Title
Spatial and Temporal Variation in Mammalian Diversity of the Colorado Plateau (USA)

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Publication Date
2015

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By

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A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

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Summer 2015

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Abstract

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Anticipating how species and ecosystems will react to continued climate change is of critical importance to biodiversity conservation and to management of the ecosystem processes on which we rely. Identifying how individual species in a community have responded in the past can be accomplished by evaluating the fossil record on a local and/or regional scale, and by examining spatial patterns of modern abundance and diversity. Here, I explore regional patterns of mammal diversity across the Colorado Plateau (CP), examine local small mammal diversity fluctuations in fossil deposits from northern San Juan County, Utah, through the late Holocene, and assess modern spatial diversity patterns across a range of San Juan County sites.

Over the past century, extraordinary global transformations have taken place, including climate change and land conversion for human use. With these unusually rapid and extreme global changes underway, it is increasingly important to understand the extent to which designated conservation areas have protected biodiversity thus far, and to gauge their potential for continuing to do so in the future. Chapter 1 examines the efficacy of biodiversity preservation in National Park Service (NPS) lands of the CP by using analysis of nested species assemblages to compare surveyed mammal communities to the range map predictions of which species should be present. I find that NPS lands are nested, and, although site diversity is correlated with area, elevational range, budget and visitation, a comparison between species lists compiled from surveys versus range map distributions reveals that the biogeographic patterns prevailing today cannot be distinguished from those prevailing when these NPS sites were established. These broad-stroke patterns define an important context in which to direct future conservation efforts as we attempt to divert and mitigate anthropogenic impacts—past, current, and future.

Modern patterns of diversity are the result of past events and processes that take place on the scale of decades, centuries, and millennia. Detailed paleoecological records from Quaternary deposits are remarkably useful in characterizing these long-term ecological dynamics, but only a handful of Quaternary localities that sample the small mammal community of the CP have been studied to date. In chapter 2, I describe my excavation and analyses of two fossil-bearing alcoves, East Canyon Rims 2 (ECR2) and Rone Bailey Alcove (RBA) (San Juan County, Utah), and quantify diversity and abundance change of the small mammal community as recorded in the fossil samples. Fossil localities with comparable mammal diversity have not been reported from this region previously, so these sites provide novel insight into Holocene mammal diversity in

southeastern Utah. Further, these localities contribute to our understanding of natural variation in this system by providing faunal data for a period of recent climate change—cool-wet to warm-dry. AMS radiocarbon dates on 33 bone samples from these sites span ~4.4 ka-present, and shed light on pre-industrial faunal dynamics in the region over the course of environmental change, most notably aridification. I test for an effect of climate on community evenness and relative abundance of 10 small mammal taxa—leporids, perognathines, small sciurids, arvicolines, *Cynomys*, *Neotoma*, *Dipodomys*, *Onychomys*, *Peromyscus*, and *Thomomys*—and find that, in spite of considerable increases in aridity and temperature, neither is significantly correlated with relative abundance or evenness when statistically tested, but there are qualitative patterns consistent with a response to increasing aridity around 1000 years ago.

The CP is home to a diverse complement of species that are experiencing increasing temperature and drought stress today. Understanding how mammal communities might be expected to respond to impending global changes requires a baseline of information on presence, abundance, and spatial variation of species on the landscape today. Chapter 3 describes the results of a preliminary analysis of spatial variation in the small mammals of northern San Juan County at a single point in time, with the objective of learning how species commonly preserved in the fossil record sort geographically in relation to variation in their abiotic environment. I conducted mark-recapture surveys at 8 sites in northern San Juan County, two of which were located in the immediate vicinity of ECR2 and RBA. Over the course of one year, I compiled abundance and presence/absence data on nine species: *Neotoma albigula*, *Onychomys leucogaster*, *Peromyscus maniculatus*, *P. truei*, *Dipodomys ordii*, *Perognathus flavescens, P. parvus*, *Ammospermophilus leucurus*, and *Tamias rufus.* In chapter 3, I evaluate spatial differences in species richness using occupancy modeling and metrics of taxonomic difference, and I assess proportional and rank abundance across sites. Although the results are preliminary, some patterns are emerging: sites spanning 50km and 550m elevation range sample the same small-mammal species pool, but abundance of those species varies non-randomly, and sites are less similar in abundance than expected by random distribution of individuals. Species evenness varies among sites, and sites with low evenness are dominated by *Peromyscus maniculatus*, a "weedy" species with broad habitat requirements. This is also the first report of *Perognathus parvus* east of the Colorado River, suggesting recent range expansion of the species. Occupancy models indicate that presence/absence of different species is determined by different aspects of their environment, and therefore species will respond idiosyncratically to future environmental changes. However, more survey data is necessary before these patterns can be considered robust or fully explained.

In chapter 4, I compare fossil diversity at ECR2 and RBA to modern diversity at the same sites. I find that evenness reached a peak in ECR2 and RBA between ~1-1.7 ka, then began to decline between ~0.7-1 ka. Evenness of the modern community at ECR2 and RBA is also significantly lower than in the fossil record between ~0.7-4.5 ka. The observed drop in evenness occurred prior to the onset of high-impact, post-European human land uses, like livestock grazing, and is coincident with the time when Ancestral Puebloan populations crashed due to long-term periodic droughts, suggesting a marked environmental change between ~0.7-1 ka. Low modern evenness is consistent spatially—modern evenness at all survey sites is lower than it is for all fossil time bins ~0.7 ka and older, suggesting that this was a landscape-level decline in diversity. These results send a cautionary message: though the basic taxonomic integrity of the small mammal community is still present, abundance and community structure are very different today.

Additional information on past and current diversity of the CP will improve forecasting and establish baselines against which to compare future surveys, allowing us to gauge rates and direction of change, and to prioritize conservation efforts in the future. This study emphasizes the enormous utility of the fossil record in understanding the extent of ecological fluctuations that can be considered "normal" through long periods of time, information which is essential as we struggle to conserve biodiversity in a rapidly changing world.

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Acknowledgements

In 1998, Dave Livermore and Chris Montague introduced me to the Dugout Ranch and a seed was planted. During the intervening years, they kept me apace of the construction of the research center there, and it was my good luck that the Canyonlands Research Center came to fruition as I was searching for the right setting for my dissertation. The research center introduced me to Heidi, Matt, and Adam Redd of the Indian Creek Cattle Company, who have contributed more to my science (and my safety) than they realize. I am lucky, also, to count them as dear friends.

I owe a tremendous debt of gratitude to Liz Hadly, who set me on this particular path of inquiry; I would not be where I am today without the strength of her mentoring and the value of her recommendation. I have so many reasons to thank Liz, not the least of which is for introducing me to my graduate advisor, Tony Barnosky. I simply could not have found a more encouraging, kind, supportive, and wise advisor.

I was fortunate to snag David Lindberg on my qualifying and dissertation committees shortly before his retirement and I thank him for many illuminating and reassuring conversations. When I needed to learn pollen extraction and analysis in the eleventh hour, Roger Byrne gave me full access to his lab, equipment, chemicals, and taught me how to "cook." From Jim Patton I learned almost everything I know about living mammals, including how to trap them. I have taken up hours of Jim's time with my questions and I am so grateful to have had an opportunity to work with him—it has been both edifying and fun. It has been a privilege to be a member of the UCMP and MVZ communities, and to share a lab with Emily Lindsey, Kaitlin Maguire, Nicholas Spano, Susumu Tomiya, Natalia Villavicencio, and Zixiang Zhang. Thanks also to my friend and collaborator, Elizabeth Ferrer: we may have accomplished more talking than working, but it made the past five years so much more enjoyable.

Tom Guilderson and Paula Zermeno of the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, taught me how to radiocarbon date and graciously hosted me many times. I thank them also for tolerating the vagaries of a graduate student's schedule and funding contortions. Chris Conroy of the Museum of Vertebrate Zoology taught me to prepare mammal specimens, calmly and without judgment as I crouched on the floor trying to blink the stars from my eyes and to keep my lunch down. Under his tutelage, I can now skin a rat, maybe not with the best of 'em, but serviceably. Mark Miller of Canyonlands National Park and ReBecca Hunt-Foster of the Bureau of Land Management ushered me painlessly through many permit applications and revisions, and improved my study design by their incisive questions and suggestions. And to whomever blessed my Utah Department of Wildlife Resources permits, most sincere thanks—I can only assume that my applications would be gathering dust somewhere in Salt Lake City without that benediction. Patrick Garcia-Luna, Molly Hardesty-Moore, and Prayerna Uppal were particularly dedicated and excellent lab and field assistants.

Funding for this research came from the Canyonlands Natural History Association, UC Berkeley Graduate Division, UC Berkeley Department of Integrative Biology, UCMP, MVZ, Sigma Xi, The Paleontological Society, Geological Society of America, the National Science Foundation (Grant DGE-1106400), International Biogeography Society, and Kappy Wells. I thank the California Desert Research Program at the Community Foundation serving Riverside and San Bernardino Counties, and the Paleobiology Database Analytical Methods course for necessary training.

Thanks to my grandfather, Wallace Stegner, whose conservation ethic has largely shaped my own, and whose writings are a reminder of what is worth saving—in ourselves and in our natural world. I thank my father, Page Stegner, for teaching me how to take no guff, to be defiantly independent, and to use all manner of useful machinery and tools, gender and age be damned. Thick skin is required for both academia and field work.

Most important, thanks to Lynn Stegner, my mother, my friend. Where would we be without each other? Like an archway, we lean together to hold each other up. You have made all of this possible for me.

Chapter 1

Efficacy of biodiversity conservation in U.S. National Park Service lands of the Colorado Plateau

M. Allison Stegner, Daniel S. Karp, Andrew J. Rominger, and Elizabeth A. Hadly

1. Introduction

The efficacy of biodiversity reserves in protecting species is an important question in conservation biology. Evaluation and re-evaluation of and identifying causal mechanisms for reserve success (Coad et al. 2013, Geldmann et al. 2013) are increasingly important in light of rapid, high-magnitude global changes now underway, including climate change, altered fire regimes and encroaching agricultural, urban, and other development. In fact, approaches to biodiversity conservation are themselves in flux. For instance, recent debates center on whether the traditional approach of setting aside land that precludes other use is preferable to conservation on so-called working landscapes, that is, areas where both human land use and biodiversity conservation take place in tandem (Polasky et al. 2005, Sayre 2006, Rissman et al. 2007, Sulak and Huntsinger 2007, Suckling 2012, Kareiva et al. 2012, Soule 2013).

One obstacle to gauging success is the fact that many reserves were originally created for reasons other than biodiversity conservation. Although ideally reserves should be located in areas where they capture the highest biological diversity and where they are likely to be able to protect that diversity in the long term (Margules and Pressey 2000), in many parts of the American West they were placed in areas that have relatively little commercial value, where land was readily available, or where scenic beauty or recreation value was (and is) high (Geldmann et al. 2013, Pressey 1994, Meir et al. 2004). This has left some species and ecosystems unprotected, has potentially reduced the conservation effectiveness of some reserves, and is purported to have raised the cost of conservation due to limited management capacity and a lack of an overarching plan for reserve creation (Pressey 1994, Le Saout et al. 2013, Geldmann et al. 2013). Such historical legacies give rise to three key questions: How well does the extensive network of existing reserves actually contribute to biodiversity conservation? Are local extirpations (see below) a sign of major disruption to the regional biodiversity? Can we extract more conservation value from these sites?

We address these questions by assessing the mammalian communities of Colorado Plateau (USA) National Parks Service (NPS) lands. These reserves were mostly established between 50 and 100 years ago. Using analysis of nested species assemblages, we compare lists of contemporary resident species from surveys (up-to-date as of 2005), to species lists generated from historical range maps, which represent a prediction of what current biodiversity should be if there have been no major changes in recent times. This comparison allows us to gauge whether NPS lands retain the mammalian biodiversity that was resident prior to park designation.

Analyzing nestedness is an appropriate approach because the method allows for the examination of how local diversity contributes to the overall regional pattern of diversity. The analysis provides information on how well a single site conforms to the regional pattern, for example if a site harbors more or fewer species than expected, and can reveal species that are becoming more or less widespread through time. To account for potential confounding factors like sampling and attributes of parks that could affect diversity, we explore the relationship between site diversity (number of species in an individual NPS unit), overall site nestedness, and parameters such as elevation range, area, and park budget.

1.1 Study Area

Approximately 49% of the Plateau is public land or privately owned conservation land (e.g., The Nature Conservancy), and the Plateau is therefore a promising region for both research and targeted conservation and management planning. It is one of the most diverse ecoregions in North America with extraordinarily high endemicity (Nabhan et al., 2005), yet it faces a variety of land use demands, including tourism and recreation, grazing, mining, renewable energy and fossil fuel development. The flora and fauna of the southwestern United States are already experiencing impacts from anthropogenic climate change, including widespread tree mortality due to drought or released abiotic pressure on pests—e.g., sudden aspen decline (Rehfeldt et al. 2009, Huang and Anderegg 2012), piñon-juniper drought-induced mortality (Floyd et al. 2009), spruce beetle outbreaks (Herbertson and Jenkins 2008)—and declines in small mammals that are losing suitable habitat or are unable to withstand extreme heat events—e.g., *Brachylagus idahoensis* (pygmy rabbit) (Larrucea and Brussard 2008) and *Ochotona princeps* (American pika) (Grayson 2005). In addition, several extirpations have taken place on the Colorado Plateau in the last 100 years; for example, the Canada lynx, jaguar, grizzly bear, gray wolf, black-footed ferret, and wolverine (Zimmerman and Carr 2004).

1.2 Nestedness

In this study, we use nestedness to: (1) determine if mammal assemblages are more nested across the Plateau with respect to a random null model; (2) clarify which properties of protected lands correlate with nestedness and species richness, and (3) evaluate the importance of taxonomic group and taxonomic scale in making conservation choices based on patterns of nestedness. We compare recent biological inventories of NPS lands with range map data that include recently extinct species and portions of ranges where species have been recently extirpated. Therefore, if both surveyed and predicted presence-absence matrices are nested to a similar degree, and exhibit species richness that is not significantly different from historic time, protected lands are maintaining historic levels and biogeographic patterns of diversity. We also use the data to examine whether the causes for the observed nested patterns are more likely to be attributable to physical aspects of the sites such as geographic area, or to management factors.

Nested metrics are a way to compare beta diversity across a collection of sites within the same region, where all sites theoretically have access to the same pool of species—the concept was originally applied to oceanic islands, where each island is a site (Atmar and Patterson 1993). Nestedness occurs when the lists of species for sites with lower diversity are predictable subsets of the species list in sites with higher diversity. Nestedness simultaneously identifies 1) sites that have low diversity or unexpected diversity patterns (e.g., a site that harbors many unusual species but few common species); and 2) species that are rare and restricted in range, and therefore at risk of extirpation or extinction. This metric also illustrates visually and mathematically how different sites and species relate to the fauna overall. Species that fall in the lower left-hand corner of a nested matrix, i.e. species that are typically found in the few, most-diverse parks, are considered at risk. Sites that are "highly nested" have lower diversity than sites that are less nested; in turn, *species* that are highly nested occur in few sites, while species that are less nested are common. Almeida-Neto et al. (2007) and Ulrich et al. (2009) provide a detailed introduction to nested species assemblages and nestedness analysis.

Causes of nestedness have typically been framed as a dichotomy between differential colonization driven by variations in site isolation, and selective extinction due to differences in geographic area (MacArthur and Wilson 1963). Many studies of nestedness only consider these two factors—isolation and area—when searching for potential causes, but other site attributes, such as abundance, latitude and habitat diversity, can influence species nestedness patterns as well (Allen et al. 2002, MacArthur and Wilson 1963, Hadly and Maurer 2001). NPS lands on the Colorado Plateau are derived from a once-connected series of habitats that transition from arid desert scrublands, through sagebrush steppe and pinyon-juniper communities, to mixed conifer and subalpine environments at the higher elevations; so selective extinction, or faunal relaxation, rather than dispersal dynamics, is a more likely cause for any observed nested patterns (Brown 1971). Based on species-area relationships, we expect that larger parks will support more species; however, if area and diversity in this system are not correlated, we would conclude that other factors affect diversity levels.

2. Methods

2.1 Data Sources

Surveyed species lists for 24 National Parks, Monuments, and Historical Sites located on the Colorado Plateau were downloaded from the NPSpecies database (NPSpecies, https://irma.nps.gov/App/Species/Search). NPSpecies species occurrences are categorized by the amount of evidence—voucher, observation, etc.—associated with the data. We included as resident species those categorized as “present in park” and “probably present” because both indicate very high confidence that the species occurs in the park as of 2005 (Loar 2011). Additionally, excluding species categorized as “probably present” had no statistical and minimal qualitative impacts on the results. NPSpecies data were potentially assembled in different ways in different parks (i.e., surveys were not necessarily conducted in a standardized way), which is a potential source of bias. However, the park species lists used in our study are all “certified,” meaning that before the data were uploaded to the NPSpecies database, each list was vetted by a taxonomic expert and reviewed for completeness and accuracy at the time of certification. Species that were historically present in the park but were extirpated at the time of the certification are listed as “historic” and not included in our study. All park species lists in our study were certified between 2005 and 2007 (Loar, 2011).

Park and monument trait data (elevation, area, year of creation, etc.) were derived from various sources (Appendix 1.1).

Range map species lists are from digital range map data (Patterson et al. 2007), available on the NatureServe Website (www.natureserve.org), and were extracted in ArcMap (ESRI 2009). For most North American Mammals, these digital maps are derived from Hall (1981) and Wilson and Ruff (1999), but where data were available, the digital maps include ranges and portions of ranges where species have been extirpated in historic times (in the last ~100 years) (Patterson et al. 2007). All statistical analyses were performed in the R language and environment for statistical computing, using the R packages vegan (Oksanen et al. 2015), maps (Becker et al., 2014), and MASS (Venables and Ripley 2002).

2.2 Nested analyses

We tested for a nested subset pattern across the 24 national parks and monuments (Figure 1.1), which range in area from 34 to 1,217,262 acres. Our analysis included a species pool of all mammals native to the Colorado Plateau, 123 species in total. Introduced species [i.e., horses (*Equus caballus*), house mice (*Mus musculus)*] were not included. Nestedness was assessed using the Nestedness based on Overlap and Decreasing Fill (NODF) metric developed by Almeida-Neto et al. (2008), and surveyed species list data were compared to 500 random matrices simulated using two null models: c0, which maintains species frequencies but allows site richness to vary (Jonsson 2001) (more generally referred to as an equiprobable-fixed model); and quasiswap, which maintains both species and site frequencies (fixed-fixed model) (Miklós & Podani 2004).

Debate as to which statistical and analytical methods should be used to evaluate nestedness has yielded many studies on the performance of different nested metrics and their associated null models. We used NODF because, unlike other metrics, NODF directly quantifies two properties of nested matrices: decreasing row and column marginals, and overlap of presences from more nested to less nested columns/rows (Almeida-Neto et al. 2008). Furthermore, although NODF is affected by matrix fill (as are most nested metrics), it is not affected by matrix size and shape, or by the orientation of the matrix (which set—species or sites—is represented by columns/rows) (Atmar and Patterson 1993, Brualdi and Sanderson 1999, Almeida-Neto et al. 2008). An additional advantage of NODF is that it calculates a nested score not just for the entire matrix, but for rows and columns separately, so we can evaluate whether the whole matrix score is most influenced by species or by site differences.

When paired with a fixed-fixed model, NODF performs slightly better than other metrics, but is markedly more conservative and less prone to Type-I error when paired with an equiprobable-equiprobable null (Almeida-Neto et al. 2008). Because these sites are not strictly isolated from one another, it seems appropriate to regard diversity (number of species) as not necessarily an inherent property of sites; therefore, a null model that allows site frequency (number of species per site) to vary, as c0 does, may be a better reflection of reality than a fixed-fixed null, in spite of the statistical advantages of a fixed-fixed null.

Nestedness was quantified for surveyed species-level and genus-level presence-absence matrices in order to assess the role of taxonomic scale in patterns of nestedness. To better understand the interplay between number of congeners and geographic prevalence of species and genera, we tested for correlation between the nested rank of taxa (the order of species in the packed nested matrix, with rank 1 representing the least-nested position) and number of sister species. We tallied the number of congeners per genus present on the Colorado Plateau in the survey data, and used these values for both the species- and genus-level correlations. Correlation was measured using a Spearman's test because the data are not normally distributed. We also tested for a correlation between species-level park rank and genus-level park rank using a Spearman's test.

To compare survey and range map data, we generated nested matrices using both datasets. We assessed similarity in two ways. First, we determined if both datasets were significantly nested using the c0 and quasiswap null models. Second, we used Spearman's tests to determine if the nested rank of sites was significantly different between the datasets. To compare species rank, we first had to remove any species that were not present in both datasets, a total of 12 species from the survey data and 21 species from the range map data; this left 111 species for the statistical test. It is not clear whether species found in the surveys but not in the range maps are the result of imperfect range maps, species introductions/immigrations, or incorrect identifications during the surveys.

2.3 Park-monument attributes

Correlations between biodiversity and park-monument (hereafter, 'park') attributes were analyzed in two ways. First, we used Spearman's tests to quantify the relationship between park nested rank and the nine park attributes, with a Holm p-value adjustment to correct for multiple tests. Second, we used multiple linear regression (mlr) models to test the ability of site attributes to explain site species richness. We then used a step-wise method to eliminate variables from the mlr models that were not explanatory, using Bayesian information criterion (BIC). All of the final variables were significant at the $\alpha=0.05$ level (with Holm p value adjustment) when correlated individually against diversity. We used BIC because Akaike information criterion (AIC) selected the same variables for the final model, but included one that was not significant at the $\alpha=0.05$ level.

3. Results

3.1 Nested analyses

Surveyed mammals are strongly nested on both the species- (Figure 1.2a) and generic-level (Figure 1.2b; Table 1.1). Using the c0 null model, column, row, and whole matrix scores are significantly more nested than random, but with the quasiswap null, only columns (sites) are significantly nested. Number of congeners is not correlated with species nested rank (Spearman correlation = 0.0782, p = 0.3899), but is significantly correlated with generic rank (Spearman's correlation = -0.3506, p = 0.009) (Figure 1.3); i.e., more nested genera also have fewer congeners.

Although there are some differences in the nested order of parks between the generic-level and species-level matrices (Figure 1.4), there is no systematic bias of increase or decrease in park rank when switching between taxonomic scales. In short, where a park falls in the species nested matrix is not correlated with whether the park increases or decreases in nested rank when switching from a species- to a generic-level analysis (Spearman's test correlation = 0.1800, p = 0.39). The perhaps counter-intuitive implication of this result is that park rank at the species level tells us nothing about park rank at the generic level.

Richness is higher in the range maps than in the surveys: discrepancies between the survey and range map data are addressed in the Discussion. Surveyed and range map presence absence matrices produced the same overall nested results (Table 1.1; Appendix 1.2-1.3), in spite of the fact that fill was higher in the range map matrix, which probably accounts for the slightly higher NODF scores for the range map data. Both survey and range map datasets were significantly nested when compared to the c0 null model, while only the order of columns was significant using the quasiswap null (Table 1.1). Spearman's tests revealed there is no significant difference between nested rank of sites (Spearman's rho=0.623, p value=0.0011) or species (Spearman's rho=0.827, p value$<1\times10^{-16}$) between datasets.

3.2 Park attributes

Both nested rank of parks and species richness of parks significantly correlate with area, budget, visitation, and elevation range (Table 1.2). However, these four independent variables are correlated with one another, so it is unclear which are meaningfully correlated with diversity and which are simply confounded. Nested rank of sites also correlates with maximum elevation. BIC selected three of these variables as explanatory: area, budget and elevation range. Upper and lower elevation were not included in the multiple linear regression modeling because elevation range is a linear combination of the two, and elevation range correlates more strongly with rank and diversity when tested in a simple linear model.

4. Discussion

Colorado Plateau park sites are nested with respect to mammals, when compared to both a semi-conservative (c0) and highly conservative (quasiswap) null model. Using the highly conservative null, only sites, but not species, are significantly nested. However, NODF scores suggest a strong pattern of nestedness regardless of the null used and statistical significance. Nested patterns are common in nature (Higgins et al. 2006, Moore and Swihart 2007, Ulrich and Gotelli 2007); but in this case, there are no hard boundaries between sites and the areas that comprise the land matrix so a nested pattern is not necessarily expected.

Survey data and range map data are very similar in nestedness pattern overall, despite the slight differences in fill and richness: there is no significant difference in the nested rank of either sites or species between the survey and range map datasets. One implication of this is that most species are found in the same number of sites in each dataset. However, there are two species that are outliers in that they are markedly less abundant in surveys: *Bison bison* (American bison) and *Lasiurus blossevilli* (Desert red bat). *Bison bison* drops from a rank of 1 (occurring in all parks) in the range map data to a rank of 105 (occurring in only one site) in the surveys—of course, this is a real and well-documented extirpation. *Lasiurus blossevilli* is considered “least concern” by the IUCN (IUCN 2015) so the reason for its absence from the surveys is unclear. However, this highlights one of the ways in which nestedness can be used by land managers to quickly identify species at risk, or species that are poorly targeted for sampling: species that become more nested over time (increase in rank) are probably experiencing unusual declines across the region and should be considered more closely.

The range map data used here include historic ranges of species that have since been extirpated. Therefore, because there are negligible differences between nested scores for surveyed and range map park species lists (Table 1.1), one possible explanation for our results is that conservation efforts at the sites have been successful up to the 2005-2007 certification period. Conversely, it is possible that the nested pattern we see in the survey data is a reflection of some physical aspects of parks, such as habitat diversity, rather than management. While the nested pattern alone does not imply effective or ineffective management, our comparison between expected and observed nested patterns can reveal if the biogeography of the Colorado Plateau has changed. Because expected and observed nestedness patterns are generally the same, NPS lands maintain the distribution of diversity that was resident when they were created. In a meta-analysis of published papers on protected area success globally, Geldmann et al. (2013) also found that protected areas effectively conserve species populations, but more data is needed overall, and causal mechanisms for reserve success are not addressed or understood in most papers.

A critical question now is how biodiversity of intervening unmanaged or differently managed lands, like open range or U.S. Forest Service holdings where more recreational activities are permitted (hunting, for instance) compares to that of NPS lands. It would also be valuable to learn whether the parks serve as sources (or sinks) relative to other lands in the region. Ultimately, it is necessary to obtain data from these multiuse lands experiencing different management regimes in order to put the status of reserves with a strict mandate for biodiversity protection, like the NPS lands assessed here, in perspective. Potentially destructive uses like mining and grazing are currently permissible on all but a third of U.S. public lands (Klinkenborg 2013), yet so-called multiuse lands form important geographic connections between islands of more strictly protected land and they may harbor biodiversity (potentially as either a sink or a source population, or both) of individuals for a range of different species. Key questions are: how diversity of protected lands compares to surrounding, multi-use lands, whether the protected areas are suffering from detrimental impacts in this matrix, and if, in turn, strictly protected lands can "rescue" biodiversity in multi-use lands. At this point, surveys outside of national parks and monuments are rare and, where they do exist, methods are not comparable.

4.1 Nestedness and Park Attributes

Our analysis does not reveal a causal mechanism for the nested pattern observed in the sites. We have shown correlations between diversity and area, elevation range, budget, and visitation; indeed, there are also correlations among these variables. If budget, area and visitation have a causal relationship, the direct mechanism is unclear, and likely has to do with funding priorities rather than overall funding amount. Larger parks do not necessarily receive more federal funding, and income generated by visitation at one park may be used to support a less-visited park. Comparisons between predicted and surveyed species lists suggest that aspects of parks that are not related to management, such as area and habitat diversity, are driving the observed biogeographic patterns. It is tempting to explain this correlation between budget and diversity as a direct mechanism: perhaps more funding does indeed lead to more biodiversity-conservation projects and therefore more successful species protection. It is also possible that larger budget allows for better sampling, which in itself is important because biodiversity management plans cannot proceed without adequate knowledge of what is on the landscape. However, the reality of this correlation is likely to be more complicated and requires data on how budgets are allocated in each site (for example, what proportion of the budget goes to conservation projects versus staff salary, maintenance, education and outreach, security, etc.). Disentangling these correlations also requires more information about how species were surveyed, if surveys were conducted in the same way at all sites, and better fine-scale data on aspects of area that contribute to diversity, such as the number of habitat types.

4.2 Species- and Genus-Level Nestedness

Comparison between species- and genus-level patterns of nestedness has important implications for conservation. At the species-level, there is no relationship between how many congeners a species has and how common the species is across parks. In contrast, genera with more species are more likely to be found in more parks (they are less-nested)—this means that species-poor genera tend to be more rare. Although this makes intuitive sense, because a genus with more species has more opportunities to occupy sites, it demonstrates that, if maintaining species presence is a conservation priority, it may be appropriate to allocate proportionately more effort towards species that have no or few congeners in a given region, and which are deeply nested on both a species and genus level [e.g., *Cynomys leucurus* (white-tailed prairie dog) or *Bison bison*), versus species with many congeners (Hadly and Barnosky 2009)].

4.3 Surveyed versus range map diversity

Range map data indicate several species that should be present are in fact missing from Colorado Plateau NPS sites. From these outlier species, two broad patterns emerge: taxa in decline are potentially absent from survey data and taxa at the edge of their ranges in the Colorado Plateau may also be absent.

Odocoileus virginianus (white-tailed deer) is the only absent large herbivore, though its sister species, *O. hemionus* (mule deer), is reported from all parks examined in this study. Even though the range of *O. virginianus* is largely peripheral to the Colorado Plateau (Reid 2006), range maps place it within parks on the southern and eastern portions of the Plateau (with the exception of Grand Canyon NP). Among the carnivores, *Vulpes velox* (swift fox), *Panthera onca* (jaguar) and *Mustela nigripes* (black-footed ferret) are not present in the survey data—indeed, both *P. onca* and *M. nigripes* have been extirpated from this region in historical times and are at risk of extinction today (IUCN 2015; Zimmerman and Carr 2004). However, *Vulpes velox* is generally restricted to the Rockies, which may explain its absence from the survey data in spite of what range maps indicate. With regard to bats, *Macrotus californicus* (California leaf-nosed bat), *Myotis velifer* (cave myotis), and *Myotis occultus* (Arizona myotis) are predicted but not reported in survey data, although both species of *Myotis* should be found in the southern portion of the Plateau and neither is considered at risk of extinction (IUCN 2015). *Dasypus novemcinctus* (nine-banded armadillo) was not surveyed in Pecos NHP, a site that is located on the western boundary of the present-day (and expanding) range of this species. If their absence is real and not an artifact of sampling, perhaps this site is too arid to sustain them (McBee and Baker 1982). *Brachylagus idahoensis* was not surveyed in sites in southwestern Utah and northwestern Arizona where range maps place them—i.e. on the border between the Colorado Plateau and the Great Basin, where *B. idahoensis* is both primarily found today and prevalent in the fossil record. However, *B. idahoensis* is present Late Pleistocene fossil deposits across the Colorado Plateau and so was, at one point, more widely distributed than today (Murray et al. 2005). *Cynomys ludovicianus* (black-tailed prairie dog), *C. parvidens* (Utah prairie dog), *Urocitellus armatus* (Uinta ground squirrel), *U. mollis* (Paiute ground squirrel), *Chaetodipus hispidus* (hispid pocket mouse), *Microtus richardsoni* (water vole), *Onychomys arenicola* (Mearns' grasshopper mouse), and *Peromyscus gratus* (Osgood's mouse) were all predicted in some parks, but absent from the survey data: these species are generally found in biogeographic provinces neighboring the Colorado Plateau. *Neotoma leucodon* (white-toothed woodrat), *N. micropus* (Southern Plains woodrat), and *Reithridontomys montanus* (Plains harvest mouse), in contrast, were not surveyed sites in New Mexico along the eastern edge of the Plateau where range maps indicate their presence. *Phenacomys intermedius* (Western heather vole) is abundant along the border of Utah and Colorado, but is not reported in any of the sites assessed here.

Range map data suggests higher diversity of shrews at most NPS sites than was found in the survey data. There are several possible explanations for this, the first being that we have detected a true decline or extirpation of shrews in these sites. Alternately, the pattern we see may stem from the fact that shrews are difficult to detect with standard sampling techniques because they are surveyed using pitfall traps (a cup inserted into the ground and baited with meat, meal worms, etc.) rather than cage-style traps (Sherman, Tomahawk; baited with oats, peanut butter, etc.) employed for nearly all other small mammals (Sikes et al. 2011). Pitfall traps require archaeological clearance on NPS and other public lands, further complicating surveying shrews. Shrews are also not easy to identify. Therefore, it is possible that the strong nestedness for shrews in the survey data is a result of insufficient surveillance and sampling in some parks. Yet a third possibility is that there are differences in habitat availability among parks, or there is spatial sampling bias: fewer traps placed in mesic areas versus dry areas. Unlike other shrew (*Sorex*) species which prefer mesic areas like riparian zones and wetlands, *Notiosorex crawfordi* (desert shrew)—the only shrew that is common in the survey data—is typically found in arid, desert environments and dry woodlands, including piñon-juniper forest (Reid 2006). Although we cannot distinguish among these possible explanations without more information, overall the shrews do not make a difference to our results: removing them from the analysis produces negligible differences in the magnitude of the NODF scores, and has no statistical impact on the results except that survey data columns are no longer significantly nested using the quasiswap null model (Appendix 1.4).

Mismatch between range map predictions and surveyed species—for example, the fact that *Odocoileus hemionus* occurs where *O. virginianus* is expected, or the over-prediction of the range for *Vulpes velox*—could indicate extirpations, but more likely highlight inexact depictions of species occurrences in the original range maps. The range maps used here, from Digital Distribution Maps of the Mammals of the Western Hemisphere (Patterson et al. 2007), are derived from digitized historical or published maps, e.g. from the Mammalian Species Accounts, but have accounted for taxonomic revisions in Wilson and Reeder (2005). Generally speaking, these maps were created based on expertise and then-current knowledge of species habits and preferences; despite revisions and updates included in the digital maps, historical inaccuracies based on taxonomic issues or incomplete knowledge of the biology of particular species, in some cases may have persisted. This is a crucial consideration for species distribution modeling and other analytical and predictive methods that rely on historical range maps.

5. Conclusions

The results we report here are encouraging; according to our analyses, Colorado Plateau NPS lands retained (up to the 2005-2007 certification) essentially the same mammalian biodiversity and the same biogeographic patterns that were present when the parks were established. This suggests that "faunal relaxation" is not taking place across these NPS sites, and that biodiversity conservation in these lands is effective for most species, despite the notable extirpation of a few (Canada lynx, jaguar, grizzly bear, gray wolf, black-footed ferret, and wolverine). Even with those extirpations, the system appears not yet demonstrably outside the historical baseline in terms of overall ecosystem composition and; however, recent anthropogenic effects may well challenge the biodiversity baselines described here. For example, anthropogenic climate change is affecting the environmental variables that influence and in some cases control species distributions, lands surrounding parks are under pressure for development for energy and agriculture, and growing numbers of visitors are using parks while financial resources are increasingly uncertain. In the face of these growing pressures, managing biodiversity into the future will require ongoing evaluation of metrics such as those used here, as well as others that take into account regional and temporal patterns. Metrics can be improved by using information from the fossil record of this region, which can reveal the effects of past climate change and establish long-term faunal and floral baselines, and by incorporating abundance data to assess population viability. It will be particularly important to add data from multi-use lands into this analysis, in order to assess the ability of species to persist in less-strictly protected lands, and to disperse from one protected area to the next.

Table 1.1: Results of nested analysis. ^{c} indicates significant using the c0 null model, ^{q} indicates significant using the quasiswap null model.

	NODF columns	NODF rows	NODF	Matrix fill
Surveyed Species	$78.72^{c,q}$	66.95^{c}	67.40^{c}	0.445
Surveyed Genus	$87.73^{c,q}$	80.95^{c}	81.83^{c}	0.629
Range Map Species	$78.40^{c,q}$	70.46^{c}	70.72^{c}	0.538

Table 1.2: Park attribute correlation test results. * indicates significant at α=0.05 with Holm p adjustment.

	Spearman's correlation (with site nested rank)	Linear Regression adjusted Rsq (with site diversity)
Year created	-0.0643	-0.0388
Budget	0.5992*	0.4726*
Latitude	0.2754	0.0243
Longitude	-0.0123	-0.0065
Minimum elevation	-0.1454	-0.0115
Maximum elevation	0.6008*	0.1922
Elevation range	0.7015*	0.5594*
visitation	0.6842*	0.4272*
Area	0.6369*	0.3724*

Figure 1.1: Map of sites. ARCH: Arches National Park (NP); AZRU: Aztec Ruins National Monument (NM); BAND: Bandelier NM; BLCA: Black Canyon of the Gunnison NP; CACH: Canyon de Chelley NM; CANY: Canyonlands NP; CARE: Capitol Reef NP; CEBR: Cedar Breaks NM; CHCU: Chaco Culture National Historical Park (NHP); COLM: Colorado NM; DINO: Dinosaur NM; ELMA: El Malpais NM; ELMO: El Morro NM; GRCA: Grand Canyon NP; HOVE: Hovenweep NM; MEVE: Mesa Verde NP; NABR: Natural Bridges NM; NAVA: Navajo NM; PECO: Pecos NHP; PISP: Pipespring NM; SUCR: Sunset Crater NM; WACA: Walnut Canyon NM; WUPA: Wupatki NM; YUHO: Yucca House; ZION: Zion NP. UT: Utah; CO: Colorado; NM: New Mexico; AZ: Arizona.

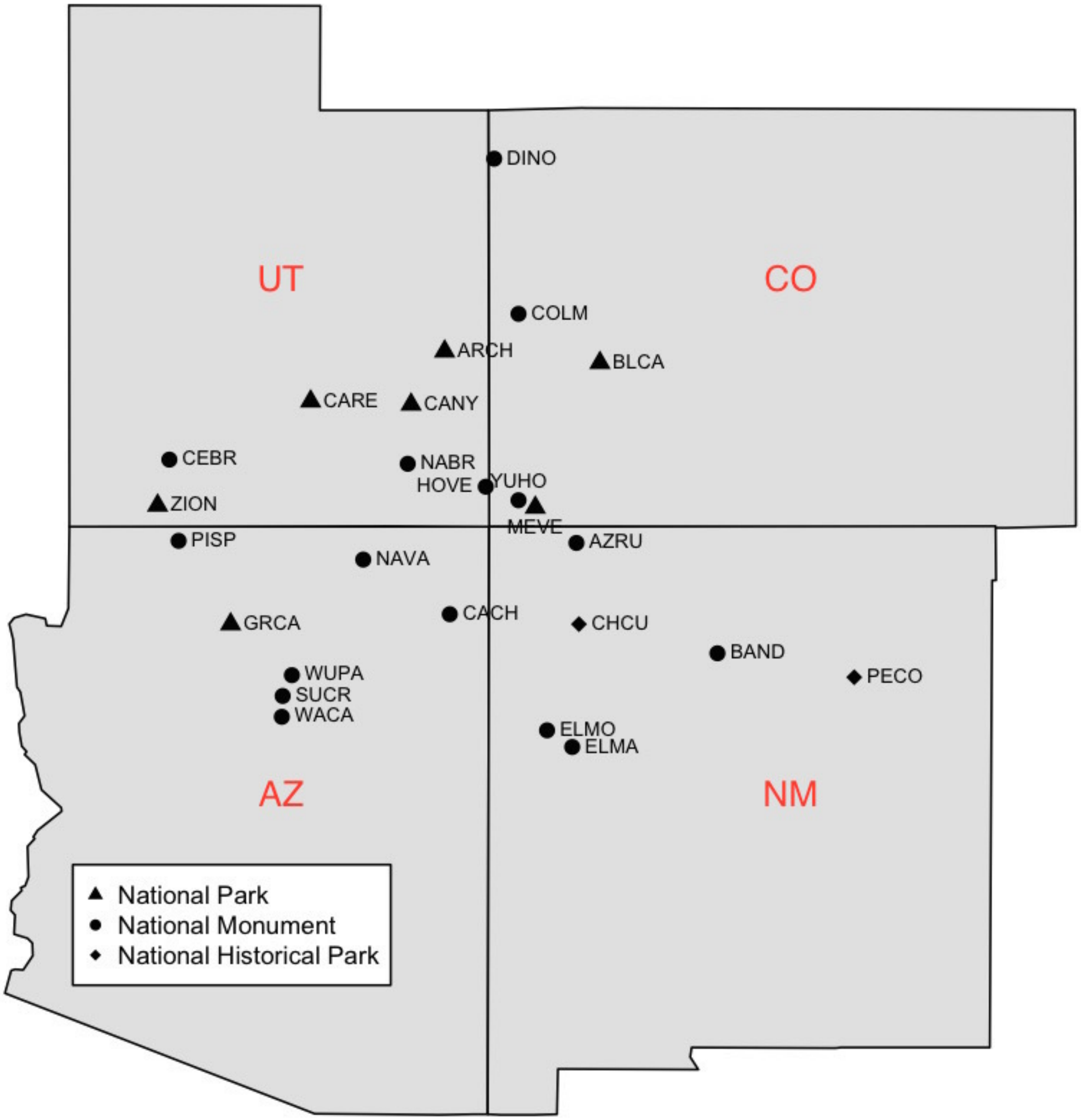
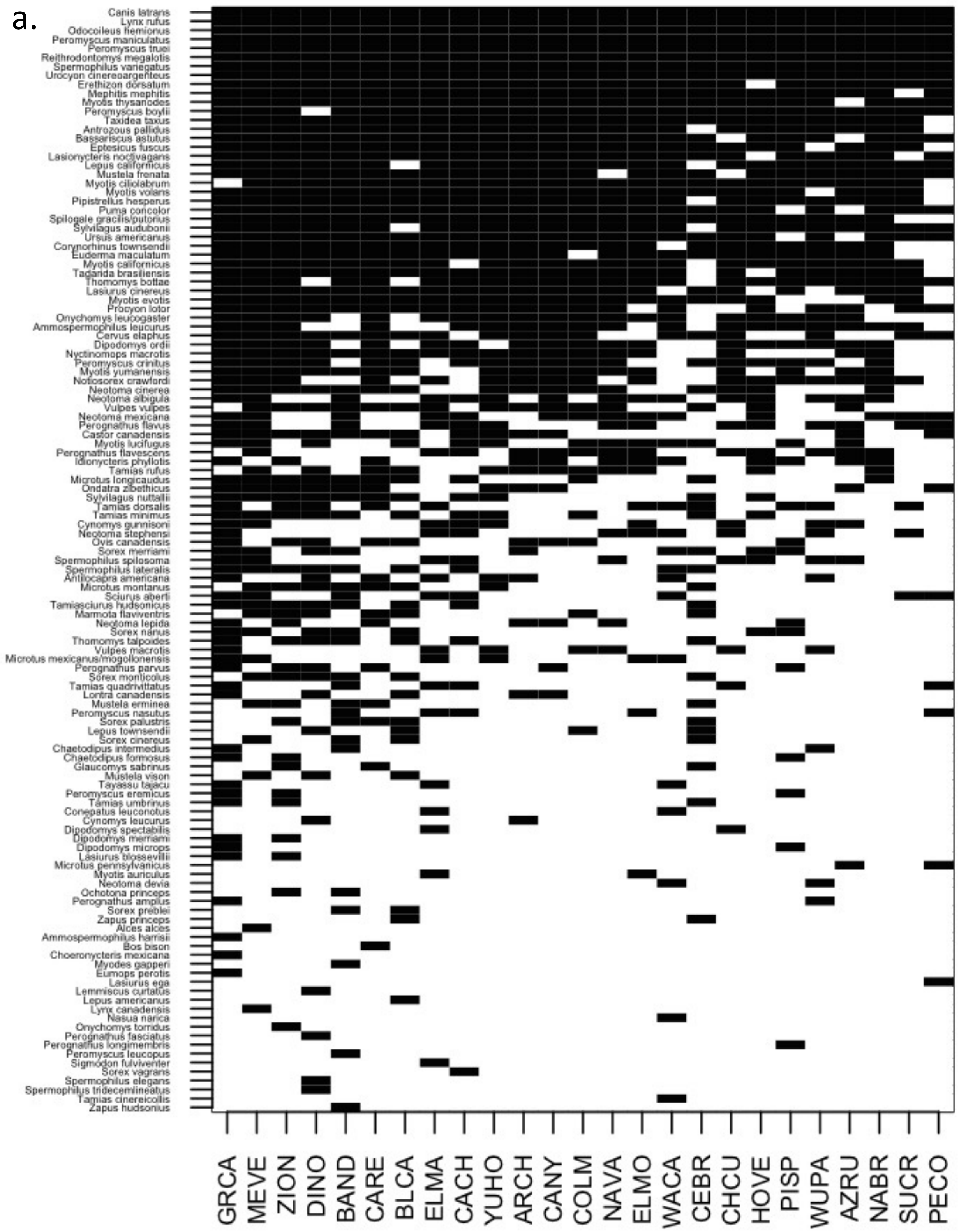


Figure 1.2a: Species-level nested community matrix. (See Figure 1 for site abbreviations). **b:** Genus-level nested community matrix. (See Figure 1.1 for site abbreviations).



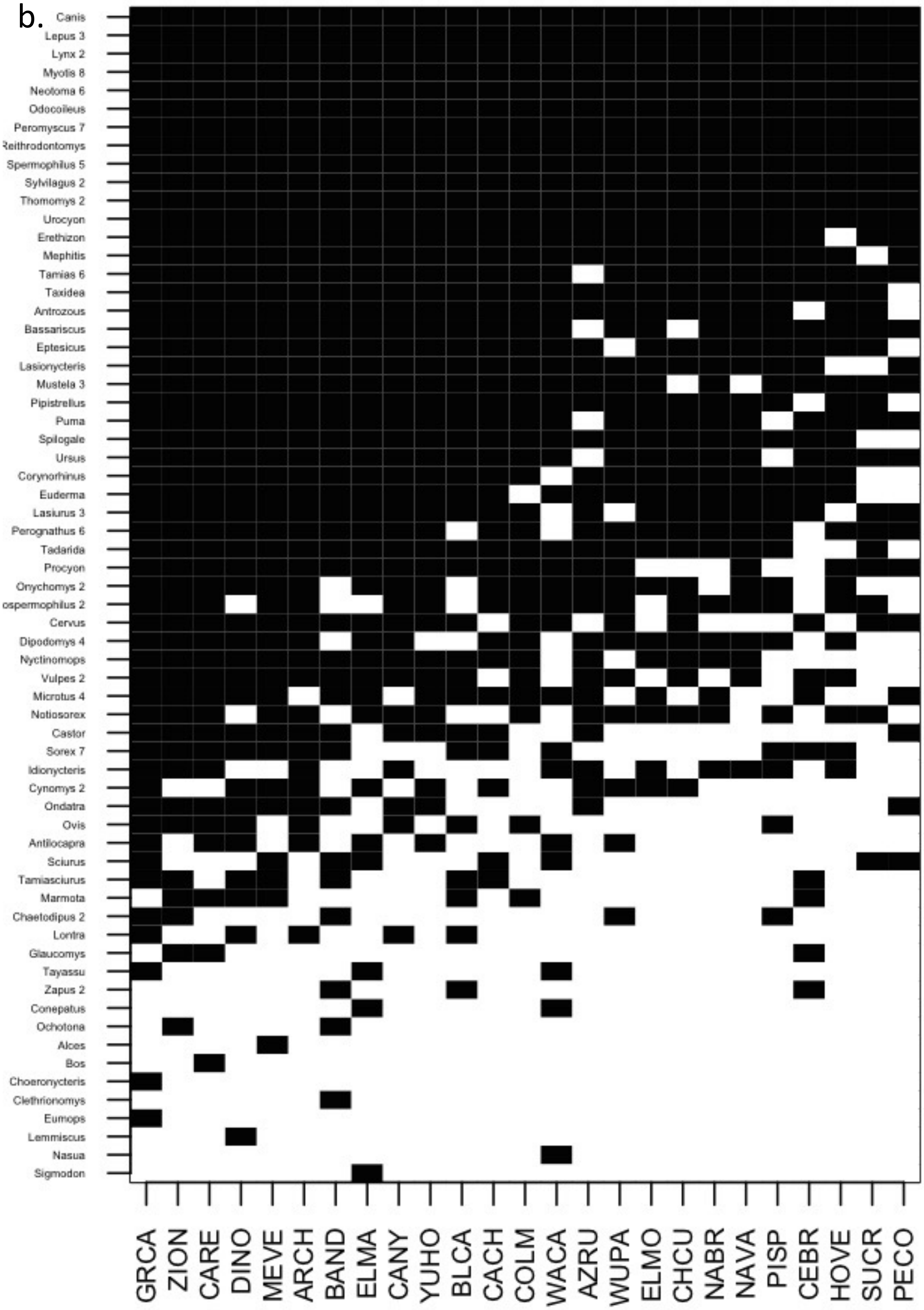

b.
Canis
Lepus 3
Lynx 2
Myotis 8
Neotoma 6
Odocoileus
Peromyscus 7
Reithrodontomys
Spermophilus 5
Sylvilagus 2
Thomomys 2
Urocyon
Erethizon
Mephitis
Tamias 6
Taxidea
Antrozous
Bassariscus
Eptesicus
Lasionycteris
Mustela 3
Pipistrellus
Puma
Spilogale
Ursus
Corynorhinus
Euderma
Lasiurus 3
Perognathus 6
Tadarida
Procyon
Onychomys 2
ospermophilus 2
Cervus
Dipodomys 4
Nyctinomops
Vulpes 2
Microtus 4
Notiosorex
Castor
Sorex 7
Idionycteris
Cynomys 2
Ondatra
Ovis
Antilocapra
Sciurus
Tamiasciurus
Marmota
Chaetodipus 2
Lontra
Glaucomys
Tayassu
Zapus 2
Conepatus
Ochotona
Alces
Bos
Choeronycteris
Clethrionomys
Eumops
Lemmiscus
Nasua
Sigmodon
GRCA
ZION
CARE
DINO
MEVE
ARCH
BAND
ELMA
CANY
YUHO
BLCA
CACH
COLM
WACA
AZRU
WUPA
ELMO
CHCU
NABR
NAVA
PISP
CEBR
HOVE
SUCR
PECO

Figure 1.3a: Species nested rank versus number of congeners. **b:** Genus rank versus number of species in the genus. Ranks are standardized to fall between 0 and 1; less nested (low) ranks fall closer to 0 while more nested (high) ranks fall near 1).

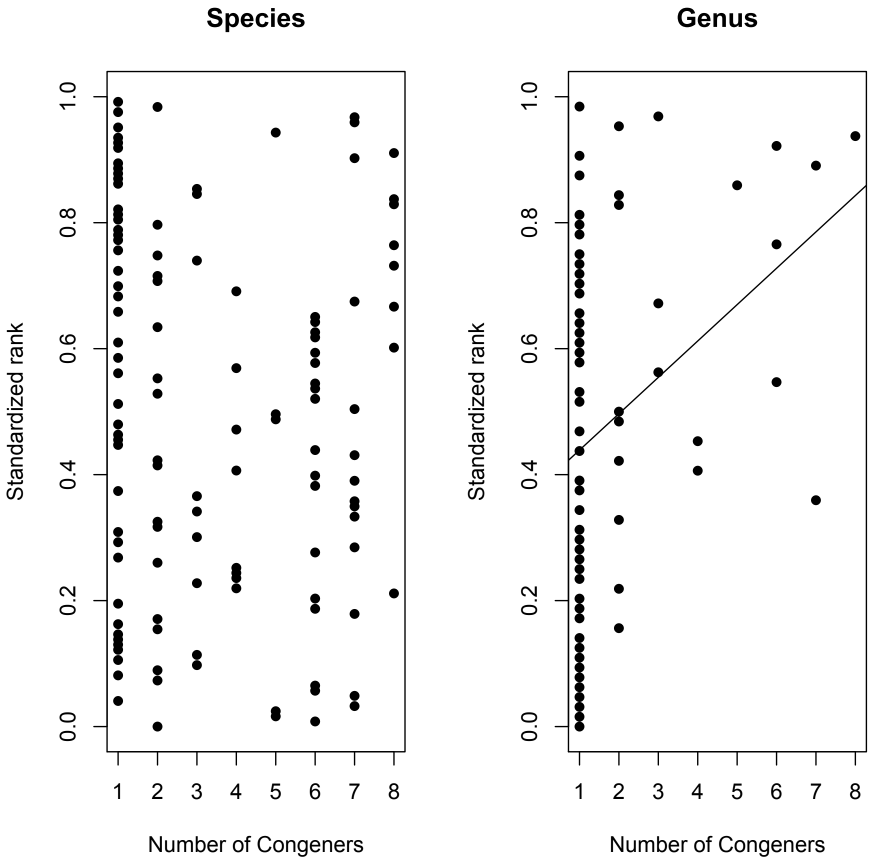
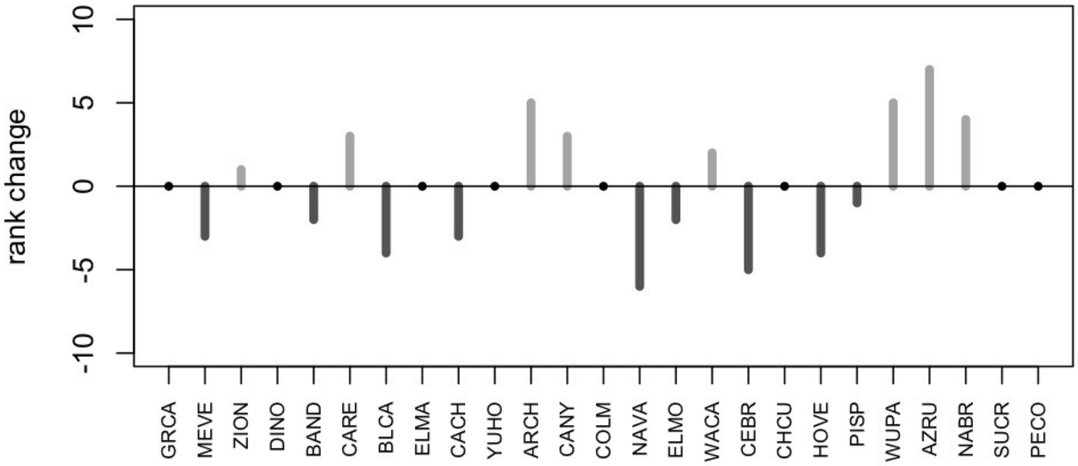


Figure 1.4: Change in site rank from species-level to genus level nested analysis (species-level rank – genus-level rank). Light gray indicates an increase in rank, dark gray indicates a decrease in rank, and black points indicate no difference in rank between taxonomic scales.



Chapter 2

Stasis and change in Holocene small mammal diversity during a period of aridification in southeastern Utah

1. Introduction

The biodiversity of the Colorado Plateau (CP; southwestern USA) is threatened by both land use and climate change impacts. This region is >50% public land, 2/3 of which is multi-use, including mining, grazing, energy development (fossil fuel and solar/wind), off-road vehicle travel, timber harvesting, hiking, fishing, hunting, and other activities (Fleischner 1994, Klinkenborg 2013). Understanding ecological dynamics on these multi-use lands is crucial for preservation of the ecosystem services and intangible benefits they provide (Nash 1967, Lawler et al. 2014, Fu et al. 2015). While much information is becoming available on ecological dynamics that operate over decadal and shorter time scales, we still know little about the over-lying longer-term dynamics that are important in conservation efforts (Swetnam et al 1999, Willis and Birks 2006, Hadly and Barnosky 2009, Dietl and Flessa 2011, Conservation Paleobiology Workshop 2012, Kidwell 2015, Rick and Lockwood 2013, Dietl et al 2015). A primary question is whether the ecological fluctuations recorded over the past few decades fall outside the range of variation expected in the absence of recent land-use and management. For example, to what extent do current relative abundances, distribution, and associations of species reflect recent adjustments of species due to anthropogenic pressures versus natural fluctuations that typify ecological dynamics that play out over millennia? Such questions can only be answered by tracing ecological dynamics through thousands of years, using the natural experiments which are preserved in the fossil record (Hadly and Barnosky 2009, Conservation Paleobiology Workshop 2012, Kidwell 2015).

Biological conservation on the CP depends on understanding and disentangling the effects of decadal- to centennial-scale dynamics, such as grazing and other human impacts, from the millenial-scale dynamics documented in the fossil record. The American Southwest is expected to become increasingly arid over the next few decades: conditions analogous to previous multi-year droughts, including the Dust Bowl, are expected to become the norm (Seager et al. 2007). Under the A2 (highest) greenhouse gas emissions scenario, precipitation is estimated to decline by around 66% by 2090 and temperatures are expected to increase ~1.5-3 C by 2041-2070 and ~3-5 C by 2070-2090 (Garfin et al. 2014).

The effects of climate on biota can take many forms: mammals can shift their geographic range, population abundance, physiology, body size, phenology, etc., or, if a species' environmental tolerances are greater than the amount of environmental change expected, they may remain observably unaffected. Assessing community-level fluctuations is one way to synthesize these many responses and compare the whole mammal community from one time period to another. Detailed paleoecological records from Quaternary deposits have been remarkably useful in characterizing these millennial-scale ecological dynamics in other regions (Betancourt 1984, Graham and Grimm 1990, Anderson 1993, Hadly 1996, Anderson et al. 1999, Anderson et al. 2000, Barnosky et al. 2004, Blois et al. 2010, Grayson 2011). Past studies have detected a strong relationship between faunal composition and climate: in Samwell Cave (California), Blois et al. (2010) show a correlation between warming climate and declining species evenness and richness from ~17-1.5 ka; Terry et al. (2011) found that cave deposits in the Great Basin record proportional increases in “southern affinity taxa” when climate warmed and dried over the last ~7.5 ka; and Porcupine Cave (Colorado) pit sequence spanning 1 ma to ~600 ka revealed little community change due to climate change except that small herbivores were less diverse during warm interglacial periods (Barnosky et al. 2004). However, while small mammals are important indicators of climate and environment, they do not always track vegetation (Graham and Grimm 1990) or temperature and precipitation predictably. For example, Lamar Cave in Yellowstone records the presence of mesic-adapted taxa during time intervals that are considered warm/arid (Hadly 1996). And at Mescal Cave in the northern Mojave desert, Stegner (2015) found that, while both *Neotoma cinerea* and *Marmota flaviventris* are considered boreal-adapted, *N. cinerea* disappeared at the end of the Pleistocene while *M. flaviventris* was present at the site during several thousand years of Holocene warming and aridification.

Few Quaternary fossil records that sample the small mammal community of the CP have been studied to date (Mead 1981, Mead and Phillips 1981, Emslie 1986, FAUNMAP Working Group 1994, Carrasco et al. 2005, Tweet et al. 2012), particularly in southeastern Utah, where only a handful of Quaternary vertebrate localities have been published. Most of these contain fewer than five taxa—primarily large bodied species—and few specimens (FAUNMAP Working Group 1994, 1996, Carrasco et al. 2005). Archaeological and fossil plant records from the Quaternary CP, in contrast, have been more-extensively studied and provide an important context for new vertebrate fossil data presented here. Holocene rockshelter deposits are common across the CP (Mead et al. 2003, Tweet et al. 2012) and contain abundant small mammal remains that can be used to track the communities through long time spans. To this end, I excavated and quantified mammal diversity change in two fossil-bearing alcoves located in San Juan County, UT. These localities, East Canyon Rims 2 (ECR2) and Rone Bailey Alcove (RBA), contribute to our understanding of natural variation in this system by providing faunal data for a period of recent climate change—a transition from cool-wet to warm-dry that occurred within the last 5000 years. AMS radiocarbon dates on 33 bone samples from these sites span ~4400 cal ybp-present, and shed light on pre-industrial faunal dynamics in the region over the course of environmental change, most notably aridification. Localities with comparable mammal diversity have not been reported from this region previously, so these sites provide novel insight into Holocene mammal diversity in southeastern Utah.

2. Study Region

The CP is a physiogeographic province in North America centered on the Four Corners Region where Utah, Colorado, New Mexico, and Arizona meet. It is an arid region with high topographic relief—from ~900-4300m—pocked with isolated laccolithic mountain ranges and creased with deep canyons formed by the Colorado River and its tributaries (Barnes 1993, Foos 1999). This CP is flanked to the west by the Great Basin, to the east by the Rocky Mountains, and to the south by the Sonoran and Chihuahuan Deserts. The western border is formed by a series of mountain ranges—the Uinta Mountains, Wasatch Range, and Fishlake and Aquarius Plateaus (Rowe 2007)—while the Mogollon Rim in Arizona and the Rio Grande Rift Valley in New Mexico form the southwestern and southeastern borders, respectively (Foos 1999).

2.1 Localities

RBA and ECR2 are large, horizontally shallow alcoves in the Slickrock Entrada Sandstone cliff face of Rone Bailey Mesa, Canyon Rims Recreation Area (BLM), San Juan County, Utah (Figure 2.1a-c). ECR2 is 1830m (±5m) in elevation, southeast-facing, and roughly ~50m across, ~30m high at the mouth, and ~20m deep (Figure 2.1c). RBA is 1905m (±5m) in elevation and faces roughly southwest. RBA (~10m high by ~3m wide by ~5m deep) is contained within a much larger alcove, and an apron of sediment roughly 10-15m high extends from a maximum height at the midden, spilling southwest to the floor of the larger alcove (Figure 2.1b). Quaternary eolian sediments have accumulated in both ECR2 and RBA and buried bone and plant material collected by roosting raptors (as evidenced by raptor pellets on the surface of the sediments) and woodrats (genus *Neotoma*). Woodrats remain active at both sites today, and mammalian carnivores also may have played a role in bone accumulation in these middens.

The vegetation surrounding these sites today is a patchy amalgamation of sagebrush-dominated areas, open perennial grassland, and pinyon-juniper woodland. Cooler and more mesic pockets harbor gambel oak (*Quercus gambelii*), barberry (*Mahonia fremonti*), squawbush (*Rhus trilobata*), Utah service berry (*Amelanchier utahensis*), and spruce *(Picea englemanii*). At ECR2, invasive Russian thistle (tumble weed, *Salsola* spp.) dominates the middle of the drainage where a primitive road passes through, and forms dense patches up to approximately a meter high in places. Russian thistle is present near RBA as well, but it is sparser and does not produce the monotypic thickets seen near ECR2. The area around Rone Bailey Mesa has been grazed by cattle and horses since the 1880s, an activity that concluded indefinitely in the year following excavations (Heidi Redd, L. Hardee Redd, *personnal communication*).

2.2 Climate and Vegetation History of Colorado Plateau

Today, the CP marks the geographic transition between summer-wet (summer monsoon) to the south and summer-dry to the northwest (Anderson et al. 2000). Southeastern Utah currently experiences summer monsoons, but the monsoon boundary shifts through time in response to temperature, snow pack in the Rocky Mountains, location of the jetstream, and other factors (Anderson et al. 2000). Because the CP has high topographic variability—deep canyons and high peaks—typical precipitation and temperature are spatially heterogeneous. However, most of the region receives between 4 and 12 inches of precipitation annually, and experiences minimum January temperatures around -10 to -4°C (13-25°F), and maximum July temperatures between roughly 29 and 38°C (84-100°F) (30 year normals from 1981-2010) (PRISM Climate Group 2015).

The CP was considerably cooler and more mesic during the last glacial period of the Pleistocene, before ~14 ka, at which time it was characterized by juniper woodland and sagebrush between ~600-1500m; pinyon, limber pine, and Douglass fir between 1500-1800m; Engelmann spruce/juniper forest around 2100m; and spruce/pine forest above 2700m (Cole 1990, Anderson et al. 2000). Since the last glacial maximum, the dominant tree and shrub species—including *Abies concolor* (white fir), *Artemisia* spp. (sagebrush), *Atriplex confertifolia* (shadscale saltbush), *Cercocarpus intricatus* (mountain mahogany), *Ephedra* spp. (Mormon tea), *Juniperus* spp. (Juniper), *Opuntia* spp. (prickly pear), *Picea* spp. (Spruce), *Pinus ponderosa* (Ponderosa pine), *Yucca angustissima* (narrow-leaf yucca) and many others—have generally moved 700-900 m higher in elevation and 400-700 km up river (Cole 1990). At the end of the

Pleistocene, middens from the Abajos and Comb Ridge (respectively ~45 and ~85 km south of Rone Bailey Mesa) record a mixture of xeric- and mesic-adapted plants; the mesic components (e.g., subalpine conifers) of the flora disappeared from lower elevations, but modern dominant trees—pinyon (*Pinus edulus* and *P. monophylla*) and ponderosa (*P. ponderosa*)—do not appear at those elevations until the mid-Holocene (~7-3 ka) (Betancourt 1984, Coats et al. 2008). Pinyon has been expanding from south to north across the CP since the end of the glacial period (Coats et al. 2008). Climatically, the early Holocene was cooler than today, but more mesic than the Late Glacial because the summer monsoon was strengthened (Weng and Jackson 1999); this is also when the modern monsoon boundary was established (Betancourt 1984). This cool mesic period gave way to an arid and warm mid-Holocene, from about 8.5-6 ka (Weng and Jackson 1999, Reheis et al 2005). From ~6-3 ka, cool-wet conditions returned (Reheis et al. 2005) and fossil plant evidence from the Abajos suggest higher effective moisture before 3 ka (Betancourt 1984). At the end of this period, around 3120 cal ybp, *Maize* agriculture arrived in this area as indicated by pollen in the Abajos records (Betancourt and Davis 1984). Analysis of eolian and alluvial deposition in Canyonlands suggests that from 2 ka to the present, drier conditions set in, as evidenced by greater mobility of dune sand (Reheis et al. 2005).

With increasing elevation in this arid region, precipitation increases and temperature decreases on average (Betancourt 1984). The fossil localities are between ~1830-1900 m in elevation, and so the plant community likely progressed from pinyon, Douglas fir, and other conifers at the end of the Pleistocene, to juniper woodland and sagebrush with smaller pockets of ponderosa and spruce over the course of the Holocene, to an assemblage dominated by sagebrush and grasslands with large pockets of pinyon-juniper today. Preliminary analysis of pollen from RBA has identified spruce in the deepest excavation level, around 4400 cal ybp, and juniper throughout the deposit.

2.3 Human influences

Humans were probably present across the CP by around 8000 ybp (Grahame and Sisk 2002). Between 1250 and 820 ybp, the Ancestral Puebloan Culture increased in population size, construction of pueblos, and extent of agriculture, and population reached a peak between 875-850 ybp (Grahame and Sisk 2002). This heyday came to a somewhat abrupt end, coincident with a series of at least six extended severe "megardroughts," the first of which occurred from 870-820 ybp (Grahame and Sisk 2002, Benson and Berry 2009). The northern San Juan Basin (southeastner Utah and southwestern Colorado, was largely abandoned by around 650 ybp (Benson and Berry 2009); whether this exodus is attributable directly (e.g. through crop failure) or indirectly (e.g. through social collapse and warfare possibly due to food shortage) to climatic changes is unclear, but climate-induced stress it is the predominant theory today (Benson et al. 2007). Spanish explorers arrived in the American Southwest in the early 1500s and European domesticated livestock—primarily cattle, sheep, pigs, and horses—were introduced around around 1540 (Barnosky et al. 2014b). In the last two centuries, large-scale livestock grazing on the CP has transformed aspects of this region—among many impacts, livestock break up soil crusts and destabilize soils, leading to increased dust, soil loss over time, and exotic plant species invasion (Belnap 2003, Belnap et al. 2009, Miller et al. 2011); grazing also changes the plant structure including dominance by weedy invasive species (Belnap et al. 2009), increases wild fire potential (Belnap et al 2009), reduces carbon storage and vegetation cover (Jones 2000, Fernández et al. 2008, Miller et al. 2011), and leads to destruction of riparian habitats and waterways as livestock congregate around water sources (Eldridge and Whitford 2009). While the midden data addressed here do not provide clear records for faunal change between 500 ybp-present, when livestock grazing began and then intensified, these localities elucidate what we might expect from the small mammal community in response to climate if grazing has no effect. The modern small mammal community and potential impacts from grazing will be addressed in Chapter 3.

3. Methods

3.1 Excavation and identification of vertebrate fossils

Middens like RBA and ECR2 provide high-fidelity records of diversity though time. These sites generally sample the small vertebrate community in ~7 km radius around the site (Hadly 1999, Porder et al. 2003, Feranec et al. 2007). Because ECR2 and RBA are ~4.7 km apart, thereby sampling an overlapping area, and they have similar taphonomic vectors, they can be treated as representative of the same community and the stratigraphic levels from the two sites can be combined to construct a chronological sequence that extends from ~4.4-0.5 ka. Taphonomic studies of woodrat- and owl-generated deposits reveals that they record relative abundance and diversity with high accuracy (less than 1% mismatch between modern middens and the living local community) (Terry 2008, Terry 2010a,b). Deposits like these are also spatially integrated, sampling small mammals from all microhabitats surrounding the deposits (Terry 2010b). Time-averaging on the scale of decades to centuries is actually an asset to studies of diversity change through time, because time-averaged middens sample rare species which are often missed by other survey techniques (Hadly 1999, Barnosky et al. 2004, Terry 2010a), smooth the effects of annual or decadal population booms and busts which are common in small mammals (Whitford 1976, Terry 2008, Dickman et al. 2010), and these sites accurately reflect the magnitude and direction of faunal baseline shifts (Terry 2010a).

RBA and ECR2 were identified as promising deposits in 2012 and 1m^2 test pits were excavated in each site in 2013. Excavation levels were an arbitrary depth based on sediment volume (ranging from 2.3 to 13.5 cm in thickness; Appendix 2.1) because sediments were extremely unconsolidated sand mingled with roof fall (large sandstone blocks), and there was no apparent natural stratigraphy. Sediments were screened (1/2 inch^2, 1/4 inch^2, and window screen) and bone was picked from the 1/2 and 1/4 inch^2 screens in the field. All material collected on the window screen was bagged, taken to the University of California Museum of Paleontology (UCMP), and processed for this study.

Fossil material was separated from matrix by hand or with forceps. Material was initially sorted into rodent scats, insect, plant macrofossils, and vertebrate bone. Using morphological criteria, bone was identified to class (Aves, Reptilia, Amphibia, and Mammalia), and mammalian bone was identified to species when possible (primarily craniodental remains), or to family or genus (in the case of postcranial or otherwise non-diagnostic fossils), by direct comparison to modern skeletal specimens of known species deposited at the Museum of Vertebrate Zoology (MVZ) and UCMP, or using published descriptions from primary paleontological and mammalogical literature. All specimens are curated at the UCMP. See Appendix 2.2 for Systematic Paleontology.

3.2 Radiocarbon dating

I radiocarbon dated 33 bone collagen specimens (16 from ECR2 and 17 from RBA; Table 2.1) using Accelerator Mass Spectrometry (AMS) dating techniques at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory (Livermore, California, USA). Seven of these specimens were subsampled and dated twice to confirm that results were consistent. Bone specimen preparation follows the modified Longin method described by Brown et al. (1988) for collagen extraction, and follows methods outlined in Vogel et al. (1987) for converting CO_2 into graphite for AMS analysis. AMS ^{14}C results include a matrix-specific background correction and an estimate of the $\delta^{13}C$ value of the material (Stuvier and Polach 1977). To convert radiocarbon ybp to calendar ybp, I used the IntCal 13 calibration curve (Reimer et al. 2013) in OxCal Online, version 4.2 (Bronk Ramsey 2009).

Faunal data for excavation levels with overlapping radiocarbon age ranges (Figure 2.3) were combined, and I developed a chronology of 6 time bins with different degrees of time averaging, dating from 4410-501 cal ybp (Table 2.2). Dates presented in Table 2.2 are derived from the most likely age for each specimen. However, there is a range of possible calibrated calendar ybp for a given ^{14}C date (Figure 2.3); I used these probability distributions and the overlap in possible calibrated ages to determine which excavation levels could reasonably be considered non-overlapping in age. The three older time bins pertain to RBA, while the younger are from ECR2. Time bin A represents excavation level 6 and has peak age probabilities at 3699.5, 3639.5, and 4184.5 cal ybp. RBA level 5 was not dated, but dates for levels 6 and 4 are consistent and non-overlapping, so here I assume that stratigraphic mixing in these older layers is either not present or very minimal, and that level 5 can be treated as a separate faunal unit (time bin B). However, additional radiocarbon dates are necessary to confirm this assumption. Level 4 encompasses time bin C with peak age probability at 2424.5 cal ybp. Time bin D represents ECR2 excavation levels 8-10, with peaks at 1024.5, 1169.5, 1179.5, 1194.5, 1214.5, 1289.5, 1529.5, and 1609.5 cal ybp. Time bin E represents ECR2 levels 4-6, and peaks at 794.5, 789.5, and 959.5 cal ybp. Time bin F is represented by ECR2 level 3. The oldest date from ECR2, 4970-4844 cal ybp, is from excavation level 3, and is ~2600 years older than the next oldest date (from level 8). If this is excluded, bin F/level 3 has peaks at 524.5 and 544.5 cal ybp. While there is no evidence that this particularly old date is inaccurate, either as a result of contamination in the lab or in the deposit (e.g. humic acid infiltration), these kinds of contamination are extremely difficult to diagnose. However, all other dates for ECR2 are consistently younger than 1704 cal ybp, and so this date of nearly 5000 cal ybp in the middle of the deposit has a few important implications. First, it suggests that stratigraphic mixing is present to a certain degree in this site, but that it occurs rarely because dates from other levels tend to be consistent and arranged in a predictable chronologic order. Younger levels in both ECR2 and RBA have wider age ranges and show more mixing than the deeper/older excavation levels. Bioturbation by people, cattle, and rodents is one possible explanation for the presence of older bones in top excavation levels. Second, while there is some mixing in these sites, dates generally get older with increasing depth, suggesting it is reasonable to assume that the majority of the material in each level has not moved dramatically up or down in the deposit. Combining neighboring excavation levels into single analysis units helps to strengthen this assumption. However, interpretation of the age of individual specimens is not possible without a date on the specimen itself.

3.3 Sample standardization

Taxon abundance was quantified as number of individual specimens (NISP) of craniodental material identified to family (Leporidae, Sciuridae), subfamily (Perognathinae, Arvicolinae), or genus (*Onychomys, Cynomys, Dipodomys, Peromyscus, Neotoma, Thomomys*). As compared to minimum number of individuals (MNI), NISP has been demonstrated to be a less-biased indicator of relative importance of a taxon in the community (Grayson 1978, Blois et al. 2010). Species-level identifications within these taxa are often only possible by comparison of skeletal elements that are seldom well-represented in the fossil record. Analysis at taxonomic levels above the species level allows incorporation of more of the fossil data represented in these deposits, improving abundance estimations by increasing sample size. Furthermore, analysis at the genus, family, and subfamily levels provides the requisite information needed to recognize the relative changes in the small mammal taxa that fill different functional roles in the ecosystem (Grayson 2000, Barnosky et al. 2004, Barnosky 2004a,b, Blois et al. 2010, Terry 2011), and which can be used as appropriate metrics of the environmental state (Badgley and Fox 2000, Barnosky et al. 2004, Barnosky and Shabel 2005, Stegner and Holmes 2013).

Because the 6 time bins have different amounts of time averaging and numbers of specimens, I standardized sample size to that in the time bin that had the fewest specimens using rarefaction (iterative subsampling without replacement, 100 iterations, sample size=12) and calculated the 95% confidence interval around the resulting sample standardized abundance ($NISP_s$). To test for an effect of low rarefaction sample size, I compared $NISP_s$ and 95% confidence intervals when using a sample size of 12 and sample size of 30, which was the second lowest number of specimens for any time bin. To compare, I scaled the $NISP_s$ and 95% bounds to a unit scale for both sample sizes. Then, for each taxon in each time bin I determined if the 95% confidence interval when n=12 overlapped with the interval when n=30. They overlap in all cases, which is the expectation because rarefaction values converge on proportion as the number of iterations increases. The advantage of rarefaction is that it produces a confidence interval describing the possible range of values for any given taxon. $NISP_s$ with n=12 was used for all subsequent diversity analyses. Time bin A has a sample size of 12, so NISP and $NISP_s$ are the same in A because resampling simply reproduces the observed data. The same analyses using unstandardized NISP and proportional abundance produce the same general results.

Sample size standardization and estimation of confidence intervals is one way to correct for differences in time bin duration, but longer time bins inevitably have more opportunity to sample more species, and low sample size, as in bins F and D, can lead to a randomly biased NISP that produces a $NISP_s$ with the same underlying biased abundance distribution structure. I tested for a correlation between duration and number of species per time bin and found no relationship between the two (Pearson's product moment correlation=0.328, p=0.5).

All analyses were performed using the R Project for Statistical Computing version 3.2.0 (R Core Team 2015), and with the vegan (Oksanen et al. 2015) and analogue (Simpson 2007, Simpson and Oksanen 2015) packages.

3.4 Analysis of diversity change

I assessed diversity change through time in several different ways. First, I used pairwise Fisher's tests to compare the relative rarefied abundance distribution from one time bin to the next (with a Monte Carlo p value simulation, 1000 replicates, and Holm p value correction). Second, I calculated Shannon, Simpson, and Hurlbert's probability of interspecific encounter

(PIE) diversity indices for each time bin and compared them across time bins. While Simpson and Shannon indices are commonly used in ecological studies and are included here for comparison, both are sensitive to sample size (Gotelli and Ellison 2013). In contrast, PIE is a measure of species evenness, and has the advantage of being independent of sample size (Hurlbert 1971, Blois et al. 2010, Gotelli and Ellison 2013).

To calculate diversity indices, I first iteratively subsampled each time bin (n=12, the minimum NISP across time bins) 1000 times, and for each iteration I calculated Shannon, Simpson, PIE, and the 95% confidence interval for each diversity index in each time bin. Because time bins are likely to be serially autocorrelated and therefore non-independent, I compared 95% confidence interval overlap to determine if the diversity indices were different among time bins (Blois et al. 2010).

I visualized faunal relationships among time bins using non-metric multidimensional scaling (NMDS). Unlike other ordination techniques (e.g., principal components or principal coordinates analysis), NMDS does not preserve true distances between objects (time bins or taxa in this case) and instead uses rank order of the distances between objects to arrange them in multidimensional space. This technique places more different objects further apart and more similar objects closer together, which is not always the case in other ordination techniques. (Gotelli and Ellison 2013).

I also made pairwise comparisons of rank-order abundance between time bins using Spearman rank correlation tests with Holm p value corrections. The Spearman coefficient ranges from -1, indicating an inverse relationship, to 1, indicating perfect correspondence (Terry 2010b). To determine if particular taxa were consistently higher or lower in rank than the others, I compared the ranks of taxa using pairwise Mann-Whitney U tests with Holm p value corrections.

3.5 Climate correlation

In order to evaluate the role of climate across all 6 times bins, I used reconstructed mean July temperature (MJT) for the Southwestern US from Viau et al. (2006), downloaded from the National Climatic Data Center (<https://www.ncdc.noaa.gov/cdo/f?p=519:1:::::P1_study_id:6377>). These reconstructions are based on 752 fossil and 4590 modern pollen records from across the continent, and estimate MJT in 100-year intervals from 14,000 ybp to the present (Viau et al. 2006). To reflect time averaging in the faunal data, I averaged the reconstructed MJT across the duration of each time bin. Because MJT estimates are in 100-year intervals, I rounded the ECR2 and RBA time bins to the nearest 100 cal ybp. I used temporal cross-correlation to test for a correlation between diversity and MJT. To test the significance of the cross-correlation coefficient, *r*, I created a null distribution of multiple *r* values by holding one time series stationary (MJT) and randomly reshuffling the diversity time series, then calculating *r*, for 1000 iterations. Values that fell above the 95% confidence interval of the distribution were considered significantly correlated. I evaluated correlation between MJT and number of species, $NISP_S$ for every taxon, rank abundance for every taxon, and PIE, Shannon, and Simpson indices.

For a local climatic signal, I used two published tree ring records as climate proxies to evaluate the relationship between faunal and climatic change in the three youngest time bins (D, E and F), from ~1700 cal ybp to the present. The first dataset is a standardized tree-ring width chronology from *Pseudotsuga menziisii* in Beef Basin (Figure 2.1; latitude 37.933, longitude -109.7999), approximately 40 km southwest of RBA and ECR2, and dating from 1600 ybp to the present (Pederson et al. 2011; https://www.ncdc.noaa.gov/paleo/study/12738). These data were downloaded from the National Climatic Data Center (https://www.ncdc. noaa.gov/paleo). The second record was downloaded from the North American Drought Atlas (Cook and Krusic 2004) (http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRL/.NADA2004/.pdsi-atlas.html). This dataset uses 835 tree ring records from across North America to model Palmer Drought Severity Index (PDSI) from 2005 cal ybp to the present. The PDSI reconstruction most proximate to Rone Bailey Alcove is from latitude 37.5, longitude -110.0, a point ~8 km south of Natural Bridges National Monument and approximately 88 km southwest of Rone Bailey Mesa (Figure 2.1).

PDSI is widely used to estimate abnormally wet or dry conditions (Cook et al. 1999). It incorporates not only temperature and precipitation, but also duration of drought conditions. A PDSI value of -0.49 to 0.49 is considered "normal," increasingly positive numbers indicate increasingly wet periods (anything above 4 is extremely wet) while more negative values indicate drier periods (any value below -4 is extreme drought) (Dai 2010). PDSI suffers from several inaccuracies (e.g., all precipitation is assumed to be rain, so temporal effects of snowfall are lost), but correlates well with soil moisture during warm months and over long time periods, as in this study, the intrannual inaccuracies in PDSI are less relevant (Dai et al. 2004).

As with MJT, I binned PDSI and standardized tree ring width values across each time bin and found the mean. PDSI data were normally distributed in each time bin (Shapiro-Wilks tests), so I used pairwise Student's t tests (with Holm p value correction) to compare bins. Tree ring widths, in contrast, were not normally distributed, so I tested for differences using pairwise Wilcoxon rank-sum tests (with Holm p value correction).

4 Results

4.1 Radiocarbon chronology

Table 2.1 summarizes radiocarbon results and associated data; Table 2.2 summarizes the connection between excavation levels and time bins, mean age ranges, and amount of time averaging.

4.2 Relative and rank-order abundance

Table 2.3 summarizes NISP and NISP_S with 95% confidence intervals. Figure 2.4 illustrates change in NISP_S through time. In time bin A, rarefied abundances (NISP_S) of arvicolines, sciurids, and *Thomomys* were at their highest, while leporids, perognathines, *Cynomys*, and *Onychomys* were not sampled at all. During B, leporids, perognathines, *Cynomys*, and *Onychomys* first appeared, and perognathines were at their most abundant across the record. *Dipodomys* also increased in abundance, while sciurids, arvicolines, *Peromyscus*, *Neotoma*, and *Thomomys* all declined. In bin C, leporids, *Cynomys*, *Neotoma*, *Onychomys*, *Peromyscus*, and arvicolines all increased, while sciurids, *Thomomys*, *Dipodomys*, and perognathines declined. Leporids and *Cynomys* continued their steady increase in bin D, along with *Neotoma* and *Peromyscus* which were at their most abundant during that time, and sciurids and perognathines slightly increased. *Dipodomys* and *Thomomys* continued to decline, both reaching their lowest abundance across the record, and arvicolines and *Onychomys* also decreased. *Cynomys* was again absent during bin E; *Neotoma*, *Onychomys*, and *Peromyscus* also declined. After relatively low abundance in the preceding time bin, *Thomomys* reached its peak abundance in E. Leporids, perognathines, *Dipodomys*, and sciurids also increased. Bin F is characterized by extremes: leporids and *Dipodomys* were at their highest abundance, but *Onychomys*, *Peromyscus*, and sciurids were entirely absent. *Cynomys* reappeared, *Thomomys* declined slightly, and perognathines, arvicolines, and *Neotoma* maintained low abundance.

Table 2.4 summarizes rank-order abundance for each time bin; Table 2.5 summarizes Spearman rank correlation test results for similarly of rank-order abundance among time bins. The rank order abundances are all positively correlated across time bins, but not significantly. Without the Holm p value correction for multiple statistical tests, the rank-order abundances of time bins A and F are not significantly correlated with the other time bins, but B, C, D, and E are all significantly correlated with one another, except for B versus C. In the comparison of the ranks of each taxon, there were no significant differences among the ranks when using a Holm p value correction, meaning that no taxa are statistically higher or lower in rank than the others on average. However, without a p value correction, the ranks of *Dipodomys* and *Thomomys* are significantly lower than all other taxa, and *Dipodomys* are significantly lower in rank than *Thomomys* (Figure 2.5). *Dipodomys* and *Thomomys* are consistently the most abundant through time but there is no apparent signal in the rank-order abundance of the other taxa.

4.3 Diversity dynamics

I detected no significant differences in abundance distribution among time bins using Fisher's tests. NMDS (Figure 2.6) illustrates the relative degree of compositional similarity among time bins: B, C, and E are most similar to each other while A, D, and F have more extreme representations of different taxa.

Shannon, Simpson and PIE produce the same overall pattern (Figure 2.7): evenness begins fairly high in time bin A (4410-3569 cal ybp), drops sharply in B (3569-2700 cal ybp), then recovers in C, D, and E (2700-959 cal ybp) before declining again in F (644-501 cal ybp). 95% confidence intervals are non-overlapping for time bin F (644-501cal ybp) which is lower than all other time bins except B (3569-2700 cal ybp); and bin D (1704-959 cal ybp) which is higher than all other time bins except C (2700-2350 cal ybp, immediately prior) and E (1054-735 cal ybp, immediately subsequent).

4.4 Climate correlations

With regard to PDSI, time bins E (mean PDSI=-1.68, range: -10.32-4.66) and F (mean PDSI=-1.64, range: -9.18-4.42) were significantly drier than D (mean PDSI=-1.00, range: -9.30-5.94), but indistinguishable from one another. There were no significant differences in mean tree ring width across the entire binned data set.

Cross-correlation revealed no correlation between MJT and diversity—whether number of species, diversity indices, or relative or rank-order abundance fluctuations within a taxon—except for leporids. Leporid relative abundance is strongly positively correlated with MJT (r=0.953, null interval=0.154-0.794).

5. Discussion

Neither diversity nor abundance in ECR2 and RBA correlate with the climate records assessed here. Most of the taxa present in these sites throughout the record are tolerant or indicative of xeric ecosystems, and only one taxon present in the fossil record is not found in the immediate vicinity of the caves today: voles, genus *Lemmiscus* and *Microtus*. *Microtus* are typically found in grasslands and meadows, often associated with montane and/or riparian ecosystems (Kays and Wilson 2009). In the fossil record, *Microtus* tends to be associated with cooler and more mesic times (Hadly 1996, Barnosky 2004b, Hadly and Barnosky 2009). In contrast, the sagebrush vole, *L. curtatus*, is found in more arid brushy environments—usually sagebrush or rabbit brush (Kays and Wilson 2009). *L. curtatus* is restricted to the Great Basin today but is found in late Pleistocene records from across the CP (Murray et al 2005, Mead et al. 2003). Teeth of *L. curtatus* are present in ECR2 level 4 (time bin E, 1054-735 cal ybp) and RBA level 4 (time bin C, 2700-2350 cal ypb). To my knowledge, these are the youngest records of *L. curtatus* on the CP (FAUNMAP 1994, 1996, Bell and Glennon 2003, Mead et al. 2003, Carrasco et al. 2005, Neotoma Paleoecological Database 2013): other occurrences of this species on the CP in the last 40 ka are Sheep Camp Shelter (Late Glacial/Holocene; Gillespie 1985), Screaming Neotoma Cave (29-25 ka; Bell and Glennon 2003, Mead et al. 2003), and Isleta Cave No. 2 (Late Glacial/Holocene; Harris and Findley 1964).

Leporids are the only group for which abundance is correlated with temperature in these sites: leporid diversity increases steadily through time as MJT increases. Whether this is a causal relationship is unclear. *Sylvilagus* and *Lepus* are both ubiquitous across the CP and in western North America generally, and are tolerant of a wide range of habitats (Kays and Wilson 2009). In a study of Chihuahuan Desert *Lepus californicus*, Hernandez et al. (2011) found a correlation between leporid abundance and both precipitation and plant productivity, and conclude that food supply has a strong effect on *L. californicus* abundance. In contrast, Lightfoot et al. (2010) also assessed leporid abundance dynamics in the Chihuahuan Desert but found no correlation between *Sylvilagus audubonii* or *L. californicus* abundance and precipitation or productivity. Rather, Lightfoot et al. (2010) observed higher diversity of both species in black gramma grassland as compared to creosote bush shrubland. At RBA and ECR2, precipitation *declined* as leporid diversity increased, but local changes in the plant community were almost certainly taking place, which may have favored leporids. Identification of the pollen from these sites will shed light on this question.

A second pattern is qualitatively evident in the relative abundance data (Figure 2.4): *Thomomys* and *Dipodomys* both tend to have lower relative abundance when *Neotoma* and *Peromyscus* are higher in abundance. However, *Dipodomys* and *Thomomys* remain the most common (1st and 2nd most abundant, respectively) throughout the record. One possible connection is that both *Thomomys* and *Dipodomys* are reliant on burrowing in the soil to a greater or lesser extent, unlike either *Peromyscus* or *Neotoma.* Climatic preferences seem less related to this relative abundance pattern: *Dipodomys* are physiologically adapted to dry environments (Vimtrup and Schmidt-Nielsen 2005), and are found in a range of arid and semi-arid habitats (Garrison and Best 1990, Kays and Wilson 2009); *D. ordii*, the only species found in San Juan County today, is almost always associated with sandy soils (Garrison and Best 1990). The two species of *Thomomys* present in Utah today are *T. talpoides*, found generally in the mountains and high valleys of Utah (Durrant 1952), and *T. bottae*, generally found in agricultural fields (such as alfalfa), lower valleys, and desert mountains (Durrant 1952, Verts and Carraway 1999). However, both have extremely wide geographic, elevational, and ecological ranges (Wilson and Ruff 1999) and so their present-day distribution in Utah is not necessarily a good indicator of their fossil distribution or habitat preferences. *Peromyscus* and *Neotoma* are fairly generalist in their climatic and dietary requirements (Sorensen et al. 2004, Blois et al. 2010). Certain species within these genera are specialists, however—for example, *P. truei* (pinyon mouse) is found associated with pinyon (Chapter 3, Hoffmeister 1981), and *N. stephensi* is associated with juniper or, occasionally, other conifers (Sorensen et al. 2004). Finer taxonomic resolution of the fossil data would certainly aid in interpretation of abundance dynamics, for example by revealing intra-generic turnover, but isolated teeth of *Peromyscus* and *Neotoma* cannot be identified to species using standard morphological criteria (Hooper 1957, Repenning 2004). Using the dental morphological criteria developed by Hooper (1957), I attempted to identify *Peromyscus* teeth from ECR2 and RBA to species. However, almost all teeth were morphologically aligned with at least two of four species, all present in this region today: *P. maniculatus, P. crinitus, P. boylei,* and *P. truei* (Appendix 2.3).

Sciurid specimens from ECR2 and RBA are almost exclusively loose cheek teeth, and have not yet been identified to genus, much less species, with the exception of *Cynomys* which are much larger and more hypsosdont than other sciurids. Today, the sciurids present in southeastern Utah include the burrowing *Ammospermophilus leucurus* (white-tailed antelope squirrel), *Otospermophilus variegatus* (rock squirrel), and *Xerospermophilus spilosoma* (spotted ground squirrel), largely ground-dwelling *Tamias mimimus* (least chipmunk), *T. quadrivitattus* (Colorado chipmunk), and *T. rufus* (Hopi chipmunk), and tree-dwelling *Sciurus aberti* (Abert's squirrel). All of these species, with the exception of *S. aberti*, are found in arid desert and scrubland habitats (Nash and Seaman 1977, Streubel and Fitzgerald 1978, Oaks et al. 1987, Belk and Smith 1991, Best et al. 1994, Burt and Best 1994, Verts and Carraway 2001, Kays and Wilson 2009). *S. aberti* is present in the Abajos today (Schaefer 1991) but not outside montane, forested regions (Kays and Wilson 2009)—the presence of *S. aberti* in the fossil record of ECR2 and RBA might indicate cool/mesic climatic conditions. Relative abundance of tree-dwelling versus ground-dwelling sciurids more generally could also be indicative of different environments, although I have trapped and observed *Tamias* and *Ammospermophilus* at both ECR2 and RBA. *Tamias* is common in patches of pinyon-juniper woodland near these sites (Chapter 3). *Cynomys* on a genus-level is unlikely to be a good indicator of climate: members of this genus can persist in semi desert (*C. leucurus*), grasslands and prairies (*C. parvidens, C. ludovicianus*), as well as montane meadows (*C. gunnisoni, C. leucurus*) (Kays and Wilson 2009).

Two arid-adapted taxa with relatively lower abundance are also present throughout the deposits. Generally, perognathines—genus *Perognathus* and *Chaetodipus*—are currently found in arid or semiarid grasslands, desert scrub or shrub steppe, but several species also occupy woodlands and chaparral (Kays and Wilson 2009). Only *Perognathus* is present on the CP today. *Onychomys* also occupies arid and semi-arid regions of North America: *O. leucogaster*, the only species currently found on the CP, prefers shrub steppes and grasslands (McCarty 1975, 1978).

Taxa with similar relative abundance dynamics group closer together in the NMDS results (Figure 2.6). Three general taxonomic groups are evident: 1) *Dipodomys* and *Thomomys* (highest rank-order abundance across the record; higher relative abundance in the beginning and end of the record, lower in the middle); 2) leporidae, perognathines, *Cynomys*, and *Onychomys* (low in the beginning, higher towards the end), and; 3) *Neotoma*, *Peromyscus*, sciurids, and arvicolines (high in the beginning and middle, an early dip in abundance, and lower in the end). These groupings do not seem to be connected to climatic affinity, at least using the measure of climate that were possible in this study, because a mixture of taxa with xeric, mesic, or neutral affinity are found in each grouping and abundance does not correlate with MJT.

Desert taxa might be expected to respond more to aridity than to temperature (Stapp 2010). Several lines of evidence indicate that conditions were relatively cool and wet during time bins A-C, then more arid and warm during D-F (Figure 2.2; fossil plants and pollen (Betancourt 1984, Betancourt and Davis 1984, Coats et al. 2008, Anderson et al. 2000), eolian and alluvial deposition (Reheis et al. 2005). Bins E and F encompass a period of time when at least 6 "mega-droughts" took place, including the droughts that are thought to have dispersed the Ancestral Puebloans at Chaco, Mesa Verde, Kayenta, and other large CP settlements (Benson et al. 2007, Benson and Berry 2009). However, time bins with similar climate (A-C versus D-F) do not plot closer to one another on the NMDS, supporting the conclusion that relative and rank-order abundance dynamics are disconnected from climate, at least with regard to the broad-scale trends discussed here. One possible explanation is that time-averaged stratigraphic layers capture short cool or mesic periods within an overall aridifying and warming trend (Hadly 1996). However, sample sizes for these cool/mesic taxa should be lower than for warm/xeric taxa if taphonomic processes are the same during wet and dry times.

PIE, Shannon, and Simpson indices also appear to be uncorrelated with climate. All three indices of evenness are lower during bin B (3569-2700 cal ybp; cool/wet) and bin F (644-501 cal ybp; warm/dry). In both cases, relative abundance of *Dipodomys* was extremely high, and *Neotoma* and *Peromyscus* were at their lowest abundance. These indices do not correlate with MJT and, while it is interesting that diversity declines as climate aridified over the last 3 time bins, more time points would be necessary for a statistical assessment, and a local precipitation proxy stretching further back in time would refine interpretation dramatically. A record of precipitation or available moisture during bins A through C would help to support or reject the hypothesis that evenness decreases during arid times (i.e., if precipitation was low during B but high during A and C).

Overall, the evidence presented here suggests that small mammal abundance at these sites was not detectably altered by the changes in climate that occurred during the interval of deposition. Other factors not tested in this study—like Ancestral Puebloan population size and land use—may influence small mammal diversity dynamics. However, Fisher's tests reveal no significant changes in the relative abundance distribution across the record and the taxonomic and functional components of this community have not changed markedly through the environmental changes represented by the time sampled by the deposits, suggesting that these groups persist in spite of natural variation and/or external perturbation in this system. However, finer taxonomic resolution might reveal a signature of climate change: for example, *Thomomys* subgenus *Megascapheus* is present in ECR2 and RBA throughout the time period encompassed by this study, but the only record of *Thomomys* subgenus *Thomomys* is during time bin F (ECR2 level 3, 644-501 cal ybp). *T.* subgenus *Thomomys* is better able to dig in harder soils than *T.* subgenus *Megascapheus*, and soils tend to get harder as climate dries (Marcy et al. 2013). While *Thomomys* abundance has remained high relative to other taxa for thousands of years, species and subspecies of *Thomomys* naturally replace one another as climate changes, so pocket gophers as a genus and functional group are important and ever-present members of the community (Hadly and Barnosky 2009).

6. Conclusions

Two newly-excavated late Holocene fossil midden localities, ECR2 and RBA, with 33 AMS ^{14}C dates provide fine-resolution information on small mammal diversity dynamics from

~4400-500 cal ybp in southeastern Utah. These sites comprise a chronology of 6 time bins; climate during the oldest three (~4400-2700 cal ybp) was relatively cool and mesic while during the younger three (1700-500 cal ybp) was increasingly warm and arid. I tested for an effect of climate on community evenness and relative abundance of 10 small mammal taxa: leporids, perognathines, small sciurids, arvicolines, *Cynomys*, *Neotoma*, *Dipodomys*, *Onychomys*, *Peromyscus*, and *Thomomys*. In spite of considerable increases in aridity—quantified as PDSI and standardized tree ring width—and temperature—measured as reconstructed mean July temperature anomaly—neither is significantly correlated with relative abundance or Shannon, Simpson and PIE indices of diversity and evenness. However, increased aridity may be connected with declining evenness from ~1700-500 cal ybp, corresponding with increasing abundance of *Dipodomys* and decreasing abundance of *Neotoma* and *Peromyscus*. Though abundance does not correlate with climate, certain groups of species have similar diversity trends through time. Identifying what drives these cross-taxa abundance patterns will be important for predicting future abundance changes.

Overall, these results indicate that climatic fluctuations of the magnitude preserved in these deposits does not significantly alter the small mammal community at least on the taxonomic level assessed here. Neither is there evidence that the presence, then exodus of Native Americans in the region significantly affected small mammals. The metrics of community structure assessed here can be monitored in the modern small mammal community of this region: if these metrics are significantly different today (Chapter 3) or in the future from those seen in the fossil record, it may indicate anthropogenic influences outside the range of natural variability.

Table 2.1: AMS 14C Results. CAMS = Center for Accelerator Mass Spectrometry; UCMP = University of California Museum of Paleontology.

Site	Level	UCMP#	CAMS #	^{14}C age	Cal ybp	Cal ybp % conf.
ECR2	1	233255	169707	1110±30	937-1072	95.4
	3	233188	169714	4335±30	4844-4970	95.4
	3	233189	169717	560±30	587-644	50.1
			170004	500±30	501-553	94.7
	4	233193	169712	905±30	744-914	95.4
			170002	895±35	735-911	95.4
	4	233196	169719	895±25	738-833	55.1
	8	233219	169709	1620±30	1412-1569	95.4
			170042	1710±35	1549-1704	95.4
	8	233217	169711	1125±30	959-1089	89.7
	9	233221	170056	1185±30	1050-1183	88.3
	9	233222	170057	1355±30	1240-1325	90.6
	10	233227	169713	1245±30	1171-1271	68.3
				1285±30	1179-1285	95.4
RBA	1	231186	169716	3330±50	3451-3649	89.5
			170041	3365±30	3557-3693	92.6
	1	231178	169720	>Modern	0	-
			170005	>Modern	0	-
	1	231187	169721	>Modern	0	-
			170006	>Modern	0	-
	2	RBA02	170054	2545±45	2489-2754	95.4
	2	231199	170055	1145±35	972-1175	95.4
	6	231224	169708	3455±30	3640-3828	95.4
	6	231230	169722	3395±30	3569-3705	95.4
	1	231173	167403	>Modern	0	-
	4	231190	167404	2420±35	2350-2700	95.4
	6	231228	167405	3825±50	4090-4410	95.4

Table 2.2: Time bins.

Time Bin	Cal ybp	Approximate time averaging (yrs)	Excavation Levels
A	3569-4410	841	RBA 6
B	unknown	unknown	RBA 5
C	2350-2700	350	RBA 4
D	959-1704	745	ECR2 8-10
E	735-1054	319	ECR2 4-6
F	501-644	143	ECR2 3

Table 2.3: Summary of NISP (above) with sample standardized abundance (NISPs) ± 95% confidence interval (below). For time bin A, NISP and NISP$_s$ are the same.

	Time Bin					
Taxon	A	B	C	D	E	F
Arvicolinae	1	1	4	1	2	1
	-	0.14±0.22	0.53±0.43	0.19±0.25	0.22±0.27	0.40±0.31
Cynomys	0	1	2	3	0	1
	-	0.16±0.23	0.26±0.30	0.61±0.43	-	0.40±0.31
Dipodomys	3	35	32	12	30	14
	-	5.42±1.02	4.41±0.96	2.55±0.80	3.23±0.91	5.55±0.86
Leporidae	0	3	5	6	16	6
	-	0.45±0.39	0.68±0.47	1.29±0.63	1.71±0.74	2.42±0.67
Neotoma	1	4	11	10	12	1
	-	0.59±0.43	1.52±0.67	2.09±0.76	1.28±0.65	0.40±0.31
Onychomys	0	2	7	2	3	0
	-	0.32±0.33	0.91±0.54	0.40±0.36	0.35±0.34	-
Perognathinae	0	6	3	2	5	1
	-	0.97±0.54	0.41±0.38	0.45±0.36	0.53±0.43	0.41±0.31
Peromyscus	1	3	6	9	8	0
	-	0.46±0.39	0.82±0.51	1.80±0.73	0.82±0.53	-
Sciuridae	1	5	2	3	6	0
	-	0.75±0.47	0.26±0.29	0.63±0.44	0.66±0.47	-
Thomomys	5	18	16	9	30	6
	-	2.75±0.85	2.20±0.80	2.00±0.74	3.21±0.89	2.43±0.72

Table 2.4: Rank abundance.

	A	B	C	D	E	F	mean rank
Dipodomys	2	1	1	1	1	1	1.17
Thomomys	1	2	2	3	2	2	2
Neotoma	6	5	3	2	4	7	4.5
Leporidae		7	6	5	3	3	4.8
Peromyscus	6	6	5	4	5		5.2
Perognathinae		3	8	8	7	4	6
Sciuridae	6	4	10	6	6		6.4
Onychomys		8	4	9	8		7.25
Cynomys		9	9	7		5	7.5
Arvicolinae	6	10	7	10	9	6	8

Table 2.5: Correlation coefficients from pairwise Spearman rank correlation tests on rank-order abundance of taxa for each time bin. * indicates statistical significant without a Holm p value correction; no comparisons were significant with p value correction.

Time bin	A	B	C	D	E
B	0.56				
C	0.56	0.44			
D	0.62	0.68*	0.65*		
E	0.61	0.76*	0.71*	0.87*	
F	0.26	0.46	0.39	0.39	0.52

Figure 2.1a: Map of localities and geographic landmarks mentioned in the text; Regional map is inset, the green line indicates the rough outline of the Colorado Plateau. ECR2= East Canyon Rims 2 (UCMP #V36221); RBA=Rone Bailey Alcove (UCMP #V36222); ARCH=Arches National Park; CANY=Canyonlands National Park, GRCA=Glen Canyon Recreation Area; NABR=Natural Bridges Nation Monument. Red Xs denote locations of climate proxy data: T=standardized tree ring data; P=reconstructed PDSI data. **b.** Rone Bailey Alcove from approximately west; arrow indicates location of woodrat midden deposit. **c.** East Canyon Rims 2 from approximately south; arrow indicates location of woodrat midden deposit.

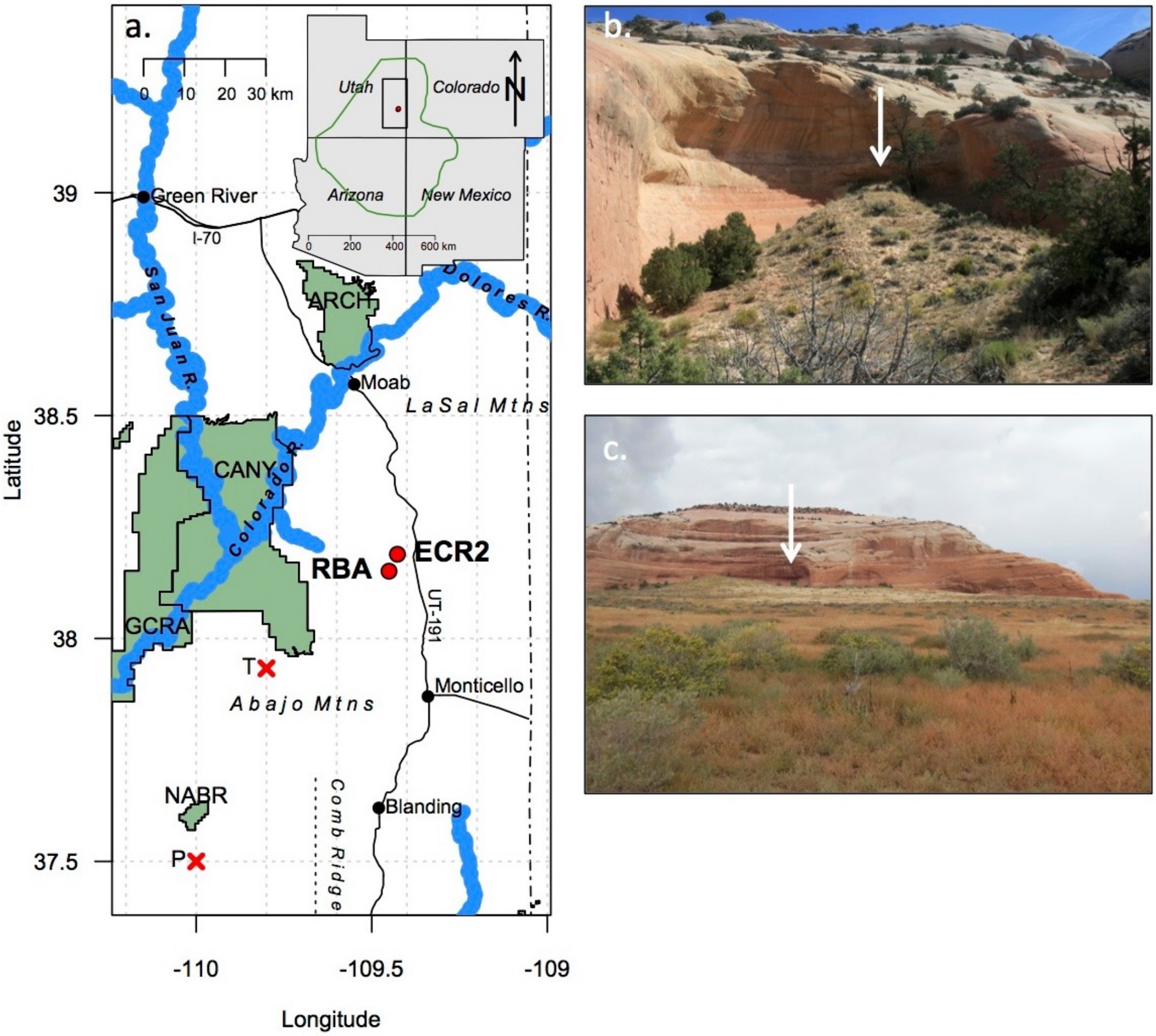
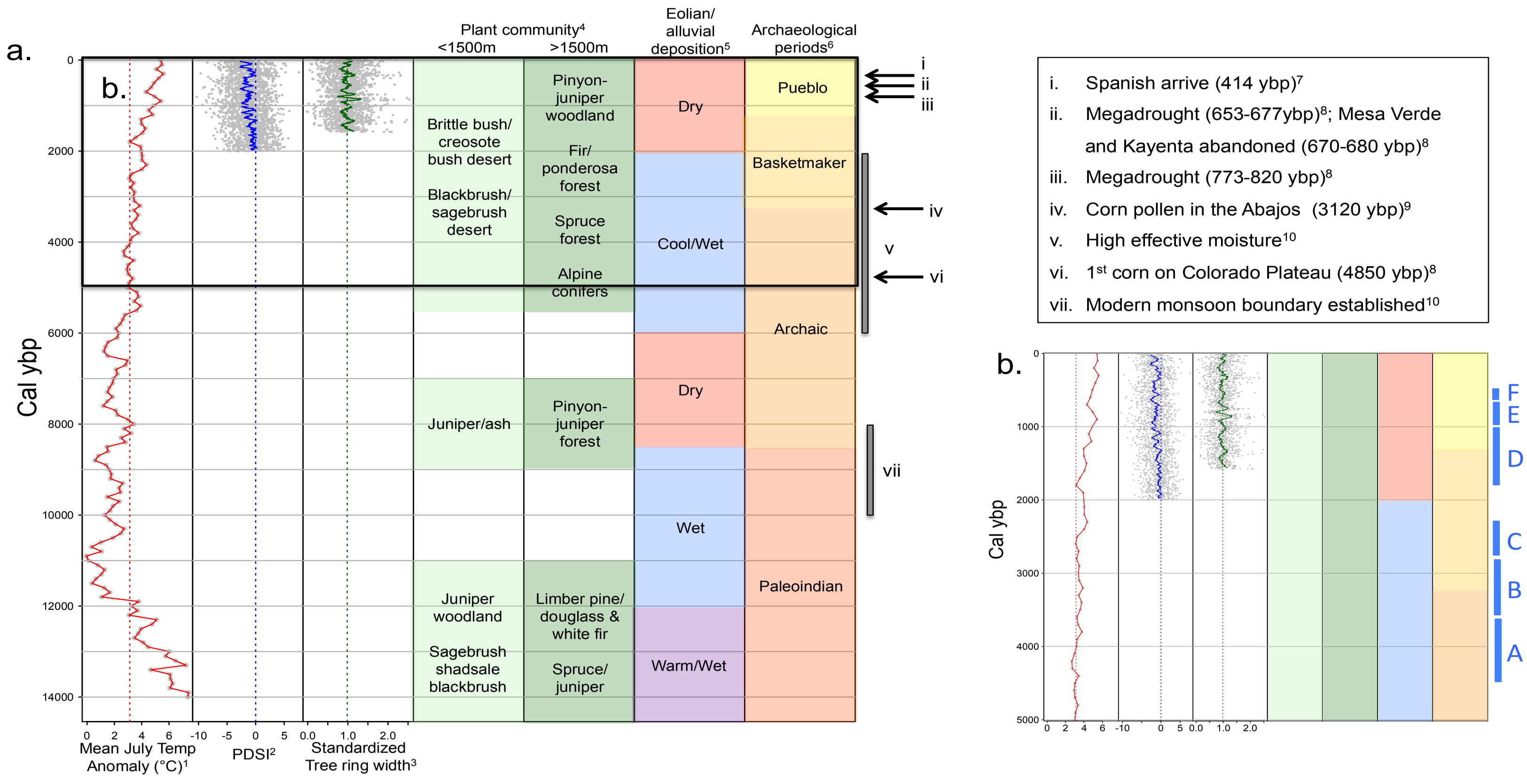


Figure 2.2a. Chronology of environmental changes on the Colorado Plateau since the last glacial maximum. Gray dots show mean July temperature anomaly (MJT), PDSI, and tree ring width values. Solid red line = MJT; dashed red line = average MJT from 14ka to the present; solid blue line = 100 year moving average of PDSI values; dashed blue line = 0, the PDSI value indicating neither wet nor dry conditions relative to normal; solid green line = 100 year moving average of standardized tree ring width; dashed green line = average tree ring width across the record. **b:** Chronology of environmental changes on the Colorado Plateau from 5 ka to the present, the time period captured by ECR2 and RBA. Blue vertical bars and lettering indicate time bins used in this study. Data are summarized from: 1.Viau et al (2006); 2. Cook and Krusic (2004) 3. Pedersen et al. (2011), 4. Cole (1990) 5. Reheis et al. (2005) 6. Crow Canyon Archaeological Center (2015) 7. Grahame and Sisk (2002) 8. Benson and Berry (2009) 9. Betancourt and Davis (1984) 10. Betancourt (1984).



i. Spanish arrive (414 ybp)[7]
ii. Megadrought (653-677ybp)[8]; Mesa Verde and Kayenta abandoned (670-680 ybp)[8]
iii. Megadrought (773-820 ybp)[8]
iv. Corn pollen in the Abajos (3120 ybp)[9]
v. High effective moisture[10]
vi. 1st corn on Colorado Plateau (4850 ybp)[8]
vii. Modern monsoon boundary established[10]

Figure 2.3. Plot illustrating probability density distribution of the calibrated calendar ybp ages based on the 14C ages. Black lines trace the probability density distribution, with higher probabilities to the right. Blue brackets indicate the excavation levels that were combined to get time bins (blue letters).

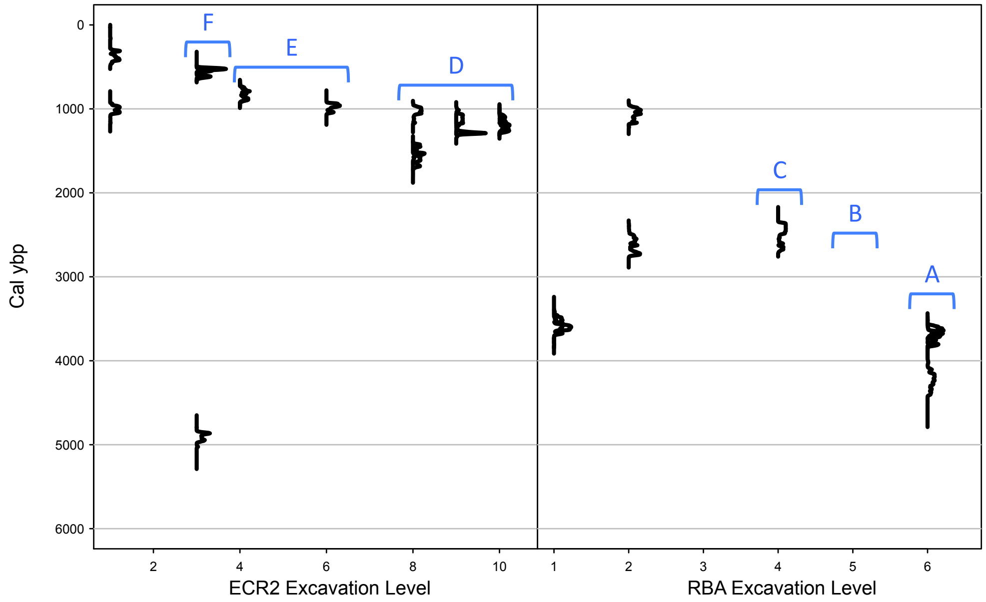


Figure 2.4: Diagram of NISPs relative abundance through time. Blue shading indicates cool/mesic conditions, red shading indicates warm/arid conditions.

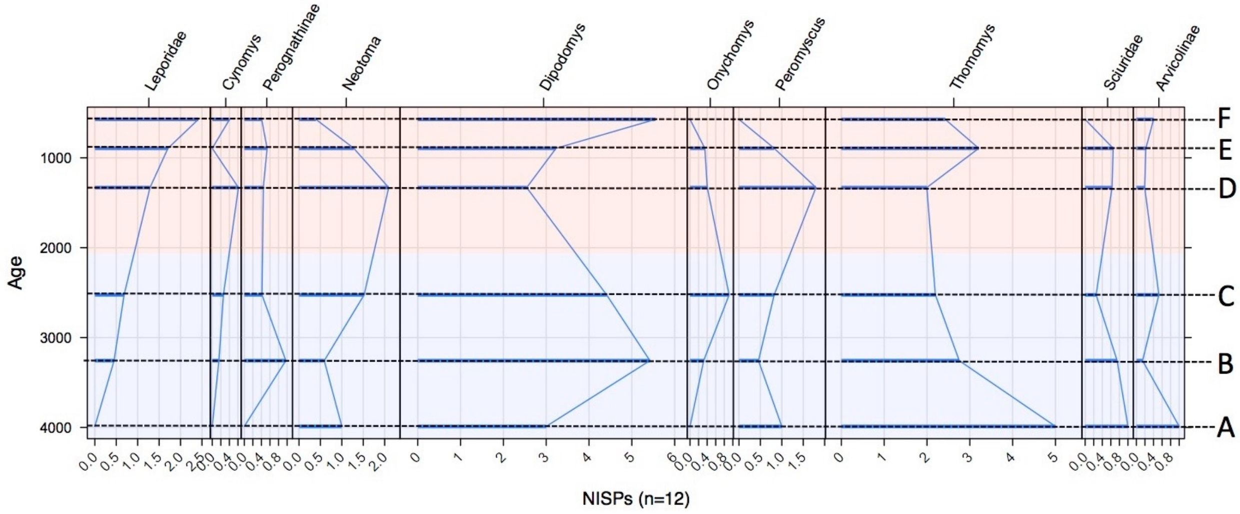


Figure 2.5: Boxplot of rank-order abundance ranks across time bins for each taxon.

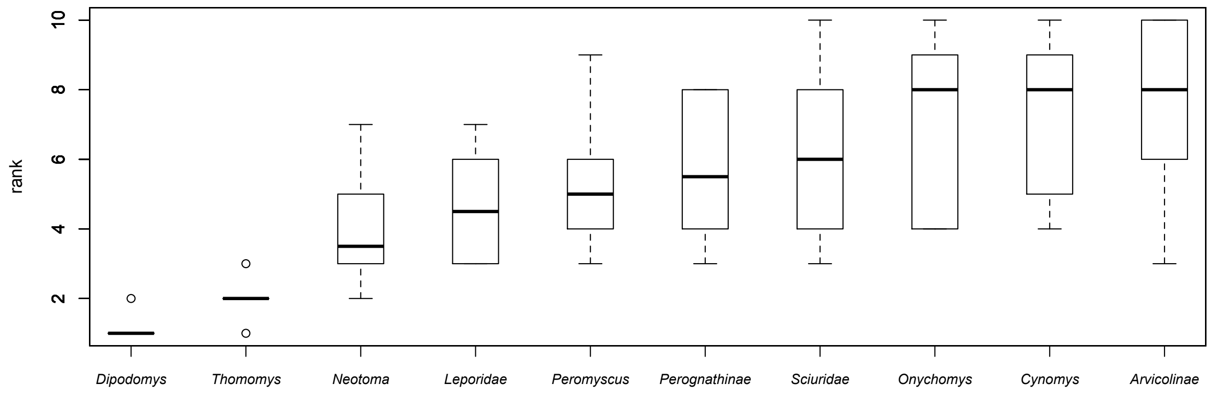


Figure 2.6: Plot of Nonmetric Multidimensional Scaling axes 1 and 2.

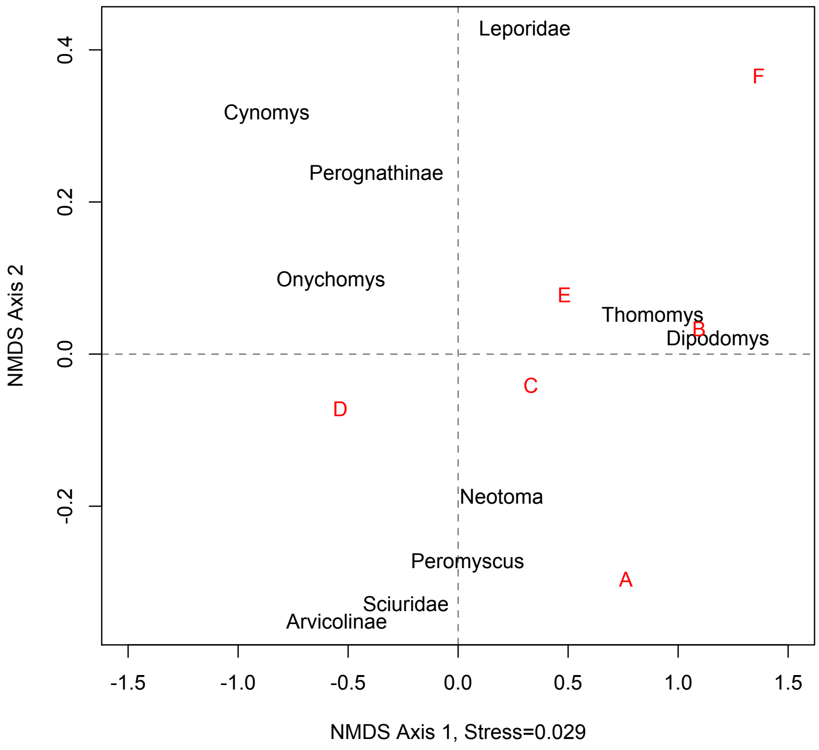
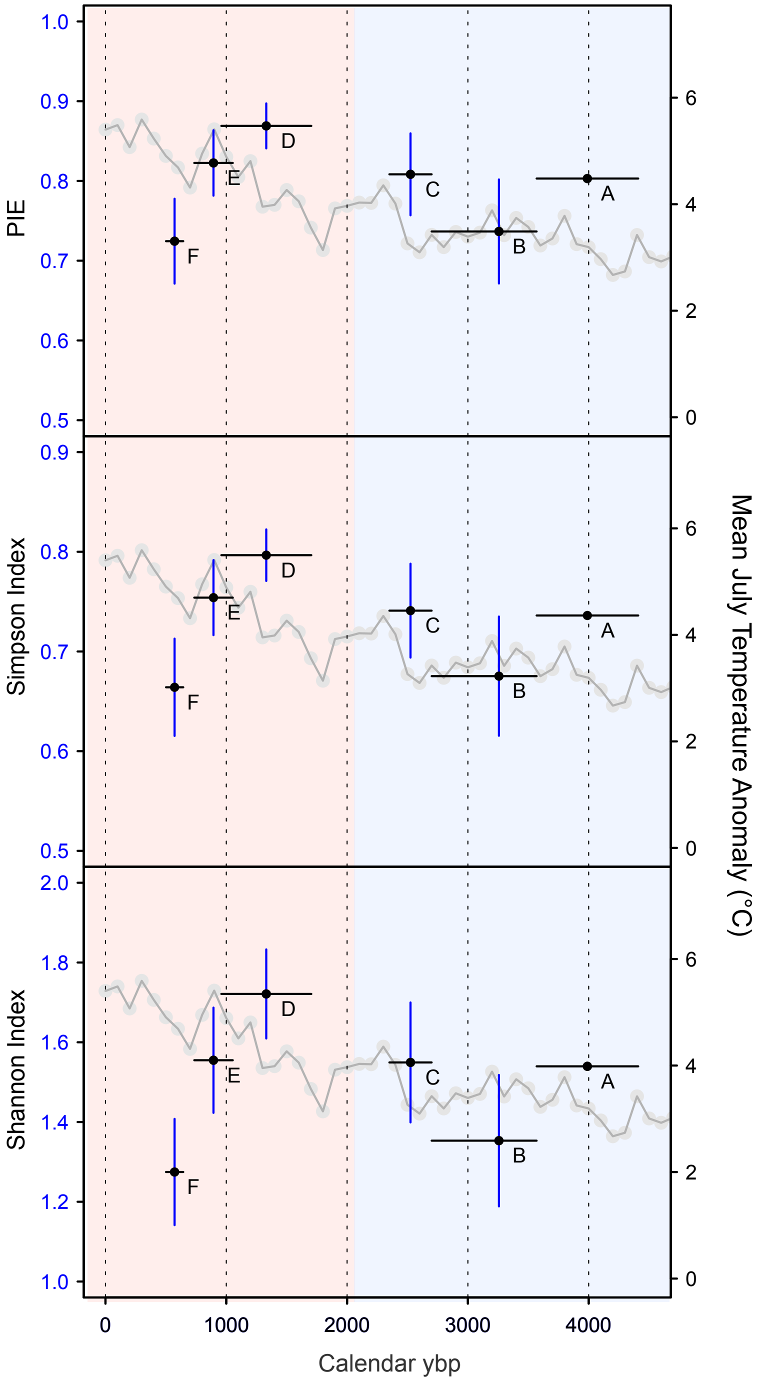


Figure 2.7: PIE, Shannon, and Simpson indices for each time bin. Letters indicate time bin. Blue shading indicates cool/mesic conditions, red shading indicates warm/arid conditions. Horizontal black bars indicate age range (cal ybp); vertical blue bars indicate 95% confidence interval for each diversity index. The gray line and points are reconstructed mean July temperature anomaly (Viau et al. 2006).



Chapter 3

Spatial variation in small mammal diversity of northern San Juan County, Utah

1. Introduction

The effects of on-going and rapid anthropogenic global change, including climate change, ecosystem transformations, extinctions, pollution, and growing human populations, are impacting the world's biota in many ways (McCarty 2001, Root et al. 2003, Parmesan 2006, Williams et al. 2007, Barnosky 2009, Barnosky et al. 2012, Barnosky et al. 2014a, Urban 2015). Of particular concern is the interaction between habitat loss and climate change. Whereas in the past, most species were able to track climate change by shifting their geographic ranges, today more than 50% of Earth's lands have been converted for human use, ranging from comparatively light (e.g., pastureland) to total transformation (e.g. cities) (Hooke et al. 2012, Barnosky et al. 2014a), prohibiting many species from tracking preferred climatic and environmental conditions. Such species will have to either adapt *in situ* or they will go extinct. Adaptation at the required rapid pace will be problematic: given current rates of global change, for example, it is estimated that, on average, species will have to adapt their niche 10,000 times faster than they have in their evolutionary history in order to keep pace with the temperature and precipitation changes projected for 2100 (Quintero and Wiens 2013).

In the southwestern US, climate change and land conversion have already progressed dramatically: in San Juan County, Utah, the focus of this study, over 34% of land is agricultural (croplands, farms, or rangeland) (Godfrey et al. 2005) and ranching has been a major part of the economy of that region for more than a hundred years. Since 1950 the southwest has been hotter than any time during the last 600 years, and the early 2000s were hotter than any time in the last 100 years (Garfin et al. 2014). This situation is expected to worsen throughout the current century: under an A2 (highest) greenhouse gas emissions scenario, precipitation is estimated to decline around 66% by 2090 and temperatures are expected to increase ~1.5-3°C by 2041-2070 and ~3-5°C by 2070-2090 (Garfin et al. 2014). This region is also home to a diverse complement of mammal species, some of them endemic subspecies, distributed through both protected and multi-use lands. Thus, a key question is how mammal communities might be expected to respond to these impending changes. Answering that question is important because, setting aside ethical issues of human-caused extinction, anthropogenic impacts may cause the loss of species that play crucial roles in ecosystem function and in maintenance of habitat states, many of which benefit humans. For example, experimental removal of kangaroo rats (genus *Dipodomys*) in Chihuahuan Desert environments causes a rapid shift in the structure and composition of the vegetation, from shrubland to perennial grassland (Brown and Heske 1990, Heske et al. 1993, Curtin et al. 1999). In contrast, prairie dogs and associated herbivorous rodents prevent mesquite encroachment and maintain the open grasslands preferred by ranchers and domestic livestock (Weltzin 1997). Thus, anticipating how these keystone species and the broader small mammal community will respond to future climate change is important for preventing the loss of these species and the ecosystem services they provide.

Mammals respond to aspects of climate in different ways. Paleontological studies have shown that so-called no-analog communities—novel species assemblages not seen today—are the rule rather than the exception in the past (FAUNMAP Working Group 1996, Stafford et al.

1999, Semken et al. 2010); this has also been well-documented in plant communities (Graham and Grimm 1990, Jackson and Overpeck 2000, Williams et al. 2001, Williams and Jackson 2007). Previous studies have found support for both individualistic (Graham and Grimm 1990, FAUNMAP Working Group 1996) and synchronized range shifts (Lyons 2003) during the Pleistocene-Holocene transition. Ecological studies of extant mammals have produced similar results: some groups of species track climate by changing their geographic or elevational range (Moritz et al. 2008) while others remain in place but adapt by altering their body size (Smith et al. 1998, Smith and Betancourt 2006), phenology (Parmesan 2006), local population density beyond variability on the scale of several years, or gene frequencies or genetic diversity (Hadly et al. 1998, Root et al. 2003, Rubidge et al. 2012, Bi et al. 2013, Oliver and Morecroft 2014). Several studies of Sierra Nevada mammals have found that even closely-related mammal species responded idiosyncratically to climate over the past ~100 years (Moritz et al. 2008, Rowe et al. 2015).

A first step in understanding such responses is establishing a baseline of information on presence, abundance, and spatial variation of mammal species in selected regions, as well as how that spatial variation compares with the temporal fluctuations of the same species through thousands of years. This study, therefore, was undertaken as a preliminary analysis of current spatial variation in the abundance of the small mammals of southeastern Utah, with the purpose of learning how species commonly preserved in the fossil record (see Chapter 2) sort geographically in relation to variation in their abiotic environment. Here, I evaluate spatial differences in species richness using occupancy modeling and metrics of taxonomic difference, and I assess proportional and rank abundance across sites. Differences in abundance are one of the first ways a species responds to its environment: declining abundance precedes extirpation and is therefore a valuable metric of early changes in a community (Blois and Hadly 2009). This study estimates the present-day level of taxonomic and abundance variation across the landscape at a single point in time. With additional surveys over the course of multiple years, this information can then be compared to past and future levels of variation to determine if mammalian diversity patterns in this region vary more than would be expected given the range of variation they exhibited over past centuries and millennia.

1.2 Study Area

San Juan County encompasses part of the southeastern corner of Utah, from the Colorado River east to the Colorado state border, and south of Moab. It is 19% multi-use public land (BLM, USFS) where cattle grazing, off-road vehicle use, hunting, mineral and fossil fuel extraction, and recreation including hiking, biking, rock-climbing, etc., occur to varying degrees across the region. Another 41% is managed by the National Parks Service, including Canyonlands National Park and Natural Bridges National Monument, where many recreation activities are also permitted (obvious exceptions include off-road vehicle use and hunting). State and Bureau of Indian Affairs land make up 5% and 26%, respectively, leaving 8% private land (Godfrey 2008). While much of this region remains un-urbanized, human impacts—both historic and ongoing—are pervasive even in the National Parks; for example, in Canyonlands NP grazing was permitted across much of the southeastern half of the park until the 1970s (Mark Miller, Canyonlands NP, Heidi Redd, Indian Creek Cattle Company, *personal communication*).

San Juan County contains predominantly semi-desert ecosystems, with a mixture of piñon-juniper, salt-desert shrub, sagebrush, shrub steppe, and patches of grassland (Ramsey and

West 2015). Montane regions like the Abajo and La Sal Mountains are characterized by subalpine conifers, oak woodland, aspen, and montane meadows (Kelson 1951). Topographically, the region is extraordinarily varied, including tablelands, vast mesas, grabens and pockets divided by cliffs, spires and fins of sandstone, and drainages incised in deep canyons (Barnes 1993).

I conducted surveys for small mammals at eight sites in northern San Juan County, in the BLM Canyon Rims Recreation Area and in Canyonlands National Park (Figure 3.1, Table 3.1). Each site has the same general vegetation and array of microhabitats— piñon-juniper woodland, sagebrush/salt desert scrub, and grassland—but sites vary in latitude, longitude, and elevation (Figure 3.2). These sites are scattered in the upland region north and west of the Abajo Mountains and southwest of the La Sal Range, east of the Colorado River, and west of a broad swath of arid highlands called the Sage Plain (Kelson 1951), or, more locally, Dry Valley. Canyon Rims spans over 100,000 acres south of Moab, Utah, and flanking the southern and eastern borders of the Canyonlands NP Needles and Island in the Sky Districts. Two surveys in Canyon Rims were conducted in Beef Basin [Middle Park (MP) and South Plain (SP)], a remote area south of the Needles District; two were near Rone Bailey Mesa east of Canyonlands NP and west of Highway 191 by ~3-5 km [West of Rone Bailey (WRB) and East of Rone Bailey (ERB)]; and 2 were at the feet of the Abajos, one directly north of Shay Mountain [Shay (SH)] and one northwest of Horse Mountain (between Beef Basin and the Abajos) [Cedar Mesa (CM)]. All sites in Canyon Rims were grazed during the year of survey and for many decades previous. Surveys in Canyonlands NP were conducted in the Needles District in two “pockets” along the Salt Creek Drainage [Tower Ruin Basin (TRB) and Salt Creek Pocket (SCP)]; these sites were last grazed in the 1970s (Mark Miller, Heidi Redd*, personal communication*).

2. Methods

2.1 Mammal Surveys

I surveyed a subset of the small mammal community at the 8 sites in San Juan County (Figure 3.1; Table 3.1) in spring (mid-April through mid-June) and fall (September-October) of 2014, a total of 8064 trap nights (4608 in spring and 3456 in fall). Preliminary surveys in Fall of 2013 were made at two of these sites, ERB and WRB. One site, TRB, was surveyed in both seasons, but no animals were captured in spring of 2014. Two sites, SH and SCP, were only surveyed in spring 2014.

Surveys were conducted using a targeted trap line approach (Wilson et al. 1996, Terry 2010a,b) with one trap line in each of the three microhabitats at these sites: grassland (a mixture of native, introduced, perennial and annual species), piñon-juniper woodland, and sagebrush/salt desert shrub (mainly salt bush (*Atriplex* spp.) and winterfat (*Krascheninnikovia lanata*)). These three microhabitats were surveyed at each site with the goal of ascertaining which mammal species are most commonly associated with particular plants or communities (e.g., chipmunks in piñon-juniper) and to compare relative abundance among microhabitats. Each trap line consisted of 40 Sherman and 8 Tomahawk live traps set 10 paces (approximately 10 meters) apart (5 Sherman followed by 1 Tomahawk, repeated along the trap line). Traps were baited with oats and peanut butter, supplied with cotton batting for insulation during cold nights, and traps were opened at dusk, checked in the morning, and then closed during the day. For all animals captured, sex, reproductive status, and weight were recorded, and the animal was marked with permanent marker, usually on the venter. These marks were typically nearly imperceptible by the final day of trapping, particularly if the weather had been wet.

I surveyed nine species of small mammals: *Neotoma albigula*, *Onychomys leucogaster*, *Peromyscus maniculatus*, *P. truei*, *Dipodomys ordii*, *Perognathus flavescens, P. parvus*, *Ammospermophilus leucurus*, and *Tamias rufus*. Taxonomy follows Wilson and Reeder (2005). These surveys targeted nocturnal and crepuscular species, but *Tamias rufus* and *Ammospermophilus leucurus*, both diurnal, were frequently captured, possibly in the early morning hours as I began checking the trap lines, which sometimes took up to 4 hours. Preliminary trapping in fall 2013 included pitfall traps for surveying shrews (genus *Sorex* and *Notiosorex*), but I did not use pitfall traps in spring and fall 2014 because 1) shrews were never captured in the preliminary surveys, 2) the environments surveyed are extremely unlikely to harbor shrews, and, 3) pitfall traps were not permitted in the National Park sites (TRB and SCP) and so shrews could not be included in cross-site comparisons. Some taxa that were observed in the area or are likely present were not included in this analysis because they require targeted trapping/survey techniques that could not be kept constant across sites in this study. This includes hares and jackrabbits (genus *Lepus* and *Sylvilagus*), pocket gophers (genus *Thomomys*), prairie dogs (genus *Cynomys*), and mesocarnivores like weasels (genus *Mustela*), skunk (genus *Spilogale* and *Mephitis*), and ringtail (*Bassariscus astutus*).

Generally, animals captured were released immediately back into the environment at the site of capture. Rare trap mortalities were prepared for skeletonization, standard measurements were recorded (total, tail, hind foot, and ear from notch length; testes length x width; and weight), and a liver sample was preserved in ethanol (Appendix 3.1). These specimens were deposited at the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ).

All trapping was done in compliance with the American Society of Mammalogists guidelines for animal care (Sikes et al. 2011), under Utah Department of Wildlife Resources permit #6COLL9140, National Parks Service permit #CANY-2014-SCI-0010, and University of California, Berkeley Animal Care and Use Committee Animal Use Protocol #R357-0314.

2.2 Occupancy modeling

I used occupancy modeling to address two over-arching questions: 1) what is the detection rate for each species and how likely is it that absences in my data are true absences; and, 2) is site occupancy predicted by measured site variables like elevation, annual precipitation, etc.? I developed detection models to estimate the detection probability for each species at each site. The input data for these models were the nightly presence/absence records for each species for each site, pooled across the three trap lines. A species was scored as present if any individual was captured on a night of the four-night trapping period, so the data were comprised of a sequence of four 0s (absences) and 1s (presences) per season, per species. The "trap history" of a species sampled only on the first night would then be "1000," a species sampled on both the first and last nights would be "1001," and so on. For a multi-season model with 2 seasons, the data for a single species would be two sets of trap histories, one for each season (Mackenzie et al. 2006).

While trap effort was the same across sites and seasons, time of year can influence species behavior: for example, foraging behavior may be influenced by cold weather and food availability: some taxa, like *Peromyscus* and *Perognathus*, enter short-term (daily to several days) torpor during food shortage or temperature extremes, while others, like ground squirrels, have seasonal aestivation/hibernation cycles so they are not active for months at a time and are thus not trappable (Schmidt-Nielsen 1964). To account for this, I used multi-season single species models and included date of survey as a covariate in the detection models. From the detection probability, p, for each site (i), species (j) and season (k), I calculated the probability of false absence, p(fa): $p(fa)_{ijk}=1-p_{ijk}$.

I developed occupancy models for each species using site elevation, latitude, and longitude as covariates. I constructed 13 geographic models that included all linear and multiplicative combinations of these terms (Appendix 3.2). I also constructed 13 climatic models using annual, spring (March-May), summer (June-August), fall (September-November, and winter precipitation (December-February), maximum summer temperature, and minimum winter temperature. To model interactions between the climatic variables, I used only annual precipitation, minimum winter temperature, and maximum summer temperature (Appendix 3.2). Climate data were download from the PRISM Climate Group (2015) and are 30-year normals, interpolated and spatially averaged over $4km^2$ around each survey site (Table 3.1). I then compared all geographic and climatic models using Akaike Information Criterion (AIC) model selection (Mortiz et al. 2008, Fisk and Chandler 2011): the best model has the lowest cumulative AIC (AICc) score (Appendix 3.2). I tested for a correlation between the three geographic variables and the seven climatic variables to ensure that there was no autocorrelation between the geographic and climatic models; there were no significant correlations using either linear regression or Spearman's tests.

The criterion for true absence was a probability of a false absence ≤0.10 (Smith et al. 2013); however, this criterion was never met.

All occupancy modeling was performed using the unmarked package (Fisk and Chandler 2011) in the R Project for Statistical Computing (R Core Team, 2015).

2.3 Comparison of diversity across sites

Because trap effort was the same across sites it was not necessary to standardize for trap effort. I compared 5 aspects of diversity across sites: a) richness, b) taxonomic composition, c) rank abundance, d) proportional abundance, and e) evenness. I made three sets of comparisons: 1) $site_{i\ (spring)}$ versus $site_{i\ (fall)}$, 2) $site_{i\ (spring)}$ versus $site_{j\ spring}$, $site_{k\ spring}$ and so on, and 3) $site_{i\ (spring\ +\ fall)}$ versus $site_{j(spring\ +\ fall)}$, $site_{k(spring\ +\ fall)}$, and so on. For all of the parameters and tests described below, my null hypothesis was that there was no difference between sampling sites.

Richness was estimated using both rarefaction (Raup 1975, Terry 2010a,b) and shareholder quorum subsampling (SQS) (Alroy 2010). Because rarefaction is the prevailing method for computing and standardizing richness estimates I have included it for comparison, but SQS gives more accurate estimates of relative standing diversity. While the goal of traditional rarefaction is uniform sampling, the purpose of SQS is "fair" sampling that is reflective of the true standing diversity. In rarefaction the sample size, n, is fixed, so one would resample the data n times, compute the number of species (richness) in that re-sample, iterate repeatedly, then average the richness across all iterations. In SQS, n is not fixed; rather, SQS fixes "coverage"—the proportion of the entire frequency distribution represented by the species in the resample. If one sets coverage to 0.4 then samples one specimen that has a proportion of 0.5, the resampling stops and the richness is 1. If the community is extremely diverse and each species represents only a small proportion of the overall distribution, it will take more draws to reach the desired coverage, and richness will be higher. Most important, rarefaction dampens the richness of very diverse samples, so relative diversity estimates are not linear, whereas in SQS a site that is twice as diverse as another has an SQS richness value that is twice as large (Alroy 2010).

Communities that are more even tend to persist longer during environmental stress, so evenness is potentially a powerful predictor of community stability over time (Blois et al. 2010). Evenness was quantified using Hurlbert's Probability of Interspecific Encounter (PIE) (Hurlbert 1971), which measures the likelihood that two specimens drawn from the sample will be from the same species (Gotelli and Ellison 2013). A major advantage of PIE over other measures of evenness is that it is independent of sample size (Hurlbert 1971, Gotelli and Ellison 2013). PIE ranges from 0 to 1, with 1 indicating a perfectly even community in which all species have the same abundance.

I used the corrected Forbes index (F') (Alroy 2015) to compare taxonomic composition. F' is more accurate than other commonly-used indices, including Dice, Simpson, and Jaccard when sampling is incomplete or uneven (Alroy 2015). The Forbe's index varies from 0 to 1, with a value of 1 meaning all species are shared between sites. Differences in rank abundance were computed using Spearman's rank-order correlation tests (Terry 2010a). Spearman's rho values vary from -1 (inverse relationship) to 1 (perfect positive correlation). I measured pairwise similarly in proportional abundance using the Bray-Curtis similarity Index, which varies from 0 to 1, where a value of 1 indicates that the two communities have the same taxonomic composition and abundance distribution (Terry 2010a). For these three metrics, I used Monte Carlo analysis to test if the metric of interest was significantly different from random. Monte Carlo analysis randomly reassigns group membership of the observed data, testing the null hypothesis that the true difference between groups is no more different than if the data were randomly shuffled. In this way, it uses the observed data to gauge how extreme the test statistic is (Stegner and Holmes 2013). More specifically, I created a null distribution of the metric for each pairwise comparison by assuming that individuals are randomly distributed across the landscape, i.e., the taxonomic identity of individuals found at each site is not determined by site attributes, but number of individuals is fixed. I generated a list of individuals sampled in both sites, then randomly re-assigned all individuals to one site or the other. I then computed the metrics of interest: F', Spearman's rho, and Bray-Curtis index. This process was repeated 1000 times to generate the null distributions. I then determined if the metric for the observed data fell with in the 95% confidence interval of the null distribution.

3. Results

Table 3.2 summarizes trapping survey results including numbers of each species captured each season and during both seasons. Number of individuals captured at a site varied from 0 (TRBspr) to 165 (ERBspr) per season, and trap success varied from 0% to 62% per night (Appendix 3.3).

3.1 Occupancy modeling

Table 3.3 summarizes the results of occupancy and detectibly models. Detection probabilities for all species are low—very low for *Ammospermophilus leucurus* (p=0.189 both spring and fall), and ranging from 0.397 to 0.753 for other species—except for *Peromyscus maniculatus* (both seasons) and *P. truei* (fall only) (Table 3.3).

In all instances where a species was not captured at a site, the likelihood of false absence, p(fa), was unacceptably high (p(fa)>0.10) (Table 3.3). However, p(fa) was below 0.50 for all species except *Onychomys leucogaster* (p(fa) between 0.251 and 0.660), *Ammospermophilus leucurus* (p(fa)=0.811), *Neotoma albigula* (p(fa)=0.529), and *Perognathus flavescens* (p(fa)=0.560). Given these results, subsequent conclusions that depend on using these modern presence/absence data must be considered suggestive rather than firm, because the probabilities of detection and false absence demonstrate high likelihood that most sites and species are incompletely sampled.

For most species (7 out of 9) detectibly was not related to the date or season of survey (Table 3.3). Exceptions were *Peromyscus truei* and *Onychomys leucogaster,* both of which were caught on fewer nights in the spring. *P. truei* and *P. maniculatus* were captured in all sites during both seasons so the best occupancy model for these species was constant (the "dot" model). Occupancy of two species, *Ammospermophilus leucurus* and *Onychomys leucogaster*, was best modeled using climate covariates. In the remaining four species, covariates of occupancy were some combination of elevation, latitude, and longitude (Table 3.3).

3.2 Spatial Variation in Diversity

Table 3.4 summarizes the results of SQS and rarefaction at different sampling levels. In this study, diversity estimates using SQS are consistently lower than rarefaction even when rarefaction sample size is low and SQS coverage is high. However, the underlying assumptions and mathematics of these two techniques are different and so they are not directly comparable. While the magnitude of richness is different, both rarefaction and SQS tend to rank diversity of sites in similar order—the most diverse sites calculated by SQS tend to also be the most diverse when using rarefaction. For rarefaction analysis (n=40), sites (across seasons) were ordered from most to least rich as follows: SP, WRB, MP, TRB, CM, ERB. For SQS (q=0.8) (and, incidentally, for the rarefaction analysis when n=9 and n=20), the order of sites from most to least rich was: SP, MP, TRB, WRB, CM, ERB. Two sites, MP and SP, had consistently high PIE scores as compared to the other sites. In contrast, ERB had low evenness during both seasons and when seasons were binned. Sites that had high evenness also tended to have higher estimated richness and vice versa: sites with low evenness had low estimated richness even when raw richness was high, like ERB and WRB.

Across seasons, sites overall had similar taxonomic diversity (corrected Forbes index), but proportional and rank order abundance (Bray-Curtis and spearman's tests, respectively) varied (Table 3.5abc). *Peromyscus maniculatus* was the most common species across sites and seasons, except for the spring survey of SP which had very low sample size, but rank abundance of other species varied across sites.

In the spring dataset (Table 3.5a), all of the Bray-Curtis similarity values resulting from pairwise comparisons are significantly higher than expected if individuals were distributed randomly, except for 2 pairwise comparisons where the Bray-Curtis index was no different from expected ($\mathrm{WRB}_{\mathrm{spr}}$ versus $\mathrm{MP}_{\mathrm{spr}}$ and $\mathrm{SCP}_{\mathrm{spr}}$) and 7 comparisons where the Bray-Curtis index was lower than expected: $\mathrm{CM}_{\mathrm{spr}}$ versus $\mathrm{MP}_{\mathrm{spr}}$, $\mathrm{SCP}_{\mathrm{spr}}$, and $\mathrm{SH}_{\mathrm{spr}}$; $\mathrm{ERB}_{\mathrm{spr}}$ versus $\mathrm{WRB}_{\mathrm{spr}}$; $\mathrm{MP}_{\mathrm{spr}}$ versus $\mathrm{SCP}_{\mathrm{spr}}$ and $\mathrm{SH}_{\mathrm{spr}}$; and $\mathrm{SCP}_{\mathrm{spr}}$ versus $\mathrm{SH}_{\mathrm{spr}}$. With regard to species composition as measured by the corrected Forbes index, $\mathrm{CM}_{\mathrm{spr}}$ and $\mathrm{WRB}_{\mathrm{spr}}$ are more similar than random while $\mathrm{SH}_{\mathrm{spr}}$ is less similar to $\mathrm{CM}_{\mathrm{spr},}$ $\mathrm{ERB}_{\mathrm{spr}}$, $\mathrm{MP}_{\mathrm{spr},}$ and $\mathrm{SCP}_{\mathrm{spr}}$ than random. This is because most sites have more or less the same set of species, but $\mathrm{SH}_{\mathrm{spr}}$ is missing 3 species common across sites (*Dipodomys* *ordii*, *Tamias rufus*, and *Onychomys leucogaster*). While spearman's rho (rank abundance) was lower than random for MP_{spr} versus SH_{spr} and SCP_{spr} versus WRB_{spr}.

In the fall (Table 3.5b), all sites were less similar in proportional abundance (Bray-Curtis) than expected if individuals were distributed randomly among sites. The only exception was CM versus ERB_{fall}, which fell within the range of expected values. As with the spring dataset, the corrected Forbe's index shows that all sites sample essentially the same taxonomic diversity and fall within the range of expected F' values, except SP_{fall} versus MP_{fall} which are less similar to one another than expected. Rank order abundance is less correlated than expected for both TRB_{fall} and MP_{fall} versus SP_{fall} and WRB_{fall}. Both TRB_{fall} and MP_{fall} Both have relatively high numbers of *Peromyscus truei* and *Onychomys leucogaster* compared to other sites, and lower raw richness but relatively high evenness.

When the survey data are binned across seasons (Table 3.5c), all pairwise comparisons of sites have significantly lower Bray-Curtis values except for ERB versus SP, CM, MP, and TRB which are more similar than random. Taxonomic similarity is lower than expected for WRB versus MP and TRB, and higher than expected from WRB versus CM. This is probably because WRB samples all nine species included in the analysis; CM only samples four, and MP and TRB both sample 6. Rank order abundance is lower than expected for WRB versus all sites except SP: this is because *Dipodomys ordii* and *N. albigula* are higher in rank abundance at WRB than at any other site. SP and TRB also have lower than expected rank order abundance correlation because TRB has extremely high numbers of *O. leucogaster*, very few *N. albigula* compared to SP, and samples neither *D. ordii* (also relatively abundant at SP) nor *Perognathus parvus*. Rank order abundance at CM is less correlated than expected with WRB and MP because CM does not sample species that are high in rank abundance at those sites (*D. ordii* at WRB and *O. leucogaster* at MP).

In assessing changes in seasonal diversity, I found that most sites are less similar than expected from spring to fall (Table 3.6). For CM, ERB, WRB, and MP Bray-Curtis indices are lower than expected, whereas SP is more similar than expected from spring to fall. Taxonomic composition (F') is less similar than expected at ERB and MP from spring to fall; conversely, similarity is higher at SP than expected. Spearman's tests rho values fall within the range of expected values, meaning rank abundance is no more similar between spring and fall than if individuals were distributed randomly among seasons

4. Discussion

In these surveys, I sampled nine taxa common in arid environments of the southwestern US. I expected to trap several additional species based on the results of other studies and museum specimen records documented in the VertNet distributed database (www.vertnet.org). Kelson (1951) made a broad survey of rodents in eastern Utah from the Uinta Range south to the Arizona border. In the following year, Durrant (1952) summarized the ranges of all mammal species and subspecies known from Utah at the time. Neither Kelson nor Durrant undertook systematic trapping; instead they compiled trapping, museum records, and other physical specimen records to evaluate the geographic distribution of subspecies across the Colorado River drainage in eastern Utah. Both identify faunal subdivision across the state: within what they called the Colorado Plateau Faunal Area, Canyonlands Province, they describe the "San Juan Subcenter" which encompasses my study sites. Species that characterize the San Juan Subcenter include species that I captured— *Dipodomys ordii* (Ord's kangaroo rat), *Peromyscus* *maniculatus* (deer mouse), *P. truei* (piñon mouse), *Neotoma albigula* (white-throated woodrat), *Tamias rufus* (Hopi chipmunk), *Ammospermophilus leucurus* (white-tailed antelope squirrel), *Onychomys leucogaster* (northern grasshopper mouse), *Perognathus flavescens* (Plains pocket mouse), and in addition, species that could have been captured in my trapping protocol, but were not: *Xerospermophilus spilosoma* (spotted ground squirrel), *Otospermophilus variegatus* (rock squirrel), *Tamias minimus* (least chipmunk), *Peromyscus boylii* (brush mouse), *P. crinitus* (canyon mouse), *Neotoma cinerea* (bushy-tailed woodrat), *N. mexicana* (Mexican woodrat), and *Reithrodontomys megalotis* (western harvest mouse). Also present in Kelson's and Durant's "San Juan Subcenter" were species that were not targeted by my trapping protocol: *Cynomys gunnisoni* (Gunnison's prairie dog) and *Thomomys bottae* (Botta's pocket gopher).

Between 1972 and 1978 Armstrong (1979) assembled faunal data for nine different vegetation zones in Canyonlands NP, including the three microhabitats included in my surveys. In concordance with Kelson (1951) and Durrant (1952), Armstrong reported all the species I sampled, along with several additional taxa that he found in environments similar to those that I surveyed. His faunal list included: *Neotoma cinerea*, *N. lepida*, *N. mexicana*, *Onychomys leucogaster*, *Peromyscus boylii*, *P. crinitus*, *P. maniculatus*, *P. truei*, *Reithrodontomys megalotis*, *Dipodomys ordii*, *Perognathus apache* (*flavescens*), *P. parvus* (but only west of the Colorado River), *Ammospermophilus leucurus*, and *Tamias quadrivittatus.*

In addition to *Perognathus flavescens*, I also capture *P. parvus*, which has never been reported east of the Colorado River. The individuals I captured had particularly long tails (tails of *P. parvus* are ~110% longer than body length, <100% in *P. flavescens*) that were slightly tufted and notably bicolored (*P. flavescens* has no tuft and is lightly bicolored) (Verts and Kirkland 1988, Monk and Jones 1996). *P. parvus* is much larger than *P. flavescens* (Monk and Jones 1996, Verts and Kirkland 1988), and weights of *P. parvus* individuals that I captured ranged from 15-21g, while *P. flavescens* individuals weighed between 5-13g. In some cases, identification was made based solely on weight. At several sites (SH, SP, and WRB) I caught both *P. flavescens* and *P. parvus*, which is of interest because Williams (1978) suggests that *P. flavescens* is prevented from expanding into *P. parvus* territory by interspecific competition.

Comparison of my surveys to these previous studies, conducted over half a century ago, raises the question: why did I encounter a smaller subset of the diversity sampled in the recent past? Several possible explanations include: 1) some species have genuinely been extirpated; 2) congeners segregate the habitat and my surveys did not sample enough microhabitats; 3) previous studies surveyed different or additional microhabitats; or, 4) the "missing" species are present in my sites but not sampled (insufficient sampling). With regard to 2) and 3), microhabitats relevant to mammal species are defined not only by the dominant vegetation, but often by more cryptic features like soils, distance to permanent and/or ephemeral water sources, etc. As noted above, occupancy modeling suggests I would record more species in my sites with additional sampling. Armstrong's surveys occurred over the course of 7 years and he included specimens collected in a variety of ways and not strictly from trap surveys, so more intensive and different sampling protocol may explain why he found higher diversity than I did.

In 1972 and 1973 Armstrong trapped specimens of *Reithrodontomys megalotis* in shrublands/grasslands less than 5km from SCP and TRB and along the same drainage (Salt Creek) (Museum of Texas Tech University Mammal Collection 2015); since then, the only other VertNet records of *R. megalotis* in the region is an individual from the northern edge of the La Sals (Museum of Southwestern Biology Mammals 2015).

I captured only two of four species of *Peromyscus* that are generally found in southeastern Utah: *P. maniculatus* and *P. truei*. Previous surveys and accounts of the fauna of this region also include *P. crinitus* and *P. boylii*. Though Armstrong found both *P. crinitus* and *P. boylii* in a range of habitats, these species are generally considered to have more specific habitat requirements than *P. maniculatus* (Kelson 1951, Smith 1981). *P. crinitus* is found in a range of plant communities, but always associated with bare dirt or rock, or even vertical cliffs (Johnson and Armstrong 1987). In Utah—Zion and Canyonlands National Parks specifically—*P. boylii* is usually found in scrub oak and canyon bottoms (Kalcounis-Rueppell and Spoon 2009) and, according to Kelson (1951), populations of this species are small and highly localized. During my preliminary trapping work in fall 2013, in addition to *P. truei* and *P. maniculatus* I also captured *P. boylii* near WRB—one of the trap lines during that season was arranged in a relatively mesic and shady canyon along the cliffs of Rone Bailey, vegetated by a mixture of piñon-juniper community species and southern mountainbrush species like squawbush (*Rhus aromatica*) and oak (*Quercus gambelii*) (van Buren et al. 2011). In 2014 my trap lines at WRB were further from the mesa and did not include slickrock or mesic pockets, which may explain why I did not capture *P. boylii* or *P. crinitus*. However, ERB, TRB, and SCP each had one trap line within 5 meters of slickrock cliffs and benches, and trap lines at SCP and CM were within 50 meters of mountainbrush communities so the appropriate microhabitats to capture these species were indeed sampled at these sites.

Competition among congeners and different habitat requirements explain at least partially why I only sampled *Neotoma albigula* while Armstrong found *N. mexicana*, *N. lepida* (desert woodrat), and *N. cinerea* in sagebrush shrublands. Dial (1988) found that *N. albigula* is behaviorally dominant to the smaller-bodied *N. stephensi* (Stephen's woodrat) and *N. devia* (Arizona woodrat); when *N. albigula* was experimentally removed other species took over the newly-vacated den sites and, conversely, when *N. albigula* was introduced to new sites it drove out other species from occupied dens. Cornely and Baker (1986) note habitat partitioning among *N. mexicana*, *N. albigula*, and *N. cinerea* in places where their ranges overlap. Further, according to Kalcounis-Rueppell and Spoon (2009), *N. mexicana* and *Peromyscus boylii* are often found co-occurring; both favor rocky scrub oak (*Quercus*) and *Mahonia* thickets.

Only a handful of *Neotoma* specimens from southeastern Utah are recorded in VertNet. Over the last century several specimens of *N. cinerea* have been collected in the region, including one about 5km north of ERB in 1982 (LSUMZ Mammals 2015) and one from Dry Valley in 1939 (Museum of Vertebrate Zoology Mammal Collection 2015). The locations of Armstrong's captures in the 1970s were unfortunately not reported. *N. mexicana* was found near Rone Bailey in 1983 (Fort Hays Sternberg Museum Mammal Collection 2015), Armstrong found this species in the Salt Creek Drainage (Museum of Texas Tech University Mammal Collection 2015), and several earlier specimens are from Monticello (University of Kansas Biodiversity Institute Mammalogy Collection 2015) and Bluff (Museum of Vertebrate Zoology Mammal Collection 2015). Specimens of *N. albigula* from Castle Valley in 1968 (University of Kansas Biodiversity Institute Mammalogy Collection 2015, University of Michigan Museum of Zoology Mammal Collection 2015), over 50km northeast of my surveys, and from Bluff in 1939 (Museum of Vertebrate Zoology Mammal Collection 2015), over 75km south of my surveys, are the only specimens of the white-throated woodrat reported in VertNet from southeastern Utah. All of the *N. lepida* captured by Armstrong were from the Island in the Sky district of Canyonlands (Museum of Texas Tech University Mammal Collection 2015), north of my sites and across the Colorado River; one other individual from southeastern Utah was collected in

1972 between Monticello and Blanding (University of Washington Burke Museum Mammal Collection 2015). *N. lepida* is generally found west of the Colorado Plateau, in the Great Basin and Mojave Desert (Verts and Carraway 2002), and Kelson (1951) describes it only from west of the Colorado, so its absence from my surveys is not particularly surprising. Overall, there is evidence for the presence of all four *Neotoma* species in southeastern Utah; why I only sampled one is not clear but may have to do with the environments where I trapped.

Also missing from my surveys were several sciurids that purportedly inhabit this region. Armstrong found *Tamias quadrivittatus* (Colorado chipmunk) in piñon-juniper and desert scrub—probably he was seeing what is now called *T. rufus,* which was split from *T. quadrivittatus* in 1980 (Patterson 1984), and which I also captured in these environments. In 1982, a specimen designated *T. quadrivittatus* was collected near Rone Bailey, but I suspect this individual is also *T. rufus*, because *T. quadrivittatus* is typically found at higher elevations in ponderosa and spruce/fir forests (Best et al. 1994) while *T. rufus* prefers lower elevations and is common in piñon-juniper woodland (Burt and Best 1994), as around Rone Bailey. Although I saw a single *Otospermophilus variegatus* at MP, which I observed at length while it ate spilled oats near my trap lines, I never captured any. Specimen records and range maps also suggest that *Xerospermophilus spilosoma* and *Tamias minimus* might be present at my sites, though the former is uncommon in Utah (Kelson 1951) and the latter is generally found at higher elevations on the Colorado Plateau (Bartels and Thompson 1993, Verts and Carraway 2001). Specimen records for these three species are from the Abajos, La Sals, and the higher elevation regions near Blanding and Monticello (Museum of Vertebrate Zoology Mammal Collection 2015, Museum of Texas Tech University Mammal Collection 2015, Museum of Southwestern Biology Mammals 2015). Although my surveys targeted nocturnal species (sciurids are diurnal), I sometimes finished checking the trap lines as late as 10 a.m. I captured chipmunks and antelope ground squirrels even in the early morning hours, suggesting that if other sciurid species were present I would have captured them occasionally. However, trap effort was much lower for diurnal than for nocturnal species, both in terms of length of time and number of traps. Traps were open for only a few hours of daylight, but open throughout the night. Additionally, fewer traps were available in the morning because some traps were occupied by animals captured during the night—this reduced the number of traps by a variable amount, depending on trap success during the night which was very high at some sites (e.g., ERB) and very low at others (e.g., SP). These biases likely explain the low probabilities of detection for *Tamias rufus* and *Ammospermophilus leucurus*, and potentially explain why I never sampled *Otospermophilus variegatus*.

Of the species not targeted by my trapping protocol, my observations suggest that they are still present in the region, though not at all sites. A large Gunnison's prairie dog town is currently occupied just southeast of ERB and fossil teeth identifiable to *Cynomys* have been recovered in deposits near ERB (East Canyon Rims 2, University of California Museum of Paleontology (UCMP) Locality #36221) and WRB (Rone Bailey Alcove, UCMP Locality # 36222) (Chapter 2). *Thomomys* teeth are also abundant in these fossil deposits, and I have noted gopher mounds at MP, indicating that gophers were present within approximately a year of the surveys.

Insufficient sampling may explain why I did not encounter several species recorded by previous researchers, but it is also problematic in modeling probability of occupancy for the species that I did capture. Detection models demonstrate that the probability of false absence is too high to confidently reject the possibility that species were present but not sampled at some sites. That said, only *Ammospermophilus leucurus, Onychomys leucogaster, Neotoma albigula,* and *Perognathus flavescens* had probabilities of false absence higher than 50%; while there is a chance that the other absences in my dataset are false, it is technically more likely that they are true absences (less than 50% probability they are false). As more surveys are added to this dataset—both additional sites and repeated visits to the eight sites discussed here—the statistical power of the occupancy models will increase and will likely confirm that some of these absences are real and reflective of differences in species habitat preferences or geographic range. Additional survey techniques, like hand surveillance with a spot light at night, are yet another means by which to improve this dataset and may reveal more taxa, like mesocarnivores and leporids.

The occupancy models I developed are challenged by several issues in addition to high probabilities of false absence, and should be considered preliminary at best. The number of sites surveyed, and the range of elevations, latitudes and longitudes covered by those sites, is insufficient for drawing meaningful conclusions about the habitat requirements of these species. However, if these occupancy models are indicative of the relationship between species and environment, they highlight the varied ways in which mammals sort across the landscape. Two species are common in all sites: *Peromyscus maniculatus*, which is a habitat generalist, and *P. truei*, which is a piñon-juniper specialist, captured everywhere because all survey sites here included piñon-juniper woodland. Occupancy of some species is predicted by temperature (*Onychomys leucogaster*), while for others precipitation is a better model (*Ammospermophilus leucurus*). The remaining species track an aspect of the environment that varies with a combination of elevation, latitude, and longitude (*Neotoma albigula*, *Dipodomys ordii*, *Perognathus parvus*, *P. flavescens*, *Tamias rufus*). It is important to emphasize that occupancy modeling selects among the parameters that I provided, which were hardly an exhaustive list of possible biotic and abiotic variables, and so these models simply show that species respond differently to their environments for as-yet unknown reasons. Additional covariates will be an important addition to this dataset. As an example of a biotic covariate, yearly abundance of *P. truei* and *T. rufus* may be linked to piñon masting events (James Patton, *personal communication*). An important abiotic covariate might be edaphic conditions: soil type probably determines site occupancy for species like *D. ordii* which requires sandy soils (reviewed in Garrison and Best 1990). Further, I would expect edaphic conditions in this region to correlate with both elevation and latitude/longitude because of the way in which the geology of the Colorado Plateau has been uplifted, folded, tilted, and eroded. At sites further to the west, the predominant outcrops are Cedar Mesa Sandstone (SP, MP, TRB, SCP), but outcrop at eastern sites is Entrada Sandstone (ERB, WRB) (Huntoon et al. 1982, Barnes 1993). Outcrops at CM are Moenkopi Formation, and at SH are Navajo Sandstone (Huntoon et al. 1982, Barnes 1993). The soils at these sites are all derived from Quaternary alluvium and eolian deposits (Huntoon et al. 1982), but the different parent materials might generate different soil properties. In addition to more sites, including more covariates would likely improve and refine the occupancy models—variables like soil type, slope and aspect, specific vegetation information including three-dimensional structure, etc. However, no amount of additional environmental information will improve occupancy models when the initial trap data are limited, as they are here.

In spite of the need for more surveys and additional site-specific information, comparison of diversity metrics among sites reveals an important pattern: although the same species are present across sites (more or less), differences in abundance are not random and sites are less similar to one another than if individuals were distributed randomly. This suggests that, although the species pool is the same, some aspect of the sites drives differences in abundance among them. However, with only two seasons of data, these non-random abundances could also be attributable to other factors not connected to site characteristics. Given the limitations of the data, it is not yet possible to determine, for example, if the observed differences in abundance might reflect short-term population booms or busts rather than site attributes. At most sites, diversity was significantly different between spring and fall in terms of proportional abundance and in 3 out of 5 sites in terms of taxonomic composition as well. This is strong support for the role of short-term population booms and busts, perhaps connected to breeding season or weather patterns like late summer monsoons. With regard to climate covariates, temperature and precipitation 30-year normals, as well as periodic extreme events like drought or extreme cold, likely govern whether a species can exist at a site in the long term, which is reflected in the occupancy models if we assume that all absences are true absences. However, yearly temperature and precipitation values—data that that is not available for these surveys—are expected to have a greater influence on the abundance dynamics captured by my single year of surveys.

Yet another possible explanation for site-by-site differences in species abundance and composition is the long tradition of rodent and carnivore extermination on rangelands. Coyotes are avidly hunted in Utah: in 2013 and 2014, 375 and 421 coyotes, respectively, were killed (and reported) in San Juan County alone, mainly along Utah highway 191 which is within 5km of ERB and WRB but far from the other survey sites (Utah Division of Wildlife Resources 2013, 2014). Ecological release from predators could explain the remarkably high abundance of *Peromyscus maniculatus* at these two sites. Additionally, between 1936 and 1938, the Civilian Conservation Corps (CCC) undertook what was, at least until that point, the largest rodent extermination project in Utah (Blanding CCC Camp DG-34 1936, 1937, 1938). In 1936, they distributed poisoned grain across 130,000 acres of rangeland between Dry Valley and Blanding (a subset of this region was treated in 1937 and 1938), and estimated a 92% eradication success rate (Blanding CCC Camp DG-34 1936, 1937, 1938). Unfortunately, exact locations were not recorded in the CCC reports, but ERB and WRB are in Dry Valley so it is highly likely that extermination took place there. The other survey sites are all in current (SP, MP, CM, SH) or former rangeland (SCP and TRB) and may very well have been included in these, or other, treatments as well. While the focus of eradication efforts was prairie dogs, kangaroo rats, jackrabbits, hares, and occasionally rock squirrels, many other species would have been impacted and recovery rates would necessarily vary depending on the extent of the population exterminated, metapopulation dynamics, and other intrinsic variables like reproductive rate. It is certainly possible that eradication treatments were repeated after the CCC efforts, though I have not seen records of it. Though many of the sites I surveyed currently harbor these “pest” species (with the exception of *Cynomys*, only found at ERB), it is possible that repeated eradication treatments impacted structural aspects of the community that are observable today, like species evenness. Blois et al. (2010) found that evenness of the small mammal community at a site in northern California was demonstrably lower after the Pleistocene-Holocene transition and remains low today even though taxonomic diversity is the same (no small mammals were extirpated/went extinct). Dominance of the “weedy” species *Peromyscus maniculatus* is responsible both for the observed low Holocene evenness in the Blois et al. (2010) study, and also in my surveys at ERB, a site that was markedly less even than the others (PIE=0.21).

5. Conclusions

The data presented here are the preliminary results of the first targeted trapping study designed to reveal fine-scale differences in species abundance and diversity in northern San Juan County, Utah. Over the course of one year, I have compiled abundance and presence/absence data on nine species: *Neotoma albigula*, *Onychomys leucogaster*, *Peromyscus maniculatus*, *P. truei*, *Dipodomys ordii*, *Perognathus flavescens, P. parvus*, *Ammospermophilus leucurus*, and *Tamias rufus.* Although the results are preliminary, some patterns are emerging: sites spanning 50km and 550m elevation range sample the same small-mammal species pool, but abundance of those species varies non-randomly, and sites are less similar in abundance than expected by random distribution of individuals. Species evenness varies among sites, and sites with low evenness are dominated by *Peromyscus maniculatus*, a "weedy" species with broad habitat requirements. Several species reported from this region in past studies are absent from my surveys, but additional field work is required to determine if these species have been extirpated or simply were not sampled. In contrast, this is the first report of *Perognathus parvus* east of the Colorado River, suggesting recent range expansion of the species. Occupancy models indicate that presence/absence of different species is determined by different aspects of their environment, and therefore species will respond idiosyncratically to future environmental changes, in concordance with a range of other studies comparing historic to modern species ranges (Moritz et al. 2008, Rowe et al. 2015). However, occupancy and detection models clearly indicate the need for more data before these patterns can be considered robust or fully explained.

Disentangling the potential effects of historical legacies, like past land use and "pest" extermination, from climate change and current land uses will require a concerted survey effort over multiple years at these and many additional sites. Necessary future work will also include day-time trapping for diurnal taxa and additional survey techniques to assess diversity of leporids, mesocarnivores, and other taxa not generally captured in folding traps. Considering the high levels of endemicity on the Colorado Plateau (Stohlgren et al. 2005) including endemic subspecies unique to the mountain ranges of southeastern Utah (Kelson 1951), these surveys should be a high priority for biological conservation. Southeastern Utah also holds high potential for the study of fundamental biogeographic principles because complex patterns of dispersal, isolation, and evolution are evident as a result of major topographic features: the Colorado River drainage and isolated laccolithic mountain ranges that have never been connected to one another (Kelson 1951).

Table 3.1: Site locations and covariates data. CM=Cedar Mesa; ERB=East of Rone Bailey; MP=Middle Park, SCP=Salt Creek Pocket; SH=Shay Mesa, SP=South Plain; TRB=Tower Ruin Basin; WRB=West of Rone Bailey. NPS=National Parks Service; BLM=Bureau of Land Management.

Site	Elevation (m)	Management	Latitude	Longitude	Precipitation (mm)					Temperature (°C)	
					Annual	Spring	Summer	Fall	Winter	Winter Min.	Summer Max.
CM	1550	NPS	37.96	-109.69	320.4	73.32	82.72	103.68	60.69	-7.23	30.4
ERB	1800	BLM	38.189	-109.427	227.45	55.09	62.29	71.18	38.9	-6.67	32.5
MP	1970	BLM	38.02	-109.91	328.59	75.2	86.9	102.28	64.21	-6.97	29.87
SCP	2100	BLM	38.137	-109.733	397.4	84.68	97.71	121.82	93.19	-7.17	28.47
SH	2040	BLM	37.98	-109.53	219.99	53.89	59.79	68.86	37.45	-6.53	32.93
SP	1880	BLM	37.95	-109.95	356.81	79.69	91.47	110.7	74.96	-6.9	29.27
TRB	1560	NPS	38.117	-109.724	320.18	73.22	82.71	103.6	60.64	-7.3	30.43
WRB	1880	BLM	38.151	-109.451	371.05	80.72	92.24	116.66	81.44	-7.13	28.27

Table 3.2: Number of individuals captured at each site during each season. SP=South Plain; CM=Cedar Mesa; ERB=East of Rone Bailey; SCP=Salt Creek Pocket; SH=Shay Mesa; TRB=Tower Ruin Basin; WRB=West of Rone Bailey; MP=Middle Park.

	Ammospermophilus leucurus			*Dipodomys ordii*			*Neotoma albigula*			*Onychomys leucogaster*			*Perognathus flavescens*			*Perognathus parvus*			*Peromyscus maniculatus*			*Peromyscus truei*			*Tamias rufus*			Total Captures		
	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.	Spr	Fall	Tot.
SP	0	0	0	0	5	5	3	2	5	1	1	2	0	2	2	1	0	1	2	26	28	2	8	10	0	0	0	9	43	52
CM	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	20	23	43	1	3	4	5	2	7	26	29	55
ERB	0	1	1	2	1	3	0	0	0	0	7	7	0	0	0	0	0	0	156	62	218	4	2	6	3	2	5	165	75	240
SCP	0			7			0			11			0			2			16			2			2			40		
SH	0			0			2			0			6			4			18			2			0			31		
TRB	0	0	0	0	0	0	0	1	1	0	9	9	1	0	1	0	0	0	0	34	34	0	8	8	0	2	2	0	54	54
WRB	1	1	2	4	7	11	3	1	4	0	1	1	2	0	2	1	0	1	69	27	96	7	5	12	1	0	1	88	42	130
MP	0	0	0	3	0	3	0	0	0	1	10	11	0	0	0	1	0	1	17	20	37	6	6	12	7	3	10	35	39	74

Table 3.3: Occupancy modeling results. AICc=cumulative AIC score. p(fa)=Probability of false absence; p=probabilility of detection.

	Ammospermo-philus leucurus		***Dipodomys ordii***		***Neotoma albigula***		***Onychomys leucogaster***		***Perognathus flavescens***		***Perognathus parvus***		***Peromyscus maniculatus***		***Peromyscus truei***		***Tamias rufus***	
Best detectibility model:	constant (AICc=0.64)		constant (AICc =0.53)		constant (AICc =0.72)		date (AICc =0.68)		constant (AICc=0.73)		constant (AICc=0.72)		constant (AICc=0.61)		date (AICc=0.99)		constant (AICc=0.73)	
Best occupancy model:	winter precip. (AICc =0.11)		lat+long (AICc =0.24)		elev+lat+long (AICc =0.19)		max. summer temp. (AICc =0.30)		elev.*long. (AICc=0.53)		elev. (AICc=0.33)		constant (AICc=0.17))		constant (AICc=0.17)		Elev.*lat. (AICc=0.21)	
Mean p	**Spr.**	**Fall**	**Spr.**	**Fall**	**Spr.**	**Fall**	**Spr.**	**Fall**	**Spr.**	**Fall**	**Fall**	**Fall**	**Spr.**	**Fall**	**Spr.**	**Fall**	**Spr.**	**Fall**
	0.189	0.189	0.626	0.626	0.472	0.472	0.397	0.753	0.440	0.440	0.550	0.550	0.964	0.964	0.751	0.998	0.534	0.534
Site p(fa)																		
CM	0.811	0.811	0.375	0.375	0.529	0.529	0.617	0.279	0.560	0.560	0.450	0.450	0.036	0.036	0.270	0.003	0.466	0.466
ERB	0.811	0.811	0.375	0.375	0.529	0.529	0.645	0.243	0.560	0.560	0.450	0.450	0.036	0.036	0.359	0.002	0.466	0.466
MP	0.811	0.811	0.375	0.375	0.529	0.529	0.536	0.251	0.560	0.560	0.450	0.450	0.036	0.036	0.107	0.002	0.466	0.466
SCP	0.811	0.811	0.375	0.375	0.529	0.529	0.593		0.560	0.560	0.450	0.450	0.036	0.036	0.208		0.466	0.466
SH	0.811	0.811	0.375	0.375	0.529	0.529	0.660		0.560	0.560	0.450	0.450	0.036	0.036	0.412		0.466	0.466
SP	0.811	0.811	0.375	0.375	0.529	0.529	0.561	0.271	0.560	0.560	0.450	0.450	0.036	0.036	0.144	0.002	0.466	0.466
TRB	0.811	0.811	0.375	0.375	0.529	0.529	0.577	0.212	0.560	0.560	0.450	0.450	0.036	0.036	0.174	0.001	0.466	0.466
WRB	0.811	0.811	0.375	0.375	0.529	0.529	0.632	0.225	0.560	0.560	0.450	0.450	0.036	0.036	0.317	0.001	0.466	0.466

Table 3.4: Species richness per site. Rarefaction values are mean ± standard error. q=quorum level; n=sample size. PIE=Probability of Interspecific Encounter.

	Raw richness	SQS			Rarefaction			PIE
		q=0.4	q=0.6	q=0.8	n=9	n=20	n=40	
SP$_{spr}$	5	1.88	3.39		5			0.96
CM$_{spr}$	3	0.98	0.98	1.38	2.25±0.54	2.77±0.42		0.55
ERB$_{spr}$	4	0.97	0.99	0.99	1.46±0.61	1.96±0.78	2.67±0.83	0.14
SCP$_{spr}$	6	1.35	2.04	3.01	4.03±0.84	5.27±0.72	6	0.87
SH$_{spr}$	5	1.12	1.38	2.83	3.62±0.80	4.72±0.48		0.78
WRB$_{spr}$	8	0.97	0.98	1.39	2.68±0.97	4.13±1.10	5.82±1.05	0.43
MP$_{spr}$	6	1.14	1.66	2.95	3.88±0.82	5.07±0.73		0.82
SP$_{fall}$	6	1.05	1.38	2.82	3.51±0.88	4.83±0.80	5.9±0.31	0.72
CM$_{fall}$	4	0.94	0.96	1.18	2.53±0.78	3.58±0.55		0.47
ERB$_{fall}$	6	0.98	0.97	0.98	2.30±0.85	3.36±0.95	4.63±0.89	0.37
TRB$_{fall}$	5	0.98	0.96	2.37	3.10±0.75	3.95±0.69	4.68±0.50	0.69
WRB$_{fall}$	6	0.98	0.99	2.62	3.21±0.84	4.39±0.86	5.86±0.36	0.65
MP$_{fall}$	4	0.97	1.55	2.34	3.33±0.63	3.89±0.32		0.86
SP	7	1.11	1.48	3.31	3.91±0.94	5.44±0.88	6.64±0.53	0.78
CM	4	0.97	0.98	1.27	2.42±0.73	3.18±0.61	3.72±0.45	0.49
ERB	6	0.97	0.97	0.98	1.77±0.76	2.54±0.96	3.59±1.00	0.21
TRB	6	1.04	1.00	2.61	3.24±0.82	4.30±0.83	5.38±0.67	0.68
WRB	9	0.97	0.98	1.53	2.88±0.96	4.25±1.07	5.72±1.12	0.49
MP	6	1.11	1.51	2.92	3.80±0.81	4.82±0.69	5.45±0.57	0.82

Table 3.5abc: Results of diversity indices Monte Carlo analysis. BC=Bray Curtis index, F'=corrected Forbe's index, rho=Spearman's rho. * indicates significant with no p value correction; ** indicates significant with a Holm p value correction; L=indicates significantly lower than the 95% confidence interval generated by Monte Carlo simulation; H=indicates significantly higher than the 95% confidence interval generated by Monte Carlo simulation. Bold font indicates comparison that were significantly higher or lower then the Monte Carlo-generated 95% confidence interval

3.5a. Spring

	SP			CM			ERB			WRB			MP			SCP		
	BC	F'	rho	BC	F'	rho	BC	F'	rho	BC	F'	rho	BC	F'	rho	BC	F'	rho
CM	**0.83**^{H}	0.79	0.23															
ERB	**0.95**^{H}	0.68	0.19	**0.75**^{H}	1.00	0.90*												
WRB	**0.84**^{H}	0.89	0.42	**0.61**^{H}	**1.00**^{H}	0.47	**0.40**^{L}	1.00	0.69*									
MP	**0.73**^{H}	0.93	0.13	**0.25**^{L}	1.00	0.86*	**0.74**^{H}	1.00	0.91*	0.54	0.93	0.42						
SCP	**0.76**^{H}	0.93	0.17	**0.42**^{L}	1.00	0.45	**0.79**^{H}	1.00	0.57	0.63	0.93	**0.19**^{L}	**0.33**^{L}	1.00	0.77*			
SH	**0.66**^{H}	0.96	0.45	**0.34**^{L}	**0.79**^{L}	0.26	**0.80**^{H}	**0.68**^{L}	0.17	**0.58**^{H}	1.00	0.52	**0.40**^{L}	**0.78**^{L}	**0.08**^{L}	**0.44**^{L}	**0.78**^{L}	0.01

3.5b. Fall

	SP			CM			ERB			WRB			MP		
	BC	F'	rho	BC	F'	rho	BC	F'	rho	BC	F'	rho	BC	F'	rho
CM	**0.26**^{L}	0.87	0.53												
ERB	**0.50**^{L}	0.88	0.34	0.48	0.87	0.53									
WRB	**0.12**^{L}	0.97	0.78*	**0.24**^{L}	0.87	0.42	**0.45**^{L}	0.97	0.55						
MP	**0.35**^{L}	**0.87**^{L}	**0.41**^{L}	**0.26**^{L}	0.94	0.64	**0.46**^{L}	1.00	0.93**	**0.36**^{L}	0.87	**0.43**^{L}			
TRB	**0.27**^{L}	0.93	**0.44**^{L}	**0.30**^{L}	1.00	0.72*	**0.30**^{L}	0.93	0.84*	**0.29**^{L}	0.93	**0.44**^{L}	**0.20**^{L}	1.00	0.95**

3.5c. Spring+Fall

	SP			CM			ERB			WRB			MP		
	BC	F'	rho	BC	F'	rho	BC	F'	rho	BC	F'	rho	BC	F'	rho
CM	**0.39**^{L}	0.84	0.43												
ERB	**0.73**^{H}	0.84	0.40	**0.65**^{H}	0.87	0.52									
WRB	**0.44**^{L}	1.00	0.85*	**0.47**^{L}	**1.00**^{H}	**0.45**^{L}	**0.42**^{L}	1.00	**0.31**^{L}						
MP	**0.31**^{L}	0.95	**0.52**^{L}	**0.26**^{L}	0.87	**0.59**^{L}	**0.63**^{H}	0.97	0.91**	**0.46**^{L}	**0.87**^{L}	**0.33**^{L}			
TRB	**0.26**^{L}	0.95	**0.49**^{L}	**0.25**^{L}	1.00	0.66	**0.67**^{H}	0.88	0.78*	**0.50**^{L}	**0.87**^{L}	**0.25**^{L}	**0.18**^{L}	0.88	0.76*

Table 3.6: Spring versus fall diversity within sites. BC=Bray Curtis index, F'=corrected Forbe's index, rho=Spearman's rho. * indicates significant with no p value correction; ** indicates significant with a Holm p value correction; L=indicates significantly lower than the 95% confidence interval generated by Monte Carlo simulation; H=indicates significantly higher than the 95% confidence interval generated by Monte Carlo simulation. Bold font indicates comparison that were significantly higher or lower then the Monte Carlo-generated 95% confidence interval.

	BC	F'	rho
SP	**0.74**^{H}	**0.99**^{H}	0.47
CM	**0.16**^{L}	0.94	0.90**
ERB	**0.44**^{L}	**0.87**^{L}	0.67*
WRB	**0.42**^{L}	0.78	0.70*
MP	**0.27**^{L}	**0.78**^{L}	0.72*

Figure 3.1: Map of survey sites. CANY=Canyonlands National Park, GRCA=Glen Canyon Recreation Area, SP=South Plain, MP=Middle Park, CM=Cedar Mesa, TRB=Tower Ruin Basin, SCP=Salt Creek Pocket, SH=Shay Mesa, WRB=West of Rone Bailey, ERB=East of Rone Bailey. Dark green=National Parks Service land; light green=Manti-La Sal National Forest.

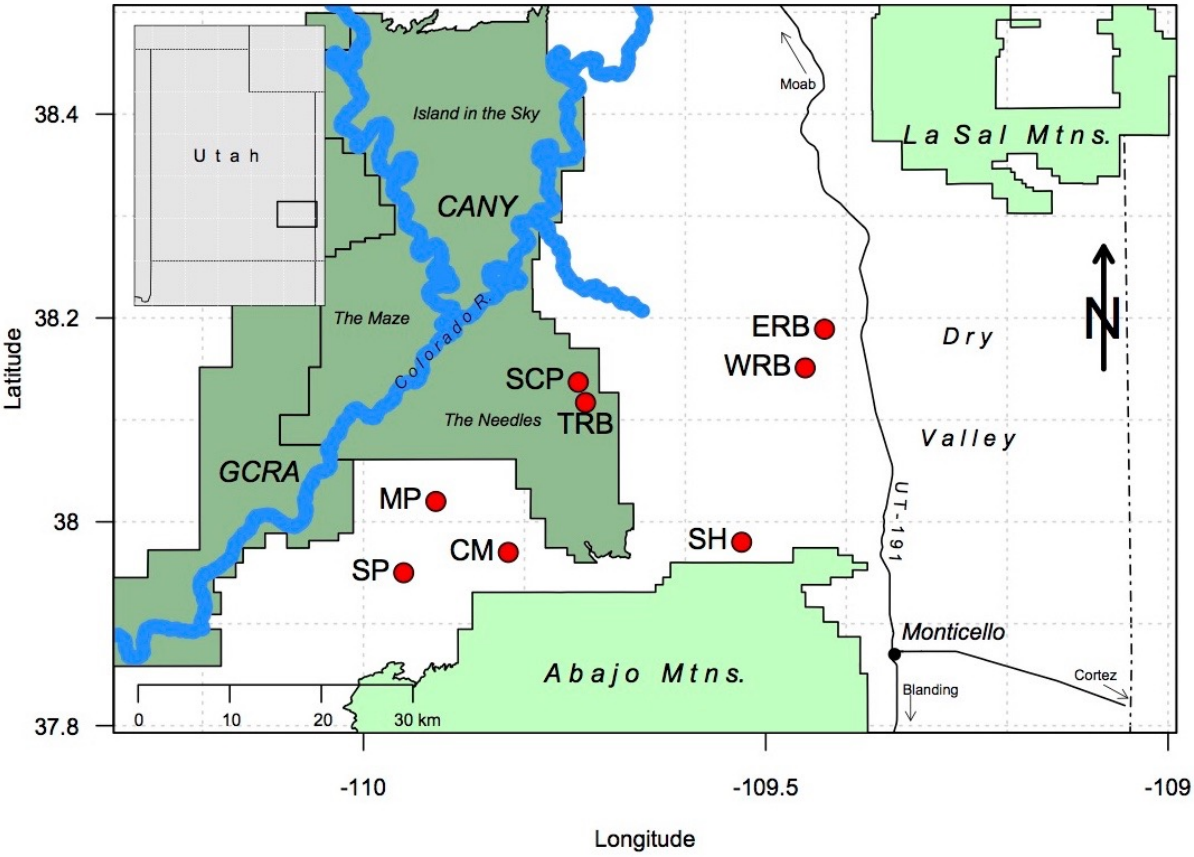


Figure 3.2a: South Plain; **b:** Middle Park; **c:** Cedar Mesa; **d:** Tower Ruin Basin; **e:** Salt Creek Pocket; **f:** Shay Mesa; **g:** West of Rone Bailey; **h:** East of Rone Bailey.

Chapter 4

Spatial and Temporal Variation in Mammalian Diversity of Northern San Juan County, Utah (USA)

Anticipating how species and ecosystems will react to continued and intensified climate and land use change is of critical importance to biodiversity conservation and to management of the ecosystem processes on which we rely. Predictive techniques, like Species Distribution Models, that employ only modern range data have had limited success in this regard, as demonstrated by the generally low agreement between hind-casted SDMs and actual fossil data used to verify the models (McGuire and Davis 2013, Davis et al. 2014). Identifying how individual species in a community have responded in the past can be accomplished by evaluating the fossil record on a local and/or regional scale, and by examining spatial patterns of abundance and diversity that are the result of ecological processes that occur over decades and centuries.

Climate change-induced range shifts over the course of the Holocene are of particular interest in light of current climate change because many of the same species are at stake today. To that end, the purpose of this study is to compare the small mammal diversity of southeastern Utah across space and over the past ~4.4 ka, using the data presented in the previous chapters. Specifically, I compare surveys of the living community at eight sites in northern San Juan County, Utah, to the fossil diversity recorded in two well-dated fossil localities, Rone Bailey Alcove (RBA) and East Canyon Rims 2 (ECR2) (Figure 4.1). As noted in previous chapters, RBA and ECR2 are woodrat (*Neotoma*) middens where bone and plant material have been accumulated by the activities of woodrats and avian and mammalian carnivores. They sample an overlapping area and have similar taphonomic vectors so they may be treated as representative of the same community. Together, these sites form a chronological sequence that extends from ~0.5-4.4 ka. Previous studies have shown that *Neotoma*- and owl-generated deposits record taxonomic diversity, relative abundance, (Terry 2008, Terry 2010a,b) and rank abundance (Hadly 1999) with high fidelity, and therefore, such data are useful in assessing climate change impacts on biota, and the magnitude and direction of shifts in faunal baselines (Terry 2010a, Terry and Rowe 2015).

On a regional scale, the taxonomic diversity of mammals on the Colorado Plateau has remained largely unchanged in the last 100 years (Chapter 1). The mammalian community of CP National Parks and Monuments (hereafter, simply called "parks") follow a species nested subset pattern in which less-diverse parks are a predictable subset of the diversity present in more-diverse parks. The same nested subset pattern present a century ago is still present today in spite of climate change and habitat fragmentation that has occurred to varying degrees across the region. "Faunal relaxation"—a consequence of fragmentation and isolation of suitable habitat (Darlington 1957)—has not taken place in these protected "islands" in the last hundred years. Though conservation was not the main purpose of creating parks originally, biodiversity conservation in these lands during historic times nevertheless has been effective for most species. Notable exceptions include extirpation of several carnivores (Canada lynx, jaguar, grizzly bear, gray wolf, black-footed ferret, and wolverine). These broad-stroke patterns define an important context in which to direct future conservation efforts as we attempt to divert and mitigate anthropogenic impacts—past, current, and future.

Reaching further back in time, few small mammal species have been lost from the regional fauna of the CP since the last glacial maximum, though range shifts have certainly taken place. *Lemmiscus curtatus*, preserved in both ECR2 and RBA, and *Brachylagus idahoensis*, found on the surface of a rock shelter near ECR2 and RBA, were both extirpated on the CP sometime during the Holocene—both species are found in the Great Basin today (Murray et al 2005, Mead et al. 2003, Chapter 2). At RBA and ECR2, taxonomic diversity and abundance (rank and proportional) were not statistically different through time, in spite of considerable increases in aridity and temperature. Declining evenness (Shannon, Simpson, and PIE indices) is apparent from ~1700 to 500 cal ybp. This coincides with a period of increasing aridity and periodic extreme drought, but it is not clear if there is a causal relationship between aridification and evenness in this case (Chapter 2). *Dipodomys*, a genus that can live indefinitely without drinking or dietary water (Schmidt-Neilsen 1964), increased in abundance at that time, suggesting that arid-adapted taxa were favored. Similar increases in *Dipodomys* were observed during Holocene aridification at Homestead Cave in the northern Great Basin (Terry and Rowe 2015). Overall, climatic fluctuations of the magnitude preserved in these deposits did not significantly alter the small mammal community at higher taxonomic levels (genus- and family-level).

Spatially, mark-recapture surveys in northern San Juan County reveal that the species pool is essentially the same across sites with similar floral communities regardless of factors like elevation, distance to permanent water, and livestock grazing. However, other measures of diversity are more different across survey sites than they would be if individuals were distributed randomly (Chapter 3). In particular, species evenness varies among sites, and sites with low evenness are dominated by the generalist species *Peromyscus maniculatus* (Chapter 3). High taxonomic similarity is also evident in comparison of fossil diversity through ECR2 and RBA to surveys of the living community at these same sites. Of the groups assessed, essentially all taxa found in the fossil deposits are present today, with the important exception of voles (*Lemmiscus* and *Microtus*) and possibly pocket gophers (*Thomomys*). However, repeated systematic surveys are needed to confirm the lack of pocket gophers, because their populations tend to blink in and out across the landscape in desert environments (James Patton, *personal communication*).

Proportional abundance varies comparatively little among the fossil time bins (Table 4.2) except bin D, which has more *Peromyscus* and fewer *Dipodomys* than B, and has higher overall diversity as well as more *Neotoma* and *Peromyscus* than F. Correspondence analysis (Figure 4.2) and Spearman's rank correlations illustrate that rank abundance varies non-linearly throughout the fossil and living record of the community at RBA and ECR2. This is because, though *Dipodomys* is highest in rank abundance for all the fossil time bins, and 2nd-most abundant in the modern, all the other taxa fluctuate in rank considerably, and most time periods are not significantly correlated with one another, with the exception of time bins D (959-1704 cal ybp) and E (735-1054 cal ybp) (spearman's rho=0.99, $p<1.0\times10^{-4}$). In contrast, proportional abundance of the modern community is dramatically different from all fossil time periods, because *Peromyscus* (*P. maniculatus* and *P. truei*) are far more abundant in the living community than they were in the past (Table 4.1). Landscapes subject to major ecological disturbance are expected to favor generalist "weedy" species like *Peromyscus*, a pattern that has been found in other North American fossil deposits like Samwell Cave in northern California (Blois et al. 2010). Yet another example of major landscape disturbance, Terry and Rowe (2015) document increases in closed grassland mammal species like *Reithrodontomys megalotis*, *P. maniculatus*, and *Chaetodipus* spp. at the expense of open grassland and shrubland species withthe introduction and spread of exotic annual grasses like *Bromus tectorum*. It remains to be seen if the high abundance of *Peromyscus* at ECR2 and RBA represents a true, long-term change to the community structure.

Evenness, measured using Probability of Interspecific Encounter (PIE) (Hurlbert 1971), reached a peak in ECR2 and RBA around time bin D (959-1704 cal ybp) then began to decline in time bin E (735-1054 cal ybp) (Figure 4.3b). The extent of 95% confidence interval (CI) overlap depends on the sample size used to sample standardize each time bin and site—because bins A and F had few specimens (7 and 17 respectively) I here include PIE results using a sample size of 7 (wide CIs), but a larger sample size (n=30; narrow CIs) is a better estimation of PIE for most time bins. When n=30, modern site evenness at ECR2 and RBA is significantly lower than evenness in all fossil time bins except for bin F (501-644 cal ybp). This drop in evenness at bin F occurred prior to the onset of high-impact, post-European human land uses, like livestock grazing, and is coincident with the time when Ancestral Puebloan populations crashed due to long-term periodic droughts (Benson and Berry 2009), suggesting a marked environmental change between ~700-1000 ybp. Low modern evenness appears to be consistent across space—modern evenness at all survey sites is lower than it is for all fossil time bins except F (Figure 4.3a), suggesting that this was a landscape-level decline in diversity.

These results send a cautionary message: though the basic taxonomic integrity of the small mammal community is still present, abundance and community structure are very different today. Changes in abundance necessarily precede extirpation and so declining abundance and evenness can be used as an early warning sign of diversity loss (Blois et al. 2010). However, in the short term, small mammal abundance can fluctuate dramatically, so long-term records are necessary to establish meaningful patterns. Currently we do not have enough information about modern abundance patterns to draw firm conclusions, and more detailed information regarding species presence/absence regionally and locally is of primary importance.

Parsing the potential effects of historical legacies, climate change, and current land uses will require a concerted survey effort over multiple years at the eight sites discussed here and at many additional sites. Necessary future work should expand the trapping protocol to include day-time trapping for diurnal species and additional survey techniques to assess diversity of leporids, mesocarnivores, and other taxa not generally captured in folding traps but often recorded in the fossil record. Additional surveys will almost certainly reveal higher resident diversity in northern San Juan County, like rock squirrels (*Otospermophilus variegatus*), western harvest mice (*Reithrodontomys megalotis*), pocket gophers (genus *Thomomys*), potentially more species of *Neotoma*, and mesocarnivores like ringtails (*Bassariscus astutus*) and weasels (genus *Mustela*). More surveys will also reveal whether the abundance differences highlighted in chapter 3 are short-term population cycles, or long-term differences in habitat characteristics of sites. Overall, the fossil record is expected to appear more homogenous than the modern, because individuals in the fossil record have been collected over a range of nearby habitats and over the course of many years (depending on the deposits, this could be decades, centuries, or millennia). While the modern trap surveys are spatially averaged (multiple microhabitats, multiple sites), the issue of time-averaging can be addressed only by repeated surveys.

Future surveys should also be conducted with the goal of comparing strictly protected land to multi-use land. Presently, it is unclear *where* small mammal species have a better chance of persisting—does strict land protection have a positive impact on small mammal populations? If not, how do we ensure their persistence in the future? Further, multi-use lands comprise the vast majority of the southwest and as climate changes we may rely on these regions for population connectivity and biodiversity reservoirs.

Whereas the modern sample currently lacks temporal coverage, the fossil sample lacks spatial breadth. More information on the Quaternary fossil record of the CP will provide the context with which to interpret modern patterns of diversity and, when paired with independent climate proxies, can be used to identify large-scale patterns of mammal response to climate change. No matter how ideal the fossil deposit, a single site necessarily only provides information about the local environment. Quaternary-age deposits, particularly woodrat middens, are common across the CP, and so we are limited only by research effort. Additional information on past and current diversity of the CP will improve forecasting and establish baselines against which to compare future surveys, allowing us to gauge rates and direction of change, and to prioritize conservation efforts in the future.

This study emphasizes the utility of the fossil record in understanding the extent of ecological fluctuations that can be considered "normal" through long periods of time. This information is essential as we struggle to conserve biodiversity in a world that is changing more over the course of a single century than is has in the past 12,000 years (Barnosky et al. 2014a).

Methods Summary

Excavation method and trapping protocol are addressed at length in Chapters 2 and 3, respectively. Some taxa are not identifiable to species in the fossil record, so I collapsed the modern survey data into broader taxonomic categories (family, subfamily, or genus) in analogy to the fossil record for direct comparison between the two. Furthermore, some species preserved in the fossil record of RBA and ECR2 were not targeted by my surveys because they require different trapping techniques. The taxa found in both datasets include: small sciurids, perognathines, arvicolines, *Neotoma*, *Dipodomys*, *Onychomys*, and *Peromyscus*.

I used Spearman's rank correlation tests to compare rank abundance, and Fisher's exact tests to compare proportional abundance between each fossil time bin and the modern. Correspondence Analysis (CA) was used to visualize differences in rank abundance between times bins. Time bins that have similar rank abundance distributions are plotted closer together.

Evenness is a measure of how similar abundance of each represented taxa is at a site: high evenness indicates a community in which most species are similar in abundance, whereas a community with low evenness is dominated by a few, very abundant taxa. I used Probability of Interspecific Encounter (PIE; Hurlburt 1971) to compare evenness across sites and time bins. PIE is independent of sample size, unlike other measures of evenness (Gotelli and Ellison 2013). I used subsampling to generate 95% confidence intervals around each PIE score: I subsampled the species list for the time bin or site of interest n times then computed PIE, for 1000 iterations. I compared the result at n=30 and n=7 (time bins F and A had sample sizes lower than 30; 7 was the minimum sample size, for time bin A).

Table 4.1: Number of individuals in each time bin.

	Sciuridae	*Dipodomys*	*Neotoma*	*Onychomys*	Perognathinae	*Peromyscus*	Arvicolines	Age (Cal ybp)
modern	9	14	4	8	3	332	0	
F	0	14	1	0	1	0	1	501-644
E	6	30	12	3	5	8	2	735-1054
D	3	12	10	2	2	9	1	959-1704
C	2	32	11	7	3	6	4	2350-2700
B	5	35	4	2	6	3	1	
A	1	3	1	0	0	1	1	3569-4410

Table 4.2: Fisher's test p values with Holm p value adjustment. * indicates significance without a p value correction; ** indicates significant with a p value correction.

	A	B	C	D	E	F
B	1					
C	1	1				
D	1	0.11*	1			
E	1	1	1	1		
F	1	1	1	0.09*	1	
modern	0.04**	0.04**	0.04**	0.04**	0.04**	0.04**

Figure 4.1: Map of survey sites. Yellow circles indicate modern survey sites; SP=South Plain, MP=Middle Park, CM=Cedar Mesa, TRB=Tower Ruin Basin, SCP=Salt Creek Pocket, SH=Shay Mesa, WRB=West of Rone Bailey, ERB=East of Rone Bailey. Red circles indicate fossil localities; ECR2=East Canyon Rims 2, RBA=Rone Bailey Alcove. Dark green=National Parks Service land; . CANY=Canyonlands National Park, GRCA=Glen Canyon Recreation Area. Light green=Manti-La Sal National Forest.

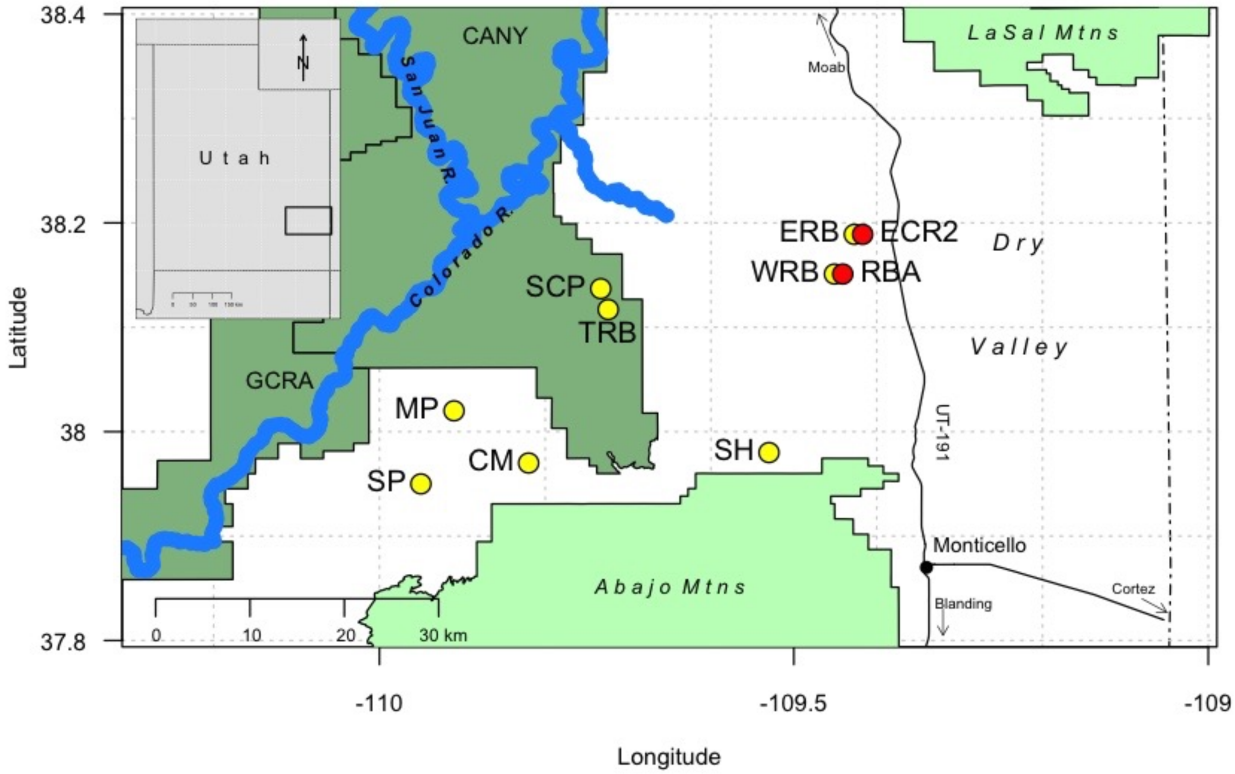


Figure 4.2: Correspondence Analysis of times bins (blue) and taxa (black).

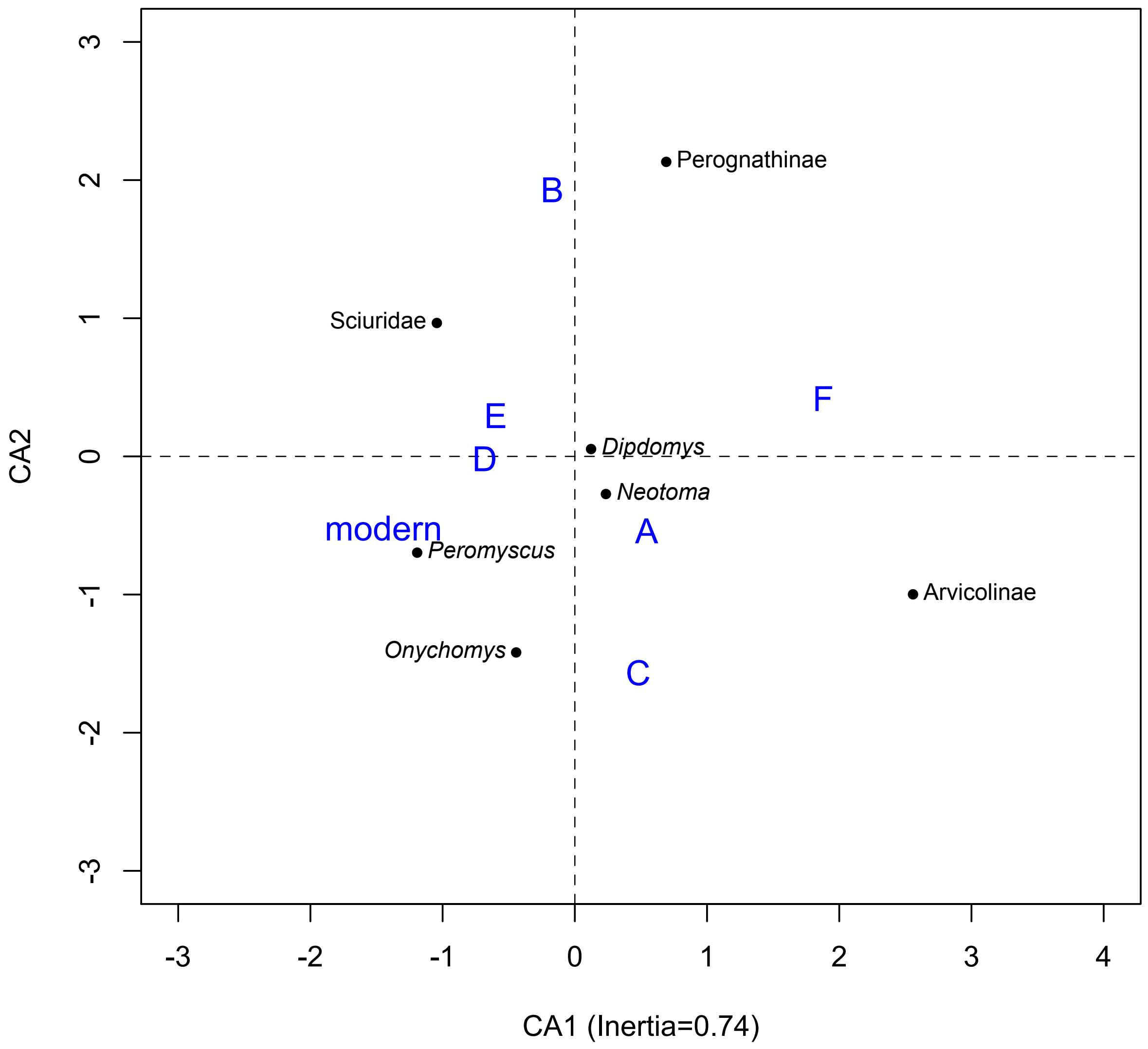
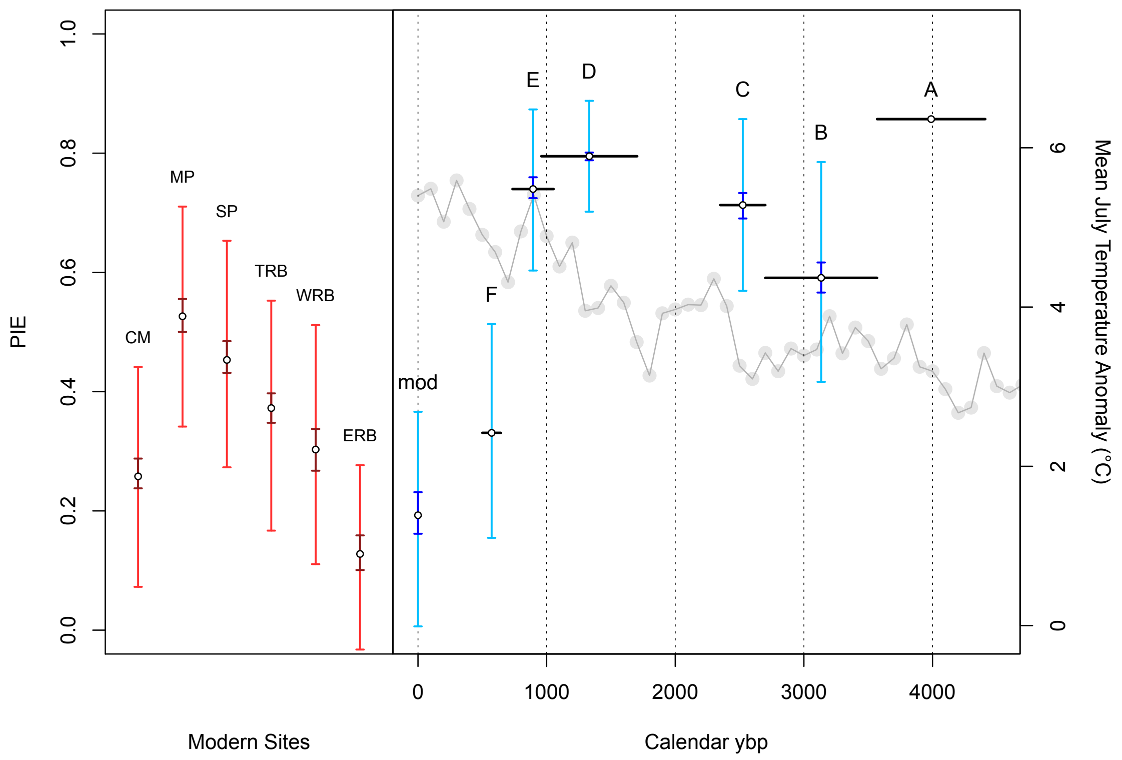


Figure 4.3a: PIE scores at each survey site. CM=Cedar Mesa, MP=Middle Park, SP=South Plain, TRB=Tower Ruin Basin, WRB=West of Rone Bailey, ERB=East of Rone Bailey. Bright red vertical bars indicate 95% CI when n=7; dark red vertical bars indicate 95% CI when n=30; black circles indicate actual PIE score without resampling. **b:** PIE scores for each time bin. mod=modern. Light blue vertical bars indicate 95% CI when n=7; dark blue vertical bars indicate 95% CI when n=30; black horizontal bars indicate age range for each time bin; black circles indicate actual PIE score without resampling; gray line and points are reconstructed mean July temperature anomaly (Viau et al. 2006).



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Appendices

Appendix 1.1: References for park attribute data.

Park attribute	**Source**
Budget	US Department of the Interior Budget Justifications home.nps.gov/applications/budgetweb/fy2012/sbtoc.htm
Visitation (5 year average)	NPS Stats https://irma.nps.gov/Stats/
Area	NPS Stats https://irma.nps.gov/Stats/
Year of park creation	US National Parks Service https://www.nps.gov/
Latitude and longitude	Google Earth*
Minimum/maximum elevation	Google Earth*

*Latitude and longitude, and minimum and maximum elevation were determined using Google Earth

Appendix 1.2: Species ranks for survey and range map data, rank change, and number of congeners present on the Colorado Plateau for each species. — signifies a species that is not present in the indicated dataset.

Species	NPS rank	Range rank	difference in rank (range – survey rank)	# of congeners
Alces alces	103	—	—	1
Ammospermophilus harrisii	104	—	—	2
Ammospermophilus leucurus	36	39	3	2
Antilocapra americana	64	61	-3	1
Antrozous pallidus	14	11	-3	1
Bassariscus astutus	15	3	-12	1
Bison bison	105	1	-104	1
Canis latrans	1	4	3	1
Castor canadensis	48	24	-24	1
Cervus elaphus	37	35	-2	1
Chaetodipus formosus	84	97	13	2
Chaetodipus intermedius	83	94	11	2
Choeronycteris mexicana	106	—	—	1
Conepatus leuconotus	90	—	—	1
Corynorhinus townsendii	27	12	-15	1
Cynomys gunnisoni	58	50	-8	1
Cynomys leucurus	91	89	-2	2
Cynomys parvidens	—	108	—	—
Dasypus novemcinctus	—	132	—	—
Dipodomys merriami	93	124	31	2

Appendix 1.2 Continued.

Dipodomys microps	94	103	9	4
Dipodomys ordii	38	25	-13	4
Dipodomys spectabilis	92	86	-6	4
Eptesicus fuscus	16	13	-3	4
Erethizon dorsatum	9	40	31	1
Euderma maculatum	28	14	-14	1
Glaucomys sabrinus	85	104	19	1
Idionycteris phyllotis	51	75	24	1
Lasionycteris noctivagans	17	15	-2	1
Lasiurus blossevillii	95	16	-79	3
Lasiurus cinereus	32	17	-15	3
Lasiurus ega	109	—	—	3
Lemmiscus curtatus	110	98	-12	1
Lepus americanus	111	93	-18	3
Lepus californicus	18	38	20	3
Lepus townsendii	81	82	1	3
Lontra canadensis	77	118	41	1
Lynx canadensis	112	119	7	2
Lynx rufus	2	5	3	2
Macrotus californicus	—	101	—	—
Marmota flaviventris	68	51	-17	1
Mephitis mephitis	10	6	-4	1
Microtus longicaudus	53	30	-23	4
Microtus mexicanus/mogollonensis	73	109	36	4
Microtus montanus	65	73	8	4
Microtus richardsoni	—	125	—	—
Microtus pennsylvanicus	96	81	-15	4
Mustela erminea	78	72	-6	3
Mustela frenata	19	36	17	3
Mustela nigripes	—	46	—	—
Mustela vison	86	120	34	3
Myodes gapperi	107	83	-24	1
Myotis auriculus	97	—	—	8
Myotis californicus	29	18	-11	8
Myotis ciliolabrum	20	19	-1	8
Myotis evotis	33	33	0	8
Myotis lucifugus	49	69	20	8
Myotis velifer	—	96	—	—
Myotis volans	21	21	0	8
Myotis yumanensis	41	37	-4	8

Appendix 1.2 Continued.

Nasua narica	113	121	8	1
Neotoma albigula	44	62	18	6
Neotoma cinerea	43	34	-9	6
Neotoma devia	98	110	12	6
Neotoma lepida	69	111	42	6
Neotoma leucodon	—	112	—	—
Neotoma mexicana	46	49	3	6
Neotoma micropus	—	105	—	—
Neotoma stephensi	59	78	19	6
Notiosorex crawfordi	42	77	35	1
Nyctinomops macrotis	39	29	-10	1
Ochotona princeps	99	76	-23	1
Odocoileus hemionus	3	2	-1	1
Odocoileus virginianus	—	85	—	—
Ondatra zibethicus	54	52	-2	1
Onychomys arenicola	—	113	—	—
Onychomys leucogaster	35	41	6	2
Onychomys torridus	114	126	12	2
Ovis canadensis	60	64	4	1
Panthera onca	—	95	—	—
Perognathus amplus	100	114	14	6
Perognathus fasciatus	115	127	12	6
Perognathus flavescens	50	55	5	6
Perognathus flavus	47	56	9	6
Perognathus longimembris	116	106	-10	6
Perognathus parvus	74	87	13	6
Peromyscus boylii	12	26	14	7
Peromyscus crinitus	40	57	17	7
Peromyscus eremicus	88	90	2	7
Peromyscus gratus	—	128	—	—
Peromyscus leucopus	117	91	-26	7
Peromyscus maniculatus	4	27	23	7
Peromyscus nasutus	79	92	13	7
Peromyscus truei	5	42	37	7
Phenacomys intermedius	—	88	—	—
Pipistrellus hesperus	22	44	22	1
Puma concolor	23	7	-16	1
Reithrodontomys megalotis	6	31	25	1
Reithrodontomys montanus	—	115	—	—
Sciurus aberti	66	67	1	1

Appendix 1.2 Continued.

Sigmodon fulviventer	118	116	-2	1
Sorex cinereus	82	100	18	7
Sorex merriami	61	28	-33	7
Sorex monticolus	75	59	-16	7
Sorex nanus	70	43	-27	7
Sorex palustris	80	80	0	7
Sorex preblei	101	—	—	7
Sorex vagrans	119	—	—	7
Urocitellus armatus	—	129	—	—
Urocitellus elegans	120	—	—	5
Callospermophilus lateralis	63	63	0	5
Urocitellus mollis	—	130	—	—
Xerospermophilus spilosoma	62	58	-4	5
Ictidomys tridecemlineatus	121	117	-4	5
Otospermophilus variegatus	7	32	25	5
Spilogale gracilis/putorius	24	8	-16	1
Sylvilagus audubonii	25	23	-2	2
Sylvilagus nuttallii	55	45	-10	2
Tadarida brasiliensis	30	22	-8	1
Tamias cinereicollis	122	131	9	6
Tamias dorsalis	56	84	28	6
Tamias minimus	57	60	3	6
Tamias quadrivittatus	76	68	-8	6
Tamias rufus	52	74	22	6
Tamias umbrinus	89	99	10	6
Tamiasciurus hudsonicus	67	53	-14	1
Taxidea taxus	13	9	-4	1
Tayassu tajacu	87	—	—	1
Thomomys bottae	31	47	16	2
Thomomys talpoides	71	71	0	2
Urocyon cinereoargenteus	8	10	2	1
Ursus americanus	26	65	39	1
Vulpes macrotis	72	66	-6	2
Vulpes velox	—	122	—	—
Vulpes vulpes	45	48	3	2
Zapus hudsonius	123	-	-	2
Zapus princeps	102	79	-23	2

Appendix 1.3: Site ranks for survey and range map data, and rank difference.

	NPS	Range	Rank change
ARCH	11	14	-3
AZRU	22	11	11
BAND	5	2	3
BLCA	7	16	-9
CACH	9	10	-1
CANY	12	8	4
CARE	6	4	2
CEBR	17	23	-6
CHCU	18	18	0
COLM	13	12	1
DINO	4	9	-5
ELMA	8	6	2
ELMO	15	17	-2
GRCA	1	1	0
HOVE	19	21	-2
MEVE	2	5	-3
NABR	23	19	4
NAVA	14	24	-10
PECO	25	3	22
PISP	20	25	-5
SUCR	24	22	2
WACA	16	15	1
WUPA	21	20	1
YUHO	10	13	-3
ZION	3	7	-4

Appendix 1.4: NODF scores with Soricidae removed from datasets. ^{c} indicates significant using the c0 null model, ^{q} indicates significant using the quasiswap null model.

	NODF columns	NODF rows	NODF	Matrix fill
Surveyed Species	$78.57^{c,q}$	68.10^{c}	68.56^{c}	0.458
Surveyed Genus	$89.82^{c,q}$	80.86^{c}	82.09^{c}	0.630
Range Map Species	79.47^{c}	70.45^{c}	70.78^{c}	0.536

Appendix 2.1: Excavation elevations.

	Level	Average Level thickness (cm)
RBA	1	9.2
	2	9.8
	3	14
	4	9.9
	5	13.5
	6	8.6
ECR2	1	5.5
	2	5.8
	3	8.3
	4	7.5
	5	6.1
	6	5
	7	4.6
	8	4.7
	9	3.4
	10	2.3

Appendix 2.2: Systematic Paleontology.

CLASS: MAMMALIA

ORDER: CHIROPTERA Blumenbach 1779

FAMILY: Vespertilionidae Gray 1821

Vespertilionidae indet.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233619, tooth. UCMP Locality V36222 (RBA): UCMP 231407.

ORDER: RODENTIA Bowditch 1821

FAMILY: HETEROMYIDAE Gray 1868

SUBFAMILY: PEROGNATHINAE Coues 1875

Perognathinae indet.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233288, 233353, 233381, 233565,233672, 233690, 257372-257373, right and left dentaries with and without cheekteeth; UCMP 233384, m1/2; UCMP 233449, Lm3; UCMP 233279, p4; UCMP 233415 palate with P4M1. UCMP Locality V36222 (RBA): UCMP 231272, 231416, 231435, 231472, 231508, 231623, 231632, m1s, m2s, m3s, p4s; UCMP 231474, 231558-231559, 237665, UCMP dentaries with and without teeth. UCMP 231554, left maxilla with P4

Remarks—Teeth of perognathines are low-crowned and rooted, with two transverse lophs. As compared to other heteromyids, teeth referred here are too small and low-crowned to be *Microdipodops*, *Liomys*, or *Dipodomys* (further, *Dipodomys* have unrooted teeth).

GENUS: *DIPODOMYS* Gray 1841

Dipodomys sp.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233266-233267, 233271, 231277, 233291, 233301-233302, 233305-233309, 233323-233324, 233332-233333, 233364, 233386-233391, 233393-233395, 233408-2333411, 233426, 233440-233442, 233450-233451, 233502-233504, 233521-233522, 233535-233537, 233553-233555, 233563, 233579233581, 233593, 233613, 233630, 233632m 233634, 233644, 233652, 233660, 233668, 233675-233678, 233686, 233691, 233696, 233697, 233699, 233705, 233712, 257400, 257422, 257436, cheekteeth; UCMP 233251-233254, 233292-233294, 233350, 257399, 257406, dentaries with cheekteeth; UCMP 233428-233429, 233714, 257369, 257389, 257391, maxillae with teeth; UCMP 257405, partial skull. UCMP Locality V36222 (RBA): UCMP 231293-231297, 231317-231319, 231333-231336, 231255-231358, 231364, 231367-231368, 231388-231390, 231400-231401, 231408-231412, 231428-231430, 231458-231461, 231463, 231465-231470, 231494-231501, 231515-231521, 231542, 231563-231565, 231568-231572, 231575-231589, 231615-231620, 231627, 231642-231644, 231664, 231666-231668, 238400-238405, cheekteeth; UCMP 231464, 231567, 231561, dentaries with cheekteeth; UCMP 231328, skull; UCMP 231562, 231566, maxillae; UCMP 231323, 231462, tooth sockets.

Remarks—Teeth of *Dipodomys* are easily distinguished from other North American Heteromyid genera because they are un-rooted. *Dipodomys* teeth are superficially similar to the cheekteeth of *Thomomys*—both are unrooted and are composed of an anterior and posterior enamel plate—with is particularly relevant for identifying broken specimens. However, *Thomomys* teeth are considerably more robust, taller, and angle strongly from root to occlusal surface.

FAMILY: CRICETIDAE Fischer 1817

SUBFAMILY: ARVICOLINAE Gray 1821

Arvicolinae indet. (aff. *Microtus* or *Lemmiscus*)

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233403, 233542, 233636, 257392, 257414, 257424, cheekteeth. UCMP Locality V36222 (RBA): UCMP 231421, 231493, 231591, 231645, cheekteeth.

GENUS: *MICROTUS* Schrank 1798

Arvicolinae indet. (aff. *Microtus*)

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 257357, m12. UCMP Locality V36222 (RBA): UCMP 231492, Rm1.

GENUS: *LEMMISCUS* Thomas 1912

Lemmiscus c.f. curtatus Cope 1868

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233404, left dentary with m12; UCMP Locality V36222 (RBA): UCMP 231452, 231512, m1s

Summary remarks for Subfamily Arvicolinae—In m1s of *Microtus,* triangle 2 is distinctly smaller than triangle 1, while in m1s of *Lemmiscus*, triangle 2 is equal in length or longer than triangle 1 (Bell et al., 2004). All other specimens are referred to Arvicolinae indet because they lack diagnostic characters.

SUBFAMILY: NEOTOMINAE Merriam 1894

Neotominae indet. (aff. *Peromyscus* or *Onychomys*)

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233354, 233356-233357, 233380, 233467, 233470, 233606, 233628-233629, 233666, 233685, 257384, 257407, 257435, left and right dentaries, some with cheekteeth; UCMP 233465-233466, 233510, 257344, left and right maxillae with cheekteeth; UCMP 233312-233313, 233455, 233506, 233509, 233526-233528, 233530, 233544, 233564, 233585, 233607, 233612, 233615, 233622, 233667, 233692, 233713, 233716, 257394, 257397, 257416, upper and lower cheekteeth. UCMP Locality V36222 (RBA): UCMP 231271, 231273, 231274, 231275, 231478-231479, 231555, 231607, fragmentary left and right dentaries; UCMP 231403, maxilla with M2; UCMP 231288, 231374-231375, 231404, 231432, 231434, 231473, 231534-231536, 231605, 231622, 231650-231651, upper and lower molars.

Remarks—Specimens referred to Neotominae indet lack morphological characters that identify them to a finer taxonomic level. Among species that occur on the Colorado Plateau today, *Peromyscus*, *Reithrodontomys*, and *Onychomys* are all morphologically similar to the specimens reported here. Teeth *Reithrodontomys* and *Baiomys* (not present on the Colorado Plateau, but ranges into southern Arizona and Texas) are smaller than those of *Peromyscus* and *Onychomys*, but are a number of morphological differences as well (Hillson 2005).

GENUS: *PEROMYSCUS* Gloger 1841

Peromyscus sp.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233256, 233269, 233355, 233430, 233444, 233468, left and right dentaries with cheekteeth; UCMP 233257, 233445, 233469, 233472, 233473, left and right maxillae with teeth; UCMP 233278, 233382-233383, 233385, 233442, 233505, 233507, 233529, 233577, 233583-233584, 233586-233588, 233621, 233641-233642, upper and lower molars. UCMP Locality V36222 (RBA): UCMP 231476, 231537, left dentaries with molars; UCMP 231347, 231560, 231649, left and right maxillae with M12; UCMP 231254, 231276, 231287, 231309-231310, 231339, 231361, 231418, 231431, 231506-231507, 231531-231532, 231608, 231631, upper and lower molars.

GENUS: *ONYCHOMYS* Baird 1858

Onychomys sp.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233255, 233414, 233647, left and right denaries with m1-3; UCMP 233342, 233508, 233661, M2s; UCMP 233413, maxilla with M1; UCMP 233471, M1; UCMP 233531, 233582, Lm1s. UCMP Locality V36222 (RBA): UCMP 231289-231290, 231475, 231477, 231480, 231606, left and right dentaries with cheekteeth; UCMP 231286, 231417, 231433, 231504-231505, 231533, 231539, 231621, upper and lower molars.

Summary remarks for *Onychomys* and *Peromyscus*—*Onychomys* and *Peromyscus* overlap in molar size, but *Peromyscus* usually has additional folds of enamel between the main cusps in both upper and lower molars (Hillson 2005, Hooper 1957). In *Onychomys*, the upper and lower 3rd molars are simplified: the M3 is peg-like and round, and the m3 is shaped like and 8, with a much larger anterior loop. In *Peromyscus*, the m3 is S-shaped, and the M3 is pocked with infundibula. The upper and lower first molars in *Peromyscus* have a more-infolded anterior loop, often with three lobes. *Onychomys* tends to have a single or, at most, double-lobed anterior loop in the first molars.

GENUS: *NEOTOMA* Say and Ord 1825

Neotoma spp.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233248, 233457, 233459, 233562, 233627, 257358, 257362, 257393, left and right dentaries, some with molars; UCMP 233222, 233241, 257401, 257427, 257432, maxillae, some with teeth; UCMP 233230, skull; UCMP 233261, 233270, 233276, 233327-233328, 233339-233340, 233349, 233367-233368, 233405-233406, 233421, 233448, 233458, 233501, 233543, 233552, 233578, 233600-233601, 233620, 233625-233626, 233683, 233698, 257366, 257368, 257370, 257387-257388, 257396, 257398, 257410, 257418, 257433, 257434, 257437, 257438, upper and lower cheekteeth. UCMP Locality V36222 (RBA): UCMP 231240, 231242, 231277, 231325, 231425, 231427, left and right dentaries, some with molars; UCMP 231442-231443, 231659, left and right maxillae, some with molars; UCMP 231247-231252, 231298-231301, 231311-231313, 231326, 231327, 231340-231342, 231344-231346, 231349, 231372-231373, 231391, 231402, 231419, 231426, 231444-231448, 231486-231488, 231511, 231546, 231590, 231610, 231626, 231634, 231661, 257491, upper and lower cheekteeth.

Remarks—*Neotoma* are semihypsodont and have no cementum in their reentrants; their teeth and cranial elements are easily morphologically distinguished from other Cricetids using criteria detailed by Repenning (2004). Because species of *Neotoma*, with the exception of *N. cinerea*, are extremely similar in size and morphology, specimens referred to *N. spp.* may represent more than one species. *Neotoma albigula* is present around Rone Bailey Mesa today.

FAMILY: GEOMYIDAE Bonaparte 1845

GENUS: *THOMOMYS* Wied-Neuwied 1839

Thomomys sp.

Referred Specimens—UCMP Locality V36221 (ECR2): 233303, 233310, 233318-233321, 233329-233331, 233341, 233351, 233369-233379, 233392, 233412, 233425, 233427, 233437, 233460-233463, 233490-233498, 233512-233520, 233538-233540, 233638, 23343, 233670-233671, 233687, 233702-233704, 233711, 233715, upper and lower cheekteeth; UCMP 233594, right dentaries. UCMP Locality V36222 (RBA): 231260-231262, 231302, 231304, 231314-231316, 231329-231332, 231352-231354, 231363, 231366, 231369, 231371, 231385-231387, 231395-231396, 231398, 231414-231415, 231420, 231423, 231436-231437, 231456, 231491, 231523, 231525-231529, 231540-231541, 231548, 231550, 231597-231604, 231614, 231629-231630, 231636-231638, 231640-231641, 237669, 238406-238407, upper and lower cheekteeth; UCMP 231278, maxilla with cheekteeth; UCMP 231305, left dentary fragment.

*Thomomys (*subgenus *Thomomys)* sp. Elliot 1903

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233352, right dentary fragment with m1-3. UCMP Locality V36222 (RBA): UCMP 231258, 231259, p4s.

*Thomomys (*subgenus *Megascapheus)* sp. Elliot 1903

Referred Specimens— UCMP Locality V36221 (ECR2): UCMP 233322, 233407, 233541, p4s; UCMP 233595, left dentary fragment with p4. UCMP Locality V36222 (RBA): UCMP 231303, 231370, 231397, 231457, 231489-231490, 231524, 231530, 231549, 231596, p4s; UCMP 231613, 231628, P4s.

Summary remarks for genus *Thomomys*—Specimens identified to subgenus are all p4s or P4s. Subgenus *Megascapheus* has a flat anterior enamel plate that is widely separated from the lingual and buccal enamel plates; in subgenus *Thomomys*, this enamel plate is broad, recurved forming a shallow reentrant, located antero-lingual, and is very close to the more posterior lingual enamel plate (Thaeler 1980). In subgenus *Megascapheus*, the P4 is strongly anteriorly angled and the infraorbital foramina are anterior to incisive foramina, and the angular process is continuous with the well-developed flange on the ventral surface of the jaw (Tomiya et al. 2011).

FAMILY: SCIURIDAE Fischer 1817

Sciuridae indet.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233317, 233334, 233614, 233635, 233656, 233659, upper cheekteeth; UCMP 233236, 233436-233447, 233499, 233598, 233653-233654, 233658, lower cheekteeth; UCMP 233347-233348, dentary fragments. UCMP Locality V36222 (RBA): UCMP 231453, 231514, 231611, 231625, 231646, upper cheekteeth; UCMP 231253, 231405, 231413, 231592-231595, lower cheekteeth.

Remarks—These small sciruid teeth overlap in size with *Ammospermophilus*, *Tamias*, and small ground squirrels. Finer taxonomic identification may be possible by morphological comparison to known modern specimens

GENUS: *CYNOMYS* Rafinesque 1817

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233235, 233289, 233596-233597, 233599, 257367, 257409, cheekteeth; UCMP 233250, left dentary with p4m1-3; UCMP

257428, 257430, maxillae. UCMP Locality V36222 (RBA): UCMP 231454-231455, 231547, cheekteeth.
Remarks—*Cynomys* is easily distinguished from other sciurids; *Cynomys* has a deep trigonid trench lingual to the ectolophid, not present in other sciurids (UCMP 233235). As compared to ground squirrels (*Otospermophilus*, *Callospermophilus*, *Xerospermophilus*, *Poliocitellus*, *Ictidomys*, *Urocitellus*, *Spermophilus*, *Notocitellus*, and *Ammospermophilus*) and *Marmota*, the cheekteeth are higher-crowned and the trigonid is higher relative to the talonid (UCMP 233250) (Goodwin 2004; Hillson 2005). Upper molars in *Cynomys* are mesiodistally compressed (UCMP 233289).

ORDER: LAGOMORPHA Brandt 1855

FAMILY: LEPORIDAE Fischer 1817

Leporidae spp.

Referred Specimens—UCMP Locality V36221 (ECR2): UCMP 233242, 23335, 233424, 233481-233483, 233523-233524, 233549, 233669, 257415, 257431, P2s; UCMP 233684, 233694, 233696, 233700, 233718, M3s; UCMP 233361, 233571, 233680, p3s; UCMP 257419, m3s; UCMP 233243-233244, 233343, 233359-233360, 233416, 233423, 233438, 233475-233478, 233500, 233548, 233556, 233589-233591, 233602-233604, 233617, 233639-233640, 233664-233665, 233688, 233709, 257386, upper cheekteeth; UCMP 233237-233238, 233264, 233272-233273, 233280-233281, 233297-231299, 233311, 233316, 233362, 233396, 233439, 233479-233480, 233546-233547, 233570, 233572, 257347, 257421, 257423, lower cheekteeth; UCMP 233258, 233296, 233358, 233363, 233456, 233474, 233605, 233682, 233710, 257342, 257343, left and right dentary fragments, some with teeth; UCMP 233249, 233295, 257404 left and right maxillae, some with teeth; UCMP 257355, 257364, 257375, 257378, cheekteeth. UCMP Locality V36222 (RBA): UCMP 231243-231244, 231267-231270, 231392-231393, 231450-231451, 231510, 231551-231553, 231655, upper cheekteeth; UCMP 231280-231283, 231291, 231365, P2s; UCMP 238408, M3; UCMP 231279, 231348, 231663, lower cheekteeth; UCMP 231255-231257, 231320, 238409, m3s; UCMP 231241, 231449, 231265-231266, fragmentary left and right dentaries with teeth; UCMP 231308, palate.
Remarks—The three genera of North American leporid—*Lepus*, *Sylvilagus*, and *Brachylagus*—are distinguishable from *Ochotona*, the only other North American Lagomorph, in that, on the lower cheekteeth the lingual reentrant is much deeper and anterior and posterior lophs are roughly the same width (buccal-lingual) in *Ochotona*, whereas in Leporids the anterior loph is wider than the posterior. Upper cheekteeth of *Ochotona* also have deeper lingual and buccal reentrants. There are no dental characters that definitively distinguish *Lepus* and *Sylvilagus*. The P2s *Brachylagus* have a single anterior reentrant, whereas in *Lepus* and *Sylvilagus* there are two. Cheekteeth in all three species are morphologically very similar, but *Brachlagus* is smaller than both *Lepus* and *Sylvilagus*. However, cheekteeth from juveniles and small individuals of *Lepus* and *Sylvilagus* could be confused with *Brachylagus*. Non-dental morphological differences between *Lepus* and *Sylvilagus* are few, and none pertain to the available fossil material. Specimens too large to be *Brachylagus* are referred to Leporidae spp. (aff. *Lepus* or *Sylvilagus*).

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Appendix 2.3: Dental patterns and morphological affinity of ECR2 and RBA fossil *Peromyscus* to known species. Dental types form Hooper (1957): a=enamel valley unobstructed; neither mesoloph/id nor mesostyle/lid present; b=a style present, unattached to neighboring cusps or lophs; no mesoloph; c=a style only, one face of it joined to the paracone (or entoconid); d=a style joined to a loph that projects from positions 4 or 5 (indicates loph projects from side of paracone and curves toward style); e=a style fused with a loph that extends from positions 6 or 7 (loph extends from the mure, not the paracone); f=style and loph not united, the style of any type the loph arising from position 5, 6, 7, but not reaching the style; g=style absent, loph arising at positions 4-7, but terminating short of the tooth's margin.

UCMP #	Site	Level	Tooth	Type of mesoloph(id)/ mesostyle(id) if present in M1	Mesoloph(id) present in M1	Mesostyle (id) Present	Type of mesoloph(id)/ mesostyle(id) , if present in M2 (see key)	Mesoloph(id) present in M2	Mesostyle (id) Present in M2	Species affinity
233257	ECR2	1	LM12	g	X		d,e	X	X	P. maniculatus P. boylei
233269	ECR2	1	Rm123	a			a			P. maniculatus P. crinitus
233256	ECR2	1	Lm123	a			a			P. maniculatus P. crinitus
233713	ECR2	3	Lm1	a						P. crinitus P. maniculatus
233383	ECR2	4	RM1	e	X	X				P. boylei P. truei
233380	ECR2	4	Rm123	a			a			P. crinitus P. maniculatus
233443	ECR2	5	LM1	e	X	X				P. boylei P. truei
233444	ECR2	5	Lm12	c		X	a			P. maniculatus
233526	ECR2	6	LM1	e	X	X				P. boylei P. truei
233472	ECR2	6	LM1	c		X				P. maniculatus

Appendix 2.3 Continued.

233507	ECR2	6	LM1	d	X	X				P. maniculatus P. boylei
233469	ECR2	6	RM1	d	X	X				P. maniculatus P. boylei
233577	ECR2	7	LM1	d	X	X				P. boylei P. maniculatus
233586	ECR2	7	LM1	e	X	X				P. boylei P. truei
233584	ECR2	7	Rm1	a						P. crinitus P. maniculatus
233588	ECR2	7	RM1	f	X	X				P. maniculatus
233587	ECR2	7	LM123	c		X	c	X		P. maniculatus
233583	ECR2	7	Lm1	a						P. maniculatus P. crinitus
233621	ECR2	8	LM1	b		X				P. crinitus
231254	RBA	1	RM1	e	X	X				P. boylei P. truei
231309	RBA	1	LM1	e	X	X				P. boylei P. truei
231287	RBA	1	LM1	a						P. crinitus
231310	RBA	1	Lm1	a						P. crinitus P. maniculatus
231276	RBA	1	Rm1	a						P. crinitus P. maniculatus
231375	RBA	2	Lm1	a						P. crinitus P. maniculatus
231339	RBA	2	Rm1	a						P. crinitus P. maniculatus
231347	RBA	2	RM12	a			c		X	P. maniculatus
231361	RBA	2	Rm1	g	X					P. maniculatus P. truei
231431	RBA	3	Rm1	g	X					P. maniculatus P. truei
231535	RBA	4	LM1	g	X					P. boylei P. maniculatus
231506	RBA	4	LM1	e	X	X				P. boylei P. truei
231537	RBA	4	Lm123	b		X	a			P. crinitus
231531	RBA	4	Rm1	b		X				P. crinitus
231532	RBA	4	Lm1	a						P. crinitus P. maniculatus
231560	RBA	5	LM12	d,e	X	X	d,e	X	X	P. boylei P. truei
231608	RBA	5	RM1	e	X	X				P. boylei P. truei
231631	RBA	6	LM1	g	X					P. boylei P. maniculatus
231649	RBA	6	LM12	e	X	X	e	X	X	P. boylei P. truei

Appendix 3.1: MVZ specimens collected in Spring and Fall 2014. All specimens were collected in the Canyon Rims Recreation Area (BLM), San Juan County, Utah, USA.

MVZ #	Accession #	Scientific Name	Sex	Site	Lat	Long	Collecton Date
230801	14964	*Peromyscus truei*	female	ERB	38.18	-109.44	6-Oct-13
230802	14964	*Peromyscus truei*	female	ERB	38.18	-109.44	11-Oct-13
230800	14964	*Peromyscus maniculatus*	male	ERB	38.19	-109.43	13-Oct-13
230799	14964	*Peromyscus maniculatus*	female	ERB	38.19	-109.43	13-Oct-13
230803	14964	*Peromyscus maniculatus*	male	WRB	38.15	-109.45	18-Oct-13
230808	14964	*Peromyscus maniculatus*	female	WRB	38.14	-109.46	18-Oct-13
230809	14964	*Peromyscus maniculatus*	female	WRB	38.14	-109.46	21-Oct-13
230807	14964	*Peromyscus maniculatus*	male	WRB	38.15	-109.45	21-Oct-13
230810	14964	*Peromyscus maniculatus*	female	WRB	38.14	-109.46	21-Oct-13
230806	14964	*Neotoma* c.f. *albigula*	unknown	WRB	38.15	-109.45	21-Oct-13
230805	14964	*Peromyscus maniculatus*	female	WRB	38.15	-109.45	21-Oct-13
230804	14964	*Peromyscus maniculatus*	male	WRB	38.15	-109.45	21-Oct-13
230866	15038	*Peromyscus maniculatus*	unknown	SH	37.98	-109.53	20-Apr-14
230864	15038	*Peromyscus maniculatus*	unknown	SH	37.98	-109.53	20-Apr-14
230865	15038	*Peromyscus maniculatus*	unknown	SH	37.98	-109.53	20-Apr-14
230862	15038	*Dipodomys ordii*	male	ERB	38.19	-109.42	24-Apr-14
230868	15038	*Peromyscus maniculatus*	male	ERB	38.18	-109.42	28-Apr-14
230867	15038	*Peromyscus maniculatus*	female	ERB	38.18	-109.44	28-Apr-14
230869	15038	*Peromyscus maniculatus*	female	WRB	38.14	-109.45	1-May-14
230870	15038	*Peromyscus maniculatus*	male	WRB	38.14	-109.45	3-May-14
230871	15038	*Peromyscus maniculatus*	female	WRB	38.14	-109.45	3-May-14
230863	15038	*Dipodomys ordii*	male	WRB	38.14	-109.45	3-May-14
231471	15081	*Peromyscus maniculatus*	male	CM	37.97	-109.83	13-Sep-14
231472	15081	*Peromyscus maniculatus*	male	CM	37.97	-109.83	13-Sep-14
231485	15081	*Peromyscus truei*	male	CM	37.97	-109.83	13-Sep-14
231473	15081	*Peromyscus maniculatus*	female	CM	37.97	-109.83	14-Sep-14
231470	15081	*Peromyscus maniculatus*	female	CM	37.95	-109.81	15-Sep-14
231474	15081	*Peromyscus maniculatus*	male	CM	37.97	-109.83	15-Sep-14
231486	15081	*Peromyscus truei*	male	MP	38.00	-109.88	28-Sep-14
231475	15081	*Peromyscus maniculatus*	male	MP	38.00	-109.88	28-Sep-14
231476	15081	*Peromyscus maniculatus*	male	MP	38.00	-109.88	28-Sep-14
231480	15081	*Peromyscus maniculatus*	male	ERB	38.18	-109.42	30-Sep-14
231479	15081	*Peromyscus maniculatus*	male	ERB	38.18	-109.42	30-Sep-14
231483	15081	*Peromyscus maniculatus*	female	ERB	38.19	-109.42	2-Oct-14
231481	15081	*Peromyscus maniculatus*	male	ERB	38.18	-109.42	2-Oct-14
231482	15081	*Peromyscus maniculatus*	male	ERB	38.18	-109.42	2-Oct-14
231484	15081	*Peromyscus maniculatus*	male	ERB	38.19	-109.42	2-Oct-14
231478	15081	*Peromyscus maniculatus*	female	WRB	38.14	-109.45	10-Oct-14
231477	15081	*Peromyscus maniculatus*	male	WRB	38.14	-109.45	10-Oct-14

Appendix 3.2: List of detection and occupancy models included in AIC model selection, and AIC results for each species (only the 10 models with the lowest AICc weights are included). elev=elevation, lat=latitude, long=longitude, pAnnual=annual precipitation, pSpring=spring precipitation, pSummer=summer precipitation, pFall=fall precipitation, pWinter=winter precipitation, tmWinter=minimum winter temperature, TMSummer=maximum summer temperature.

Detection Models:

- ~1 (dot)
- ~date

Occupancy Models:

- ~1 (dot)
- ~elev
- ~long
- ~lat
- ~elev+long+lat
- ~elev*long*lat
- ~long+lat
- ~elev+long
- ~elev+lat
- ~long+lat
- ~elev*long
- ~elev*lat
- ~long*lat
- ~pAnnual
- ~pSpring
- ~pSummer
- ~pFall
- ~pWinter
- ~tmWinter
- ~TMSummer
- ~pAnnual+tmWinter
- ~pAnnual+TMSummer
- ~pAnnual+tmWinter+TMSummer
- ~pAnnual*tmWinter
- ~pAnnual*TMSummer
- ~pAnnual*tmWinter*TMSummer

Ammospermophilus leucurus

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~1 (dot)	4	34.79	0.00	0.64	0.64

~date	5	35.94	1.15	0.36	1.00

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~pWinter	5	31.71	0.000	0.112	0.11
2 ~pAnnual	5	31.73	0.021	0.110	0.22
3 ~pSpring	5	31.73	0.026	0.110	0.33
4 ~TMSummer	5	31.73	0.027	0.110	0.44
5 ~pSummer	5	31.75	0.041	0.109	0.55
6 ~pFall	5	33.01	1.300	0.058	0.61
7 ~tmWinter	5	33.02	1.317	0.058	0.67
8 ~pAnnual+TMSummer	6	33.71	2.006	0.041	0.71
9 ~pAnnual+tmWinter	6	33.71	2.009	0.041	0.75
10 ~elev	5	34.07	2.369	0.034	0.78

Dipodomys ordii

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~1 (dot)	4	79.350	0.000	0.530	0.530
~date	5	79.570	0.220	0.470	1.000

Occupancy Models

	nPars	AIC	delta	AICwt	cumltvWt
1 ~long+lat	6	74.590	0.000	0.245	0.240
2 ~long+lat	6	74.590	0.000	0.245	0.490
3 ~long*lat	7	76.580	1.980	0.091	0.580
4 ~elev+long+lat	7	76.590	1.990	0.090	0.670
5 ~lat	5	78.000	3.410	0.045	0.720
6 ~pAnnual+TMSummer	6	78.400	3.810	0.037	0.750
7 ~TMSummer	5	79.330	4.740	0.023	0.770
8 ~1 (dot)	4	79.350	4.760	0.023	0.800
9 ~pWinter	5	79.450	4.860	0.022	0.820
10 ~pSummer	5	79.630	5.040	0.020	0.840

Neotoma albigula

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~1 (dot)	4	62.240	0.000	0.720	0.720
~date	5	64.180	1.940	0.280	1.000

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~elev+long+lat	7	58.300	0.000	0.195	0.190

2 ~pAnnual+tmWinter+TMSummer	7	58.340	0.039	0.191	0.390
3 ~elev*long	7	58.810	0.515	0.151	0.540
4 ~long+lat	6	59.590	1.290	0.102	0.640
5 ~long+lat	6	59.590	1.290	0.102	0.740
6 ~long*lat	7	61.670	3.373	0.036	0.780
7 ~1 (dot)	4	62.240	3.945	0.027	0.800
8 ~pAnnual+tmWinter	6	62.290	3.991	0.027	0.830
9 ~tmWinter	5	63.200	4.898	0.017	0.850
10 ~elev	5	63.290	4.996	0.016	0.860

Onychomys leucogaster

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~date	5	68.310	0.000	0.680	0.680
~1 (dot)	4	69.800	1.490	0.320	1.000

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~TMSummer	6	60.260	0.000	0.148	0.150
2 ~pSummer	6	60.260	0.002	0.148	0.300
3 ~pWinter	6	60.330	0.069	0.143	0.440
4 ~pSpring	6	60.350	0.086	0.142	0.580
5 ~pAnnual	6	60.410	0.149	0.137	0.720
6 ~pAnnual+tmWinter	7	62.220	1.957	0.056	0.770
7 ~pAnnual+TMSummer	7	62.260	1.996	0.055	0.830
8 ~elev	6	63.890	3.629	0.024	0.850
9 ~pAnnual+tmWinter+TMSummer	8	64.210	3.945	0.021	0.870
10 ~pAnnual*tmWinter	8	64.210	3.952	0.021	0.890

Perognathus flavescens

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~1 (dot)	4	49.55	0.00	0.73	0.73
~date	5	51.55	2.0	0.27	1.00

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~elev*long	7	45.34	0	0.5315	0.53
2 ~1 (dot)	4	49.55	4.21	0.0649	0.6
3 ~elev+lat+long	7	50.08	4.74	0.0497	0.65
4 ~lat	5	51.39	6.05	0.0258	0.67
5 ~tmWinter	5	51.51	6.16	0.0244	0.7
6 ~long	5	51.51	6.17	0.0243	0.72

7 ~TMSummer	5	51.54	6.2	0.024	0.74
8 ~elev	5	51.54	6.2	0.0239	0.77
9 ~pSummer	5	51.55	6.2	0.0239	0.79
10 ~pFall	5	51.55	6.2	0.0239	0.82

Perognathus parvus

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~1 (dot)	4	45.66	0	0.72	0.72
~date	5	47.56	1.89	0.28	1

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~elev	5	37.61	0	3.3E-01	0.33
2 ~elev+lat	6	39.6	1.99	1.2E-01	0.45
3 ~elev+long	6	39.61	2	1.2E-01	0.57
4 ~pAnnual+tmWinter	6	39.63	2.02	1.2E-01	0.69
5 ~elev*lat	7	41.59	3.98	4.5E-02	0.74
6 ~elev*long	7	41.59	3.98	4.5E-02	0.78
7 ~elelv+lat+long	7	41.59	3.98	4.5E-02	0.83
8 ~pAnnual*tmWinter	7	41.61	4	4.5E-02	0.87
9 ~pAnnual+tmWinter+TMSummer	7	41.64	4.04	4.4E-02	0.92
10 ~pAnnual*TMSummer	7	41.67	4.07	4.3E-02	0.96

Peromyscus maniculatus

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~1 (dot)	4	25.290	0.000	0.610	0.610
~date	5	26.220	0.930	0.390	1.000

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~1 (dot)	4	25.29	0.000	0.171	0.170
2 ~elev	5	27.29	2.000	0.063	0.230
3 ~pAnnual	5	27.29	2.000	0.063	0.300
4 ~lat	5	27.29	2.000	0.063	0.360
5 ~tmWinter	5	27.29	2.000	0.063	0.420
6 ~pSummer	5	27.29	2.000	0.063	0.490
7 ~TMSummer	5	27.29	2.000	0.063	0.550
8 ~pWinter	5	27.29	2.000	0.063	0.610
9 ~long	5	27.29	2.000	0.063	0.680
10 ~pSpring	5	27.29	2.000	0.063	0.740

Peromyscus truei

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~date	5	44.730	0.000	0.990	0.990
~1 (dot)	4	53.960	9.230	0.010	1.000

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~1 (dot)	5	44.730	0.000	0.171	0.170
2 ~pFall	6	46.730	2.000	0.063	0.230
3 ~TMSummer	6	46.730	2.000	0.063	0.300
4 ~pSummer	6	46.730	2.000	0.063	0.360
5 ~pAnnual	6	46.730	2.000	0.063	0.420
6 ~pSpring	6	46.730	2.000	0.063	0.490
7 ~long	6	46.730	2.000	0.063	0.550
8 ~lat	6	46.730	2.000	0.063	0.610
9 ~tmWinter	6	46.730	2.000	0.063	0.680
10 ~elev	6	46.730	2.000	0.063	0.740

Tamias rufus

Detection models:

	nPars	AIC	delta	AICwt	cumltvWt
~1 (dot)	4	75.890	0.000	0.730	0.730
~date	5	77.880	1.990	0.270	1.000

Occupancy Models:

	nPars	AIC	delta	AICwt	cumltvWt
1 ~elev*lat	7	71.810	0.000	0.208	0.210
2 ~elev*long	7	71.830	0.021	0.206	0.410
3 ~pAnnual+tmWinter	6	73.090	1.281	0.110	0.520
4 ~elev+lat	6	73.110	1.296	0.109	0.630
5 ~pAnnual+tmWinter+TMSummer	7	75.090	3.278	0.040	0.670
6 ~pAnnual*tmWinter	7	75.090	3.280	0.040	0.710
7 ~elev+long+lat	7	75.110	3.300	0.040	0.750
8 ~lat	5	75.530	3.714	0.033	0.790
9 ~1 (dot)	4	75.890	4.076	0.027	0.810
10 ~long*lat	7	76.030	4.215	0.025	0.840

Appendix 3.3: Number of animal captures per site per trap night. SP=South Plain, MP=Middle Park, CM=Cedar Mesa, TRB=Tower Ruin Basin, SCP=Salt Creek Pocket, SH=Shay Mesa, WRB=West of Rone Bailey, ERB=East of Rone Bailey.

Season	Site	trap night	# captures	Capture rate
Spring	SP	1	1	0.74%
		2	3	2.21%
		3	6	4.41%
		4	4	2.94%
	CM	1	8	5.88%
		2	10	7.35%
		3	16	11.76%
		4	14	10.29%
	ERB	1	42	30.88%
		2	79	58.09%
		3	78	57.35%
		4	84	61.76%
	SCP	1	7	5.15%
		2	16	11.76%
		3	24	17.65%
		4	33	24.26%
	SH	1	9	6.62%
		2	10	7.35%
		3	14	10.29%
		4	22	16.18%
	TRB	1	0	0.00%
		2	0	0.00%
		3	0	0.00%
		4	0	0.00%
	WRB	1	39	28.68%
		2	58	42.65%
		3	55	40.44%
		4	40	29.41%
	MP	1	9	6.62%
		2	17	12.50%
		3	23	16.91%
		4	24	17.65%
Fall	SP	1	12	8.82%
		2	20	14.71%
		3	21	15.44%
		4	26	19.12%

Appendix 3.3 Continued.

	CM	1	26	19.12%
		2	27	19.85%
		3	36	26.47%
		4	34	25.00%
	ERB	1	21	15.44%
		2	31	22.79%
		3	52	38.24%
		4	56	41.18%
	TRB	1	20	14.71%
		2	31	22.79%
		3	29	21.32%
		4	39	28.68%
	WRB	1	17	12.50%
		2	33	24.26%
		3	24	17.65%
		4	25	18.38%
	MP	1	15	11.03%
		2	25	18.38%
		3	28	20.59%
		4	36	26.47%