***Introduction, Questions, and Merits of the Proposed Research***

Ecologists often attempt to link animal population dynamics to resource systems becauseconsumer life histories are intimately tied to resource quantity and quality (Simpson et al. 2009). Establishing mechanistic connections between resource availability and consumer population growth, however, involves understanding a complicated set of interactions mediated by individuals’ physiological processes. It is a challenge to correlate physiological processes to ecological conditions that dictate resource use because it requires linking population and community ecology with animal eco-physiology at the organismal scale. Such research involves the collection of longitudinal data at multiple levels of ecological organization (individual to community), which is nearly impossible using traditional methods.

Our study will bridge two gaps: one between disciplines (animal ecology and physiology) and another between empirical data and process-based models. We will do this by coupling empirical data derived from a variety of emergent technologies that directly measure resource use and body condition with a stochastic dynamic model that will link environmental conditions to foraging behavior, fitness, and ultimately population dynamics. This combined empirical and theoretical framework will allow us to explore how such metrics are impacted by future climate scenarios and the new resource landscape they will produce are likely to affect desert consumer communities over the next century.

Desert ecosystems often support diverse and dynamic small mammal communities in spite of low and unpredictable resource availability (Fox 2011). These communities exemplify how resource-limited ecosystems can support consumers with a diverse range of life-history modes and functional traits associated with strategies for resource procurement. In the arid ecosystems of the American Southwest, for example, Heteromyid rodents are food-hoarding granivores that range in body size from ~5–125g and have long gestation times and small litter sizes, but they typically out-compete other species for high-quality seeds. In particular, kangaroo rats (*Dipodomys spp.*) use both scatter and larder-hoarding strategies to store food in caches that can persist across seasons and even years to provide reliable sources of food during periods of resource scarcity (Schroder 1979, Vander Wall 1990). In contrast, Cricetids such as deer mice (*Peromyscus spp.*) and grasshopper mice (*Onychomys spp.*) do not hoard food in the desert ecosystem we propose to study and thus must forage continuously to survive, but have evolved to be more omnivorous and occupy multiple trophic levels, which grants them access to high quality foods with high protein contents. With shorter gestation times and larger litter sizes, Cricetids typically have higher reproductive potential than sympatric Heteromyids (Hoffmeister 1986).

Research to date shows that arid ecosystems are regulated primarily from the bottom-up and are subject to highly stochastic variation in seasonal rainfall and productivity (e.g.,Guo and Grown 1996, Guo et al. 2002), which makes them model systems for examining how abiotic factors influence consumer community dynamics and structure (Polis 1991, Meserve et al. 1995, 1996, 2003, 2011, Chesson et al. 2004, Letnic et al. 2004, Thibault et al. 2004, Dickman et al. 2011, Kelt 2011). For example, small mammal populations respond rapidly and positively to rainfall-driven increases in resources (Brown 1973, Ernest et al. 2000, Lima et al. 2008, Previtali et al. 2009, Thibault et al. 2010), and while temporal variation in resource abundance can produce shifts in community composition, energy use by the community appears homeostatic over time (Ernest et al. 2001, Brown et al. 2002, Ernest 2005).

While much descriptive information exists on the diets of small mammals in the American Southwest (e.g., Vorhies and Taylor 1922, Brown and Lieberman 1973, Reichman 1975, 1979, Stamp and Ohmart 1978, Price and Reichman 1987, Price and Joyner 1997, Hope and Parmenter 2007), the relative importance of winter/spring versus summer monsoon resource production to consumer function and fitness within and among species is not known. Most studies have relied on a correlative approach to link precipitation or primary production to numerical responses in small mammal abundance or community composition (Ernest et al. 2000, Lima et al. 2008, Thibault et al. 2010) and have not directly examined, even at coarse resolution, inter- or intra-specific variation in diet. Furthermore, little is known about how the timing and quality or quantity of seasonal resource production influence consumer body condition, which is often used to predict reproductive performance, survival, and overall fitness (Ritchie 1990, Millar et al. 1991, Newton 1993, Dobson and Michener 1995, Wauters and Dhondt 1995, Atkinson and Ramsay 1995, Keech et al. 2000). To our knowledge, no study has quantitatively linked vertebrate resource use with body condition at seasonal timescales, likely because the simultaneous collection of both types of data is highly invasive and time-intensive using traditional techniques (Millar and Schieck 1986, Hickling et al. 1991, Batzli and Esseks 1992, Schulte-Hostedde et al. 2001).

Though ecologists have a solid understanding of how both abiotic and biotic processes structure desert small mammal communities, how functional traits regulate intra- and inter-specific variation in individual fitness, and by extension how population and community dynamics respond to changing environmental conditions, is unknown (McGill et al. 2006, Kearney and Porter 2006, Messier et al. 2010, Violle et al. 2012). To achieve such an understanding requires knowing how specific resources affect individual condition and performance, and how these metrics translate into survival and reproduction, which ultimately regulate population and community dynamics. Such a framework would be powerful, as it could be used to generate predictions of population and community dynamics in alternative environmental conditions, and establish a general theory of consumer foraging behaviors in resource-limited systems: this is one of our primary goals. By using a desert small mammal community as a model system, our project will focus on three general questions that ecologists often consider when studying consumers in any ecosystem:

* ***How does variation in the availability of relatively nutritious C3 versus non-nutritious C4 plants influence individual and population-level niche partitioning in this small mammal community?***
* ***Does diet composition influence key physiological traits, namely body condition and gut microbiome composition, and how do these variables impact individual survival?***
* ***Use mechanistic foraging models that incorporate ecological and physiological constraints to develop a consumer strategy-niche space, from which empirical measures can be assessed***

We anticipate that our project will produce significant insights into the field of animal ecology because it will demonstrate how resources are mechanistically linked to body condition and fitness in a dynamic resource landscape. These topics have never been examined in a single consumer species, much less an entire community. Our mark-recapture data will allow us to link quantitative data on resource selection and body condition to individual survival and population dynamics. Lastly, our empirically-grounded stochastic dynamic models will provide novel insight into how species may respond to future shifts in climate conditions that are predicted to decrease C3 resources, which are strongly preferred by small mammals and other abundant consumers in many desert ecosystems.

***Study System***

Our study will use ecological data collected at the individual level to link rainfall-driven variation in resource availability with traditional metrics of fitness such as body condition and survival, which in turn influence population size and consumer community composition. Figure 1 presents a conceptual diagram of how precipitation-driven resource inputs are linked to community ecology at our field site. We will assess consumer diet composition in the context of well-established theory that provides predictions for how population and individual niche width vary in response to resource quantity and quality (ecological opportunity), as well as inter- and intra-specific competition (REFS). This will enable us to identify foraging generalists and specialists along two primary axes – plant photosynthetic pathway and trophic level – that are closely associated with forage quality quantified with an index constructed from foliar and seed nitrogen (protein) content (Fig. A), soluble carbohydrate concentration, and seed mass. Consumer resource selection will be quantified with a combination of metabarcoding and isotope data to identify dietary strategies used by both primary (Fig. X) and secondary (Fig. Y) consumers. Metabarcoding will also enable us to characterize gut microbiome composition that will be used as a physiologically mediated phenotypic trait in models used to identify fitness maximizing decisions and predict how future conditions will alter community dynamics. Consumer body condition will be directly measured via quantitative magnetic resonance to construct a body condition index (e.g., percent body fat and lean mass) that can be directly compared with data on resource selection and gut microbiome composition. Finally, we will estimate individual survival and population size with mark-recapture models, which will also quantify intra- and inter-specific competition within this consumer community. Finally, these data streams will be included in a mechanistic state-dependent model that determines how species-specific body condition and caching behaviors, as well as environmental uncertainty, impacts foraging.



Figure 1. Conceptual schematic highlighting data streams our proposed project will use to link resource inputs to community dynamics at the Sevilleta LTER.

Our small mammal trapping program in the shrubland-grassland transition zone at the Sevilleta National Wildlife Refuge (NWR) routinely captures four Heteromyids and six Cricetids (Table 1). We capture and process ~100-125 individuals every month and the most common species we have captured from 2014-2020 (n=2756) in order of decreasing relative abundance are *Perognathus flavus* (50%)*, D. merriami* (12%)*, Peromyscus spp.* (10%)*, Onychomys arenicola* (9%)*, Dipodomys ordii* (8%)*, D. spectabilis* (5%)*,* *Reithrodontomys megalotis* (5%), and *Neotoma albigula* (2%)*.* Recapture rates are also high: during the same period, the number of individuals (*N*) of each species that have been captured 3 or more times during trapping in 2014: PGFV (*359*), DIME (*100*), DISP (*67*), DIOR (*66*), ONAR (*48*), and PM (*24*); see Table 1 for species acronyms.

The high seasonal and inter-annual climate variability in the northern Chihuahuan Desert (Sala et al. 2012) provides an ideal system to quantify the effects of resource quantity and quality on the functional and community ecology of a diverse small mammal community. Precipitation is bimodal, with ~60% of annual rainfall on average being delivered by the summer monsoon from Jul–Oct (REFS). Monthly averages for more unpredictable winter and spring precipitation (Feb-Apr) are lower than the monsoon, while the driest and hottest period of the year is typically in May–Jun. Another attribute of this bimodal system is variability, which is a common attribute of precipitation regimes in arid ecosystems and one reason why such environments have served as the backdrop for field-based experiments examining the influence of abiotic factors such as precipitation and temperature on plant (e.g., McDowell et al. 2008) and consumer communities (Meserve et al. 2003, Chesson et al. 2004, Thibault et al. 2004, Kelt 2011). This high degree of inter-annual variability suggests that even relatively short-term (3–5 year) datasets can capture a significant amount of natural variability.

These two distinct periods of annual precipitation produce resources of differing quantity and quality that can be traced through the consumer community with scat metabarcoding and d13C analysis of consumer tissues with rapid isotopic incorporation rates (e.g., blood plasma). Highly unpredictable winter/spring rains fuel a spring period of C3 primary productivity, namely perennial shrubs and annual forbs (Fig. 1). Later in the summer, a second more reliable period of monsoonal precipitation drives the production of C4 perennial grasses and (mostly annual) forbs with limited C3 growth. C3 and C4 plants vary in their nutritional quality, energy content, and persistence in the environment. The leaves of C3 plants are more nutritious with higher nitrogen and digestible carbohydrate contents than C4 grasses (Caswell et al. 1973, Caswell and Reed 1975, 1976, Barbehenn et al. 2004a, 2004b). Preliminary data for weight percent nitrogen content [N] of leaves and seeds of plants collected from our field site show that (1) seeds generally have higher [N] than leaves, and importantly the [N] of seeds or leaves from C3 perennials/annuals are higher than their C4 counterparts. C3 perennials and annuals also produce larger seeds than C4 perennials Reichman 1976, Harper 1977, Davidson et al. 1985, Samson et al. 1992). In contrast, the leaves of C4 grasses are harder for consumers to process and digest, but are more resistant to decomposition (Vanderbilt et al. 2008) and may serve as a fallback food for rodents during periods of resource scarcity (Yeakel et al. 2020). C4 perennial biomass at our study site is dominated by a single grama grass species (*Bouteloua eripoda*) that contributes ~40% of the annual ANPP (Fig. 1). Lastly, C3 versus C4 plant functional types have very different d13C values, which can be used to quantify the transfer of primary production into consumer tissues in arid monsoonal ecosystems (e.g., Warne et al. 2010, Orr et al. 2015, Noble et al. 2019). Mean d13C values of leaves and seeds collected from dominant/abundant C3 perennials and annuals at our field site (Fig. 1) ranged from -25.5‰ to -27.5‰. Mean d13C values of the dominant/abundant C4 perennials and annuals ranged from -13.0‰ to -15.0‰. SDs for C3 or C4 perennials or annuals were ≤1.5‰.

Figure 2. Aboveground net primary production (ANPP) of dominant/abundant perennials and annuals in the spring (green bars, Mar-May) and summer/fall (blue bars, July-Oct) growing seasons at our mixed shrubland-grassland Sevilleta study site. C4 species are identified with an asterisk (\*), CAM species (n=1) with two asterisks (\*\*). Note differences in the scale of the y-axis (ANPP) among panels. Plant codes are adopted from the USDA Plants Database.



Regional climate models predict rapidly increasing air temperatures, significant decreases of 15–20% in winter precipitation, increased inter-annual variability in the strength of the summer monsoon, and higher drought risk (Gutzler and Robbins 2007, Seager et al. 2007, Cook et al. 2015). These directional shifts in abiotic conditions could push some flora and fauna beyond their physiological or ecological limits for local occupancy, but to date most studies on this topic have focused on strict physiological tolerances to water limitation (trees) or temperature (birds) (McDowell et al. 2008, Breshears et al. 2009, McKechnie and Wolf 2010). To our knowledge, no study has investigated how a climate-mediated shift in resource base could affect an entire consumer community.

Lastly, our project will utilize a well-established theoretical framework for quantifying foraging strategies at both the individual and population level. Briefly, the full array of individual-level foraging strategies in a population collectively contribute to its total niche width (TNW, Roughgarden 1972, Bolnick et al. 2007). Foraging strategies may differ among individuals in a population because of individual variation in physiological and/or behavioral traits (Araújo et al. 2011, Maldonado et al. 2017). Specifically, individuals may uniformly consume all resource types that are available to the population or they may specialize on subsets with little overlap, the latter often reffered to as Individual Specialization or ‘IS’ (Roughgarden 1972, Bolnick et al. 2003). The population’s total niche width reflect the balance of two opposing phenomena: (1) the diversifying effect of intraspecific competition that minimizes niche overlap between conspecifics and yields an increase in population niche width; (2) the effect of interspecific competition that prevents population niche expansion (Araújo et al. 2011, Kernaléguen et al. 2015). Accordingly, when animals are constrained by intraspecific competition in the use of a common optimal resource, individuals begin to feed on alternative resourcesleading to an expansion of population niche width (i.e., Optimal Foraging Theory, ‘OFT’; MacArthur and Pianka 1966), which can be achieved via an increase in dietary variation among individuals (Svanbäck and Bolnick 2005, 2007). Moreover, IS may differ among foraging guilds, with omnivores expected to have greater IS than primary consumers (Maldonado et al. 2017). A plausible explanation for the difference in IS among guilds is that omnivores have a higher degree of ecological opportunity (EO)—defined as the diversity of available resources—since they are able to specialize on resources derived from a greater number of trophic levels (Van Valen 1965, Roughgarden 1974, Araújo et al. 2011, Layman et al. 2015, Maldonado et al. 2017).



Figure 3. Weight percent nitrogen concent [N] of leaves (gray) and seeds (white) of dominant and abundant C3 or C4 perennials and annuals collected from our mixed shrubland-grassland field site at the Sevilleta. Dataset includes 23/25 of the perennial and 11/15 of the annual species shown in Fig. 2. Error bars represent SD and sample sizes are shown in each bar.

In arid and semiarid environments with stochastic rainfall, there can be quick and dramatic changes in the relative availability of different foods (e.g., Fig. 2). These changes are likely to alter the quantity and quality of resources to influence the degree of IS, and thus the total niche width of the population (MacArthur & Levins 1967). Resource partitioning has long been understood to affect the outcomes of ecological interactions between species (MacArthur & Levins 1967), and a recent meta-analysis showed that the ecological effects of inter- vs. intraspecific dietary variation are often of similar magnitude (Des Roches et al. 2018). Theory predicts that the effects of resource partitioning both within and between species on population and community dynamics should be strongest when access to resources is limited and/or when competition for resources is enhanced in diverse consumer communities (Wiens 1977, Heske et al. 1994). The potential for within- and between-species dietary specialization and resource partitioning to stabilize population sizes and promote species coexistence has not been systematically explored.

***Specific Questions, Interpretive Framework, and Predictions***

* ***How does variation in the availability of relatively nutritious C3 versus versus non-nutritious C4 plants influence dietary breadth and niche partitioning among small mammals, and how does forage quality impact individual body condition and survival?***
  + *How does specialization or generalization on C3 versus C4 resources and/or omnivory facilitate individual- and population-level niche partitioning?*

*Empirical Approach.* Our goal is to build an quantiative framework for combining scat metabarcoding and stable isotope data that will transform how animal ecologists measure diet, an multi-proxy approach that we anticipate will provide unprecedented insighings into the foraging strategies of consumers. The advantage of combining these two dietary proxies is that their respective strengths complement the weaknesses of the other. Specifically, scat metabarcoding provides high-resolution taxonomic information for recently consumed (~12–24 hours) resources, but estimating the relative proportion of how much of each resource was assimilated is difficult and is confounded by assumptions about the relative digestibility of different foods. In contrast, isotope analysis provides a time-integrated measure of resource assimilation, but often times can only reliably discriminate between plant functional groups (e.g., C3 or C4) or provide an estimate of relative trophic level.

*Theoretical Approach:* Mechanistic foraging models provide a means to quantify the potential niche space of a consumer given a range of constraints in the albeit simplified manner of mathematical models. If the constraints captured by a foraging model play a central role in shaping the foraging behaviors of consumers in natural systems, the niche-space enumerated by the model can be used as a lens by which the larger community can be understood. However, even a simple foraging model can result in an enormous complexity of foraging strategies, and a central challenge in understanding both model and natural ecological systems resides in excising low-dimensional relationships from high-dimensional data, particularly when such data are generated from interactions with nonlinear dependencies.

We propose to devise a series of foraging models that range from simple to complex, to explore and enumerate the dietary consequences of a large range of foraging strategies. We will then use this range of strategies to construct a low-dimensional realization of a high-dimensional niche space using diffusion mapping techniques. Diffusion mapping constitutes a class of data analytics capable of reconstructing nonlinear relationships governing high-dimensional datasets when the generative processes underlying the data are unknown. We will use this perspective to reconstruct a low-dimensional embedding of consumer strategies, or strategy-niche manifold, capturing the structural similarities of a range of foraging strategies. Understanding how different strategies relate to one another when the mechanics are simple and well-defined provides a null expectation by which to classify and evaluate the more complex strategies observed among consumers in natural systems. Our procedure thus consists of four parts: 1) build a class of foraging models to systematically capture a range of foraging strategies given known physical and biological constraints; 2) reconstruct a low-dimensional embedding of the range of modeled foraging behaviors to capture the associated strategy-niche manifold; 3) measure the diets of local consumers and assess their ecological roles by their proximity to modeled strategies on the niche manifold.

*Confronting Theory with Data:* Because both the underlying generative models and resulting foraging strategies of model systems within the embedding are known, in addition to assessment, we can use the constructed niche manifold in a predictive capacity. For instance, the foraging constraints that give rise to different strategies also allow us to assess the fitness consequences of those strategies. By relating the fitness consequences of simulated strategies occupying different locations along the niche manifold, we can associate empirically measured strategies with modeled values nearby. The resultant fitness landscape assessed along the niche manifold can thus be used to evaluate and ultimately predict life history characteristics of consumers foraging in natural systems. By incorporating foraging data from stable isotopes and scat metabarcoding with estimates of fitness from Sevilleta consumers alongside those simulated within the context of the niche manifold, we will directly assess the predictive value of the manifold niche concept in a natural community.

As applied to the monsoonal mixed C3/C4 ecosystems that dominate the Sevilleta LTER, our multi-proxy approach will enable us to place individuals into categories that represent their seasonal (or annual) resource selection strategy (Fig. X). We acknowledge that our framework is designed for habitats characterized by mixed C3/C4 production, however, such ecosystems are uniquitous at temperate latitudes around the world – American Southwest and Midwest in North America, East Africa, Australia, central Asia, and central-southern South America. For primary consumers (Heteromyidae), we will use combine metabarcoding with plasma d13C analysis to identify six resource procurement strategies as either generalists or specialists that focus on C3, C4, or a combination of the two plant functional types (Mixed). For example, a C3 Generalist (Fig. XB) or C4 Generalist (Fig. XC) will have consistently low of high plasma d13C values, respectively, but scat metabarcoding will consistently yield high C3 or C4 plant species richness. Furthermore, a Mixed Generalist (Fig. XA) individual will have intermediate isotope values and consistently consume a diet with high C3 and C4 plant species richness. In contrast, dietary specialists (Fig. XD-XE) in the mixed, C3, or C4 categories will have isotope values that mimic their generalist counteparts, however, metabarcoding will consistently yield low (n<5) plant species richness. Important to note that individuals could switch between discrete strategies over time.



Figure Y. Predictions for six primary consumer dietary classifications that can be identified using a combination of scat metabarcoding and blood plasma d13C analysis of samples collected through time (T1 to T3). Letters denote hypothetical species of eight C3 plants (A-H) and eight C4 plants (J-Q) based on metabarcoding data. Circles represent blood plasma d13C values collected from generalists (white circles) and specialists (black circles). d13C values range from -26‰ for C3 to -12‰ for C4 plants based on preliminary data for abundant plants collected from our mixed shrubland-grassland study site.

We will use DNA metabarcoding to quantify each individual’s (recent) relative utilization of fast-growing ephemeral plant species versus slow-growing perennial shrubs. We will be able to quantify forage selectivity based on matches between dietary DNA, the plant and arthropod reference libraries, and the abundances of plants recorded during contemporaneous field surveys. Based on these data, we will evaluate how climatic variation influences individual- and population-level foraging. For individual-level analyses, we will use a mixed-modeling approach to evaluate the responses of individual diets to variation in recent rainfall and vegetation abundance, using each of the two energy channels as response variables and treating individual identity as a random effect. For population-level analyses, we will use a mixed-modeling approach to evaluate variation in the utilization of each of the two energy channels.

By re-sampling individuals on different days within a trapping bout, we will evaluate short-term, intra-individual dietary flexibility. For example, with two fecal samples collected within a trapping bout, a plant taxon can be present in 0/2, 1/2, or 2/2 samples. Thus, process variance (i.e., day-to-day range of plant taxa that individuals consume) can be distinguished from sample variance (i.e., random changes in diet profiles due to sample acquisition and processing). We will also assess DNA sequence relative read abundance (RRA), which can provide a valuable proxy for proportional consumption of different plant and arthropod species (Deagle et al. 2019). Strategies for converting DNA sequence reads to relative abundance dietary data have been controversial—the reliability of this approach cannot be assumed a priori—but computer simulations and experimental data reveal that interpretations based on the presence/absence and RRA of food species will often lead to similar conclusions in highly replicated studies like the one proposed (Deagle et al. 2019, Kelly et al. 2019).

We will evaluate individual specialization using Shannon’s index (*H*’) to calculate population total niche width (TNW) and the proportion of TNW that is distributed across individuals (within individual component, WIC). We will compare the degrees of specialization at both levels across treatments and season using general linear models (e.g., TNW ~ treatment + (1|season)).

To examine dietary strategies along a trophic axis, we will use an approach recently developed for our work on small mammal community dynamics in Fray Jorge National Park, Chile in collaboration with Douglas Kelt (UC Davis). For likely omnivores (Cricetidae) and secondary consumers (*Onychomys*), we will identify diet categories along the tophic axis niche using two analytical approaches. First, we will directly compare metabarcoding-based estimates of population total niche width with isotopic niche space for each species (e.g., Fig. YA). d13C versus d15N isotopic niche space will be quantified with Bayesian standard ellipse areas (SEAB; Jackson et al. 2011). We predict a positive relationship between diet diversity as measured from fecal DNA and isotopic niche breadth (SEAB), with omnivorous species having the highest values for these two variables.



Figure Y. Diagram of expectations when comparing percent frequency of occurrence of arthropods in small mammal scats (via metabarcoding) versus d15N of blood plasma.

Additionally, we will examine omnivory in finer detail by comparing the percent frequency of occurrence (%FO) of arthropod functional groups in fecal samples against d15N values in small mammal blood plasma (Fig. Y). We predict a positive relationship between %FO and plasma d15N, and that the slope of the relationship will vary depending on the arthropod functional group consumed; that is, a relatively shallow slope with consumption of herbivorous arthropods (H), but a steeper slope for individuals consuming predacious arthropods (P). Baseline variation in the d15N of plants (Fig. Y, arrows and black circle) should cascade up to herbivores (Fig. Y, white circle), but increased omnivory will yield higher d15N in blood plasma in comparison to the highest d15N values observed in herbivorous individuals. We will train this approach with a concentration-dependent mixing model (Phillips and Koch 2002) that uses d15N data and weight percent nitrogen concentration by weight for local plants and ground-dwelling arthropods to estimate the expected increase in plasma d15N values with increased arthropod consumption. We will perform these analyses at both the population- and individual-level.

*Predictions.*

* ***Does forage quality impact the gut microbiome composition of small mammal consumers, and what is the relationship between gut microbiome composition and body condition?***

*Approach.*

*Predictions.*

* ***Use mechanistic foraging models incorporating ecological and physiological constraints as a consumer strategy-niche space, to assess and predict empirical measures***

***Approach.*** We present a minimal consumer foraging model to illustrate how our framework can be used to uncover a simulated consumer’s niche manifold – which we will identify using diffusion mapping techniques – and treat this as a null expectation by which we will subsequently evaluate empirical consumer strategies. We note that mechanistic foraging models of arbitrary complexity could be used to establish this null expectation, and while we will identify in what direction we aim to build additional complexity, a simpler framework best suits our illustration of the core approach.

We simulate a consumer foraging in a seasonal environment given a set of resource functional groups (see xx) with differing spatial distributions during fall (non-monsoonal) and spring (monsoonal) seasons, such that mu\_si is the mean encounter rate where s denotes season and i=1…N functional groups. A consumer of mass M forages within this landscape, targeting a particular functional group with weight tau. The targeting weight tau indicates that for each consumer-resource interaction, the consumer will find and acquire its targeted resource with probability tau, and target the closest resource group (regardless of preference) with probably 1-tau. Once a consumer-resource interaction is drawn, the consumer travels the distance to the resource with velocity v(M), and assimilates both bulk energy (kJ) and nitrogen content based on the resource’s energy density and nitrogen concentration, respectively. Consumer-resource interactions continue until a predetermined time threshold for the foraging bout, tmax, is reached, whereupon the consumer ceases its foraging activity for the day. We track 300 days of consumer foraging, with 100 days committed to each season in a fall-spring-fall cycle.

***Predictions.*** The simplistic foraging model described above allows us to track both temporal changes in diet as well as daily energetic gains as a function of consumer resource targeting strategies. Where a given consumer targeting strategy is characterized by the temporal sequence of the proportional contribution of each resource group to the consumer’s diet, we then use a diffusion mapping approach to compare alternative consumer targeting strategies. In the example we present here, there are 7 resource groups and we explore targeting strategies ranging from tau=0 (a consumer that always targets the nearest resource) to tau=1 (a consumer that always targets one of the 7 resource groups regardless of distance). Resource groups include C3/C4 perennial/annual shrubs, forbs, and grasses with seasonal encounter rates scaled to seasonal densities. Accordingly a single consumer strategy is described by the targeting of a specific resource group with weight tau, and exists as a single point within the diffusion space.

[this part might go into methods] After averaging biweekly dietary vectors of each targeting strategy across n=500 replicate foraging simulations, and following the principles of diffusion mapping, we first establish a similarity matrix across targeting strategy pairs. A given targeting strategy can be represented by a matrix of biweekly proportional contribution averages (with rows being resource groups, and columns being biweekly averages), and we calculate pairwise similarity between each matrix pair using Jaccard distance. The similarity matrix can be treated as an Adjacency matrix **A** - defining how nodes in a network are linked - where strategies (nodes) are linked together if they have a similarity greater than a particular value, and are not linked if they fall below that value. In this case, each targeting strategy is linked to the k=10 most similar targeting strategies, and we note that our results are not particularly sensitive to the choice of k. We then imagine a diffusive process taking place on this `strategy network’, where the diffusive modes can be used to construct a consumer strategy space where alternative strategies can be directly compared to one another. To obtain these diffusive modes, we transform the strategy matrix into a Laplacian matrix, such that **L** = **A** - **D**, where **D** is the diagonal matrix of **A**. The eigenvectors of **L** (v\_0 to v\_n) provide the modes of the diffusive process operating on the strategy space, which are scaled by the Laplacian eigenvalues (lambda\_0 to lambda\_n). From the the n-dimensional diffusion space and following Fahimipour et al. (2020), we finally construct a 2-dimensional embedding of the consumer strategy-niche manifold, to permit easier visualization. Strategies that share greater temporal similarity with each other will thus fall closer within the diffusion eigenspace, and form the basis by which alternative empirical strategies can then be assessed.

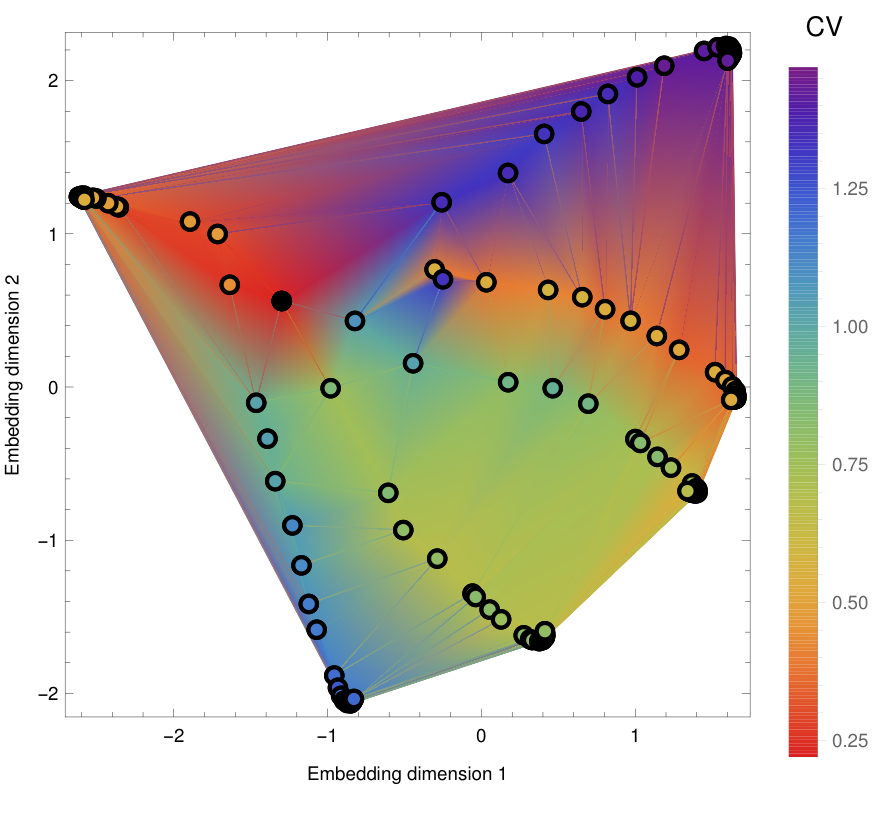


Figure XX. A) Consumer strategy-niche manifold. Each color denotes a strategy targeting a different resource group, whereas increased opacity denotes greater targeting strength tau. The black point represents the strategy where the closest resources are always targeted. B) Estimated fitness landscape (measured as the CV of nitrogenous returns) for consumer strategies. Higher CV corresponds to lower fitness; lower CV corresponds to higher fitness. The rodent silhouette illustrates placement of an empirical datum, which is evaluated with respect to the simulated strategy-niche manifold. Arrows denote trends towards increasing fitness between spines.

***Preliminary Results.*** The 2-D embedding of the consumer strategy-niche manifold depicts the array of simulated consumer targeting strategies as points, where point color denotes the resource group targeted and opacity denotes targeting weight (increased opacity means that the consumer targets the resource more strongly; Fig XXA). We find that consumer targeting strategies for different resource groups orient as spines emerging from a central point given by tau=0, i.e. a consumer that always targets the closest resource (black point). The spines that branch out from the central point are those strategies targeting different resource groups. Specialists on these resources are those farthest from the center, thus representing the most divergent strategies in this strategy-niche space.

How do different targeting strategies relate to estimates of consumer fitness, and is this predictive of consumer fitness in natural systems? We next demonstrate how a simple measure of fitness for simulated consumers can - in principle - be used as an expectation for those observed at the Sevilleta. Here we use the coefficient of variation (CV) of nitrogenous returns as a measure of fitness, such that lower values reflect smaller fluctuations relative to the mean (higher fitness), and higher values denote larger fluctuations relative to the mean (lower fitness). Along the spines radiating from the central cluster, fitness values are generally consistent (Fig. XXB). Across spines, this fitness landscape is roughly partitioned by two opposing resource groups that result in lower fitness (higher CV; C4 perennial and annual grasses), moving away from which (following the arrows in Fig. XXB) fitness increases towards two opposing resource groups that result in higher fitness (lower CV; C3 perennial forbs and shrubs). The diet of a hypothetical empirically-measured consumer is represented by the rodent silhouette. Our establishment of the strategy-niche manifold in this context would thus offer an interpretation of this hypothetical consumer. We would first note that the consumer is targeting C3 and C4 annual forbs, but that its strategy is one where roughly 75% of foraging effort is oriented towards opportunistic resources. Moreover, our foraging model predicts a fitness gradient with respect to these resource groups, where increased effort on C4 forbs is expected to promote fitness, whereas increased reliance on C3 forbs decreases fitness (arrows). Integrating individual-level ontogenetic information (Section xx) will allow us to directly assess the accuracy of this prediction.

While the simple foraging model that we describe here provides a useful heuristic for describing our approach, we intend to incorporate modeling frameworks that include more realistic physical and biological constraints, which can be either combined to form a larger strategy-niche manifold or assessed independently. For example, we intend to adapt a consumer foraging model described in Yeakel et al. (2020), where we use fitness maximization principles and stochastic dynamic programming to establish consumer strategies in environments with seasonal uncertainty. In this case, our framework directly incorporates consumer energetic constraints, caching behaviors, and state-dependent foraging strategies, from which fitness is directly estimated. Using more complex models such as this, in tandem with the simpler mechanics of the model described here, will not only enlarge our perspective of the universe of potential foraging strategies, but also enable us to pinpoint which biological and/or physical constraints play larger or smaller roles in driving consumer behaviors.

***Methods***

A novel aspect of our proposed work is the simultaneous quantification of resource use and diet-switching at the individual level in an environment with stochastic variation in resource availability and quality. Most measurements of individual specialization have focused on single species in environments with relatively stable—or at least seasonally predictable variation in—resource availability (Bolnick et al. 2003, Araújo et al. 2011). A review of these studies revealed a broad spectrum of responses to changes in resource availability, ranging from strong increases in individual specialization to strong decreases (Araujo et al 2001). Comparative studies across species in the same environment will provide a unique window into the ecological factors that promote and maintain the diversity of foraging strategies observed across studies, especially in systems that experience extreme temporal variation in resource availability and consumer population size, such as Fray Jorge. Furthermore, the data will provide insight into how individual-level foraging behaviors contribute to ecosystem-level energy flow, trophic networks, and small mammal community stability.

*Field Site and Small Mammal Trapping Protocol.* Our fieldwork will occur in the northern Chihuahuan Desert at the Sevilleta NWR located ~100km south of Albuquerque, NM. Our small mammal trapping webs are located in a mixed shrubland-grassland ecosystem and we will use ANPP estimates routinely collected by the Sevilleta LTER program in Apr-May and Sep-Oct to estimate seasonal production of C3 and C4 biomass. We will live-trap and tag small mammals nine times per year with monthly trapping bouts occurring from Mar to Nov. Two webs of 145 traps each (Parmenter et al. 2003) will be set for three consecutive nights and individual animals will be marked with a pit-tag, identified to species, weighed, and reproductive condition and blood will be collected via periorbital (Cricetidae) or retroorbital (Heteromyidae) bleeding. Scats will be opportunistically collected while handling animals and stored in cryovials immersed in liquid nitrogen. Using mark-recapture methods, we will estimate occupancy, abundance, survival probabilities, and population growth (λ) of each species with robust design models in the R-based MARK package (Lebreton et al. 1992, Kendall et al. 1997, MacKenzie et al. 2006).

*Plant and Arthropod DNA Reference Libraries*. Using well-established methods (e.g., Gill et al. 2019), we will collect duplicate vouchers of all plant species occurring in and around our study site. We anticipate collecting up to four replicate vouchers per species; within the first year we will collect and process the 25 predominant perrenials (shrubs, grasses, and forbs) and 15 predominant annuals (forbs and grasses), which collectively represent >99% of the annual aboveground net primary production (ANPP) at our site over the past 20 years (Fig. A). Fertile herbarium vouchers will be archived at the UNM Museum of Southwestern Biology (MSB). Specimens will be identified by LTER botanists and DNA-barcoded to refine taxonomic identifications and facilitate dietary analysis; we will sequence both the *trn*L sequence and the standard 3-region plant DNA barcode: chloroplast *rbc*L, *mat*K, and *psb*A-*trn*H (Kress & Erickson 2012, Gill et al. 2019). A similar approach will be used to develop a reference library for arthropod species collected using pitfall traps (Kartzinel and Pringle 2015, Pringle et al 2019). Replicate specimens of each species will be taxonomically identified and archived by specialists at the UNM Museum of Southwestern Biology. We will sequence COI and 16S barcodes to aid taxonomic identifications and provide reference sequences for dietary analysis.

*DNA Metabarcoding*. We plan to use methods that we have successfully employed to study herbivore and insectivore diets in multiple ecosystems (e.g., Kartzinel et al. 2015, 2019, Pansu et al. 2019). We anticipate collecting 100 small mammal fecal samples from 50 captured or recaptured individuals per trapping bout. Plant and arthropod DNA in the fecal samples will be preserved in the field using Zymo Soil/Fecal kits and then transported to a specially designed laboratory for extraction. For plant determination, the *trn*L-P6 chloroplast DNA marker will be amplified by PCR (Taberlet et al. 2007). For arthropods, we will amplify a small section of mitochondrial 16S rRNA that we specifically designed to enable sequencing of invertebrate DNA from vertebrate dietary samples (Kartzinel and Pringle 2015; Pringle et al 2019, Silva et al 2019). Additional loci will be considered if taxonomic coverage or resolution is insufficient based on this one alone (Marquina et al. 2019). Sequences will be obtained using an Illumina MiSeq. Data will be processed using OBITools software (Boyer et al. 2016) and identified based on extensive plant and arthropod DNA reference libraries for Fray Jorge (see below). Laboratory analyses will include crucial quality controls: extraction blanks to monitor for cross-contamination, repeat-sequencing a subset of samples, sequencing of positive and negative controls (Pompanon et al. 2012, Kartzinel et al. 2015, Deagle et al. 2019). As food passage times in mice are brief (~6-8 h—Padmanabhan et al. 2013), dietary DNA should reflect resource use over the previous day, and is sufficiently rapid to allow accurate assessments of diet variation during the course of daily recaptures. Prior and ongoing analyses of small mammal diets using this approach have shown that bait from traps does not influence diet profiles of repeatedly sampled individuals (Budischak et al. 2018), although sampling schedules will be adjusted if bait is detected after the first sequencing bout.

*Stable Isotope Analysis and Mixing Models.* We will analyze small mammal blood plasma because it provides a short-term integrated record of dietary inputs consumed during the ~2–3-week period prior to capture (Tsahar et al. 2007, Martinez del Rio et al. 2009, Klaasen et al. 2010). Our trapping frequency will thus provide a near continuous individual- and population-level dietary record from Mar through Nov for four consecutive years. d13C and d15N values will be measured using a Costech 4010 elemental analyzer interfaced with a Thermo Scientific Delta V isotope ratio mass spectrometer (EA-IRMS) at the UNM Center for Stable Isotopes (UNM-CSI; Albuquerque, NM). We will use a two-source Bayesian-based stable isotope mixing model in R (SIAR; Parnell et al. 2010) to quantify the relative contribution of C3 and C4 resources in individual small mammal diets (e.g., Orr et al. 2015) and standard ellipse areas to quantify population-level diet variation (Jackson et al. 2011).

*Plant Collections for Stable Isotope and Forage Quality Analysis.* Plants will be sampled a minimum of three times per year on each of our trapping webs: in February, when plants are dormant; in Apr–May, when spring production peaks; and in Sep–Oct when summer production peaks. We will use scat metabarcoding data to identify the plant species most often consumed by small mammals to guide our analysis of resource quality. We will create a forage quality index by combining direct measurements of weight percent nitrogen content (e.g., Fig X), soluble carbohydrate concentrations, crude fiber, and seed mass (mg) with published estimates of digestibility and energy content (e.g., Karasov 1990). Foliar and seed d13C and d15N values as well as weight percent carbon and nitrogen concentrations will be measured via the EA-IRMS system described above at UNM-CSI. For soluble carbohydrates, concentrations of monosaccharides (e.g., glucose and fructose) and disaccharides (sucrose and lactose) will be measured via gas chromatography mass spectrometry (Churms 1982) at the University of Missouri Agicultural Experiment Station Chemical Laboratories. Seed mass will be measured to the nearest 0.1mg with a Sartorius microbalance in UNM-CSI.

*Body Composition/Condition via Quantitative Magnetic Resonance (QMR).*After initial processing and blood collection, each individual will be placed into a Plexiglas tube that is inserted into our QMR to obtain a measurement of total lipid, lean muscle mass, and total body water accurate to better than ±0.1g for each substrate (Fig. 4). After analysis, animals are returned to the exact location of capture. Such QMR systems have been used in the laboratory for over a decade (Taicher et al. 2003) and are based on the same principles employed by any magnetic resonance system (Guglielmo et al. 2011). Our field-portable QMR system is manufactured by EchoMRI™ (Houston, TX) and has been previously validated on passerine birds, bats, and small terrestrial mammals (Tinsley et al. 2004, McGuire and Guglielmo 2010, Guglielmo et al. 2011). Instrument validation with reference materials show that our QMR system can accurately and precisely analyze samples that contain as little as 0.2g of fat or water. It is equipped with two antennas (small and large) capable of quantifying body condition in animals that range from 5g to 500g. The system has been installed in a Mercedes™ Sprinter Van for field-based analysis. Our data show that metal ear tags and internal electronic pit tags do not affect measurement accuracy.

*Foraging Model (Diffusion Mapping).*

*Stochastic Dynamic Program (SDP).*To develop a predictive understanding of both foraging and population dynamics within the Sevilleta small mammal community, the physiological and environmental conditions driving alternative foraging behaviors among both caching and non-caching rodent species can be incorporated into a mechanistic state-dependent model. We have developed a stochastic dynamic program (SDP) that determines how species-specific body condition and caching behaviors, as well as environmental uncertainty (e.g., ANPP), impacts foraging. We will first introduce the underlying framework of a flexible proof-of-concept model, and describe some initial insights that this framework provides.

In our framework, an individual must balance maintaining its body condition while establishing a buffer of endogenous and/or exogenous reserves to survive a stochastically varying environment. Foraging decisions maximize the individual’s future fitness integrated over the course of its lifetime, thus predicting behaviors representative of the evolutionary endpoint of natural selection. The goals of our SDP are threefold, and involve determining: 1) which resource type (C3 vegetation, C3 seeds, C4 vegetation, C4 seeds, or insects) maximizes an individual’s fitness with respect to its age and its current endogenous and exogenous (cache) energetic state, 2) whether a given resource should be consumed or cached, and 3) the population-level consequences of the predicted strategies.

We model the foraging decisions of an organism as a function of three principle state variables: 1) the time *t* at which a foraging decision is made, 2) net endogenous energetic reserves at time *t*, *X(t) = x*, and 3) net exogenous energetic (cache) reserves at time *t* (if available), Θ*(t)* = θ, where a unit increase in *x* or θ is an increase in 10 kJ. Here and throughout, upper case notation refers to a stochastic variable and the lower case refers to a particular value. Accordingly, the cache accounts for only the consumable energetic yields of stored resources, such that units for exogenous and endogenous stores are of like currency. As an illustrative example, we set the maximum endogenous energetic storage (*xmax*) to be equivalent to the energetic yield contained in both lean and fatty body mass (e.g., 316 kJ for a 40g *Dipodomys merriami*), while the minimum determines the threshold for starvation (*xc* = 0.5xmax), below which we assume the individual dies. In contrast, the cache can be much larger than the individual’s body size, such that *θmax* >> *xmax*, and the minimum size of the cache is zero. At each time step, there is loss of endogenous energetic stores via metabolic costs (*aMb*), where M is body mass in grams, and *a* and *b* are allometric constants. Similarly, the cache is not static and can decline due to random loss, theft, or decay (Ô).

In the proof-of-concept SDP, we use *Dipodomys merriamii* as an example and assume three potential behaviors determine the forager’s interaction with a given resource, conditioned on whether a particular resource is found in the time interval: 1) if the resource is not found, the forager consumes a yield of energy from its cache if available, where the yield is bounded by the organism’s daily digestive capacity *xs* (Yθ = min[*Θ(t)*, *xs*]; red equation in Fig. 6); 2) if the resource is found, it can either store the yield (*Yk* = min[energetic gain of food *j*, *xp,s*]) in its cache, bounded by the capacity of its cheek pouches (*xp*; blue equation in Fig. 6) or 3) it can consume the yield, again bounded by *xs* (green equation in Fig. 6). Whether a resource (if found) is cached or consumed is thus determined by which decision maximizes fitness.

Environmental conditions such as precipitation and associated ANPP impact predicted foraging behaviors by modifying the distribution and abundance of resources, altering the potential energetic gain of food type *j*. We let the random variable *K*=*k* represent the amount (in grams) of food found within a particular interval, and with probability *pK*(*k*)*j* an individual finds *k* grams of food type *j*, where *pK* is distributed as a Negative Binomial with mean *mj* and dispersion *vj*. We used relative standing biomass of resources to parameterize *mj* for both the winter/spring and summer monsoon seasons. In the winter/spring, C3 standing biomass is dominant (>90% of available biomass), while during the monsoon C4 biomass is dominant (~75% of available biomass). In both cases, we assumed that C3 and C4 vegetation were more evenly distributed (high dispersion; *vj* = 10) than C3 and C4 seeds (*vj* = 5), while insects were highly patchy (low dispersion; *vj* = 1). Finally, the energetic gain of a particular food must be modified by its digestibility (ε), which varies across food groups: C3 leaves = 33%; C3 seeds = 75%; C4 leaves = 25%; C4 seeds = 75%; insects = 77%. Thus the potential energetic gain of food type *j* is (*K\**ε*\*g*), where *g* is the energetic content for each food type, and *K* varies stochastically (Karasov 1990).

We consider an interval of length *T* during which only foraging decisions influence fitness. Fitness (*W*) at the terminal time interval is assumed to be an increasing function of *x* and *θ* determined by the general function *W(x,θ,t=T) =* Ψ*(x*,*θ)*, such that an organism with maximal endogenous and exogenous energetic storage has maximum fitness. We scaled the terminal fitness function to be unity, so it is easiest to consider it as survival after *T* for an individual whose end state is *X(T) = x*, *Θ(T)* = *θ*. The fitness function for both the terminal time period, and periods prior to the terminal time is as shown in Fig. 6, where maximization over *j* chooses the food that maximizes fitness given endogenous (x) and exogenous (θ) energetic state. As the fitness function is solved from *t<T* to *t=1*, we obtain the decision array *D(x,θ,t)*, which denotes the optimal foraging decision at time *t*, given *X(t) = x* and *Θ(t)* = *θ*. Moreover, we are able to determine which allocation strategy (cache or consume resource) maximizes fitness for a particular food type given *K=k>0* grams of resources are obtained.

***Summary of Intellectual Merits***

***Broader Impacts***

This project will provide an engaging platform for engaging and training undergraduates and under-represented groups in STEM disciplines. First, our field-based project lies at the interface between ecology and physiology and thus provides many opportunities for teaching undergraduate students integrative biology through hands-on research and classroom experiences. Our project will take place on the Sevilleta NWR just south of UNM, which grants undergraduate students immediate access to field-based ecological research. Both UNM and UC-Merced are minority-majority universities and certified Hispanic serving institutions, and UNM also has a large Native American population. First-generation undergraduate students often struggle to find relevance and purpose in their classroom curriculum; our project will engage a minimum of 6–8 undergraduates in research each year and teach them practical field skills such as handling and processing small mammals, as well as identifying and collecting plants. They will also learn how several cutting-edge technologies (QMR, ultrasound imaging, stable isotopes) can be implemented to study ecology. We have found that these experiences tend to be transformative for undergraduates as they gain knowledge and confidence that helps them nurture an identity as an independent and creative scientist, and many pursue senior honors thesis projects as a result. Although PI Newsome has only been an assistant professor at UNM since 2013, he has an active lab containing five graduate (all women), five undergraduate students (four women, two minority), and one postdoctoral scientist, all of which are pursuing independent research projects. This project will directly support three graduate students, who in addition to acquiring the skills described above will help manage a large field- and lab-intensive project, and mentor the four part-time undergraduate students the project will also support.

The PIs will also teach a new two-week intensive field course in mid-May of each year of the project, which will be designed to expose undergraduates to cutting-edge field and lab-based research. This course will be offered to any biology major at UNM and incoming Sevilleta Research Experiences for Undergraduates (REU) students; we expect that it will attract ~10–20 students per year. The course will be organized into three sessions. Mornings will be spent at our field sites at the Sevilleta, where students will learn how to identify and process small mammals and plants, collect plant and consumer (small mammals, grasshoppers, ants) tissues for stable isotope analysis, operate the QMR and ultrasonography equipment, and quantify aboveground net primary production. After lunch, students will attend one lecture given by the PIs and their graduate students and then spend 2–3 hours in the laboratory learning data management and analysis skills as well as how to process plant and animal tissue samples for stable isotope analysis. With support from UNM and NSF (DBI-1429042), the PIs have recently helped to establish the UNM Center for Stable Isotopes (CSI), an interdisciplinary facility dedicated to enhancing research and training in the application of stable isotope analysis in the biological, geological, anthropological, and medical sciences (http://csi.unm.edu). For the purposes of our short course, CSI will provide students with hands-on training on how to operate and maintain isotope ratio mass spectrometers. In doing so, students will produce isotope data for the samples they collect during the field portion of the course, which they will learn how to analyze and interpret using mixing models and spatial metrics to quantify variation in resource use within and among desert consumers. CSI also provides grants for undergraduate and graduate projects to cover analytical costs, thus encouraging students to take on field and laboratory projects that may result in peer-reviewed publications or presentations.

Results of this study will be incorporated into ecology courses taught in the U.S. and abroad, including a one-week short course taught by the PIs on stable isotope ecology to graduate students and faculty at the Centro Austral de Investigaciones Cientificas in Ushuaia, Argentina in 2016. Over the past five years, PI Newsome has taught six short courses in four Latin American countries that have attracted >300 graduate students, postdoctoral researchers, and faculty. Relationships forged during these short courses have resulted in eight graduate students coming to the U.S. to train in laboratories Newsome has been associated with. These interactions have also produced ~10 publications in peer-reviewed journals, but more importantly they have led to the transfer of knowledge and technology between the U.S. and Latin America, where the use of and analytical capability for stable isotope analysis is rapidly growing. PI Newsome also contributes to IsoCamp, a two-week short course taught each summer at the University of Utah to an international group of graduate students and postdoctoral researchers.

***Project Timeline***

***Results of Prior NSF Support***

**Newsome.** DEB–1120760 (2011–2016; Co-PI M.L. Fogel). *Collaborative Research: Extending the potential for hydrogen isotope tracers in ecology* ($380,000)*.**Intellectual Merit:* This project uncovered some of the fundamental underpinnings of using hydrogen isotopes (d2H) to study movement patterns, habitat use, and diet in vertebrates. We developed new methods to analyze d2H of individual amino acids and executed a series of lab experiments and field collections to examine the biochemical mechanisms responsible for creating observed d2H patterns among animal tissues. We have published eleven papers (Newsome et al. 2014, 2015, 2017; Fogel et al. 2016; Villegas et al. 2016; Gadek et al. 2018; Graves et al. 2018; Rodriguez Curras et al. 2018, Poblete et al. 2018; Poblete et al. 2018; Newsome et al. in press) and six more are in preparation. 60% of these published papers were led by undergraduate or graduate students. *Broader Impacts:*Support for 2 postdoctoral scientists (1 woman), 4 graduate students (1 woman), and 8 undergraduate students (6 women). PIs taught 3 isotope ecology short courses in La Paz, Mexico (3/2012), Santiago, Chile (11/2012), and Ushuaia, Argentina (5/2013).

**Kartzinel**. DEB–1930820 (2020–2021; Co-PI J.R. Goheen). *Collaborative Research: Testing predictions of the core-satellite and resource-breadth hypotheses in small mammal communities: field tests of a macroecological pattern* ($150,000). This award focuses on the responses of small mammal communities to a large-scale field experiment that has excluded large mammalian herbivores from plots in Kenya since 2009. Kartzinel began collaborating on this experiment as a postdoc in 2013 and has published 9 papers related to this work, including two data papers (Kartzinel et al. 2014 and Gill et al. 2019). This is Kartzinel’s first NSF award as PI and has already contributed to one accepted paper (Kartzinel and Pringle, in press). *Broader Impacts:* funding supports thesis research by 2 current Ph.D. students at Brown University, including an NSF GRF recipient and a member of a historically underrepresented group. It also supports a Kenyan MSc student who is co-supervised by Kartzinel and one post-baccalaureate recipient of a prestigious scholarship from Malaysia to train in Kartzinel’s lab.

**Yeakel.** SGP–1623852 (2016-2020; Co-PI J.D. Yeakel). *Collaborative Research: Assessing millennial-scale community dynamics using highly-resolved mammal and vegetation food webs* ($431,800). *Intellectual Merit*: The primary objective of this work is to integrate recently discovered small mammal fossil material into understandings of the La Brea ecosystem before the Last Glacial Maximum, and to reconstruct consumer-resource interactions among plant functional groups, herbivores, meso-, and apex carnivores. This project has not yet produced any publications. This is Yeakel's first NSF award as PI. *Broader Impacts*: co-PIs on the award stablished a Teachers’ Workshop at the La Brea Tar Pits and Museum to introduce the Community Science microfossil sorting initiative.