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

Ecologists have long attempted to connect animal population dynamics to resource landscapes becauseconsumer life histories are inextricably linked to resource quantity and quality (Simpson et al. 2009). Establishing mechanistic connections between resources and consumer population growth remains a challenge, however, because it requires linking population and community ecology with animal eco-physiology at the organismal scale. Indeed, linking resources to population dynamics involves understanding a complicated set of interactions mediated by individuals’ physiological processes, and then connecting these physiological processes to the ecological conditions that dictate foraging and resource use. Such research generally involves the collection of longitudinal data at multiple levels of ecological organization (individual to community), which is nearly impossible using traditional methods.

Our proposed 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 and theoretical toolkits to directly measure resource use and body condition with a series of mechanistic foraging models 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 foraging and population dynamics are impacted by future climate scenarios, and how the emergent resource landscapes they produce are likely to affect desert consumer communities over the next century.

Desert ecosystems often support diverse and dynamic small mammal communities despite 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 that range in body size from ~5–150g are food-hoarding granivores with “slow” life histories with long gestation times and small litter sizes. Kangaroo rats (*Dipodomys spp.*) use both scatter and larder-hoarding strategies to store procured seeds 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, cricetid rodents like deer (*Peromyscus spp.*) and grasshopper mice (*Onychomys spp.*) range in size from 20–40g and exhibit “fast” life histories with short gestation times and large litter sizes, resulting in higher reproductive potential than sympatric heteromyids (Hoffmeister 1986). Cricetids, in contrast to heteromyids, do not hoard food in the desert ecosystem we propose to study, and therefore must forage continuously to survive. Further, cricetids are more omnivorous and occupy multiple trophic levels, granting them access to higher quality foods with high protein content. Given the increasing resource stochasticity of our proposed desert system (Rudgers et al 2018), tradeoffs in these opposing foraging and life-history strategies have significant potential to structure population and community dynamics.

Arid ecosystems are regulated primarily from the bottom-up and are subject to highly variable 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, and temporal variation in resource abundance can produce shifts in community composition (Brown 1973, Ernest et al. 2000, Lima et al. 2008, Previtali et al. 2009, Thibault et al. 2010). 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), proportional resource use and the relative importance of seasonal resource production to consumer function and fitness - both within and between species - is not known. Indeed, most studies of aridland ecosystems have relied on correlative approaches 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 resolutions, the mechanistic relationships between foraging, fitness, and population dynamics. Furthermore, little is known about how the timing, quality, and quantity of seasonal resource production influence consumer body condition, which is often used to predict survival, reproductive performance, 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 and survival at seasonal timescales in stochastic aridland ecosystems, likely because the simultaneous collection of these data streams 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 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 unclear (McGill et al. 2006, Kearney and Porter 2006, Messier et al. 2010, Violle et al. 2012). Better understanding requires knowing how specific resources affect individual condition, 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 under alternative environmental conditions and to establish a general theory of consumer foraging behaviors in resource-limited systems. This is a primary goal of our proposed research. Using a desert small mammal community as a model system, our project will focus on three questions central to connecting animal population dynamics to resource landscapes:

* ***How does temporal variation in the availability of C3 versus C4 plants influence individual- and population-level resource use in this small mammal community?***
* ***Is the use of resources with different nutritional traits––nitrogen content, seed size, secondary metabolites––correlated with consumer phenotypic traits, namely body condition and gut microbiome composition, and how do these variables influence individual survival?***
* ***Can mechanistic foraging models that incorporate ecological and physiological constraints be used to establish a consumer strategy-niche space that correlates with expected fitness, from which empirical measures can be assessed?***

Our study will use ecological data collected at the individual level to link climate-mediated variation in resource availability with traditional metrics of fitness such as body condition and survival, as well as their cascading impacts on population size and consumer community composition. We will assess empirical observations against fitness expectations derived from mechanistic foraging models where consumer strategies can be explicitly defined and predicted fitness consequences are enumerated. Figure 1 presents a schematic diagram of our approach. 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 (Bolnick et al. 2003, Araujo et al. 2011). 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. 2), soluble carbohydrate concentration, and seed mass. Consumer resource selection will be quantified with a combination of fecal metabarcoding and isotope data to identify dietary strategies used by both primary and secondary consumers. Fecal metabarcoding will also enable us to characterize gut microbiomes as a physiologically mediated phenotype, while consumer body condition (e.g., fat and lean mass) will be directly measured via quantitative magnetic resonance (QMR) to construct a robust body condition index that can be directly compared with data on resource selection, gut microbiome composition, and survival. We will estimate individual survival and population size with mark-recapture models, which will also quantify density dependent intra- and inter-specific competition within this consumer community. Finally, we will construct mechanistic consumer foraging models parameterized by measured resource availability, stoichiometry, and nutritional content where both consumer microbiome state and body condition constrain foraging strategies. Assessing observed consumer strategies against those generated by mechanistic models and their associated fitness consequences will enable us to link consumer dynamics to population dynamics. 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 jointly in a single consumer species, let alone an entire community.

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Description automatically generated]()In addition to answering the questions listed above, our project will constitute a major methodological and theoretical advance in animal ecology by combining several types of empirical data streams on diet and body composition. These empirical approaches will be evaluated against mechanistic foraging models using recent advances in nonlinear dimensional reduction to derive a strategy-niche space that may correlate with aspects of fitness. Our approach will allow us to predict how foraging strategies will be impacted by future environmental conditions, as well as to establish predictions on consumer fitness, from which population-level expectations will be explored. First, we will build a quantitative framework for combining fecal metabarcoding and isotope data into a multi-proxy metric that will transform how animal ecologists use diet composition data to understand foraging strategies. 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 proportional consumption and assimilation of individual resources is confounded by assumptions about the relative digestibility of different foods. In contrast, isotope analysis provides a time-integrated measure of resource assimilation with low taxonomic resolution often only capable of discriminating between plant functional groups (e.g., C3 or C4) and providing an estimate of relative trophic level for consumers. Combining these two approaches with direct measurements of body condition and mark-recapture models will allow us to link high-resolution data on resource selection and assimilation to individual survival and population dynamics.

Figure 1. Schematic diagram illustrating how empirical data on resource availability (ANPP), diet composition derived from fecal metabarcoding and stable isotope analysis, and plant nutritional traits will be combined with a mechanistic foraging model based on diffusion mapping to evaluate how resource selection influences small mammal physiological (body condition, gut microbiome composition) traits and ecological (survival, population size) outcomes.

Second, we will establish a series of foraging models that range from simple to complex to explore and enumerate the dietary consequences of a large range of potential foraging strategies and their dietary and fitness consequences in response to known physiological and ecological constraints. We will then use diffusion mapping techniques (Fahimipour et al. 2020, others) to reduce both observed and simulated multi-dimensional resource use data into quantifiable fundamental and realized niche spaces. Diffusion mapping is an algorithmic framework capable of extracting 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 - the strategy-niche manifold - that captures the structural similarities of a range of simulated and observed 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 theoretical framework consists of three 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 dynamics and resulting foraging strategies of simulated systems within the niche manifold are known, in addition to assessment, we can use the constructed manifold in a predictive capacity. For instance, the foraging constraints that give rise to different strategies 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. We will leverage independent estimates of fitness from consumers and their observed foraging strategies using mark-recapture data to test and validate model predictions. By assessing the predictive value of the manifold niche concept in a natural community, we will be well-positioned to firmly establish causal links between different consumers and their foraging strategies with population-level (and ultimately community-level) consequences.

***Study System: Sevilleta Long-Term Ecological Research (LTER) Site***

Our small mammal trapping program is situated at an ecotone between a creosote bush (*Larrea tridentata*) shrubland and black grama (*Bouteloua eriopoda*) grassland in the northern Chihuahuan Desert (Sevilleta LTER), and we routinely capture four species of Heteromyids and six Cricetids. We capture and process ~50–75 unique 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%, PGFV)*, Dipodomys merriami* (12%, DIME)*, Peromyscus spp.* (10%, PEXX)*, Onychomys arenicola* (9%, ONAR)*, D. ordii* (8%, DIOR)*, D. spectabilis* (5%, DISP)*,* and *Reithrodontomys megalotis* (5%, REME). Recapture rates are also high. A large number of individuals (*N*) were captured 3 or more times across species from 2014–2020, including PGFV (*359*), DIME (*100*), DISP (*67*), DIOR (*66*), ONAR (*48*), and PM (*24*). Lastly, plant resources are measured seasonally by the Sevilleta LTER, providing a direct longitudinal record of resource diversity and availability with which consumer resource use can be compared.

The high seasonal and inter-annual climate variability in the northern Chihuahuan Desert (Sala et al. 2012) provides an ideal system to link climate-mediated resource quantity and quality to small mammal population and community dynamics. 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. In addition, inter-annual variance in monsoon timing, strength, and duration has increased due to anthropogenic climate change (Rudgers, Collins, etc.). This stochasticity in turn drives variability in primary production and resource availability for small mammal consumers, and is the defining characteristic of many dryland ecosystems. Indeed, environmental stochasticity and tightly coupled consumer-resource dynamics is one reason why dryland ecosystems have served as the backdrop for field-based experiments examining the influence of 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- and intra-annual stochasticity 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 fecal DNA 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. More than 20 years of data on aboveground net primary production (ANPP) at our study site show that there are ~14 perennial shrubs and forbs that consistently contribute to ANPP. The four dominate shrubs include creosote bush, Mormon tea (*Ephedra torreyana*), broom snakeweed (*Gutierrezia sarothrae*), and winterfat (*Krascheninnikovia lanata*) that combined contribute >95% of the production of C3 plant functional groups. 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 perennial C3 growth. Long-term data show that while 10 species of C4 grasses consistently contribute to ANPP at our study site, black grama provides >90% of the production among this plant functional group. The importance of annual C3 or C4 forbs for small mammals has not been systematically studied in this environment, although pilot data for nutritional traits (e.g., nitrogen content and seed size) of these plant functional groups suggest they could be very important for consumers.

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Description automatically generatedC3 and C4 plants vary in their nutritional quality, energy content, and persistence in the environment. The leaves and seeds 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 perennial/annual shrubs and forbs also produce larger seeds than C4 perennials (Reichman 1976, Harper 1977, Davidson et al. 1985, Samson et al. 1992). The mean weight of individual seeds of C3 shrubs/forbs (1.05g; n=32 species) at the Sevilleta are ~7X larger than those C4 grasses (0.15g; n=11 species). The leaves of C4 grasses are also 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 in our study system (Yeakel et al. 2020). C3 perennial shrubs in aridland ecosystems of the American Southwest generally have higher concentrations of unpalatable secondary compounds (e.g., phenolics) than C4 grasses or C3 annual forbs (REFS). For example, consistent consumption of creosote bush, a dominant shrub at our study site, by desert woodrats (*Neotoma spp.)* requires extensive detoxification (Mangione et al. 2001, Kohl and Dearing 2016). Most small mammals do not possess such energy-intensive physiological pathways (REFS), and previous work shows that concentrations of secondary metabolites (along with protein content and size) influences seed preference in DIOR (Henderson 1990). Lastly, C3 versus C4 plant functional types have distinct d13C values that have been used to quantify the transfer of primary production into desert consumers in the American Southwest (e.g., Warne et al. 2010, Orr et al. 2015, Noble et al. 2019). Mean d13C values of leaves and seeds collected from ~30 common C3 perennials/annuals at our field study range from -25.5‰ to -27.5‰, while those of the ~10 common C4 grasses and annual (n=1) range from -13.0‰ to -15.0‰. Standard deviation of d13C values for individual C3 or C4 species were ≤1.5‰.

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

Regional climate models predict rapidly increasing air temperatures, significant decreases in winter precipitation (15–20%), 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 by mechanistically linking resource availability and use via direct measurements of diet.