Area Description:
Elevation:
Landform: Mixed Creosote grassland
Geology: Transition zone from Chihuahua desert to prairie steppe.
Soils: Alkaline, Calcite, Nutrient Poor
Hydrology: Water limiting resource reliant on rain
Vegetation: Mixed Creosote/Black grama grassland (More Creosote than grass)
Climate: Desert, hot arid, low precipitation and humidity.
Site history: Established in 2005 by Blair Wolf.
*GPS coordinates in decimal degrees:
Center Point:
Latitude: 34.1838.62
Longitude: 106.4149.23

Study Area 2:
*Study Area Name: Web 2
*Study Area Location: Southeast of five points
*Study Area Description:
Elevation:
Landform: Mixed Creosote grassland
Geology: Transition zone from Chihuahua desert to prairie steppe.
Soils: Alkaline, Calcite, Nutrient Poor
Hydrology: Water limiting resource reliant on rain
Vegetation: Mixed Creosote/Black grama grassland (More grass than Creosote)
Climate: Desert, hot arid, low precipitation and humidity.

Site history: Established in 2005 by Blair Wolf.
*GPS coordinates in decimal degrees:
Center Point:
Latitude: 34.195.02
Longitude: 106.4154.68

7] How the Data were Collected:

Small mammals were trapped monthly from July, 2013 to May, 2016 excluding months with nighttime temperatures below freezing. Traps were set over three consecutive nights on the weekend closest to the new moon when small mammals are most active. Two permanent trapping webs are established that cross a creosote shrubland to black grama grassland ecotone. Webs are designed with 145 traps distributed on 12 equally spaced spokes containing 12 traps apiece that radiate out from a central stake where a single trap is placed (Parmenter et al. 2003). During each trapping bout, Sherman live traps are baited with rolled oats, peanut butter, and heat-treated millet. Traps are checked at dawn each day, closed during the day, and reset just before dusk. Upon capture, each individual is marked with a unique identifier in the form of an electronic pit-tag or ear-tag and species, sex, age (adult or juvenile), mass, reproductive condition (males: scrotal or non-scrotal; females: lactating, pregnant, or not pregnant), and ear/pit tag number are recorded. Only trap number and pit tag are recorded for subsequent captures of a single individual within a trapping bout (Appendix 1: Field Trapping Data). During processing, a 50 μL blood sample will be obtained by slipping a heparinized micro capillary tube behind the eye to puncture the pre- (Cricetids) or retro-orbital (Heteromyids) sinus. Capillary tubes are capped, labeled, and placed on ice for transport to the lab. All animals were released at their original trapping location in accordance with animal trapping and processing protocols approved by the UNM Institutional Animal Care and Use Committee (IACUC #A4023-01). Toward the end of the study, we were collecting feces for analysis of DNA in comparison to plants and we collected parasites. All parasites are at the Musuem of Southwestern Biology. All feces are stored at UNM with Dr. Tina Vesbach.

8] Variable Descriptions:

Variable 1:
*Name: Year
*Label: Year the animal was trapped
*Definition: Trapping occurred over four years
*Data Type: Datetime
*Units of Measure: Calendar dates
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 2:
*Name: Date

*Label: Day the animal was trapped
*Definition: Trapping occurred four days a month in July, August, September, October, November and December of 2013 and in March of 2014. From April 2014 through project completion, trapping occurred for three days each month
*Data Type: Datetime
*Units of Measure: Calendar dates
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 3:
Name: Month
*Label: Month the animal was trapped
*Definition: Trapping occurs once a month on the closest weekend to a New Moon minus months where nighttime temperatures go below freezing. For some trapping months, the data may span two months. For example in May 2014 we trapped May 31, June 1, and June 2 all of these dates have May in the month column for the May trapping bout.
*Data Type: Datetime
*Units of Measure: Calendar
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 4:
*Name: Web
*Label: One of two webs where animals were trapped.
*Definition: Web 1, Web 2
*Data Type: Nominal
*Units of Measure: Web 1, 2
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 5:
*Name: Trap
*Label: 1.1A
*Definition: This would be the first trap on the first spoke on web 1, spokes go from 1.1 to 1.12. Spoke one always points toward the road, then the spokes go clock wise. The traps start from the center (1.0C or 2.0C) and go from A to L with L being the last trap along a spoke.
*Data Type: Nominal
*Units of Measure: Web 1-2, Spoke 1-12, Trap A-L, Center spoke 1.0C or 2.0C
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 6:
*Name: Species
*Label: The type of small mammal it is
*Definition: Two to four letter code for small mammal
*Data Type: Nominal
*Units of Measure: PM = Peromyscus sp., PGFV = Perognathus flavus, SPSP=Spermophius spilosoma, DIOR = dipodomys ordii, DIME = Dipodomys merriami, DISP = Dipodomys spectabilis, ONAR = Onychomys arenicola, NEAL = Neotoma albigula, REMG = Reithrodontomys megaotis, PMTR = Peromyscus truei, SIHI = Sigmodon hispidus, BUNNY = Sylvilagus audubonii, Quail = Coturnix sp., Rattlesnake = Crotalus sp., SPARROW = Amphispiza bilineata
*Precision of Measurements: Dependent on personnel doing the identification
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 7:
*Name: (N/C/R)
*Label: N, C, or R
*Definition: N = new, this would be a mouse that has never been caught before, C = a mouse captured in previous months, but that is new to this trapping month, R = a recapture for a second or third time within a single trapping month.
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Based on ear-tag or electronic pit tag for mark/recapture
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 8:
*Name: Sex
*Label: M or F
*Definition: Male or Female
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Dependent on personnel handling the animal
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 9:
*Name: Condition
*Label: S = Scrotal, NS = Non-scrotal, P = Pregnant, NP = Not pregnant, L = Lactating, NL = Non-lactating, N = neither pregnant nor lactating
*Definition: A description of the reproductive status of the animal
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Dependent on personnel handling the animal
*Missing Data Code: NA

*Computational Method for Derived Data: NA

Variable 10:
*Name: Age
*Label: Age of Mammal A = Adult J = Juvenile
*Definition: Given a letter to indicate Juvenile or Adult
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Dependent on personnel handling the animal
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 11:
*Name: Mass
*Label: Mass (g)
*Definition: The mass of the mammal in grams
*Data Type: Numeric
*Units of Measure: Grams
*Precision of Measurements: .01
*Missing Data Code: NA
*Computational Method for Derived Data: The animal was massed in a plastic bag, then the weight of the bag was collected and subtracted along with any food from pouches or traps in the original mass.

Variable 12:
*Name: Right Tag
*Label: four digit number, seven digit number or eight digit number
*Definition: The number of the tag in the right ear, or the number on a digital pit tag inserted subcutaneously between the shoulder blades and read with a bar code reader.
*Data Type: Numeric
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: blank, tag was ripped out of ear
*Computational Method for Derived Data: NA

Variable 13:
*Name: Left Tag
*Label: four digit number
*Definition: the number of the tag in the left ear
*Data Type: numeric
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: blank means the ear tag has been ripped out and cannot be replaced.
*Computational Method for Derived Data: NA

Variable 14:
*Name: Blood
*Label: Y or N
*Definition: Blood was collected retro-orbitally while processeing
*Data Type: Nominal
*Units of Measure: Y or N
*Precision of Measurements: We did not collect from recaptures, or if a mouse was not doing well.
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 15:
* Name: Hair
*Label: Y or N
*Definition: Hair was cut from the rump if there was not an obvious previous hair cut
*Data Type: Nominal
*Units of Measure: Y or N
*Precision of Measurements: We did not collect hair if there was an obvious hair cut from a previous bout.
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 16:
*Name: Left Hindfoot
*Label: Length of foot from heel to toe in mm
*Definition: A measurement of the left hindfoot of the rodent, only done for Peromyscus to help identify to species.
*Data Type: Numeric
*Units of Measure: mm
*Precision of Measurements: 1.0 mm
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 17:
*Name: Tail Length
*Label: Length of tail from base to tip
*Definition: A measurement of the length of the tail of the rodent, only done for Peromyscus to help identify to species.
*Data Type: Numeric
*Units of Measure: mm
*Precision of Measurements: 1.0 mm
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 18:
*Name: Body Length

*Label: Length of body from base of tail to tip of snout
*Definition: A measurement of the length of body of the rodent, only done for Peromyscus to help identify to species.
*Data Type: Numeric
*Units of Measure: mm
*Precision of Measurements: 1.0 mm
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 19:
*Name: Comments
*Label: Comments in the field
*Definition: This is where we noted if an ear tag was changed or added, the mouse was dead, or we collected parasites which are stored at the Museum of Southwestern Biology
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 20:
* Name: Feces
*Label: Y or N
*Definition: We collected feces while processing and put them in liquid nitrogen in the field, they are stored in a -80 freezer at the University of New Mexico biology department.
*Data Type: Nominal
*Units of Measure: Y or N
*Precision of Measurements: If we were unable to get the feces directly from the mouse, we would get the freshest piece we could find from the plastic bag the mouse was placed in to get its weight.
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 21:
* Name: QMR
*Label: Scanned
*Definition: This was if a mouse was placed into a quantum magnetic resonance machine.
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: radiomagnetic waves are used to determine the percentage of different tissue types based on their hydrogen concentrations.

9] QA/QC Procedures?

Individual columns are periodically spot checked to make sure the same descriptors are used over time, and by different people recording data in the field.

10] Additional metadata: There will be a similar data sheet for plant data analyzing plants by plant part, leaf and seed for use in comparison with mouse plasma to determine relationships between primary production and dietary composition of mouse plasma.

11] Maintenance: File created by Jenny Noble on May 14th, 2014, and updated monthly until project completion (May, 2016).

Appendix 3.2: All Small Mammal Isotope Data

This data will be available on the Sevilleta LTER data portal as data set 313 (http://sev.lternet.edu/data/sev-313). There are 3,560 small mammal isotope analyses from July 2013 through May 2016. I am including the metadata here for reference purposes.

1] Data Set Code: *{Information manager will enter this field}*

2] Data Set Title: Five Points Small Mammal Blood Plasma Isotopic Values for Carbon, Nitrogen and Hydrogen

3] Abstract: There has been little comprehensive research undertaken to quantify resource use by small mammal communities in a nutrient limited, highly stochastic ecosystem. The most abundant small mammals in this ecosystem are Heteromyids, food-caching granivores, and Cricetids, omnivores that must utilize on board fat stores as energy reserves. Heteromyid populations co-vary with primary production whereas the cricetids can forage at multiple trophic levels reducing their dependence on primary productivity. Using isotopic values for Carbon, □^{13}C (a ratio of ^{13}C to ^{12}C), of primary producers consistent within a photosynthetic pathway, C_3 = -26.6 +/- 1.8‰ and $C_{4,}$ = -14.4 +/- 0.8‰ we can track mouse dietary assimilation of forage by plant functional type (Craig et al. 1953, Farquhar 1989). Nitrogen isotopic values □^{15}N (a ratio of ^{15}N to ^{14}N) fluctuate constantly, reflecting the landscape of primary production. Therefore, tracking nitrogen values in small mammal plasma provides a landscape level tool for studying diet by trophic level and nutritional value.

4] When the samples/data were collected:

Date Range: Begin Date: **07/03/2013** End Date: **07/06/2013**
Date Range: Begin Date: **08/02/2013** End Date: **08/05/2013**
Date Range: Begin Date: **08/30/2013** End Date: **09/02/2013**
Date Range: Begin Date: **10/18/2013** End Date: **10/21/2013**
Date Range: Begin Date: **11/15/2013** End Date: **11/18/2013**
Date Range: Begin Date: **12/13/2013** End Date: **12/16/2013**
Date Range: Begin Date: **03/28/2014** End Date: **03/31/2014**
Date Range: Begin Date: **04/25/2014** End Date: **04/27/2014**
Date Range: Begin Date: **05/31/2014** End Date: **06/02/2014**
Date Range: Begin Date: **06/28/2014** End Date: **06/30/2014**
Date Range: Begin Date: **07/26/2014** End Date: **07/28/2014**
Date Range: Begin Date: **08/23/2014** End Date: **08/25/2014**
Date Range: Begin Date: **03/20/2015** End Date: **03/23/2015**
Date Range: Begin Date: **04/17/2015** End Date: **04/20/2015**
Date Range: Begin Date: **05/15/2015** End Date: **05/18/2015**
Date Range: Begin Date: **06/19/2015** End Date: **06/22/2015**
Date Range: Begin Date: **07/17/2015** End Date: **07/20/2015**
Date Range: Begin Date: **08/14/2015** End Date: **08/17/2015**
Date Range: Begin Date: **09/11/2015** End Date: **09/14/2015**
Date Range: Begin Date: **10/09/2015** End Date: **10/12/2015**

Date Range: Begin Date: **11/06/2015** End Date: **11/09/2015**
Date Range: Begin Date: **03/10/2016** End Date: **03/13/2016**
Date Range: Begin Date: **04/07/2016** End Date: **04/10/2016**
Date Range: Begin Date: **05/05/2016** End Date: **05/08/2016**

5] Who is Involved with the Samples/Data: Noble, Jenny; Richins, Allyson; Wilson, Nick; Rodriquez Curras, Mauriel; Lujan, Sarah; Newsome, Seth; Volunteers as Needed.

Principle Investigator(s): Jennifer Noble

Field Crew: Jenny Noble, Allyson Richins, Nick Wilson, Emma Elliot Smith, Laura Pages, Ilyssa Nelson, Mauriel Rodriquez, Sarah Lujan, and Catalina Tome.

Data Manager: Jennifer Noble

Contact: Jennifer Noble; j1noble@yahoo.com, 505-917-3206

6] Where the Data were Collected:

Sites: Two trapping webs established by Blair Wolf in 2005/2006. These are located slightly southeast of the Five Points junction.

6a] Additional Geographic Metadata:
Study Area 1:
*Study Area Name: Web 1
*Study Area Location: Southeast of five points
*Study Area Description:
Elevation:
Landform: Mixed Creosote grassland
Geology: Transition zone from Chihuahua desert to prairie steppe.
Soils: Alkaline, Calcite, Nutrient Poor
Hydrology: Water limiting resource reliant on rain
Vegetation: Mixed Creosote/Black grama grassland (More Creosote than grass)
Climate: Desert, hot arid, low precipitation and humidity.
Site history: Established in 2005 by Blair Wolf.
*GPS coordinates in decimal degrees:
Center Point:
North Coordinate: 34.1838.62
West Coordinate: 106.4149.23

Study Area 2:
*Study Area Name: Web 2
*Study Area Location: Southeast of five points
*Study Area Description:
Elevation:
Landform: Mixed Creosote grassland

Geology: Transition zone from Chihuahua desert to prairie steppe.
Soils: Alkaline, Calcite, Nutrient Poor
Hydrology: Water limiting resource reliant on rain
Vegetation: Mixed Creosote/Black grama grassland (More grass than Creosote)
Climate: Desert, hot arid, low precipitation and humidity.
Site history: Established in 2005 by Blair Wolf.
*GPS coordinates in decimal degrees:
Center Point:
North Coordinate: 34.195.02
West Coordinate: 106.4154.68

7] How the Data were Collected:

Small mammals were trapped monthly from July, 2013 to May, 2016 excluding months with nighttime temperatures below freezing. Traps were set over three consecutive nights on the weekend closest to the new moon when small mammals are most active. Two permanent trapping webs are established that cross a creosote shrubland to black grama grassland ecotone. Webs are designed with 145 traps distributed on 12 equally spaced spokes containing 12 traps apiece that radiate out from a central stake where a single trap is placed (Parmenter et al. 2003). During each trapping bout, Sherman live traps are baited with rolled oats, peanut butter, and heat-treated millet. Traps are checked at dawn each day, closed during the day, and reset just before dusk. Upon capture, each individual is marked with a unique identifier in the form of an electronic pit-tag or ear-tag and species, sex, age (adult or juvenile), mass, reproductive condition (males: scrotal or non-scrotal; females: lactating, pregnant, or not pregnant), and ear/pit tag number are recorded. Only trap number and pit tag are recorded for subsequent captures of a single individual within a trapping bout (Appendix 1: Field Trapping Data). During processing, a 50 μL blood sample will be obtained by slipping a heparinized micro capillary tube behind the eye to puncture the pre- (Cricetids) or retro-orbital (Heteromyids) sinus. Capillary tubes are capped, labeled, and placed on ice for transport to the lab. Within ten hours of capture, blood samples are centrifuged to separate red blood cells from plasma. Red blood cells are placed into micro capillary tubes sealed with paraffin and frozen for future analysis. Plasma is pipetted into pre-weighed tin capsules for isotopic analysis of □^{13}C for dietary width and□□^{15}N for dietary breadth (Appendix 2: Isotopic Values for Mice Plasma). Plasma □^{13}C turnover in laboratory mice *Mus musculus* has a half-life of approximately 17 days, so monthly sampling provides a near continuous dietary record (MacAvoy et al. 2005, Tsahar et al 2008, Parnell et al 2010). All animals were released at their original trapping location in accordance with animal trapping and processing protocols approved by the UNM Institutional Animal Care and Use Committee (IACUC #A4023-01).

8] Variable Descriptions:

Variable 1:
*Name: Year
*Label: Year the animal was trapped

*Definition: Trapping occurred over four years
*Data Type: Datetime
*Units of Measure: Calendar dates
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 2:
*Name: Date
*Label: Day the animal was trapped
*Definition: Trapping occurred four days a month in July, August, September, October, November and December of 2013 and in March of 2014. From April 2014 through project completion, trapping occurred for three days each month
*Data Type: Datetime
*Units of Measure: Calendar dates
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 3:
Name: Month
*Label: Month the animal was trapped
*Definition: Trapping occurs once a month on the closest weekend to a New Moon minus months where nighttime temperatures go below freezing. For some trappig months, the data may span two months. For example in May 2014 we trapped May 31, June 1, and June 2 all of these dates have May in the month column for the May trapping bout.
*Data Type: Datetime
*Units of Measure: Calendar dates
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 4:
*Name: Species
*Label: The type of small mammal it is
*Definition: Two to four letter code for small mammal
*Data Type: Nominal
*Units of Measure: PM = Peromyscus sp., PGFV = Perognathus flavus, SPSP=Spermophius spilosoma, DIOR = dipodomys ordii, DIME = Dipodomys merriami, DISP = Dipodomys spectabilis, ONAR = Onychomys arenicola, NEAL = Neotoma albigula, REMG = Reithrodontomys megaotis, PMTR = Peromyscus truei
*Precision of Measurements: Dependent on personnel doing the identification
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 5:
*Name: Web
*Label: One of two webs where animals were trapped.
*Definition: Web 1, Web 2
*Data Type: Nominal
*Units of Measure: Web 1, 2
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 6:
*Name: Trap
*Label: 1.1A
*Definition: This would be the first trap on the first spoke on web 1, spokes go from 1.1 to 1.12. Spoke one always points toward the road, then the spokes go clock wise. The traps start from the center (1.0C or 2.0C) and go from A to L with L being the last trap along a spoke.
*Data Type: Nominal
*Units of Measure: Web 1-2, Spoke 1-12, Trap A-L, Center spoke 1.0C or 2.0C
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 7:
*Name: Sample ID
*Label: Always has a standard ID, SpeciesTrapDate for example (PGFV1.4L111513)
*Definition: The example provided above would be a Perognathus flavus caught on web 1 (1) on the fourth spoke (4) in the end trap (L) on November 15, 2013 (111513)
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 8:
*Name: New? (N/C/R)
*Label: N, C, or R
*Definition: N = new, this would be a mouse that has never been caught before, C = a mouse captured in previous months, but that is new to this trapping month, R = a recapture for a second or third time within a single trapping month.
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Based on ear-tag or electronic pit tag for mark/recapture
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 9:
*Name: Sex
*Label: M or F
*Definition: Male or Female
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Dependent on personnel handling the animal
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 10:
*Name: Condition
*Label: S = Scrotal, NS = Non-scrotal, P = Pregnant, NP = Not pregnant, L = Lactating, NL = Non-lactating, N = neither pregnant nor lactating
*Definition: A description of the reproductive status of the animal
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Dependent on personnel handling the animal
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 11:
*Name: Age
*Label: Age of Mammal A = Adult J = Juvenile
*Definition: Given a letter to indicate Juvenile or Adult
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: Dependent on personnel handling the animal
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 12:
*Name: Mass
*Label: Mass (g)
*Definition: The mass of the mammal in grams
*Data Type: Numeric
*Units of Measure: Grams
*Precision of Measurements: 0.01
*Missing Data Code: NA
*Computational Method for Derived Data: The animal was massed in a plastic bag, then the weight of the bag was collected and subtracted along with any food from pouches or traps in the original mass.

Variable 13:
*Name: Tag Right
*Label: four digit number, seven digit number or eight digit number

*Definition: The number of the tag in the right ear, or the number on a digital pit tag inserted subcutaneously between the shoulder blades and read with a bar code reader.
*Data Type: Numeric
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: blank, tag was ripped out of ear
*Computational Method for Derived Data: NA

Variable 14:
*Name: Tag left
*Label: four digit number
*Definition: the number of the tag in the left ear
*Data Type: numeric
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: blank means the ear tag has been ripped out and cannot be replaced.
*Computational Method for Derived Data: NA

Variable 15:
*Name: Plasma D13C
*Label: Numeric value
*Definition: the isotopic value of the ratio of C13 to C12 in mouse plasma
*Data Type: Ratio
*Units of Measure: Ratio of C13 to C12 in parts per mil (‰)
*Precision of Measurements: 0.2‰
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: The Carbon 13 of the sample is compared to the Carbon 12 by weight to compute a ratio, this is done at the Center for Stable Isotopes, University of New Mexico.

Variable 16:
* Name: Plasma D15N
*Label: Numeric value
*Definition: the isotopic value of the ratio of N15 to N14 in mouse plasma
*Data Type: Ratio
*Units of Measure: Ratio of N15 to N14 in parts per mil
*Precision of Measurements: 0.2‰
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: The Nitrogen 15 of the sample is compared to the Nitrogen 14 by weight to compute a ratio.

Variable 17:
*Name: Plasma [C]
*Label: concentration of carbon in plasma
*Definition: this is the amount of carbon by weight percent in the sample
*Data Type: Numeric

*Units of Measure: percent
*Precision of Measurements: NA
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: NA

Variable 18:
*Name: Plasma [N]
*Label: concentration of Nitrogen in plasma
*Definition: this is the amount of nitrogen by weight percent in the sample
*Data Type: Numeric
*Units of Measure: percent
*Precision of Measurements: NA
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: NA

Variable 19:
*Name: Plasma C/N
*Label: The ratio of carbon to nitrogen in plasma
*Definition: ratio of carbon to nitrogen in the sample by weight
*Data Type: numeric
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: NA

Variable 20:
* Name: Plasma D2H
*Label: Numeric value
*Definition: the isotopic value of the ratio of H2 to H1 in the plasma
*Data Type: Ratio
*Units of Measure: Ratio of H1 to H2 in parts per mil
*Precision of Measurements: 0.2‰
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: The Hydrogen 2 of the sample is compared to the Hydrogen 1 by weight to compute a ratio at the Center for Stable Isotopes, University of New Mexico.

Variable 21:
*Name: Plasma [H]
*Label: concentration of hydrogen in plasma
*Definition: this is the amount by weight percent of hydrogen in the sample
*Data Type: Numeric
*Units of Measure: percent
*Precision of Measurements: NA
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: NA

9] QA/QC Procedures?

The specific data per animal is spot checked against the field data sheets for accuracy. Isotope values are referenced against international standards of Vienna Pee-Dee Belemnite (VPDB) for carbon and AIR for nitrogen. Measured isotope values were calibrated against international standards using internal reference materials analyzed alongside plasma and plant material samples to correct for within-run instrument drift. Repeated within-run measurement of these reference materials yielded an analytical precision (SD) of 0.2‰ for both δ^{13}C and δ^{15}N values.

10] Additional metadata: There will be a similar data sheet for plant data analyzing plants by plant part, leaf and seed for use in comparison with mouse plasma to determine relationships between primary production and dietary composition of mouse plasma.

11] Maintenance: File created by Jenny Noble on May 14th, 2014, and updated monthly until project completion (May, 2016).

Appendix 3.3: All Plant Isotopes

This data will be available on the Sevilleta LTER data portal as data set 315 (http://sev.lternet.edu/data/sev-315). There are 698 plant isotope analyses from September 2013 through May 2016. I am including the metadata here for reference purposes.

1] Data Set Code: 315

2] Data Set Title: Five Points Plant Isotopic Values for Carbon and Nitrogen

3] Abstract: To quantify foraging strategies in the small mammal community of the Sevilleta National Wildlife Refuge, plant samples were collected at green-up (generally March for forbs and July for grasses), and when going to seed (generally May for forbs and October for grasses). Plants were analyzed for C:N ratio, □^{15}N and □^{13}C isotopic values and for carbon and nitrogen percent content by mass in both leaf and seed. These isotopic values can be compared to mouse plasma values to determine forage width (Carbon) and forage breadth (Nitrogen). Please see Sevilleta Dataset 313 on small mammal plasma to quantify resource preferences within and between small mammal communities.

4] When the samples/data were collected:
Date Range: Begin Date: **09/29/2013** End Date: **09/29/2013**
Date Range: Begin Date: **05/20/2014** End Date: **05/20/2014**
Date Range: Begin Date: **05/22/2014** End Date: **05/22/2014**
Date Range: Begin Date: **11/16/2014** End Date: **11/16/2014**
Date Range: Begin Date: **03/31/2015** End Date: **03/31/2015**
Date Range: Begin Date: **05/25/2015** End Date: **05/25/2015**
Date Range: Begin Date: **07/30/2015** End Date: **07/30/2015**
Date Range: Begin Date: **10/02/2015** End Date: **10/02/2015**
Date Range: Begin Date: **10/09/2015** End Date: **10/09/2015**
Date Range: Begin Date: **03/15/2016** End Date: **03/15/2016**
Date Range: Begin Date: **05/24/2016** End Date: **05/24/2016**
Date Range: Begin Date: **10/22/2016** End Date: **10/22/2016**

5] Who is Involved with the Samples/Data: Noble, Jenny; Richins, Allyson; Wilson, Nick; Rodriquez Curras, Mauriel; Lujan, Sarah; Newsome, Seth; Volunteers as Needed.

Principle Investigator(s): Jennifer Noble

Field Crew: Jenny Noble, Allyson Richins, Nick Wilson, Emma Elliot Smith, Laura Pages, Ilyssa Nelson, Mauriel Rodriquez, Sarah Lujan, and Catalina Tome.

Data Manager: Jennifer Noble

Contact: Jennifer Noble; j1noble@yahoo.com, 505-917-3206

6] Where the Data were Collected:

Sites: Two trapping webs established by Blair Wolf in 2005/2006. These are located slightly southeast of the Five Points junction.

6a] Additional Geographic Metadata:
Study Area 1:
*Study Area Name: Web 1
*Study Area Location: Southeast of five points
*Study Area Description:
Elevation:
Landform: Mixed Creosote grassland
Geology: Transition zone from Chihuahua desert to prairie steppe.
Soils: Alkaline, Calcite, Nutrient Poor
Hydrology: Water limiting resource reliant on rain
Vegetation: Mixed Creosote/Black grama grassland (More Creosote than grass)
Climate: Desert, hot arid, low precipitation and humidity.
Site history: Established in 2005 by Blair Wolf.
*GPS coordinates in decimal degrees:
Center Point:
North Coordinate: 34.1838.62
West Coordinate: 106.4149.23

Study Area 2:
*Study Area Name: Web 2
*Study Area Location: Southeast of five points
*Study Area Description:
Elevation:
Landform: Mixed Creosote grassland
Geology: Transition zone from Chihuahua desert to prairie steppe.
Soils: Alkaline, Calcite, Nutrient Poor
Hydrology: Water limiting resource reliant on rain
Vegetation: Mixed Creosote/Black grama grassland (More grass than Creosote)
Climate: Desert, hot arid, low precipitation and humidity.
Site history: Established in 2005 by Blair Wolf.
*GPS coordinates in decimal degrees:
Center Point:
North Coordinate: 34.195.02
West Coordinate: 106.4154.68

7] How the Data were Collected: Primary producers were sampled by species throughout the year, at green up (March, May, and September), when flowering (May and September/October), and when going to seed (May/June and September/October). Plants were collected from each of the trapping webs in the cardinal directions (spokes 1, 4, 7, and 10). A minimum of ten samples from each functional type were collected from both trapping webs, along four spokes in the cardinal directions. Samples were placed in coin envelopes in the field and then placed in a 40ºC drying oven for 48 hours in the laboratory. We collected leaves and seeds for □^{13}C and □^{15}N isotopic analysis as well as percent carbon and nitrogen by weight and C:N ratios to establish a baseline of variation in nitrogen between tissue types and across time for comparison with plasma values. Plant species with high relative abundance were selected for analysis (http://sev.lternet.edu/data/sev-129). Plants were collected from the trapping webs

8] Variable Descriptions: *Each variable description should include the following information:*
Variable 1:
*Name: Sample #
*Label: this is a consecutive number I am assigning to each plant sample I collect
*Definition: This sample number will is a unique ID for each sample collected to prevent multiple analysis of the same plant.
*Data Type: Numeric
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 2:
Name: Date Collected
*Label: Date the sample was collected
*Definition: Sampling occurs at green up, and when plants go to seed approximately three times a year, in March/April, in May/June, and in September/October
*Data Type: Date time
*Units of Measure: Calendar
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 3:
Name: Month Collected
*Label: Month the sample was collected
*Definition: Sampling occurs at green up, and when plants go to seed approximately three times a year, in March/April, in May/June, and in September/October
*Data Type: Date time
*Units of Measure: Calendar
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 4:
*Name: USDA Code
*Label: The code for the plant assigned by the United States Department of Agriculture
*Definition: 4 to 6 letter code based on the USDA website and codes used by the Sevilleta field crew.

*Data Type: Nominal
*Units of Measure: Codes found on Sevilleta plant list (Sevilleta LTER Dataset #51) or the USDA website.
*Precision of Measurements: Dependent on personnel doing the identification
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 5:
*Name: Plant Part
*Label: This indicates what part of the plant was sent for isotopic analysis.
*Definition: It will either be the whole plant ground into a powder from the Sevilleta field crew, or Leaf, Seed or Flower
*Data Type: Nominal
*Units of Measure: Plant Powder (whole plant was ground up together), Leaf, Flower, or Seed
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 6:
*Name: Web
*Label: B, G, L, 1, 2
*Definition: 1, and 2 represent my webs detailed above, B is the blue gramma core site, G is the black grama core site, and L is the creosote core site that are established as part of the Sevilleta LTER.
*Data Type: Nominal
*Units of Measure: Web 1-4, Spoke 1-12, Trap A-L
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 7:
*Name: Scientific Name
*Label: Scientific name reported in standard binomial nomenclature (Genus Species) spp. indicates unable to identify to species.
*Definition: The scientific name of the plant based on the Sevilleta LTER dataset #51 and the USDA website.
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 8:
*Name: Common name
*Label: Common name or names included to aid in identification..

*Definition: The common name of the plant based on the Sevilleta LTER dataset #51 and the USDA website.
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 9:
*Name: Growth Form
*Label: a or p
*Definition: Plants are characterized as annual (a) or perennial (p)
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 10:
*Name: Photo Path
*Label: C3, C4, CAM
*Definition: The photosynthetic pathway utilized by the plant as determined by Sevillta dataset #51, Dr. Rudges' Plant Species List, and expert opinion
*Data Type: Nominal
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: NA
*Computational Method for Derived Data: NA

Variable 11:
*Name: $d^{13}C$
*Label: Numeric value
*Definition: the isotopic ratio of ^{13}C to ^{12}C in the plant
*Data Type: Ratio
*Units of Measure: Ratio of ^{13}C to ^{12}C in parts per mil (‰)
*Precision of Measurements: 0.2‰
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: The Carbon 13 of the sample is compared to the Carbon 12 by weight to compute a ratio done in a mass spectrometer at the center for stable isotopes.

Variable 12:
* Name: $d^{15}N$
*Label: Numeric value
*Definition: the isotopic value of ^{15}N to ^{14}N in the plant
*Data Type: Ratio

*Units of Measure: Ratio of ^{15}N to ^{14}N in parts per mil (‰)
*Precision of Measurements: 0.2‰
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: The Nitrogen 15 of the sample is compared to the Nitrogen 14 by weight to compute a ratio.

Variable 13:
*Name: % C
*Label: concentration of carbon in plant
*Definition: this is the amount of or concentration of carbon in the sample, by weight percent
*Data Type: Numeric
*Units of Measure: percent
*Precision of Measurements: NA
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: percent mass by weight as calculated by the mass spectrometer in the center for stable isotopes

Variable 14:
*Name: %N
*Label: concentration of Nitrogen in plant
*Definition: this is the amount of or concentration of nitrogen in the sample, by weight percent
*Data Type: Numeric
*Units of Measure: percent
*Precision of Measurements: NA
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: percent mass by weight as calculated by the mass spectrometer in the center for stable isotopes

Variable 15:
*Name: C:N
*Label: The ratio of carbon to nitrogen in the plant
*Definition: ratio of carbon to nitrogen in the sample by weight
*Data Type: numeric
*Units of Measure: NA
*Precision of Measurements: NA
*Missing Data Code: blank, not analyzed
*Computational Method for Derived Data: the ratio of the percent mass for carbon and nitrogen derived by the mass spectrometer in the center for stable isotopes

9] QA/QC Procedures? *{Describe how the data were checked for accuracy}*

The specific data per plant is spot checked against the field data sheets for accuracy. Isotope values are referenced against international standards of Vienna Pee-Dee Belemnite (VPDB) for carbon and AIR for nitrogen. Measured isotope values were calibrated against international standards using internal reference materials analyzed alongside plasma and plant material samples to correct for within-run instrument drift. Repeated within-run measurement of these reference materials yielded an analytical precision (SD) of 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

10] Additional metadata: There is a meta data sheet for small mammal plasma for comparison with plant data to determine relationships between primary production and the dietary composition of mouse plasma.

11] Maintenance: File created by Jenny Noble on May 14th, 2014, and updated monthly until project completion (May, 2016).

Appendix 3.4: Seed Attributes

Species	Scientific Name	mean area	mean length	mean width	C3 C4	a/p	life form	# of seeds	weight (mg)	mg seed	d15N	d13C	%N	%C	C:N
APRAH	*Aphanostephus ramosissimus*	0.83	2.49	0.43	C3	p	forb	33	0.91	0.03	1.05	-26.83	3.89	43.86	11.26
ARPU9	*Aristida purpurea*	0.20	1.08	0.23	C4	p	grass	11	0.93	0.08	3.88	-14.59	3.89	43.69	11.22
ATCA2	*Atriplex canescens*	14.70	6.51	2.86	C4	p	shrub	2	15.98	7.99	2.46	-20.71	3.89	43.78	11.24
BOER4	*Bouteloua eriopoda*	0.88	2.59	0.43	C4	p	grass	95	2.49	0.03	4.99	-14.04	0.71	39.34	55.45
BOER4	*Bouteloua eriopoda*	0.88	2.59	0.43	C4	p	grass	9	2.23	0.25	2.90	-14.59	5.09	47.68	9.36
BOGR2	*Bouteloua gracilis*	0.46	1.83	0.31	C4	p	grass	12	0.44	0.04	2.87	-16.76	3.27	46.70	14.28
CHER2	*Chaetopappa ericoides*	1.03	3.03	0.43	C3	p	forb	60	9.21	0.15	1.81	-27.14	2.71	44.82	19.92
CHRE4	*Chamaesyce revoluta*	0.64	1.49	0.54	C4	a	forb	29	1.92	0.07	3.01	-19.56	2.26	41.35	18.32
CHSE7	*Chamaesyce serrula*	1.28	1.72	0.97	C4	a	forb	25	8.97	0.36	3.20	-12.73	2.73	45.12	16.69
CRCR3	*Cryptantha crassisepala*	0.99	1.46	0.85	C3	a	forb	44	10.91	0.25	3.29	-26.49	4.07	50.76	12.54
CYACF	*Cymopterus acaulis*	10.90	7.18	1.93	C3	p	forb	7	49.49	7.07	4.32	-28.49	3.28	52.27	16.05
DAFO	*Dalea formosa*	0.88	1.77	0.62	C3	p	forb	39	9.90	0.25	-0.07	-26.19	2.49	40.27	16.15
DANAV	*Dalea nana*	4.91	3.52	1.76	C3	p	forb	15	10.65	0.71	-0.49	-25.23	3.13	41.88	13.46
DAPU7	*Dasyochloa pulchella*	0.43	1.10	0.50	C4	p	grass	20	3.07	0.15	2.94	-15.57	4.82	44.32	9.20
DEPI	*Descurainia pinnata*	0.34	0.92	0.47	C3	p	forb	94	6.07	0.06	5.26	-26.33	3.93	55.22	14.06
EPTO	*Ephedra torreyana*	11.93	6.94	2.18	C3	p	shrub	6	7.70	1.28	2.47	-23.40	4.74	48.78	10.55

Species	Scientific Name	mean area	mean length	mean width	C3 C4	a/p	life form	# of seeds	weight (mg)	mg seed	d15N	d13C	%N	%C	C:N
EUEX4	*Euphorbia exstipulata*	2.47	2.19	1.44	C3	a	forb	6	10.12	1.69	1.71	-26.05	3.44	47.40	13.93
GRCL	*Grusonia clavata*	7.43	3.41	2.77	CAM	p	shrub	9	101.80	11.31	4.90	-12.69	1.22	28.59	27.26
GUSA2	*Gutierrezia sarothrae*	0.72	1.79	0.51	C3	p	shrub	24	5.07	0.21	2.92	-22.67	4.01	51.16	16.30
GUSP	*Gutierrezia sphaerocephala*	0.81	1.42	0.72	C3	a	forb	47	7.91	0.17	0.53	-22.76	2.66	50.69	19.40
HODR	*Hoffmannseggia drepanocarpa*	5.62	3.14	2.26	C3	p	forb	8	56.09	7.01	3.70	-25.46	4.88	45.41	9.30
IPPU4	*Ipomopsis pumila*	0.83	1.42	0.74	C3	a	forb	29	9.54	0.33	0.91	-26.00	2.81	49.33	17.61
KRLA2	*Krascheninnikovia lanata*	3.30	2.63	1.60	C3	p	shrub	3	6.14	2.05	7.48	-25.61	6.53	46.20	7.09
LAOCO	*Lappula occidentalis*	1.97	1.77	1.42	C3	a	forb	12	11.56	0.96	2.78	-25.73	2.14	40.23	18.80
LAOCO	*Lappula occidentalis*	1.97	1.77	1.42	C3	a	forb	5	0.29	0.06	2.43	-25.71	5.84	47.39	8.12
LATR2	*Larrea tridentata*	4.19	3.38	1.57	C3	p	shrub	6	12.66	2.11	7.97	-25.02	3.98	43.25	11.05
LEFE	*Lesquerella fendleri*	1.06	1.27	1.06	C3	p	forb	19	9.61	0.51	2.30	-23.30	2.61	45.31	17.35
LIPU4	*Linum puberulum*	2.24	2.73	1.04	C3	a	forb	32	10.55	0.33	3.44	-23.71	3.90	49.70	12.74
MALLOW	*Sphaeralcea sp.*	1.43	1.51	1.20	C3	p	forb	26	9.89	0.38	6.40	-24.41	4.58	44.58	9.74
MAPIP	*Machaeranthera pinnatifida*	1.15	2.28	0.65	C3	p	forb	85	6.44	0.08	5.08	-23.52	2.28	46.27	22.17
MUAR2	*Muhlenbergia arenicola*	0.74	2.21	0.42	C4	p	grass	26	6.25	0.24	2.46	-14.27	4.15	43.75	10.55
MUPO2	*Muhlenbergia porteri*	0.68	2.45	0.35	C4	p	grass	17	3.32	0.20	6.06	-15.06	3.70	41.89	11.34
NAHI	*Nama hispidum*	1.41	2.15	0.84	C3	a	forb	11	3.55	0.32	17.39	-26.53	1.73	36.25	21.25

Species	Scientific Name	mean area	mean length	mean width	C3 C4	a/p	life form	# of seeds	weight (mg)	mg seed	d15N	d13C	%N	%C	C:N
OECA10	*Oenothera caespitosa*	0.74	1.13	0.84	C3	p	forb	24	9.95	0.41	3.28	-25.29	2.78	49.44	17.78
PEFE	*Penstemon fendleri*	2.48	2.35	1.33	C3	p	forb	19	6.89	0.36	3.81	-25.85	2.76	44.00	15.93
PHACE	*Phacelia sp.*	2.74	2.56	1.36	C3	p	forb	18	9.66	0.54	4.98	-26.33	2.10	48.01	22.88
PLJA	*Pleuraphis jamesii*	1.06	3.16	0.43	C4	p	grass	8	0.80	0.10	2.80	-15.68	4.07	45.51	11.19
PLPA2	*Plantago patagonica*	1.80	2.25	1.02	C3	a	forb	23	10.44	0.45	2.85	-24.81	2.92	42.30	14.50
SATR12	*Salsola tragus*	2.48	2.35	1.33	C4	a	forb	19	9.91	0.52	3.40	-14.50	1.15	33.79	29.44
SCBR2	*Scleropogon brevifolius*	1.35	4.60	0.37	C4	p	grass	22	9.16	0.42	0.24	-14.88	4.94	42.68	8.65
SOEL	*Solanum elaeagnifolium*	5.88	3.10	2.42	C3	p	forb	5	15.29	3.06	3.78	-25.86	2.73	49.42	18.14
SPFL2	*Sporobolus flexuosus*	0.27	0.69	0.49	C4	p	grass	17	1.56	0.09	1.41	-14.63	3.35	40.44	12.07
SPHA	*Sphaeralcea hastulata*	1.27	1.43	1.13	C3	p	forb	4	3.37	0.84	2.21	-21.16	4.53	49.49	10.91
SPLE	*Sphaeralcea leptophylla*	1.74	1.71	1.29	C3	p	forb	12	9.37	0.78	5.56	-23.69	4.05	41.86	10.36
SPORO	*Sporobolus sp.*	0.35	0.81	0.54	C4	p	grass	90	9.30	0.10	2.66	-13.77	3.55	41.37	11.64
SPPO6	*Sphaeralcea polychroma*	1.31	1.51	1.11	C3	p	forb	12	11.28	0.94	4.39	-22.19	4.56	49.45	10.84
THAC	*Thymophylla acerosa*	1.60	2.92	0.70	C3	p	forb	23	3.20	0.14	2.11	-26.89	2.15	44.96	21.09
TOAN	*Townsendia annua*	0.34	1.35	0.32	C3	a	forb	20	1.13	0.06	5.08	-28.14	4.07	44.39	10.91

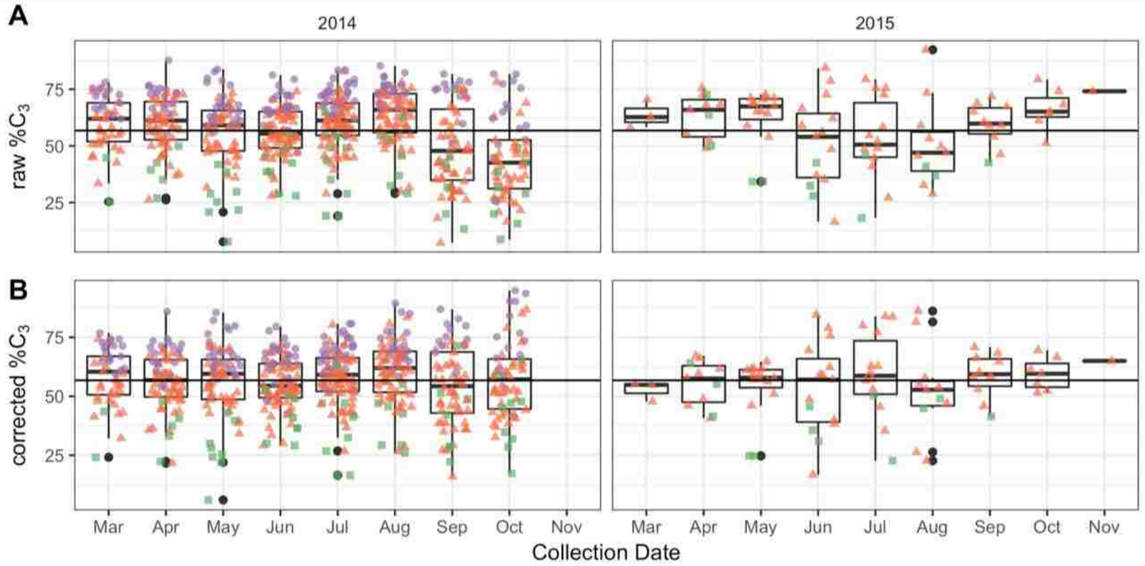
Appendix 4.1: Correction Factor Calculations

Repeated measurements of individuals over time, for example, plasma samples taken from individual *P. flavus* over the course of several months, are called panel data. This type of longitudinal time series data needs to be corrected for temporal and spatial autocorrelation before calculating summary statistics. The percent of C_3 forage incorporated into the diets of mice varies by trapping month and web as resource availability changes on the landscape. As expected, the average percent C_3 in the diets of mice throughout the population tended to be higher in spring when more C_3 forage was available and relatively lower in summer and late fall when C_4 grasses were abundant. There was no significant difference in the percent C_3 incorporated into diets of mice based on gender or mass.

To allow for accurate calculation of summary statistics, we corrected percent C_3 values of mouse plasma per trap month and web by calculating a monthly mean percent C_3 from all mouse plasma values. By comparing the monthly mean to an annual mean we could determine a monthly percent difference which we use as a correction factor. The correction factor was added to the percent C_3 in the diet of each individual to compensate for fluctuations in resource availability. This process provides values that reflect true differences in mouse foraging behavior by correcting for temporal and spatial variance in resource availability. The table below shows the raw difference between monthly mean percent C_3 in diet, and the annual mean percent C_3 in diet. The percent difference is used to correct individual mouse dietary percent C_3 (see figure).

Variable	Web	Year	Month	Monthly Mean	Difference from all-time average	Percent difference
PC3	1	2014	March	56.13545	1.2589302	2.2941144
PC3	1	2014	April	56.83391	1.9573921	3.5669026
PC3	1	2014	May	52.30837	-2.5681476	-4.6798659
PC3	1	2014	June	56.53184	1.6553165	3.0164385
PC3	1	2014	July	57.49683	2.6203101	4.7749202
PC3	1	2014	August	62.51907	7.6425465	13.9268057
PC3	1	2014	September	58.25895	3.3824286	6.1637081
PC3	1	2014	October	46.31226	-8.5642617	-15.6064224
PC3	2	2014	March	57.3765	2.4999756	4.5556379
PC3	2	2014	April	59.5097	4.6331781	8.4429151
PC3	2	2014	May	54.75417	-0.1223493	-0.2229538
PC3	2	2014	June	53.81088	-1.0656421	-1.9418909
PC3	2	2014	July	56.98	2.1034758	3.833107
PC3	2	2014	August	57.94778	3.0712606	5.5966751
PC3	2	2014	September	46.08664	-8.7898783	-16.0175574
PC3	2	2014	October	38.71886	-16.1576591	-29.443665
PC3	1	2015	March	58.25895	3.3824286	6.1637081
PC3	1	2015	April	63.28626	8.4097366	15.3248354
PC3	1	2015	May	64.42172	9.5452006	17.3939608
PC3	1	2015	June	51.8322	-3.0443251	-5.5475912
PC3	1	2015	July	50.36306	-4.5134594	-8.2247549
PC3	1	2015	August	46.77815	-8.0983741	-14.7574479
PC3	1	2015	September	55.95922	1.0827026	1.9729796
PC3	1	2015	October	46.52856	-8.3479567	-15.2122557
PC3	1	2015	November	56.76145	1.8849326	3.4348617
PC3	2	2015	March	69.86454	14.9880226	27.312268
PC3	2	2015	April	61.40369	6.5271702	11.8942856
PC3	2	2015	May	62.87623	7.9997079	14.5776513

PC3	2	2015	June	54.6816	-0.194923	-0.3552028
PC3	2	2015	July	46.74695	-8.1295719	-14.8142989
PC3	2	2015	August	61.14698	6.2704566	11.4264834
PC3	2	2015	September	55.33203	0.4555046	0.8300537
PC3	2	2015	October	66.63131	11.7547926	21.4204405
PC3	2	2015	November	63.99935	9.1228299	16.6242861



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