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Diversity and Relative Abundance of the Dark Kangaroo Mouse, *Microdipodops megacephalus*, in Communities of Nocturnal Granivorous Rodents in Western North America

Ashley S. Haug

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Diversity and Relative Abundance of the Dark Kangaroo Mouse, *Microdipodops megacephalus*, in Communities of Nocturnal Granivorous Rodents in Western North America

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The dark kangaroo mouse, *Microdipodops megacephalus*, is a sensitive species in the Great Basin Desert. This thesis explores the structure of desert rodent communities of the Great Basin to better understand *M. megacephalus'* place in the community and the conditions that promote large and stable populations. To determine community structure, I used nestedness analysis to evaluate 99 communities of nocturnal granivorous rodents. I found that the community structure was non-random, indicating the existence of assembly rules and ecological constraints. I also found that *M. megacephalus* was the second most vulnerable species in the community. To explore the correlation between species diversity and relative abundance, I performed regression analyses on *M. megacephalus* and five commonly co-occurring species of the nocturnal granivore guild: *Perognathus longimembris* (little pocket mouse)*, Perognathus parvus* (Great Basin pocket mouse)*, Dipodomys ordii* (Ord's kangaroo rat)*, Dipodomys microps* (chisel-toothed kangaroo rat)*,* and *Peromyscus maniculatus* (deer mouse). Results showed a positive correlation between rodent species diversity and relative abundance for *M. megacephalus, P. longimembris, P. parvus,* and *D. microps*, and a negative correlation for *D. ordii* and *P. maniculatus*. To further understand community composition, I ran interspecific association analyses based on presence-absence data for the six species using chi-square to determine strength of interspecific associations. I found positive interspecific associations between *M. megacephalus* and *P. parvus*, between *P. longimembris* and *P. parvus*, between *P. longimembris* and *D. microps*, and between *D. microps* and *P. maniculatus*, and a negative association between *P. longimembris* and *P. maniculatus*. A species cluster dendogram with respect to sites in common further supports the interspecific association results. A site cluster dendogram with respect to species abundances implies that dune habitat promotes diversity but not uniformity. All results indicate that *M. megacephalus* is more abundant and stable at sites with high species richness. The results also provide evidence for the existence of assembly rules, competition, and niche partitioning in desert rodent communities.

Keywords: *Microdipodops megacephalus*, nocturnal granivore guild, assembly rules, community structure, nestedness, species diversity, relative abundance, regression, interspecific associations, competition, cluster analyses, conservation, Great Basin Desert.

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Nestedness and Community Structure in Nocturnal Granivorous Rodent Systems of the Great Basin Desert, with Focus on the Dark Kangaroo Mouse, *Microdipodops megacephalus*

Abstract The existence of assembly rules has been debated since the idea's conception, but there has been strong evidence that constraints such as competition and niche partitioning influence community structure in desert rodent communities. A non-random community structure indicates that constraints and ecological processes and interactions are shaping community composition. Nestedness analysis is one tool that can test for non-random community structure, and it was used to evaluate data from 99 nocturnal granivorous rodent communities of the Great Basin Desert. An extinction order of the species in the communities was also predicted. Special attention was given to the position of the dark kangaroo mouse, *Microdipodops megacephalus*, in the predicted extinction order because it is listed as a sensitive species in Utah and Nevada. In addition, I also tested for the type of correlation between rodent species diversity and the relative abundance of each nocturnal granivorous rodent species in the community. Besides *M. megacephalus,* five other rodent species were analyzed: *Perognathus longimembris* (little pocket mouse)*, Perognathus parvus* (Great Basin pocket mouse)*, Dipodomys ordii* (Ord's kangaroo rat)*, Dipodomys microps* (chisel-toothed kangaroo rat)*,* and *Peromyscus maniculatus* (deer mouse). Results showed only a 19.15% deviation from complete nestedness and predictability of structure among the communities ($p < 0.001$). *Microdipodops megacephalus* was the second most vulnerable species in the community, and was present in higher abundances at sites with greater species richness. Species diversity was positively correlated with relative abundances of *M. megacephalus, P. longimembris, P. parvus,* and *D. microps*. These variables were negatively correlated for *D. ordii* and *P. maniculatus.* The results provide evidence for the role of assembly rules in desert rodent communities. Diversity levels may be used as a measure of the quality or stability of a community. These results will aid conservationists in promoting large and stable populations of *M. megacephalus*.

Key words: abundance, community structure, competition, conservation, diversity, *Microdipodops megacephalus*, nestedness, nocturnal granivores

Introduction

During the last decade, there has been renewed interest in community assembly rules and their influences on community structure (Ernest et al. 2008). A much-debated idea that marks a turning point in the history of ecology, the concept of assembly rules suggests that there are certain processes and constraints that define and shape communities of species. Examples of possible assembly rules include, “a combination that is stable on a large or species-rich island may be unstable on a small or species-poor island”, and “some pairs of species never coexist, either by themselves or as part of a larger combination” (Diamond 1975a, p. 344). Theoretically, some types of processes or community dynamics are the reasons for the existence of assembly rules. Two of the most commonly examined constraints behind such assembly rules are competition and niche partitioning, which have often been studied and appear to be present in granivorous desert rodent communities (Goheen et al. 2005; Ernest et al. 2008). It is difficult to determine whether interspecific competition is the driving force in the assembly of any specific rodent community, but one strong indicator of competition is the appearance of non-random community structures. A non-random community structure may provide evidence that various factors are shaping the composition of a community, including, but not limited to, competition, niche partitioning, species morphology, and species diversity.

Interspecific competition has been shown to drive non-random assemblages of granivorous rodent communities in many studies (Bowers and Brown 1982; Patterson and Brown 1991; Goheen 2005). For example, nocturnal granivorous rodents of similar sizes coexist less frequently in local communities than expected by chance, suggesting interspecific competition due to similar niche utilization (Bowers and Brown 1982). Niche complementarity, or resource partitioning based on consumer morphology, has also been found to be important in maintaining species richness (Goheen 2005).

Species diversity also plays a role in determining rodent community structure; the more diverse the community, the greater the non-random community structure (Goheen 2005). This idea suggests a correlation between diversity in communities and the relative abundance of a species. As diversity increases or decreases, the proportion of the community that each species represents will also change. Common species most likely dominate the community when diversity is low should decrease in abundance relative to the number of individuals in the entire community. Similarly, while diversity increases, rare species should increase in relative abundance.

The main processes that maintain species diversity are interspecific competition and niche complementarity, or niche partitioning based on species' morphology, i.e. body size (Goheen 2005). Body size is often correlated with species diversity in rodent communities. Ernest et al. (2008) suggest that the same level of resources can either support few large species or many small ones. Thus, when diversity is low, large-bodied species should dominate. With increased species diversity, small-bodied species will increase in number. Furthermore, there is an inverse relationship between the number of species a community can support and the differences in body size among rodent species (Brown 1973).

In other words, the greater the rodent diversity, the more homogeneous in size the species become. A site that can support a greater number of species is most likely larger in area and more productive. Therefore, species that would not normally coexist because of similar niche and body size would be able to find enough space and food resources for coexistence. For example, similarly sized species may target seeds of similar size, although this idea has been criticized as being too simplistic (Brown and Lieberman 1973; Lemen 1978).

Nestedness is an ecological concept that describes the amount of order or disorder in the composition of species among many sites. Nestedness analysis is one method for testing for non-random community assemblages. Nestedness analysis can also predict the extinction order of species within the community in the case of a local extinction event. Many communities exhibit non-random assemblages, or some degree of nestedness (Patterson and Brown 1991).

Nestedness can be examined by applying the concept of island biogeography. Sites or communities are compared to islands of an archipelago, implying that the species on the "islands", or sites, are immediately isolated from other sites (MacArthur and Wilson 1967). In a perfectly nested "archipelago", or system of sites, the sites with less species richness will contain species that are subsets of the species at the richer sites. Less rich sites will never contain species that are absent from more rich sites.

Therefore, species found where richness is small are expected to be everywhere that richness is equal to or greater than that site. This idea can be understood by visualizing a set of kitchen bowls, each bowl fitting perfectly within the next largest bowl (Wright and Reeves 1992). Rare species are theoretically found at more diverse (and typically larger) sites. Such species may be in need of preservation (Patterson 1987).

Nestedness analysis can also be used to determine the extinction order of the species in a system of sites in the case of a local extinction event (Atmar and Patterson 1993). Every site contains a species that is closest to its minimum sustainable population size, and this species is the most vulnerable in the event of a local extinction. If a system of sites is perfectly nested, the extinction order should be duplicated on every site.

It is expected that the extinction order would be affected by events such as immigration and natural disturbances (Atmar and Patterson 1993). Referred to as the “statistical noise of local opportunity and catastrophe”, this disturbance can be compared to molecules (Atmar and Patterson 1993, p. 373). At a temperature of 0°, particles are completely at rest. As the temperature increases, the particles begin to move faster, farther apart, and more chaotically. The amount of disturbance in a system of populated communities can be compared to a “temperature” that reflects the amount of entropy in the system. Using this analogy, it follows that a completely “cold” system (temperature = 0°) is perfectly nested with the extinction order replicated across all sites. Likewise, a “hot” system is one where the number of unexpected presences and absences of species across sites in the system is very high. The highest possible temperature estimated with nestedness temperature calculators is 100°, which indicates total disorder and unpredictability. Since the temperature range is 0° to 100°, these values can also be viewed as percentages of entropy in the system. The general extinction order will hold at all temperatures less than 100°. However, the cooler the temperature, the more confident one can be about the extinction order (Atmar and Patterson 1993).

Desert granivorous rodent communities of the Great Basin Desert are excellent models for exploring assembly rules. These communities are typically comprised of five to eight species of nocturnal rodents, primarily from the family Heteromyidae. The members of these communities include common and rare species of varying body sizes. The fact that the communities are generally isolated from one another, along with the comparative ease in locating and sampling them makes these communities ideal systems in which to explore assembly rules and constraints on community structure.

Understanding community structure in these desert systems is particularly important because they are home to a rare heteromyid, the dark kangaroo mouse (*Microdipodops megacephalus*). The dark kangaroo mouse, one of only two species of *Microdipodops*, is found less frequently and in smaller abundances than other heteromyids. It is restricted to "ecological refugia, or specialized or unique habitats" in parts of Utah, Nevada, California, and Oregon (O'Farrell and Blaustein 1974; Bureau of Land Management 2003, p. 1). Both the states of Nevada and Utah list *M. megacephalus* as a sensitive species. The primary rationale for this listing includes the decline in population sizes, the alteration and destruction of suitable habitat, and the proliferation of invasive species, particularly cheatgrass, *Bromus tectorum* (Bureau of Land Management 2003; State of Utah Department of Natural Resources 2007).

This paper examines the nestedness and dynamics of relative abundance in nocturnal granivorous rodent communities at many sites in the Great Basin Desert. Species diversity has been related to changes in the relative abundances of species, but the direction of this relationship in the context of *M. megacephalus* and the nocturnal granivore guild of the Great Basin has not previously been investigated (Ernest et al. 2008). Examination of community structures could provide evidence for the existence of assembly rules and constraints in systems of nocturnal granivorous rodents of the Great Basin. Moreover, any study of the vulnerability of *M. megacephalus* and conditions that are correlated with large populations will assist in the conservation of this species.

The specific objectives of this study are: 1) to test for non-randomness in nocturnal granivorous rodent communities of the Great Basin Desert using nestedness analysis; 2) to predict the extinction order of the species in communities (focusing on the stability of *M. megacephalus* in relation to the other nocturnal granivorous rodents) using nestedness analysis;

3) to look for a pattern in abundance of different body sizes with varying levels of species diversity; and 4) to further support the findings of the nestedness analysis by testing for any correlation between the relative abundance of nocturnal granivorous rodent species (including *M. megacephalus*) and rodent species diversity in desert rodent communities of the Great Basin.

For the first objective, I hypothesize that the nocturnal granivorous rodent community structure in the Great Basin will be significantly non-random. For the second objective, I hypothesize that there will be a significant extinction order among the species in the nocturnal granivorous rodent community. Rare species are likely more sensitive to disturbances or changes in habitat than common species. Knowing that *M. megacephalus* is a rare, sensitive species, I predict that it will be the species most vulnerable to extinction and found more frequently at sites with greater species richness. I also predict that the species that are the most stable and most resistant to extinction will likely be ubiquitous across the greatest number of sites.

For the third objective, I hypothesize that there will be a pattern in the abundance of various body sizes with changing diversity, and that this will mirror the patterns found with the nestedness analysis. Since species diversity may imply more available space and resources, I predict that species of similar size will more frequently coexist with greater species diversity. An example of two species that may only coexist given enough space and resources is *M. megacephalus* and *Perognathus longimembris* (little pocket mouse). The two nocturnal granivores occupy the same type of habitat and overlap in size: *M. megacephalus* ranges from 138 to 177 millimeters in length and 10 to 16.9 grams in mass, while *P. longimembris* ranges from 110 to 151 millimeters in length and 6.5 to 10.5 grams in mass (Wilson and Ruff 1999).

For the fourth objective, I hypothesize a significant correlation between species' relative abundances and site diversity of nocturnal granivores. It is known that population increases of one species are compensated for by decreases in populations among other species (Hubbell 2001; Ernest et al. 2008). I predict that the most stable species found in the nestedness analysis will decrease in abundance when diversity increases, and that the most vulnerable species found in the nestedness analysis (predicted to be *M. megacephalus*) will increase in abundance when diversity increases, since rare species are generally found at more diverse sites (Patterson 1987).

Materials and Methods

Data collection—I compiled the data for this study from data collected by myself in Utah, R. David Waltz (2005) who researched in Oregon, and Debra K. Lawhon (1984) who researched in California. This collection of data will make the findings applicable over a broad geographic and temporal range. The combination of the Utah, Oregon, and California data results in a total of 99 sites trapped for rodent presences and abundances in the Great Basin Desert (Table 1).

In 2005, rodents were trapped in west-central Utah at and around historical locations of *M. megacephalus* provided by the Natural Heritage Program, UT. Habitats ranged from windblown sand dunes with *Artemisia* (sagebrush), hardpan soil, “desert pavement”, and grass-covered terrain. Sites were sampled throughout the summer. Sherman live traps baited with commercial birdseed were used to catch rodents, and the number of traps and placement of linear transects varied from site to site (Price et al. 2000). Traps were set at dusk and collected in the morning before strong daylight to minimize heat exposure to captured animals.

In 2006 and 2007, I focused on dune habitats in west-central Utah, re-trapping some historical sites and also seeking out un-trapped places that had dune-like qualities (sandy soil, vegetated edges of bare dunes, and small sandy rises and ridges within typical Great Basin valleys). In 2008, I sampled 14 sites in west-central Utah (Iron County), which were selected because they included typical habitat for *M. megacephalus,* and because they were known sites of prior captures of *M. megacephalus*. Sites were flat to steep windblown sand dunes dominated by desert shrubs, particularly *Artemisia, Atriplex, Chrysothamnus, Rhus,* and *Sarcobatus* species. Sites were trapped through May and June. Traps were set in two linear transects of 120 traps each. Transects were placed 100 meters apart, with each trap 10 meters from its nearest neighbor (Figure 1, Table 2). Only data from the first night of trapping were analyzed in this study because new individuals and recaptures were not always distinguished.

Waltz trapped at nine sites in Pueblo Valley, Oregon (Harney County) during the summers of 2001 and 2002 (Waltz 2005; Figure 2). In Waltz's research, four main study habitats were represented: Basin big sagebrush-steppe, shadscale habitat, mixed shrub sand dunes, and alkali saltgrass flats. At each of the nine sites, Waltz set an 11x11 trapping grid (121 traps) 50–150 meters from a road that covered one hectare of ground. Sherman live traps were baited with birdseed and left overnight to capture nocturnal species. He marked and released captured animals and counted the minimum number known alive (MNKA), or total number of individuals, at each site. I used these MNKA data in my analyses, and I combined data across years for each site.

Lawhon trapped at two study sites in Mono County, California: one near Benton Valley Ranch and the other along the north shore of Mono Lake (Lawhon 1984; Figure 3). These sites were selected because of known *M. megacephalus* populations and because they were characterized by windblown sand dunes and *Artemisia*, typical habitat for *M. megacephalus* (Hall and Linsdale 1929). Lawhon built permanent 10x10 trapping grids at the Benton site and 10x6 trapping grids at the Mono Lake site. She placed traps 15 meters apart, both in the open and under shrubs. Lawhon's sampling extended through all seasons, from April of 1982 to October of 1983. Her thesis does not indicate the MKNA for each species; therefore, I analyzed the total number captures for every species at each site.

Nestedness analyses—Numerous authors have introduced metrics for quantifying the degree of nestedness in the hypothetical archipelago (Wright and Reeves 1992; Atmar and Patterson 1993). A common feature to all of these metrics is the presence-absence matrix. In this matrix, sites are row headers and species are column headers. A software program rearranges the matrix to minimize the distance of unexpected presences and absences from a calculated extinction threshold line (Atmar and Patterson 1993). This is called optimal packing, and it ensures that the software provides the lowest matrix temperature possible for the provided data. Once packed, the most species-rich site is on the top row of the matrix, while the least rich site is on the bottom row. Also, the species on the far left column is the most stable and widely distributed, while the species on the far right column is the most vulnerable to extinction. The species' position in the matrix is the most valuable information for conservationists (Atmar and Patterson 1993).

I created a presence-absence matrix that consisted of 99 rows (study sites) and 6 columns (species). The computer software BINMATNEST (Rodríguez-Gironés and Santamaría 2006) optimally packed the presence-absence matrix, estimated the matrix temperature, and computed the probability of the matrix temperature occurring in a random matrix. BINMATNEST, a prompt-command style program, was created as an alternative to the Nestedness Temperature Calculator, which Rodríguez-Gironés and Santamaría claim has deficiencies in matrix packing and mathematical accuracy (Atmar and Patterson 1993; Rodríguez-Gironés and Santamaría 2006). BINMATNEST uses a genetic algorithm (GA) to optimally pack the presence-absence matrix (Soak and Ahn 2004; Rodríguez-Gironés and Santamaría 2006). When optimally packing the matrix, it deletes identical rows and columns (except for one) for a more accurate analysis (Rodríguez-Gironés, personal communication).

The number of Monte Carlo simulations (number of null matrices used to calculate a *p*-value) was 1000 (>50 recommended by BINMATNEST); the population size for use in the GA to calculate matrix temperature was 30 (recommended); the number of individuals selected at each generation of the GA was 7 (recommended); and the number of generations for the GA was 2000 (recommended). The output included the optimally packed matrix, the matrix temperature, and the probability that the given matrix arrangement could be random.

Regression analyses of relative abundance on species diversity—I used regression analysis to determine the significance and direction of the correlation between the diversity of nocturnal granivorous rodent species in the Great Basin and the relative abundance of each species. Since trapping effort differed across data sets, I used relative abundance rather than raw capture data for normalization. I calculated the relative abundance for each species at each site by dividing the number of captures of one species by the total number of captures for all species (Table 3). Because the statistical program R required this variable to be an integer, I multiplied relative abundance by 100, and then rounded to the nearest integer (R Development Core Team 2009).

I regressed each species' relative abundance integer value by two measures of diversity for each site: species richness (*s*) and the Shannon-Wiener index of diversity (*H'*) (Shannon and Weaver 1949; Table 4). I chose species richness as the most basic and commonly used measure of diversity, as it is simply a count of the total number of species caught in a trapping session (Magurran 1988). Rarefaction or other types of transformations on *s* were not performed because of unequal catchability among all the species and the low number of rodent species observed at trapping sites. I chose the Shannon-Wiener index of diversity as a second measure of diversity because of its ability to describe the diversity of communities with rare species and its prevalent use in ecological studies (Shannon and Weaver 1949; Magurran 1988).

Data were loaded into Tinn-R, a software program that organizes the data for analysis by the program R (Faria 2009). I used regression models in R to evaluate the relationship between relative abundance and diversity. I tested five models: general linear, Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial. I included a zero-inflated Poisson and a zero-inflated negative binomial because of the zero-heavy data that were being analyzed; the number of captures for many species was zero (Figure 4). Distribution problems created by a large amount of zeros are not adequately solved by statistical transformations. The zero-inflated versions of the models, however, are effective solutions for zero-heavy data (Welsh et al. 1996).

After testing with each regression model, I chose the regression model that best fit each data set. To do this, I selected the model with the lowest Akaike's Information Criterion (AIC) value (Akaike 1973). Program R provided the AIC values for the general linear, the Poisson, and the negative binomial. I calculated the AIC values for the zero-inflated Poison and the zero-inflated negative binomial with the log likelihood provided by R and the equation AIC = –2(log likelihood) + 2n, where n is the number of parameters in the regression model (n=4 for the zero-inflated Poisson and n=5 for the zero-inflated negative binomial).

The zero-inflated negative binomial returns a *p*-value for two additional types of models: the first predicts the actual counts of relative abundance, and the second predicts the probability of a zero occurring in the relative abundance variable. The general linear only generates a *p*-value for the count model. The sign of the estimate indicates whether the relationship between relative abundance and diversity is positive or negative. A positive estimate for the count model indicates that relative abundance increases with species diversity. A positive estimate for the probability of a zero model indicates that as diversity increases, the probability of a zero in the relative abundance variable increases; essentially, a positive estimate for this model indicates a negative relationship between the two variables. Results contradict if the *p*-value is significant for both the count and probability of a zero model and the sign of the estimate is the same for both models.

Results

Nestedness analyses— Six commonly co-occurring nocturnal granivores were considered in this study because they were the only species captured to a great extent by all researchers. They were: *M. megacephalus, P. longimembris*, *Perognathus parvus* (Great Basin pocket mouse), *Dipodomys ordii* (Ord's kangaroo rat), *Dipodomys microps* (chisel-toothed kangaroo rat), and *Peromyscus maniculatus* (deer mouse). The analyses of nestedness among 99 rodent communities revealed the most common to least common species to be as follows: *D. ordii* (present at 88% of all sites), *P. maniculatus* (82%), *D. microps* (55%), *P. longimembris* (38%), *M. megacephalus* (23%), and *P. parvus* (21%). The frequency of richness values resembles a bell curve, with the majority of the sites (~ 60%) having a species richness of two or three (Figure 5). Sites with high diversity were rare; only five out of 99 sites had a richness of six. *Microdipodops megacephalus* was present at 0% of sites with a richness of one, and the likelihood of this species' presence increased with increasing species richness. For example, as richness increases from four to five species, the percentage of sites where *M. megacephalus* was present increases from 21% to 78% (Table 5).

BINMATNEST optimally packed the presence-absence matrix (Tables 6 and 7). The resulting matrix displays 95 rows/sites, rather than the original 99. The identical rows that were removed represented four out of the five sites that had a species richness of six. The calculated temperature of the matrix was cool: 19.15° in a range of 0° to 100°. This indicates that the amount of entropy in the matrix, or the trend away from nestedness, is only 19.15%.

The p-value that a random matrix would have the same level of nestedness based on 1000 Monte Carlo simulations is < 0.001. The extinction order of species in the packed matrix from most to least stable was: *D. ordii, P. maniculatus, D. microps, P. longimembris, M. megacephalus,* and *P. parvus*. The first five sites in the matrix were the most diverse, with all six species present. The sites in the bottom six rows were the least rich, with only *D. ordii* (the most stable species) present.

Regression analyses of relative abundance on species diversity—Rodent species diversity was positively correlated with the relative abundance of *M. megacephalus, P. longimembris, P. parvus,* and *D. microps.* These regressions were all significant ($p < 0.001$). Species diversity was negatively correlated with relative abundance of *D. ordii* ($p < 0.001$) and *P. maniculatus* ($p = 0.004$; Table 8).

The zero-inflated negative binomial model best fit the data for most cases. However, this model failed to converge on three occasions: for *D. ordii* when relative abundance was regressed on both s and H', and for *P. maniculatus* when relative abundance was regressed on s. On these occasions, the model with the second lowest AIC was chosen, which in all three cases was the general linear model (Table 9).

Results of the count model and the probability of a zero model contradicted most often when species richness was used as the diversity index. For *P. parvus, P. longimembris,* and *D. microps,* the sign of the estimate was negative for both models, and both *p*-values were significant. The Shannon-Wiener index only showed such a contradiction for *P. maniculatus*. Because it resulted in fewer contradictions, the Shannon-Wiener index was used for interpretation of the data in this study.

When the relative abundance of each species was regressed on the Shannon-Wiener index of diversity, all species showed significant results. Results were most often significant for the probability of a zero model only, with the exception of *D. ordii.* This type of model was not available for *D. ordii* because the general linear was used; however, *D. ordii* still showed significant results with the count model. *Peromyscus maniculatus* was the only species to show contradictory results when the Shannon-Wiener index was used, so results from this species are taken from the general linear model using species richness.

Scatter plots of relative abundance vs. site diversity (*H'*) allow for visual interpretation of results (Figure 6). The scatter plots displaying relative abundance vs. *H*' for *M. megacephalus* and *P. parvus* show a spike in relative abundance at *H'* = 0.6 and *H'* = 0.8, respectively. The scatter plot for *P. longimembris* displays a more gradual increase in relative abundance with diversity. The scatter plot for *D. microps* appears to show a negative correlation between relative abundance and diversity. The scatter plots for *D. ordii* and *P. maniculatus* also indicate gradual decreases in relative abundance with increased diversity.

Discussion

The results of this study provide further evidence that ecological processes and species interactions create non-random community structures in systems of nocturnal granivorous desert rodents from the Great Basin. These rodent communities are most likely shaped by competition and niche partitioning based on morphological and behavioral differences, such as body size and foraging habits. The findings of this study support the argument for the existence of assembly rules in communities of nocturnal granivorous rodents of the Great Basin.

The hypothesis of a non-random nocturnal granivorous rodent community structure was supported. The cool matrix temperature of 19.15° in a range of 0° to 100° indicates that the amount of entropy in the matrix, or the trend away from complete nestedness, is only 19.15%. This is comparable to the significant temperature of 15.37° calculated with the Nestedness Temperature Calculator with data from desert rodent communities by Kelt and Brown (1999). The small p-value of < 0.001 shows that the arrangement of the matrix and its corresponding temperature differ significantly from a randomly packed matrix, and that the probability of a factor other than chance influencing community structure is very high.

The hypothesis that a significantly predictable species extinction order existed was supported, as well as the prediction that the most stable species would be found across the greatest number of sites and the most vulnerable species would be rare. The Ord's kangaroo rat (*D. ordii*) and the deer mouse's (*P. maniculatus*) positions as the most stable species were expected since researchers captured them at the majority of the sites and in the greatest abundances. The little pocket mouse (*P. longimembris*) and the chisel-toothed kangaroo rat's (*D. microps*) positions in the middle of the matrix suggest stability; however, these species may still deserve further research since they were not common across all sites. The prediction that *M.*

megacephalus would be most vulnerable to extinction was also supported. *Microdipodops megacephalus* is one of the two most vulnerable species, along with *P. parvus*, the Great Basin pocket mouse. This placement in the matrix provides further support for *M. megacephalus'* status as a species of concern. The Great Basin pocket mouse's position as the one of the two most vulnerable species in the matrix also warrants further study of its habitat, resource requirements, and behavioral ecology.

The significance of the nestedness results may extend beyond extinction order and species vulnerability to the SLOSS (single large or several small) debate over the size of nature reserves (Diamond 1975b). As the presence-absence matrix becomes more nested and its temperature cools, the decision for the single large reserve becomes increasingly favored (Atmar and Patterson 1993). The cool temperatures calculated in this study and by Kelt and Brown (1999) suggest that a single large reserve would theoretically promote the greatest diversity among this group of granivorous rodents, and thereby promote stable populations of *M. megacephalus*. However, this conclusion may not be optimal in this case, since *M. megacephalus* is a rare species. Due to the sporadic presences and vulnerability of *M. megacephalus*, as many reserves as possible would likely better guarantee the taxon's continued existence. To determine the optimal size of reserves that would allow for strong populations of *M. megacephalus*, existing and future research on home range, foraging distances, and dispersal should be considered.

The matrix also shows that the likelihood of *M. megacephalus* being present increases with increased species richness. At sites where richness is equal to one, *M. megacephalus* is never that lone species. As richness increases from four to five species, the percentage of sites where *M. megacephalus* is present increases from 21% to 78% (Table 5). This clear pattern indicates a relationship between relative abundance and diversity and is supported by the regression analyses discussed below.

The hypothesis that patterns in abundance of different body sizes with varying diversity would reflect the patterns found with the nestedness analysis was also supported. The nestedness analysis returned the order in which species appeared in communities with increased species diversity: *D. ordii, P. maniculatus, D. microps, P. longimembris, M. megacephalus,* and *P. parvus.* The same ordering of species also shows a general decreasing trend in body size. To return to Brown's prediction, the more diverse a dune, the more similar in body size the species become (Brown 1973). From this study, it appears that smaller species like *M. megacephalus, P. longimembris*, and *P. parvus* coexist most frequently when species diversity is the highest. Rodents of similar size and niche that are potential competitors seem to be more likely to coexist at a more diverse dune, possibly because of the increased availability of resources.

Finally, the hypothesis of a significant correlation between rodent species diversity and relative abundance of each species was supported. Also supported was the prediction that the most stable species from the nestedness analysis would decrease in abundance with increased diversity, and the most vulnerable species would increase in abundance with increased diversity. Further examination of the regression results may reveal important information on the position of each species within nocturnal granivorous rodent communities of the Great Basin. There was a positive relationship between relative abundance and diversity for *M. megacephalus*. The scatter plot displaying relative abundance vs. *H*' for *M. megacephalus* shows a spike in relative abundance at a certain level of diversity, approximately *H'* = 0.6 (Figure 6). In fact, *M. megacephalus* does not seem to be present until species diversity reaches this threshold. An increase in the relative abundance of *M. megacephalus* with increased diversity may be because diversity reflects more available resources and the opportunity to establish populations. It is possible that *M. megacephalus* plays one or more of the following indicator roles: 1) its presence/absence may indicate the presence/absence of certain species; 2) its presence/absence may indicate certain environmental conditions (for example, the lack of *B. tectorum* or the presence of a preferred plant or soil type); and 3) it may be a species sensitive to environmental changes and thus may be a management indicator species that reflects disturbance (Lindenmayer et al. 2000).

There was also a positive relationship between rodent species diversity and relative abundance for *P. parvus*. The scatter plot for *P. parvus* is similar to that of *M. megacephalus,* including the near complete absence of the species until a certain level of diversity is reached at approximately *H'* = 0.8 (Figure 6). There was a positive relationship between relative abundance and diversity for *P. longimembris*. The scatter plot for *P. longimembris* shows a more gradual increase in relative abundance with diversity compared to the scatter plots of *M. megacephalus* and *P. parvus*.

There were negative relationships for *D. ordii* and *P. maniculatus*. The scatter plots for both of these species reflect these results and show a general downward trend in relative abundance with increased diversity. The results for *D. microps* should be noted, since the regression resulted in a positive relationship between relative abundance and diversity while the scatter plot for this species suggests a negative correlation. It is possible that the few data points on the scatter plot displaying high relative abundance of *D. microps* at sites with low diversity may be outliers. Outliers may be due to either the site having particularly suitable habitat for this species, or to *D. microps* comprising a large percentage of low total capture numbers. Ignoring these points, the scatter plot shows a slight increase in relative abundance with diversity, which supports the regression results. Since none of the scatter plots suggest completely linear relationships, non-linear regressions may be useful and enlightening choices for further statistical analyses.

It appears that because of their ubiquity across the majority of sites sampled, *D. ordii* and *P. maniculatus* dominate when species diversity is low and decrease in relative abundance when diversity increases. This supports my prediction, since *D. ordii* and *P. maniculatus* were also the most stable species in the extinction order. The relative abundance of *Perognathus* species increases with species diversity, possibly for the same reasons described for *M. megacephalus*: more diversity reflects more available resources and the opportunity to establish populations. As predicted, the regression results also indicate that *D. microps* increases in relative abundance with diversity. *Dipodomys microps* is less common than *D. ordii*, perhaps because it prefers more specific resources, such as *Atriplex confertifolia* (shadscale; Hayssen 1991). However, the results do not necessarily suggest a complete absence of *D. microps* when diversity is low. Additional uncertainty arises from the fact that the scatter plot for *D. microps* is not as suggestive of an increase in relative abundance with diversity as for other species. More research needs to be directed toward *D. microps* to better understand its place in the relative abundance-diversity relationship.

All analyses suggest that *M. megacephalus* comprises a larger portion of the desert rodent community when communities have greater rodent species diversity. While this idea may seem counterintuitive—more neighbors implying more competition—both the regression and the nestedness analyses show that *M. megacephalus* increases in relative abundance with increased species diversity at a site. If this is true, a possible explanation could be that habitats maintain high species diversity because of an abundance of space and resources that allows potential competitors to coexist. It seems more probable that what allows for the presence of *M. megacephalus* is a collection of certain habitat traits, or a threshold of diversity (connected to habitat and resources), rather than the presence of specific species. These habitat traits should be topics for future research.

It was observed that sites with high diversity are rare (Figure 5), so these sites should receive careful inspection. For example, one generally undisturbed dune system in Beryl, UT revealed high relative abundances of *M. megacephalus* as well as a high diversity of rodent species (Area 19 in Figure 1). This dune system is characterized by wind-swept dunes of fine sand and desert shrubs, mainly *Artemisia*, *Chrysothamnus*, and small annual plants, including members of the mustard family, Brassicaceae. At dune systems like this, with high diversity and strong populations of *M. megacephalus*, a multitude of studies could be conducted to discover additional factors that influence population size. These studies should include soil and vegetation analyses and comparisons, seed preference experiments, observations of interspecific interactions in the field and in captivity, and the effects of off-road-vehicles, especially on the shallow burrow systems created by *M. megacephalus* (personal observation).

Because *M. megacephalus* is a rare and sensitive species, it is important that large and stable populations are able to persist in undisturbed habitats. Further studies on factors that contribute to large populations of this species are vital to its conservation. It was found from this study that *M. megacephalus* was one of the most vulnerable species of its community, and that the promotion of species diversity in suitable habitat will likely aid in ensuring strong populations of *M. megacephalus*. Conservationists wishing to create reserves for this sensitive species and to better understand what allows large populations of *M. megacephalus* to exist may find the results of this study valuable. By promoting as much species diversity as possible (by protecting land, preventing habitat alteration, preventing invasive species, etc.) ecologists and conservationists may provide *M. megacephalus* with a better opportunity at maintaining stable populations and ultimately, species persistence.

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Literature Cited

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN and Csáki F (eds) Second international symposium on information theory, Akadémiai Kiadó, Budapest, Hungary

Atmar W; Patterson BD (1993) The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96:373–382

Bowers, MA; Brown, JH (1982) Body size and coexistence in desert rodents: chance or community structure? Ecology 63:391–400

Brown, JH (1973) Species diversity of seed-eating desert rodents in sand dune habitats. Ecology 54:775–787

Brown, JH; Lieberman, GA (1973) Utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology 54:788–797

Bureau of Land Management (2003) Nevada BLM sensitive species.

Diamond, JM (1975a) Assembly of species communities. In: Cody, ML; Diamond, JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, MA

Diamond, JM (1975b) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol Conserv 7:129–146

Ernest, SKM; Brown, JH; Thibault, KM; White, EP; Goheen, JR (2008) Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. Am Nat 172:E258-E269

Faria, JC (2009) Resources of Tinn-R GUI/Editor for R Environment. UESC, Ilheus, Brazil

Goheen, JR; White, EP; Ernest, SKM; Brown, JH (2005) Intra-guild compensation regulates species richness in desert rodents. Ecology 86:567-573

Hall, ER; Linsdale, JM (1929) Notes on the life history of the kangaroo mouse (*Microdipodops*). J Mammal 10:298–305

Hayssen, V (1991) *Dipodomys microps*. Mammalian species 39:1–9

Hubbell, SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ

Kelt, DA; Brown, JH (1999) Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. In: Weiher, E; Keddy, PH (eds) Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, UK

Lawhon, DK (1984) Spatial and temporal patterns of *Microdipodops megacephalus* in two California rodent communities. Unpublished doctoral dissertation. University of California, Irvine

Lemen, C (1978) Seed size selection in heteromyids, a second look. Oecologia 35:13-19

Lindenmayer, DB; Margules, CR; Botkin, DB (2000) Indicators of biodiversity for ecologically sustainable forest management. Conserv Biol 14:941–950

MacArthur, RH; Wilson, EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

Magurran, AE (1998) Ecological diversity and its measurement. Princeton University Press, Princeton, NJ

O'Farrell, MJ; Blaustein, AR (1974) *Microdipodops megacephalus*. Mammalian Species 46:1–3

Patterson, BD (1987) The principle of nested subsets and its implications for biological conservation. Conserv Biol 1:323–334

Patterson, BD; Brown, JH (1991) Regionally nested patterns of species composition in granivorous rodent assemblages. J Biogeogr 18:395-402

Price MV; Waser, NM; McDonald, SA (2000) Elevational distributions of kangaroo rats (genus *Dipodomys*): long-term trends at a Mojave Desert site. Am Midl Nat 144:352–361

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Rodríguez-Gironés, MA; Santamaría, L (2006) A new algorithm to calculate the nestedness temperature of presence-absence matrices. J Biogeogr 33:924–935

Shannon, CE; Weaver, W. (1949) The mathematical theory of communication. University of Illinois Press, Urbana, IL

Soak, SM; Ahn, BH (2004) New genetic crossover operator for the TSP. Lecture notes in artificial intelligence 3070:480–485

State of Utah Department of Natural Resources: Department of Wildlife Resources (2007) Utah sensitive species list

Waltz, RD (2005) Habitat characteristics and the species richness and abundance of desert rodents in the Alvord Basin, Oregon. Unpublished doctoral dissertation. Western Washington University

Welsh, A; Cunningham, R; Donnelly, C; Lindenmayer, D (1996) Modelling the abundance of rare species—statistical models for counts with extra zeros. Ecol Modell 88:297–308

Wilson, DE; Ruff, S (1999) The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, D.C.

Wright, DH; Reeves, JH (1992) On the meaning and measurement of nestedness of species assemblages. Oecologia 92:416–42

Table 1. Names and GPS coordinates of the 99 sites where nocturnal granivorous rodents were trapped in Utah (2005–2008), Oregon (2001–2002), and California (1983–1984) (Oregon and California sites are designated as such).

Site	Latitude	Longitude
AA	37°56'53.16"N	113°25'39.00"W
AS	37°56'34.50"N	113°26'7.20"W
ATCO-1 (OR)	42°19'34.21"N	118°37'17.85"W
ATCO-2 (OR)	42°19'9.25"N	118°36'41.61"W
AW	37°57'8.94"N	113°26'38.52"W
B1A	37°54'6.78"N	113°32'0.48"W
B1B+B1C	37°54'5.53"N	113°32'15.35"W
B1D	37°53'56.16"N	113°32'22.92"W
B1E+B1F+BC	37°54'10.22"N	113°32'33.14"W
B2A+B2B	37°53'59.24"N	113°39'7.98"W
B2C	37°53'55.92"N	113°39'2.52"W
B2D	37°54'4.44"N	113°39'19.08"W
B2E+BTS	37°53'49.21"N	113°39'3.89"W
BDE	37°56'58.56"N	113°29'24.90"W
BDW	37°56'40.44"N	113°29'59.34"W
BE	37°53'53.52"N	113°31'44.76"W
BENTON (CA)	37°50'17.00"N	118°20'49.00"W
BFW	37°54'8.70"	113°35'1.56"W
BNE	37°54'15.36"N	113°31'38.76"W
BNW	37°55'4.98"N	113°32'56.64"W
BP	37°53'10.98"N	113°28'14.28"W
BSW	37°53'55.44"N	113°33'2.76"W
BTN	37°53'56.52"N	113°39'26.28"W
BW	37°54'17.88"N	113°32'49.26"W
C1A	39° 0'24.54"N	112°37'30.00"W
C1B	39° 0'14.28"N	112°37'38.58"W
C1C	39° 0'21.30"N	112°37'1.74"W
C1D	39° 1'14.28"N	112°35'48.96"W
C1E	38°59'55.50"N	112°37'25.98"W
D1A+D1B	40° 1'39.48"N	112°54'57.23"W
D1C	40° 1'39.30"N	112°55'8.28"W
D1D	40° 1'47.52"N	112°54'56.10"W
DUG1	39°58'14.04"N	112°53'12.18"W
DUG2	39°57'5.66"N	112°54'57.37"W
DUG3	39°57'20.06"N	112°54'12.56"W
DUG4	39°57'57.96"N	112°53'47.81"W
DUNE-N (OR)	42°18'2.66"N	118°36'57.87"W
DUNE-S (OR)	42°17'48.79"N	118°36'10.40"W
DW-1 (OR)	42°18'19.03"N	118°37'22.26"W
ESC1	38° 9'48.60"N	113°11'25.38"W
ESC2	38° 9'15.13"N	113°13'3.14"W
EXP1	38°39'54.48"N	113°40'29.74"W
EXP2	38°35'10.16"N	113°42'40.74"W
F1A+F1B+ F1C+F1D	38°54'43.67"N	113°37'4.81"W
F2A+F2B	38°52'24.06"N	113°33'17.98"W
F2C+F2D	38°51'27.04"N	113°32'15.57"W
FS1+FS2	39°46'25.50"N	113°24'28.40"W
FS4+FS4B	39°37'18.14"N	113°23'58.91"W
FS5+FS6	39°37'57.79"N	113°22'51.79"W
GAN1	39°23'17.94"N	113°58'54.18"W
GAN2	39°22'24.33"N	113°58'12.18"W
L1A	37°55'18.54"N	113°17'29.64"W
L1B	37°55'30.24"N	113°17'23.52"W
LPL	37°55'6.30"N	113°17'35.70"W
LS1A	39°38'43.50"N	112°32'41.10"W
LS1B	39°38'58.50"N	112°32'33.36"W
LS1C	39°38'49.08"N	112°32'43.92"W
MONO (CA)	38° 4'3.64"N	119° 4'46.09"W
MIL	38°27'51.30"N	112°59'9.56"W
O1A+O1B+O1C	39°22'57.55"N	112°22'42.50"W
S1A	40°15'20.40"N	112°44'4.20"W
S1B	40°15'27.84"N	112°44'9.18"W
S1C+S1D	40°19'33.66"N	112°44'45.20"W
SAGE-1 (OR)	42°17'44.20"N	118°37'52.05"W
SAGE-2 (OR)	42°17'39.54"N	118°38'8.31"W
SALT-1 (OR)	42°17'44.28"N	118°36'39.95"W
SALT-2 (OR)	42°18'7.78"N	118°36'37.12"W
SI1	40°55'15.20"N	113°55'11.37"W
SI1A+SI1B	40°52'4.69"N	114° 0'22.07"W
SI1C+SI1D	40°50'3.90"N	114° 0'10.85"W
SI1E	40°48'42.84"N	114° 0'14.46"W
SI1F	40°48'39.66"N	114° 0'2.64"W
SI2	40°54'7.84"N	113°55'13.27"W
SI3	40°53'6.34"N	113°55'47.35"W
SI4	40°58'47.17"N	113°52'37.71"W
SI5	40°58'2.01"N	113°52'50.29"W
SI6+SI7	40°56'48.93"N	113°53'59.85"W
SR	37°52'38.22"N	113°39'16.02"W
SV1A+SV1B+ SV1C	38°51'24.69"N	113°59'3.66"W
SV1D+SV1E	38°51'12.39"N	113°55'25.79"W
T1A+T1B	39°44'27.25"N	113°42'19.39"W
T1C	39°44'21.54"N	113°42'26.58"W
T1D	39°44'15.18"N	113°42'28.68"W
T1E	39°44'25.56"N	113°42'26.46"W
T1F	39°44'29.70"N	113°42'25.56"W
TC1	39°38'1.04"N	113°53'54.32"W
TC2	39°38'47.87"N	113°53'33.45"W
TC3	39°39'25.97"N	113°52'39.83"W
TC4	39°37'51.36"N	113°53'58.65"W
TS1	39°20'39.59"N	113°26'6.62"W
TS2	39°20'59.72"N	113°30'29.74"W
TS3+TS4+TS5	39° 6'34.39"N	113°27'52.45"W
W1A+W1B	38°18'46.02"N	113°23'9.88"W
W1C	38°19'0.00"N	113°23'7.56"W
W1D	38°19'13.20"N	113°23'4.98"W
W1E+W1F	38°18'55.11"N	113°23'19.98"W
WAH1	38°34'17.53"N	113°27'3.70"W
WAH2	38°34'21.12"N	113°28'53.48"W
WAH3	38°32'7.79"N	113°24'55.70"W

Table 2. Key to the 88 study sites in Utah labeled on the map in Figure 1, where nocturnal granivorous rodents were trapped from 2005–2008.

Area Number	**Sites in Area**
1	SI1, SI1A+SI1B, SI1C+SI1D, SI1E, SI1F, SI2, SI3, SI4, SI5, SI6+SI7
2	S1A, S1B, S1C+S1D
3	D1A+D1B, D1C, D1D, DUG1, DUG2, DUG3, DUG4
4	T1A+T1B, T1C, T1D, T1E, T1F, TC1, TC2, TC3, TC4
5	FS1+FS2, FS4+FS4B, FS5+FS6
6	LS1A, LS1B, LS1C
7	GAN1, GAN2
8	TS1, TS2
9	O1A+O1B+O1C
10	TS3+TS4+TS5
11	C1A, C1B, C1C, C1D, C1E
12	SV1A+SV1B+SV1C, SV1D+SV1E
13	F1A+F1B+F1C+F1D, F2A+F2B, F2C+F2D
14	EXP1, EXP2
15	WAH1, WAH2, WAH3
16	MIL
17	W1A+W1B, W1C, W1D, W1E+W1F
18	ESC1, ESC2
19	AA, AS, AW, B1A, B1B+B1C, B1D, B1E+B1F+BC, B2A+B2B, B2C, B2D, B2E+BTS, BDE, BDW, BE, BFW, BNE, BNW, BP, BSW, BTN, BW, SR
20	L1A, L1B, LPL

Table 3. Counts of individuals captured and the relative abundances (RA) of six nocturnal granivorous rodent species (*Microdipodops megacephalus, Perognathus longimembris, Perognathus parvus, Dipodomys ordii, Dipodomys microps,* and *Peromyscus maniculatus*) at 99 study sites in Utah, Oregon, and California, continued on the following page (sites in Oregon and California are designated as such).

	M. megacephalus		***P. longimembris***		***P. parvus***		***D. ordii***		***D. microps***		***P. maniculatus***	
Site	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**
AA	1	0.08	0	0.00	1	0.08	7	0.58	1	0.08	2	0.17
AS	21	0.23	4	0.04	7	0.08	7	0.08	33	0.37	8	0.09
ATCO-1 (OR)	0	0.00	19	0.49	9	0.23	0	0.00	10	0.26	1	0.03
ATCO-2 (OR)	0	0.00	20	0.42	18	0.38	0	0.00	9	0.19	1	0.02
AW	2	0.08	1	0.04	4	0.17	3	0.13	11	0.46	2	0.08
B1A	0	0.00	0	0.00	0	0.00	22	0.59	0	0.00	15	0.41
B1B+B1C	0	0.00	0	0.00	0	0.00	23	0.79	0	0.00	6	0.21
B1D	2	0.08	0	0.00	0	0.00	11	0.42	0	0.00	13	0.50
B1E+B1F+BC	53	0.11	6	0.01	1	0.00	280	0.60	3	0.01	121	0.26
B2A+B2B	0	0.00	0	0.00	0	0.00	8	0.29	3	0.11	17	0.61
B2C	0	0.00	0	0.00	0	0.00	7	0.29	6	0.25	11	0.46
B2D	0	0.00	0	0.00	0	0.00	10	0.29	2	0.06	22	0.65
B2E+BTS	2	0.05	0	0.00	0	0.00	9	0.21	18	0.42	14	0.33
BDE	0	0.00	3	0.04	0	0.00	21	0.26	27	0.33	4	0.05
BDW	3	0.08	2	0.05	0	0.00	21	0.55	10	0.26	1	0.03
BE	23	0.28	2	0.02	15	0.19	34	0.42	0	0.00	7	0.09
BENTON (CA)	155	0.17	258	0.29	136	0.15	49	0.05	0	0.00	135	0.15
BFW	5	0.17	0	0.00	0	0.00	24	0.80	0	0.00	1	0.03
BNE	5	0.19	0	0.00	3	0.12	11	0.42	0	0.00	7	0.27
BNW	11	0.28	4	0.10	0	0.00	23	0.58	1	0.03	1	0.03
BP	1	0.08	0	0.00	1	0.08	5	0.38	6	0.46	0	0.00
BSW	16	0.44	0	0.00	2	0.06	13	0.36	0	0.00	5	0.14
BTN	0	0.00	0	0.00	0	0.00	5	0.22	7	0.30	11	0.48
BW	18	0.39	1	0.02	1	0.02	25	0.54	0	0.00	1	0.02
C1A	0	0.00	0	0.00	0	0.00	54	0.87	0	0.00	8	0.13
C1B	0	0.00	0	0.00	0	0.00	10	0.91	0	0.00	1	0.09
C1C	0	0.00	0	0.00	0	0.00	6	0.67	0	0.00	3	0.33
C1D	0	0.00	0	0.00	0	0.00	4	0.67	0	0.00	2	0.33
C1E	0	0.00	0	0.00	0	0.00	12	1.00	0	0.00	0	0.00
D1A+D1B	0	0.00	0	0.00	0	0.00	15	0.79	1	0.05	3	0.16
D1C	0	0.00	0	0.00	0	0.00	23	0.72	2	0.06	7	0.22
D1D	0	0.00	0	0.00	0	0.00	13	0.72	0	0.00	5	0.28
DUG1	0	0.00	0	0.00	0	0.00	18	0.64	2	0.07	8	0.29
DUG2	0	0.00	0	0.00	0	0.00	3	0.33	0	0.00	6	0.67
DUG3	0	0.00	0	0.00	0	0.00	7	0.88	0	0.00	1	0.13
DUG4	0	0.00	0	0.00	0	0.00	1	0.33	0	0.00	2	0.67
DUNE-N (OR)	52	0.43	17	0.14	17	0.14	21	0.17	13	0.11	2	0.02
DUNE-S (OR)	38	0.63	2	0.03	5	0.08	7	0.12	7	0.12	1	0.02
DW-1 (OR)	4	0.20	1	0.05	6	0.30	4	0.20	5	0.25	0	0.00
ESC1	0	0.00	0	0.00	0	0.00	2	0.40	1	0.20	2	0.40
ESC2	0	0.00	1	0.06	0	0.00	1	0.06	15	0.88	0	0.00
EXP1	0	0.00	11	0.21	0	0.00	41	0.79	0	0.00	0	0.00
EXP2	0	0.00	0	0.00	0	0.00	14	1.00	0	0.00	0	0.00
F1A+F1B+F1C+F1D	0	0.00	6	0.08	0	0.00	54	0.68	2	0.03	17	0.22
F2A+F2B	0	0.00	4	0.13	0	0.00	27	0.84	1	0.03	0	0.00
F2C+F2D	0	0.00	0	0.00	0	0.00	18	0.90	0	0.00	2	0.10
FS1+FS2	0	0.00	0	0.00	0	0.00	0	0.00	3	0.75	1	0.25
FS4+FS4B	0	0.00	1	0.03	0	0.00	31	0.97	0	0.00	0	0.00

(Table 3, continued)

	M. megacephalus		*P. longimembris*		*P. parvus*		*D. ordii*		*D. microps*		*P. maniculatus*	
Site	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**	**Count**	**RA**
FS5+FS6	0	0.00	0	0.00	0	0.00	9	1.00	0	0.00	0	0.00
GAN1	0	0.00	0	0.00	0	0.00	2	0.13	12	0.75	2	0.13
GAN2	0	0.00	2	0.06	0	0.00	19	0.58	11	0.33	1	0.03
L1A	0	0.00	0	0.00	0	0.00	37	0.66	0	0.00	19	0.34
L1B	0	0.00	0	0.00	0	0.00	36	0.49	0	0.00	37	0.51
LPL	0	0.00	1	0.02	7	0.12	22	0.39	9	0.16	18	0.32
LS1A	0	0.00	0	0.00	0	0.00	5	0.38	4	0.31	4	0.31
LS1B	0	0.00	0	0.00	0	0.00	11	0.46	2	0.08	11	0.46
LS1C	0	0.00	0	0.00	0	0.00	14	0.37	5	0.13	19	0.50
MIL	0	0.00	0	0.00	0	0.00	20	1.00	0	0.00	0	0.00
MONO (CA)	152	0.35	0	0.00	49	0.11	0	0.00	0	0.00	152	0.35
O1A+O1B+O1C	0	0.00	0	0.00	0	0.00	27	0.33	0	0.00	54	0.67
S1A	0	0.00	0	0.00	0	0.00	18	0.32	2	0.04	37	0.65
S1B	0	0.00	0	0.00	0	0.00	19	0.45	0	0.00	23	0.55
S1C+S1D	0	0.00	0	0.00	0	0.00	30	0.73	0	0.00	11	0.27
SAGE-1 (OR)	1	0.01	4	0.06	37	0.52	29	0.41	0	0.00	0	0.00
SAGE-2 (OR)	0	0.00	2	0.03	39	0.57	27	0.40	0	0.00	0	0.00
SALT-1 (OR)	3	0.60	0	0.00	0	0.00	0	0.00	0	0.00	2	0.40
SALT-2 (OR)	4	0.36	0	0.00	0	0.00	0	0.00	0	0.00	7	0.64
SI1	0	0.00	0	0.00	0	0.00	0	0.00	1	0.50	1	0.50
SI1A+SI1B	0	0.00	7	0.17	0	0.00	17	0.41	6	0.15	11	0.27
SI1C+SI1D	0	0.00	7	0.15	0	0.00	16	0.34	15	0.32	9	0.19
SI1E	0	0.00	3	0.12	0	0.00	9	0.36	6	0.24	7	0.28
SI1F	0	0.00	2	0.12	0	0.00	9	0.53	3	0.18	3	0.18
SI2	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	1.00
SI3	0	0.00	4	0.24	0	0.00	12	0.71	1	0.06	0	0.00
SI4	0	0.00	0	0.00	0	0.00	2	0.20	2	0.20	6	0.60
SI5	0	0.00	0	0.00	0	0.00	7	0.33	10	0.48	4	0.19
SI6+SI7	0	0.00	1	0.07	0	0.00	2	0.13	7	0.47	4	0.27
SR	2	0.04	0	0.00	0	0.00	23	0.41	18	0.32	12	0.21
SV1A+SV1B+SV1C	0	0.00	39	0.89	0	0.00	2	0.05	0	0.00	3	0.07
SV1D+SV1E	0	0.00	5	0.42	0	0.00	2	0.17	0	0.00	5	0.42
T1A+T1B	0	0.00	11	0.37	0	0.00	13	0.43	2	0.07	4	0.13
T1C	0	0.00	7	0.47	0	0.00	5	0.33	2	0.13	1	0.07
T1D	0	0.00	4	0.18	0	0.00	15	0.68	3	0.14	0	0.00
T1E	0	0.00	2	0.13	0	0.00	13	0.87	0	0.00	0	0.00
T1F	0	0.00	4	0.44	0	0.00	5	0.56	0	0.00	0	0.00
TC1	0	0.00	0	0.00	0	0.00	4	0.57	0	0.00	3	0.43
TC2	0	0.00	0	0.00	0	0.00	4	0.67	0	0.00	2	0.33
TC3	0	0.00	0	0.00	0	0.00	1	0.20	0	0.00	4	0.80
TC4	0	0.00	0	0.00	0	0.00	7	1.00	0	0.00	0	0.00
TS1	0	0.00	0	0.00	0	0.00	12	1.00	0	0.00	0	0.00
TS2	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	18	1.00
TS3+TS4+TS5	0	0.00	2	0.07	1	0.04	11	0.41	3	0.11	10	0.37
W1A+W1B	0	0.00	0	0.00	0	0.00	2	0.17	6	0.50	4	0.33
W1C	0	0.00	0	0.00	0	0.00	3	0.17	7	0.39	8	0.44
W1D	0	0.00	0	0.00	0	0.00	5	0.45	2	0.18	4	0.36
W1E+W1F	0	0.00	0	0.00	0	0.00	4	0.50	3	0.38	1	0.13
WAH1	0	0.00	0	0.00	3	0.43	0	0.00	3	0.43	1	0.14
WAH2	0	0.00	0	0.00	0	0.00	0	0.00	2	0.67	1	0.33
WAH3	0	0.00	1	0.33	0	0.00	0	0.00	1	0.33	1	0.33

Table 4. Nocturnal granivorous rodent species richness (*s*) and Shannon-Wiener diversity index (*H'*) at 99 study sites in Utah, Oregon, and California where nocturnal granivorous rodents were trapped (sites in Oregon and California are designated as such).

Site	***s***	***H'***	***Site***	***s***	***H'***
AA	5	1.234	GAN2	4	0.960
AS	6	1.458	L1A	2	0.641
ATCO-1 (OR)	4	1.132	L1B	2	0.693
ATCO-2 (OR)	4	1.127	LPL	5	1.351
AW	6	1.463	LS1A	3	1.093
B1A	2	0.675	LS1B	3	0.922
B1B+B1C	2	0.510	LS1C	3	0.981
B1D	3	0.908	MIL	1	0.000
B1E+B1F+BC	6	0.903	MONO (CA)	4	0.981
B2A+B2B	3	0.900	O1A+O1B+O1C	2	0.637
B2C	3	1.064	S1A	3	0.762
B2D	3	0.808	S1B	2	0.689
B2E+BTS	4	0.730	S1C+S1D	2	0.582
BDE	4	0.983	SAGE-1 (OR)	4	0.867
BDW	5	1.034	SAGE-2 (OR)	3	0.789
BE	5	1.337	SALT-1 (OR)	2	0.673
BENTON (CA)	7	1.388	SALT-2 (OR)	2	0.655
BFW	3	0.591	SI1	2	0.693
BNE	4	0.717	SI1A+SI1B	4	1.301
BNW	5	1.088	SI1C+SI1D	4	1.331
BP	4	1.119	SI1E	4	1.321
BSW	4	1.163	SI1F	4	1.201
BTN	3	1.047	SI2	1	0.000
BW	5	0.865	SI3	3	0.753
C1A	2	0.385	SI4	3	0.950
C1B	2	0.305	SI5	3	1.035
C1C	2	0.637	SI6+SI7	4	1.157
C1D	2	0.637	SR	4	1.060
C1E	1	0.000	SV1A+SV1B+SV1C	3	0.431
D1A+D1B	3	0.478	SV1D+SV1E	3	1.028
D1C	3	0.743	T1A+T1B	4	1.179
D1D	2	0.591	T1C	4	1.171
DUG1	3	0.830	T1D	3	0.843
DUG2	2	0.637	T1E	2	0.393
DUG3	2	0.377	T1F	2	0.687
DUG4	2	0.637	TC1	2	0.683
DUNE-N (OR)	6	1.454	TC2	2	0.637
DUNE-S (OR)	6	1.179	TC3	2	0.500
DW-1 (OR)	5	1.501	TC4	1	0.000
ESC1	3	1.055	TS1	1	0.000
ESC2	3	0.277	TS2	1	0.000
EXP1	2	0.516	TS3+TS4+TS5	5	1.293
EXP2	1	0.000	W1A+W1B	3	1.011
F1A+F1B+F1C+F1D	4	0.456	W1C	3	1.026
F2A+F2B	3	0.512	W1D	3	1.036
F2C+F2D	2	0.095	W1E+W1F	3	0.714
FS1+FS2	2	0.562	WAH1	3	1.004
FS4+FS4B	2	0.139	WAH2	2	0.637
FS5+FS6	1	0.000	WAH3	3	1.099
GAN1	3	0.736			

Table 5. The number of study sites out of 99 sites sampled in the Great Basin with species richness values from 1–6, the number of these sites where *Microdipodops megacephalus* was present, and the percentage of sites of each species richness value at which *M. megacephalus* was present.

Species richness value	1	2	3	4	5	6	**Totals**
Number of sites with species richness value	8	28	31	18	9	5	99
Number of above sites where *M. megacephalus* was present	0	2	3	6	7	5	23
Proportion of *M. megacephalus* presence to number of sites	0	0.071	0.097	0.214	0.778	1	0.232

Table 6. The presence-absence matrix packed by the software BINMATNEST; rows refer to the 99 study sites in the Great Basin (Key in Table 7), and species richness decreases with advancing rows; columns display presence-absence data for six nocturnal granivores (*Dipodomys ordii, Peromyscus maniculatus, Dipodomys microps, Perognathus longimembris, Microdipodops megacephalus,* and *Perognathus parvus*), and species stability decreases with advancing columns.

	D. ordii	***P. maniculatus***	***D. microps***	***P. longimembris***	***M. megacephalus***	***P. parvus***
1	1	1	1	1	1	1
2	1	1	0	1	1	1
3	1	1	1	1	0	1
4	1	0	1	1	1	1
5	1	1	1	1	0	1
6	0	1	1	1	0	1
7	1	1	1	1	1	0
8	1	1	1	1	1	0
9	1	1	0	1	1	1
10	1	1	0	1	1	1
11	1	1	1	1	0	1
12	1	1	1	1	0	0
13	1	1	1	0	1	1
14	1	1	1	1	0	0
15	0	1	1	1	0	0
16	1	1	1	1	0	0
17	1	1	1	0	1	0
18	1	1	1	1	0	0
19	1	1	1	1	0	0
20	1	1	1	1	0	0
21	1	1	1	1	0	0
22	1	1	1	0	1	0
23	1	1	1	1	0	0
24	0	0	0	1	1	1
25	1	1	1	1	0	0
26	1	1	0	0	1	1
27	1	1	0	0	1	1
28	1	1	1	0	0	1
29	1	0	1	0	1	1
30	1	1	1	0	0	0
31	1	1	1	0	0	0
32	1	1	1	0	0	0
33	0	1	0	0	1	0
34	1	1	0	0	1	0
35	1	1	1	0	0	0
36	1	1	1	0	0	0
37	1	1	1	0	0	0
38	1	1	1	0	0	0
39	1	1	0	1	0	0
40	1	1	0	0	1	1
41	1	1	1	0	0	0
42	0	1	0	1	0	0
43	1	1	1	0	0	0
44	1	1	1	0	0	0
45	1	1	1	0	0	0
46	1	1	1	0	0	0
47	1	1	1	0	0	0
48	1	1	1	0	0	0
49	1	1	1	0	0	0
50	1	1	1	0	0	0
51	0	1	0	0	0	0
52	1	0	0	1	0	1
53	1	1	1	0	0	0
54	1	1	1	0	0	0
55	1	1	1	0	0	0
56	1	0	1	1	0	0
57	1	0	1	1	0	0
58	1	0	1	1	0	0
59	1	0	0	1	0	0
60	0	0	1	1	0	0
61	1	1	1	1	0	0
62	1	0	0	1	0	0
63	1	0	0	1	0	0
64	1	0	0	1	0	0
65	1	1	0	0	0	0
66	1	1	0	0	0	0
67	1	1	0	0	0	0
68	1	1	0	0	0	0
69	0	1	0	0	1	0
70	1	1	0	0	0	0
71	1	1	1	0	0	0
72	1	1	0	0	0	0
73	1	1	1	0	0	0
74	1	1	0	0	0	0
75	1	1	0	0	1	0
76	1	1	1	0	0	0
77	1	1	0	0	0	0
78	0	1	0	0	0	0
79	1	1	0	0	0	0
80	1	1	0	0	0	0
81	1	1	0	0	0	0
82	1	1	0	0	0	0
83	1	1	0	0	0	0
84	1	1	0	0	0	0
85	1	1	0	0	0	0
86	1	1	0	0	0	0
87	0	1	0	0	0	0
88	1	1	0	0	0	0
89	1	1	0	0	0	0
90	1	0	0	0	0	0
91	1	0	0	0	0	0
92	1	0	0	0	0	0
93	1	0	0	0	0	0
94	1	0	0	0	0	0
95	1	0	0	0	0	0

Table 7. Key to the sites that correspond with the rows in the presence-absence matrix in Table 6.

Row	**Site**	**Row**	**Site**
1	AS, AW, DUNE-N, DUNE-S, B1E+B1F+BC	*49*	LS1B
2	BW	*50*	SI5
3	TS3+TS4+TS5	*51*	DUG3
4	DW-1	*52*	SAGE-2
5	L1B	*53*	LPL
6	ATCO-2	*54*	D1A+D1B
7	BDW	*55*	BTN
8	BNW	*56*	ESC2
9	BENTON	*57*	T1D
10	BE	*58*	F1A+F1B+F1C+F1D
11	ATCO-1	*59*	EXP1
12	T1A+T1B	*60*	SI3
13	AA	*61*	WAH3
14	T1C	*62*	FS1+FS2
15	SI6+SI7	*63*	T1F
16	SI1F	*64*	T1E
17	SR	*65*	C1B
18	SI1E	*66*	C1D
19	SI1C+SI1D	*67*	B1A
20	SI1A+SI1B	*68*	C1A
21	GAN1	*69*	SALT-2
22	B2E+BTS	*70*	DUG2
23	F	*71*	SI1
24	SAGE-1	*72*	F2A+F2B
25	BDE	*73*	F2C+F2D
26	BNE	*74*	D1D
27	BSW	*75*	SALT-1
28	WAH1	*76*	WAH2
29	BP	*77*	TC3
30	W1E+W1F	*78*	DUG4
31	W1D	*79*	B1B+B1C
32	W1A+W1B	*80*	TC1
33	BFW	*81*	C1C
34	B1D	*82*	S1C+S1D
35	W1C	*83*	S1B
36	LS1A	*84*	TC2
37	B2A+B2B	*85*	L1A
38	FS5+FS6	*86*	O1A+O1B+O1C
39	SV1D+SV1E	*87*	GAN2
40	MONO	*88*	TS2
41	ESC1	*89*	SI2
42	SV1A+SV1B+SV1C	*90*	TS1
43	D1C	*91*	EXP2
44	B2C	*92*	LS1C
45	SI4	*93*	FS4+FS4B
46	DUG1	*94*	C1E
47	B2D	*95*	TC4
48	S1A		

Table 8. *P*-values and estimates for two models (count and probability of a zero) for the linear regression of relative abundance on both species richness and the Shannon-Wiener index of diversity for six nocturnal granivorous rodent species (*Microdipodops megacephalus, Perognathus longimembris, Perognathus parvus, Dipodomys ordii, Dipodomys microps,* and *Peromyscus maniculatus*) trapped at 99 sites in the Great Basin.

Species Richness, *s*

Species	**Estimate (count)**	***p*-value (count)**	**Estimate (probability of a zero)**	***p*-value (probability of a zero)**
M. megacephalus	–0.033	0.777	–1.543	< 0.001
P. parvus	–0.363	0.00731	–1.816	< 0.001
P. longimembris	–0.277	0.0227	–1.518	< 0.001
D. ordii	–8.328	< 0.001	NA	NA
D. microps	–0.266	0.0294	–3.903	< 0.001
P. maniculatus	–5.133	0.0037	NA	NA

Shannon-Wiener index, *H'*

Species	**Estimate (count)**	***p*-value (count)**	**Estimate (probability of a zero)**	***p*-value (probability of a zero)**
M. megacephalus	–0.024	0.968	–3.197	< 0.001
P. parvus	–1.054	0.1214	–5.839	< 0.001
P. longimembris	–0.409	0.44	–2.960	< 0.001
D. ordii	–40.065	< 0.001	NA	NA
D. microps	–0.479	0.2169	–4.831	< 0.001
P. maniculatus	–0.951	< 0.001	–3.392	< 0.001

Table 9. Akaike's Information Criterion values for each of five linear regression models (general linear, Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial) for the linear regression of species' relative abundance on both species richness (*s*) and the Shannon-Wiener index of diversity (*H'*) for six nocturnal granivorous rodents (*Microdipodops megacephalus, Perognathus longimembris, Perognathus parvus, Dipodomys ordii, Dipodomys microps,* and *Peromyscus maniculatus*) trapped at 99 sites in the Great Basin (values for the most appropriate model for each species are in bold).

	Relative abundance vs. *s*				
	General Linear	Poisson	Negative Binomial	Zero-inflated Poisson	Zero-inflated Negative Binomial
M. megacephalus	771.65	1453.6	313.8	479	**264.6**
P. parvus	740.9	1283.5	267.68	306.8	**215.6**
P. longimembris	808.81	1927.1	433.38	790	**386**
D. ordii	**944.1**	2631.1	2633	1426.2	865.2*
D. microps	873.73	2673.4	627.52	1106	**556**
P. maniculatus	**901.93**	2526.2	2528.2	1334.8	774.2*

	Relative abundance vs. *H'*				
	General Linear	Poisson	Negative Binomial	Zero-inflated Poisson	Zero-inflated Negative Binomial
M. megacephalus	784.48	1678.6	313.72	504.8	**288.6**
P. parvus	743.26	1260.1	267.65	365.6	**230.4**
P. longimembris	809.27	1924.2	434.49	882	**411.8**
D. ordii	**927.77**	2403.8	2405.7	1273.6	854.2*
D. microps	868.5	2515.2	624.77	1142.2	**560.4**
P. maniculatus	910.27	2709.8	834.48	1607.2	**784.8**

* Model did not converge

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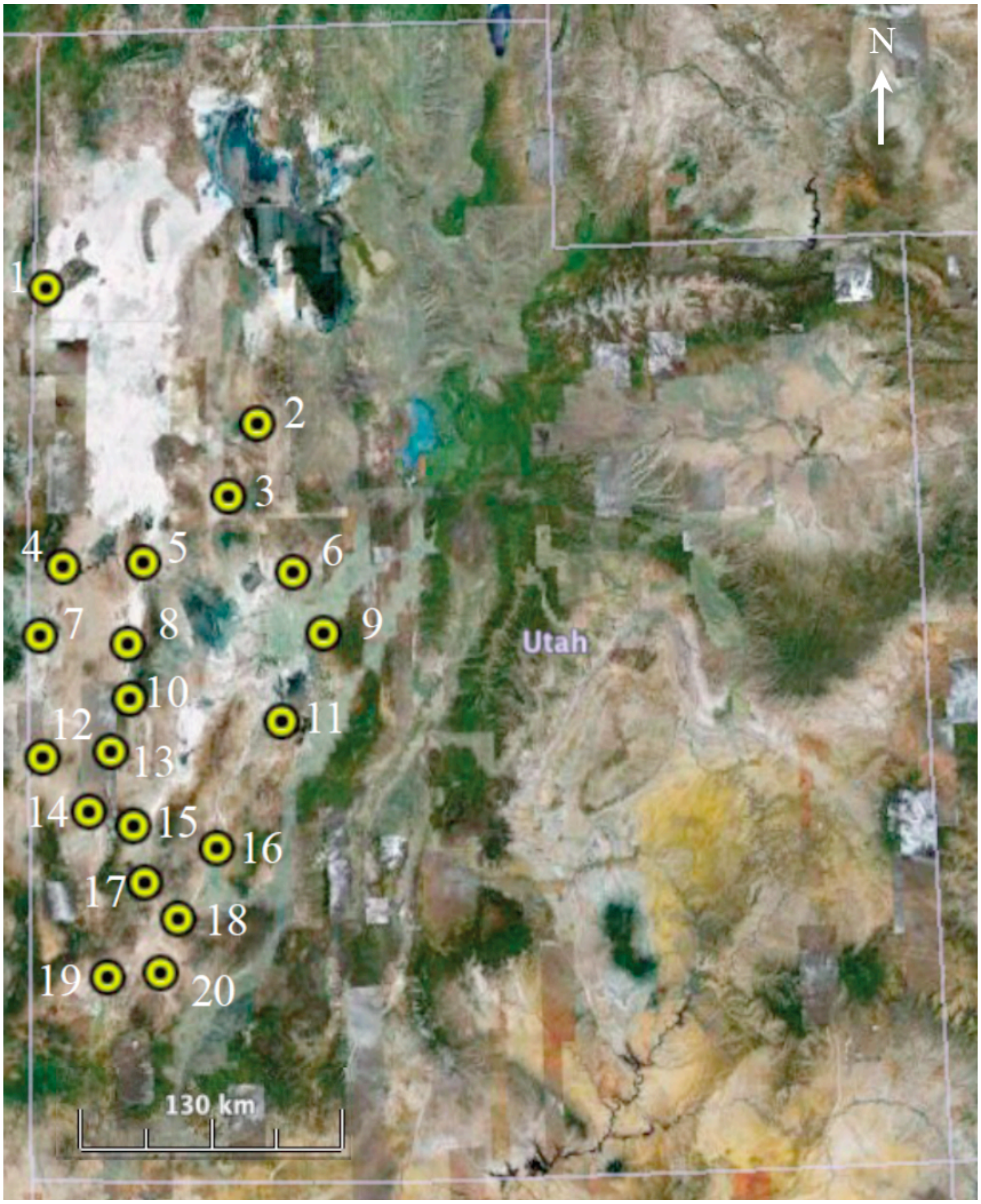


Figure 1

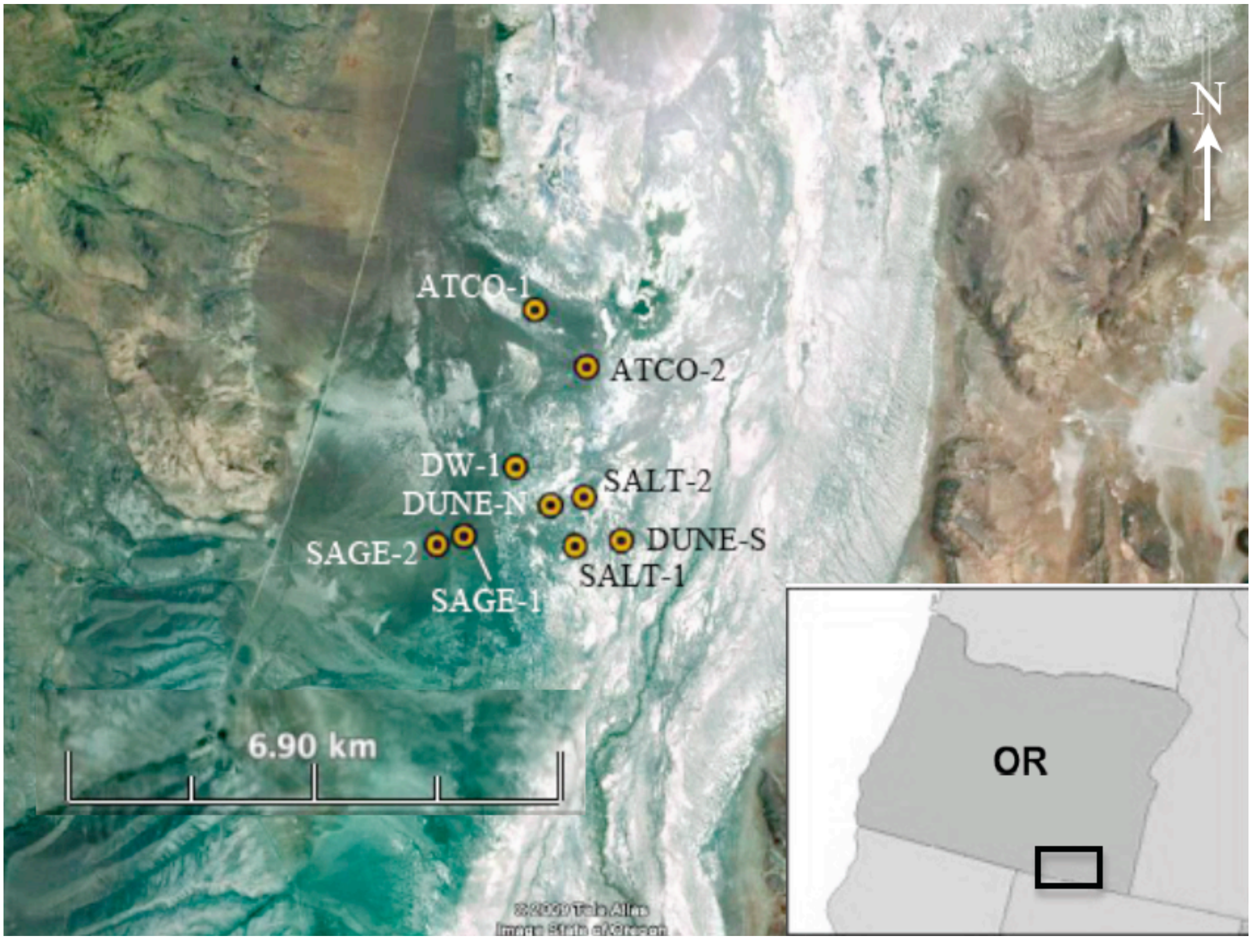

N
ATCO-1
ATCO-2
DW-1
SALT-2
DUNE-N
DUNE-S
SAGE-2
SALT-1
SAGE-1
6.90 km
OR
© 2009 Tele Atlas
Image State of Oregon

Figure 2

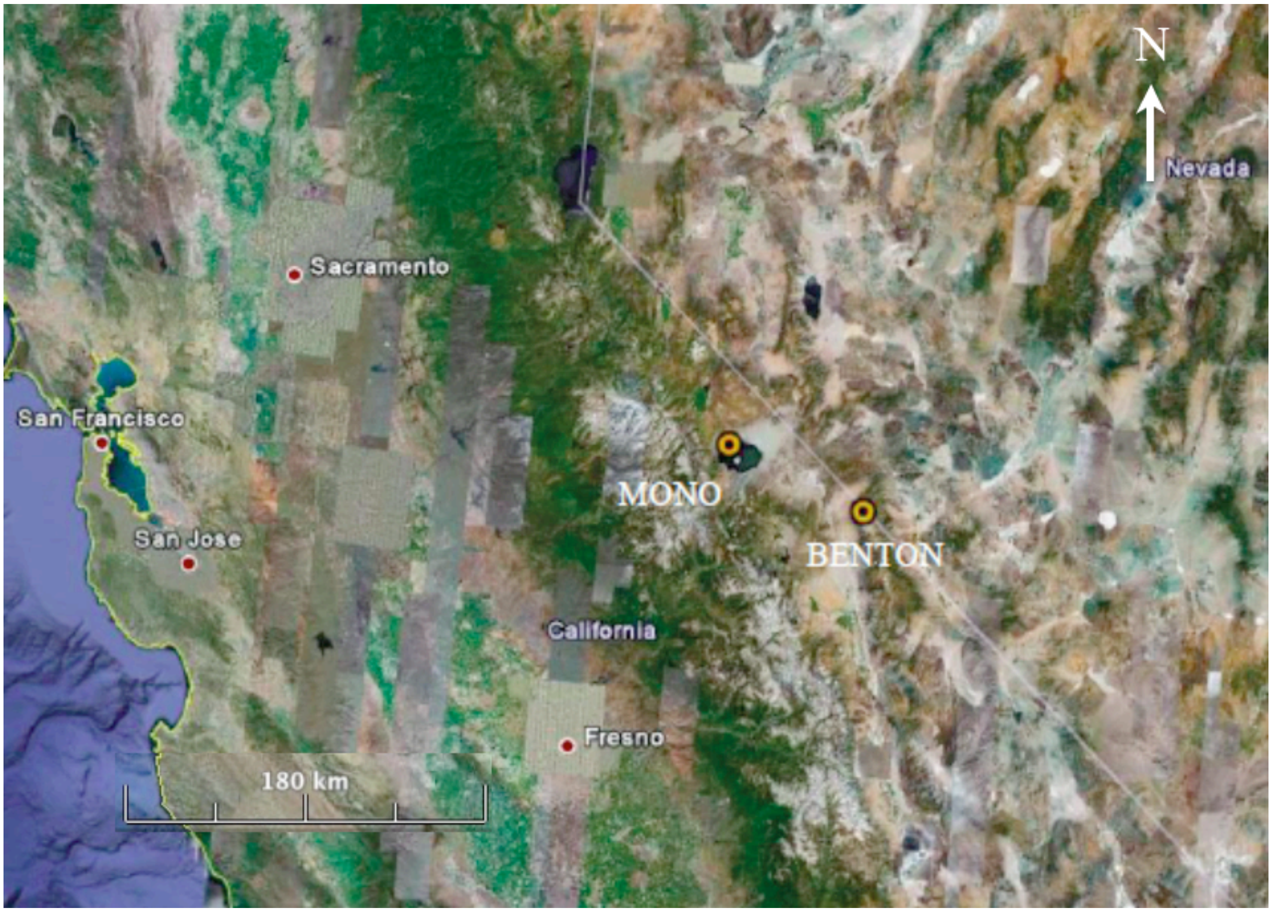

N
Nevada
Sacramento
San Francisco
MONO
BENTON
San Jose
California
Fresno
180 km

Figure 3

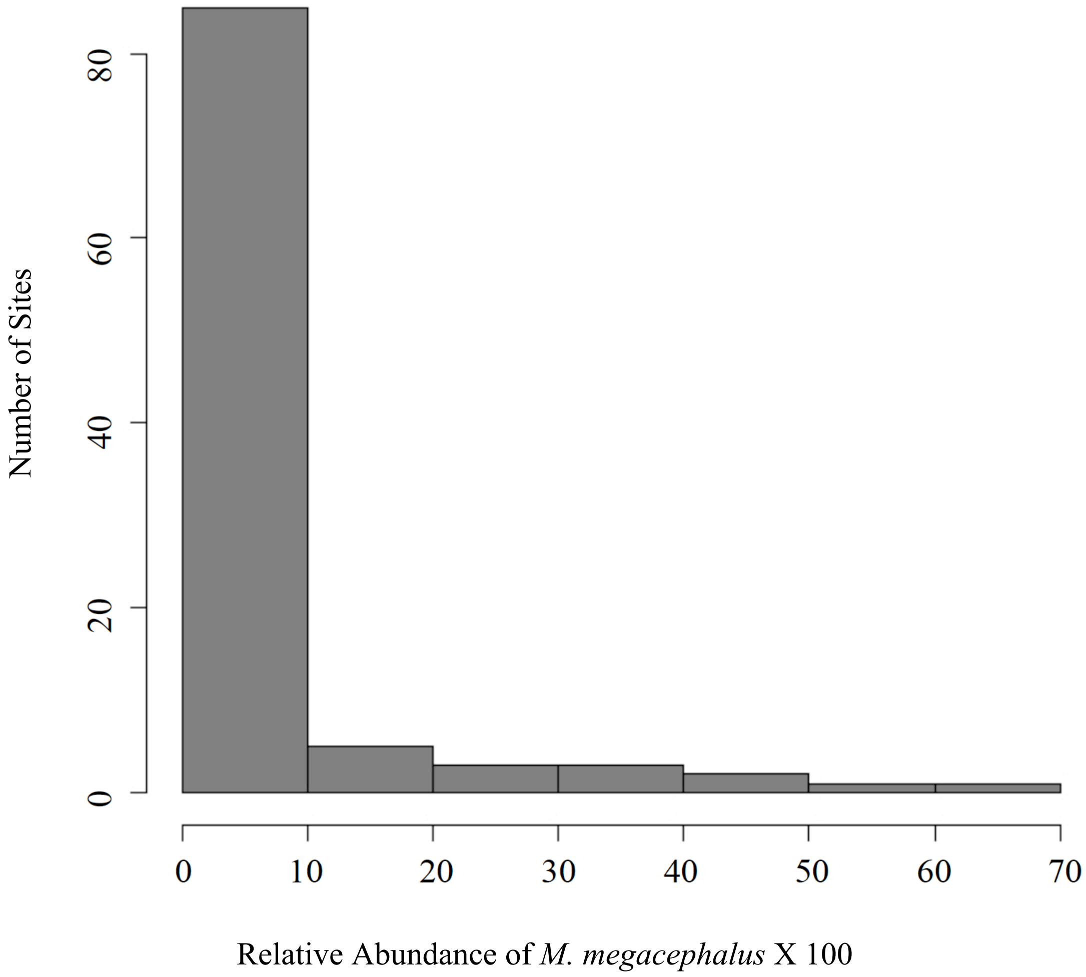
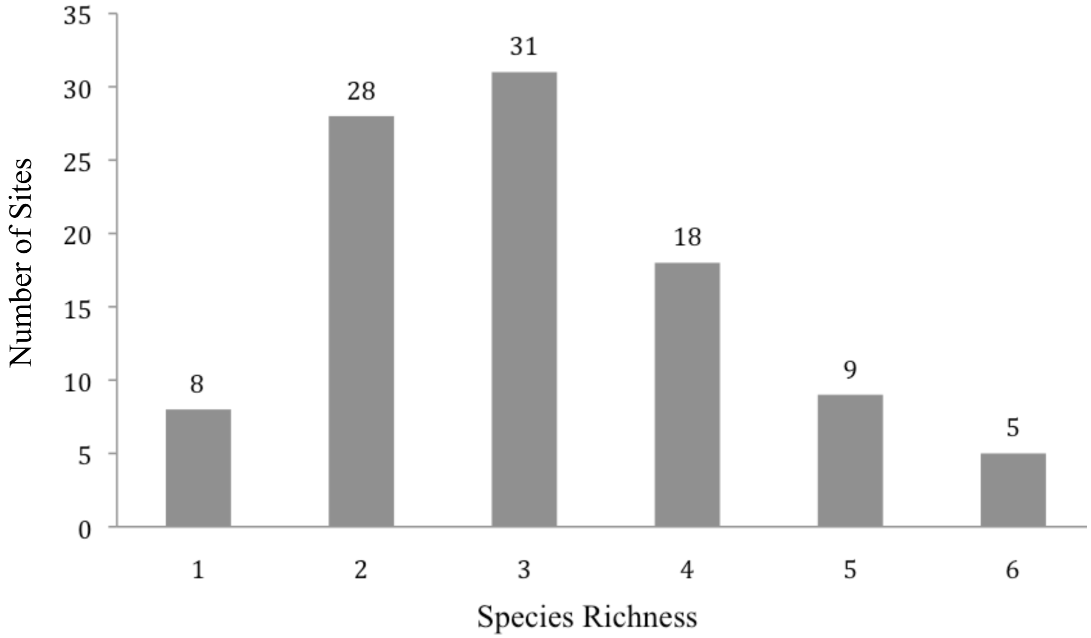

Number of Sites
0
20
40
60
80
0
10
20
30
40
50
60
70
Relative Abundance of *M. megacephalus* X 100

Figure 4


35
30
25
20
15
10
5
0
Number of Sites
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28
31
18
9
5
1
2
3
4
5
6
Species Richness

Figure 5

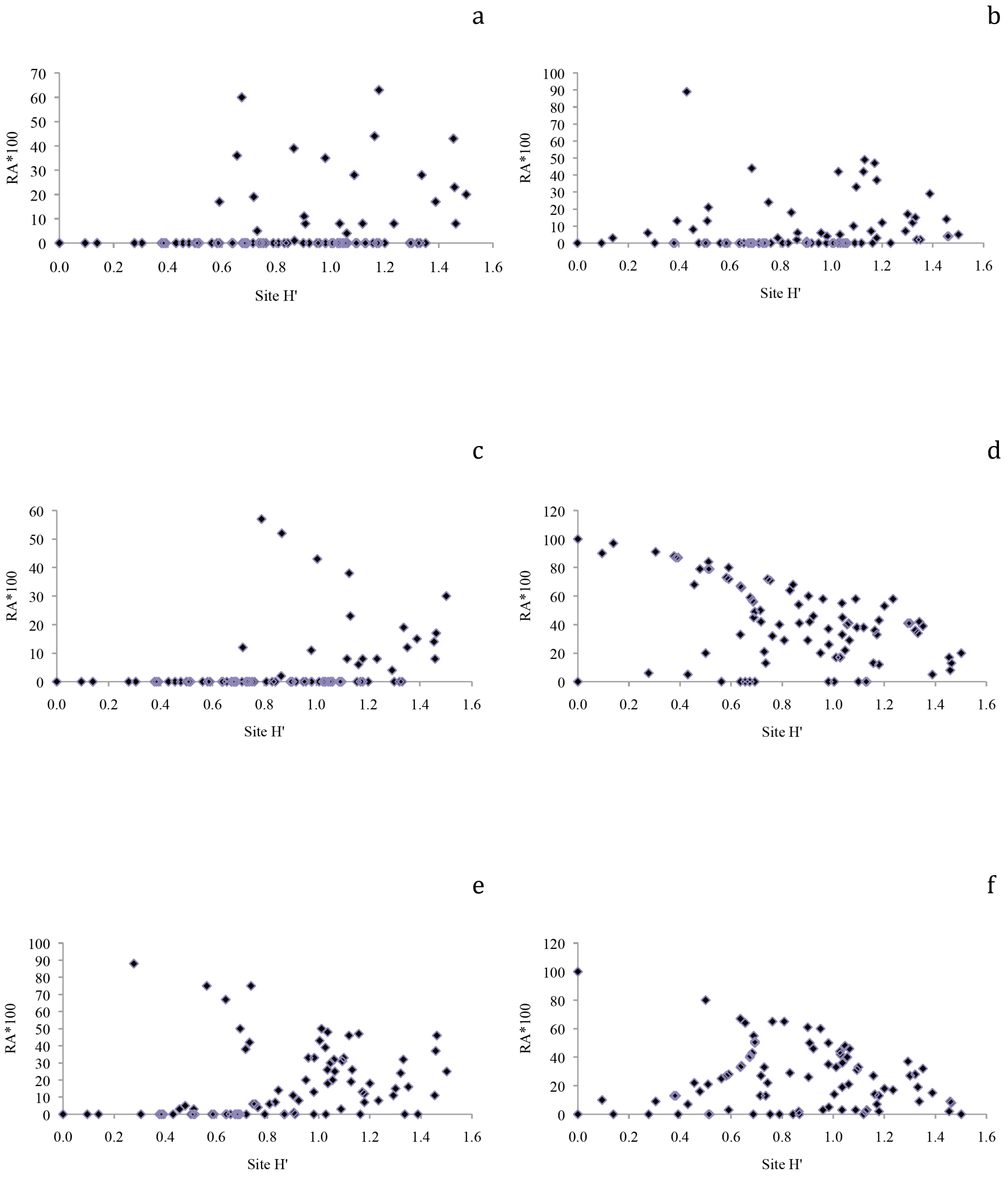
a
b
c
d
e
f
RA*100
Site H'
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0
10
20
30
40
50
60
70
80
90
100
120

Figure 6

(Formatted for submission to *Western North American Naturalist*)

INTERSPECIFIC ASSOCIATIONS BETWEEN THE DARK KANGAROO MOUSE, *MICRODIPODOPS MEGACEPHALUS*, AND OTHER NOCTURNAL GRANIVOROUS RODENTS OF THE GREAT BASIN DESERT

ABSTRACT

The behavioral dynamics between nocturnal granivorous rodents in the Great Basin Desert have historically been studied through manipulative experiments and observations in both the laboratory and the field. Ecological constraints such as niche partitioning and competition are believed to be present among species of the community and driving forces that shape the desert rodent community. One rodent of interest is the dark kangaroo mouse, *Microdipodops megacephalus*, which is listed as a species of concern in Nevada and Utah. To determine the nocturnal granivores with which it is associated and possibly competes, I ran quantitative analyses of interspecific association for six rodents species: *M. megacephalus, Perognathus longimembris* (little pocket mouse)*, Perognathus parvus* (Great Basin pocket mouse)*, Dipodomys ordii* (Ord's kangaroo rat)*, Dipodomys microps* (chisel-toothed kangaroo rat)*,* and *Peromyscus maniculatus* (deer mouse). Five out of 15 possible species pair-wise comparisons resulted in significant interspecific associations. I found positive interspecific associations between *M. megacephalus* and *P. parvus*, between *P. longimembris* and *P. parvus*, between *P. longimembris* and *D. microps*, and between *D. microps* and *P. maniculatus*. I found a negative interspecific association between *P. longimembris* and *P. maniculatus*. I also ran cluster analyses based on similarity for species and sites: the species cluster dendogram further illustrates these associations between species, while the site cluster dendogram shows little similarity between dune and non-dune habitat in abundances of species. These results imply that the presence or absence of other species is not crucial for facilitating the presence of *M. megacephalus*. There may be habitat characteristics that attract many species that utilize various behavioral and morphological ways of avoiding intense competition.

Key words: Microdipodops megacephalus, *nocturnal granivorous rodents, interspecific associations, competition, cluster analysis, conservation, Great Basin Desert.*

INTRODUCTION

The concept that assembly rules influence the assemblages of species in communities has been debated and applied to various ecological systems. It suggests that there are certain processes and constraints that define and shape a community of species, including desert rodent communities in western North America (Diamond 1975). Two major theoretical assembly constraints, competition and niche partitioning, should be considered (Ernest et al. 2008). Although one cannot assume that competition for resources is entirely responsible for the structure and organization of a community, competition has been shown to play an influential role in most communities (Connell 1975). Experimental studies on resource partitioning, food addition, and species removal illustrate that desert rodent species do compete in communities (Davidson et al. 1980, Frye 1983, Lemen and Freeman 1983, Brown and Munger 1985). While manipulative studies have been employed by ecologists to investigate the subject of associations and competition in desert rodent communities, there have been few non-manipulative, descriptive studies (Brown et al. 2000).

Nocturnal granivorous rodent communities of the Great Basin Desert are comprised mainly of species in the family Heteromyidae. Genera include *Dipodomys spp.* (kangaroo rats), *Microdipodops spp.* (kangaroo mice), and *Perognathus spp.* (pocket mice). Nocturnal granivorous rodent species differ in body size and the partitioning of resources and space. Theoretically, species that are more similar in all these respects are more likely to have direct competition, while species that are able to partition resources in different ways are more likely to avoid competition. Studies in the laboratory and in the field reveal apparent assembly rule constraints, specifically competition and niche partitioning between both conspecifics and heterospecifics of the same or different genera (Frye 1983, Lemen and Freeman 1983, Brown and Munger 1985, Lemen and Freeman 1987).

In theory, body size is proportional to the size of seeds selected for food, although this idea has been criticized as being too simplistic (Brown and Lieberman 1973, Lemen 1978). However, body size may still be a general indicator of food preference. For example, *Microdipodops megacephalus* (dark kangaroo mouse) and *Perognathus longimembris* (little pocket mouse) overlap in size and fill a similar niche in communities of nocturnal granivores (Reichman and Price 1993). *Microdipodops megacephalus* ranges from 138 to 177 millimeters in length and 10 to 16.9 grams in mass, while *P. longimembris* ranges from 110 to 151 millimeters in length and 6.5 to 10.5 grams in mass (Wilson and Ruff 1999). *Microdipodops megacephalus* has also been observed to be submissive to *P. longimembris.* In a controlled lab setting, *P. longimembris* was the aggressor in 11 out of 12 encounters with *M. megacephalus*, and neither species was the aggressor in the twelfth confrontation (Blaustein and Risser 1974).

Food resources are partitioned by species that forage for either clumped seeds or scattered seeds. For example, *M. megacephalus* and *Dipodomys ordii* (Ord's kangaroo rat) generally forage for clumped seeds, but when *D. ordii* increases in relative abundance, *M. megacephalus* shifts its foraging to scattered seeds (Bowers 1982, Harris 1984). *Peromyscus maniculatus* (deer mouse) makes little discrimination between scattered and clumped seeds (Harris 1984). Species also prefer different foraging microhabitats. *Perognathus* species forage more often near or under shrubs, while *M. megacephalus* forages in more open areas (Thompson 1982, Harris 1984). *Peromyscus maniculatus* tends to forage in shrubby microhabitat (Harris 1984).

Microdipodops megacephalus is a heteromyid of particular interest because it inhabits "ecological refugia, or specialized or unique habitats" and has been listed by both the states of Nevada and Utah as a sensitive species (Bureau of Land Management 2003 p. 1, State of Utah Department of Natural Resources 2007). Rationale for these listings includes: 1) declining populations, 2) the taxon's reliance on specialized habitat, and 3) alteration of its existing habitat, including the increase of invasive plants, such as cheatgrass, *Bromus tectorum* (State of Utah Department of Natural Resources 2007). As a rare and infrequently trapped species, the dark kangaroo mouse is less understood than many other rodents that comprise nocturnal granivorous rodent communities of the Great Basin. While field and laboratory observations indicate competitive relationships and possibly significant interspecific associations, a method of quantitative measurement is desirable to further clarify the nature of the dynamics between *M. megacephalus* and other nocturnal granivorous rodents.

The objectives of this study are: 1) to quantify interspecific associations between *M. megacephalus* and commonly co-occurring nocturnal granivores using non-experimental data; 2) to examine how these species are clustered with respect to similarities in relative abundances across sites; and 3) to examine how study sites are clustered with respect to species abundances and similarities in community structure. Six species are analyzed in this study. The smallest rodent is *P. longimembris* (6.5-10.5 grams), followed by *M. megacephalus* (10-16.9 grams), *P. maniculatus* (10-30 grams), *Perognathus parvus* (Great Basin pocket mouse; 16.5-31 grams), *D. ordii* (52 grams), and *Dipodomys microps* (chisel-toothed kangaroo rat; 40-70 grams) (Wilson and Ruff 1999).

For my first objective, I hypothesize positive associations for species that do not overlap in body size or that partition resources and space differently, thereby reducing the chance of a competitive encounter (Brown and Lieberman 1973, Blaustein and Risser 1974, Bowers 1982, Thompson 1982, Harris 1984, Reichman and Price 1993). Conversely, I hypothesize negative associations for species that overlap in body size, utilize similar resources, or have been observed to display aggression towards one another, since these species are more likely to strongly compete within a community. Therefore, I predict a positive association between *M. megacephalus* and *P. parvus*, between *M. megacephalus* and *D. microps,* and between *M. megacephalus* and *P. maniculatus*. I predict a negative association between *M. megacephalus* and *P. longimembris* and between *M. megacephalus* and *D. ordii.* The understanding of which species are significantly associated with *M. megacephalus* will reveal more about competitive relationships and the causes governing competition and coexistence. It will also aid in identifying sites where *M. megacephalus* is likely to be present.

For my second objective, I hypothesize that rodent species will cluster with respect to similarities in body size, morphology, and behavior. I predict that the most similar cluster of species will be comprised of *M. megacephalus, P. longimembris,* and *P. parvus*. Because of these species' similar body sizes and niche utilizations, I expect them to be present and abundant at many of the same sites. I predict *D. ordii* and *P. maniculatus* to be the least similar to the other species with respect to habitat type because of the diversity of habitat in which they are found. I predict *D. microps* to be clustered in the middle of the six species, since it is found in more habitat types than are *M. megacephalus, P. longimembris,* and *P. parvus,* but is not as widespread as *D. ordii* and *P. maniculatus*.

For my third objective, I hypothesize that sites will cluster according to habitat type due to species' abundances. I predict that sites will cluster into dune habitat and non-dune habitat. I expect that dune habitat will host one group of species while non-dune habitat will host another, because all six species are often seen occupying dune habitat, while *D. ordii* and *P. maniculatus* are common across a wide variety of habitat types (personal observation).

MATERIALS AND METHODS

DATA COLLECTION

I compiled the data for this study from data collected by myself in Utah, R. David Waltz (2005) who researched in Oregon, and Debra K. Lawhon (1984) who researched in California. This collection of data will make the findings applicable over a broad geographic and temporal range. The combination of the Utah, Oregon, and California data results in a total of 99 sites trapped for rodent presences and abundances in the Great Basin Desert (Table 1).

In 2005, rodents were trapped in west-central Utah at and around historical locations of *M. megacephalus* provided by the Natural Heritage Program, UT. Habitat ranged from windblown sand dunes with *Artemisia* (sagebrush), hardpan soil, “desert pavement”, and grass-covered terrain. Sites were sampled throughout the summer. Sherman live traps baited with commercial birdseed were used to catch rodents, and the number of traps and placement of linear transects varied from site to site (Price et al. 2000). Traps were set at dusk and collected in the morning before strong daylight to minimize heat exposure to captured animals.

In 2006 and 2007, I focused on dune areas in west-central Utah, re-trapping some historical sites and also seeking out un-trapped places that had dune-like qualities (sandy soil, vegetated edges of bare dunes, and small sandy rises and ridges within typical Great Basin valleys). In 2008, I sampled 14 sites in west-central Utah (Iron County), which were selected because they included typical habitat for *M. megacephalus,* and because they were known sites of prior captures of *M. megacephalus*. Sites were flat to steep windblown sand dunes dominated by desert shrubs, particularly *Artemisia, Atriplex, Chrysothamnus, Rhus,* and *Sarcobatus* species. Sites were trapped through May and June. Traps were set in two linear transects of 120 traps each. Transects were placed 100 meters apart, with each trap 10 meters from its nearest neighbor (Figure 1, Table 2). Only data from the first night of trapping are analyzed in this study because new individuals and recaptures were not always distinguished.

Waltz trapped at nine sites in Pueblo Valley, Oregon (Harney County) during the summers of 2001 and 2002 (Waltz 2005; Figure 2). In Waltz's research, four main study habitats were represented: Basin big sagebrush-steppe, shadscale habitat, mixed shrub sand dunes, and alkali saltgrass flats. At each of the nine sites, Waltz set an 11x11 trapping grid (121 traps) 50–150 meters from a road that covered one hectare of ground. Sherman live traps were baited with birdseed and left overnight to capture nocturnal species. He marked and released captured animals and counted the minimum number known alive (MNKA), or total number of individuals, at each site. I use these MNKA data in my analyses. I combined data across years for each site as well.

Lawhon trapped at two study sites in Mono County, California: one near Benton Valley Ranch and the other along the north shore of Mono Lake (Lawhon 1984; Figure 3). These sites were selected because of known *M. megacephalus* populations and because they were characterized by windblown sand dunes and *Artemisia*, typical habitat for *M. megacephalus* (Hall and Linsdale 1929). Lawhon built permanent 10x10 trapping grids at the Benton site and 10x6 trapping grids at the Mono Lake site. She placed traps 15 meters apart, both in the open and under shrubs. Lawhon's sampling extended through all seasons, from April of 1982 to October of 1983. Her thesis does not indicate the MKNA for each species, so I analyzed the total number captures for every species at each site.

INTERSPECIFIC ASSOCIATIONS WITH PAIR-WISE CONTINGENCY TABLES

I used Cole's 2x2 contingency table to organize presence-absence data for the analysis of the interspecific associations (1949; Table 3). The interspecific association is examined between species A and species B. The table quantifies presences and absences, where a = the number of sites where both species are present, b = the number of sites where species A is present and species B is absent, c = the number of sites where species B is present and species A is absent, d = the number of sites where both species are absent, and n = the total number of sites.

I used Cole's equation (1949) for chi-square to determine whether there was a significant interspecific association: $\chi^2 = \dfrac{(ad - bc)^2 n}{(a + b)(a + c)(c + d)(b + d)}$.

If the interspecific association was statistically significant, I then determined if the association was positive or negative. I did this by comparing the observed value of a to the expected value of a, which I calculated with Cole's equation: $\left(\dfrac{(a + b)(a + c)}{n}\right)$. If the observed value of a was greater than the expected value of a, the interspecific association was positive; if the observed value was less than the expected value, the association was negative.

CLUSTER ANALYSES

Cluster analysis is a method that can generate classifications from a series of samples (Krebs 1999). I used the software SYSTAT 11 (2004) to generate cluster dendograms for both species and sites with the data from the 88 study sites in Utah. The purpose of the species cluster is to show the similarities between species with respect to sites where the species were present. The data for the species cluster contained the number of sites at which each species was caught.

The purpose of the site cluster is to show similarities between sites with respect to the types and abundances of species found at the sites. It will also show any distinction in species' presence between dune habitat and non-dune habitat. The data for the site cluster contained the relative abundance of each species caught at each site. I labeled sites as either dune or non-dune in order to reveal any possible clustering among habitat type. I characterized dune sites as having loose, sandy soil, sparse desert shrubs (particularly *Artemisia* and *Atriplex*), and little to no grasses. I characterized non-dune sites as having hard, crusty soil, "desert pavement", or a thick cover of grasses or weeds.

The percentage similarity index was computed from relative abundance data for all species, and cluster analysis was performed on a similarity matrix (Renkonken 1938, Krebs 1999). Using SYSTAT 11, I applied an unweighted pair group method of averaging method (UPGMA) to create an average linkage cluster based on the percentage similarity index between entries (Sneath and Sokal 1973, Romesburg 1984). Romesburg recommends the UPGMA method for most cluster analyses (1984). The resulting cluster dendograms are based on the percent of dissimilarity, which is simply 1 – % similarity (Renkonken 1938).

RESULTS

INTERSPECIFIC ASSOCIATIONS WITH PAIR-WISE CONTINGENCY TABLES

The six species analyzed in this study were *M. megacephalus, P. longimembris, P. parvus, D. ordii, D. microps,* and *P. maniculatus*. These species were all nocturnal granivores that co-existed in various combinations. In addition, they represented the majority of captures by all three researchers in Utah, Oregon, and California. *Microdipodops megacephalus* was captured at only 25 of the 99 sites sampled. It was also significantly associated with only one species: *P. parvus.* Of all of the 15 pair-wise comparisons of species, five returned significant results. The following pairs of species were positively associated: *M. megacephalus* and *P. parvus; P. longimembris* and *P. parvus; P. longimembris* and *D. microps, P. longimembris* and *P. maniculatus;* and *D. microps* and *P. maniculatus* (Table 4). The other 11 pairings did not return a large enough chi-square value to deem the associations significant (Table 5).

CLUSTER ANALYSES

Species cluster—In the species cluster dendogram, *M. megacephalus* and *P. parvus* were the most similar species with respect to degree of capture across sites. These two species made up the first cluster at only 20% dissimilarity (Figure 4). This group was joined by *P. longimembris* (42.5% dissimilarity), followed by *D. microps* (52.5%)*, P. maniculatus* (85%), and finally *D. ordii* (95%).

Site cluster—The site cluster dendogram did not cluster between dune and non-dune habitat according to distribution and abundance of nocturnal granivorous rodents as expected (Figure 5). There was no apparent pattern in the similarity of dune habitat or non-dune habitat. Dune sites occasionally clustered farther out, at 30–40% dissimilarity; however, a clear distinction between dune and non-dune habitat was not drawn. The greatest amount of similarity found between sites was approximately 18%, but this was among a mixture of habitat type. Notably, the sites with dune habitat were very dissimilar in terms of species. For example, the last 14 sites in the cluster dendogram were all dune sites, yet as a group they were approximately 92% dissimilar with respect to species type and abundance (Figure 5). Similar sites were also not necessarily close geographically.

DISCUSSION

Five of the fifteen pair-wise comparisons of interspecific association were significant. A significant positive association was found between *M. megacephalus* and *P. parvus*. This was the only pairing out of five with *M. megacephalus* that was significant. This result supports the prediction for this pair of species. *Microdipodops megacephalus* may be positively associated with *P. parvus* because of niche partitioning that allows for coexistence. *Perognathus parvus* forages mainly in areas of densely clustered shrubs, while *M. megacephalus* forages more often in intershrub areas (Thompson 1982, Harris 1984). There is also a slight difference in body size between *M. megacephalus* (138 to 177 mm, 10 to 16.9 g) and *P. parvus* (160 to 190 mm, 21.5 to 28.5 g; Wilson and Ruff 1999), and species of different sizes are less likely to compete. The knowledge that *M. megacephalus* was positively associated with *P. parvus* is evidence for assembly rule constraints, such as niche partitioning, that enable these two species to coexist and utilize the same resources.

A lack of association between *M. megacephalus* and the remaining four species may be because the other species are successful or adaptable enough to be found at sites both with and without *M. megacephalus*, or that *M. megacephalus* and the other species are behaviorally and/or morphologically dissimilar enough to avoid placing significant competitive pressure on each other. Perhaps the most surprising of these results was the lack of an association between *M. megacephalus* and *P. longimembris*. I predicted a negative association based on the aggressive interactions in the laboratory and the similarity in size (Blaustein and Risser 1974). Mechanisms in behavior and morphology may allow for coexistence through partitioning of space, time, and resources. For example, *M. megacephalus'* bipedal gait allows it to traverse open intershrub terrain while *P. longimembris* more often remains in protected, shrubby areas (Thompson 1982, Harris 1984). Furthermore, *M. megacephalus* forages for both scattered and clumped seeds, while *P. longimembris* favors clumped seeds (Bowers 1982, Harris 1984). A difference in seasonal and daily activity between the two species has also been documented (O'Farrell 1974).

It should be noted that although *M. megacephalus* and *P. longimembris* are often found in similar habitat, a positive association between the two species was lacking (Schmidley et al. 1993). Besides habitat type, there may be other conditions that each species needs for a sustainable population to be possible. For example, there must be enough space to avoid competitive interactions, habitat boundaries that allow for minimum home range size, specific vegetation species, a certain soil texture and density, and/or isolation from predators and environmental disturbances. Further association and relative abundance studies with more data on habitat variables beyond the labels of dune and non-dune will assist in the determining requirements of each species.

The clustering of species compliments the interspecific association results and supports the hypothesis that species would cluster with respect to similarities in body size, morphology, and behavior. *Microdipodops megacephalus* and *P. parvus* were the most similar species in terms of sites at which they were both present, further supporting the positive interspecific association (Figure 4). *Perognathus longimembris* was clustered next, which was expected because of similarities to *P. longimembris* and *M. megacephalus* in behavior and morphology. The cluster was then joined by *D. microps*, followed by *P. maniculatus*, and lastly, *D. ordii.*

It was expected that *P. maniculatus* and *D. ordii* would be clustered least similarly to the other species because they were found at a wider variety of sites and seemed to be less discriminatory in choosing habitat. This means that while they were sometimes found with species like *M. megacephalus* and *P. parvus*, they were also as likely to be found in areas where these species were absent. *Dipodomys ordii* and *P. maniculatus* appear to be more generalist, while *M. megacephalus* and the *Perognathus* species appear to be more specialist. *Dipodomys microps* has been found to be a specialist as well, utilizing shadscale (*Atriplex confertifolia*; Hayssen 1991); however, *M. megacephalus* and *Perognathus spp*. were not commonly found in shadscale habitat, hence the distance between these species and *D. microps* in the species cluster dendogram.

The site dendogram did not cluster by habitat type, which did not support the hypothesis. Sites with dune habitat were very dissimilar in terms of species (Figure 5). This suggests that while dune sites as a group promote a large amount of species diversity, there is little evenness or uniformity among sites. While richness was high at dunes in general, some individual dunes had low richness, hence the high dissimilarity between sites in the cluster dendogram. A lack of pattern was also found among non-dune habitat types. In fact, some of the more similar clusters were actually a mixture of dune and non-dune habitat. This may reflect the presence of *D. ordii* and *P. maniculatus* at these sites. These species were found at a larger variety of sites than the other species, and therefore have a more ubiquitous presence. When diversity is low, as is often the case, these species are the most likely to be present. It is also important to note that sites did not cluster geographically; that is, sites in close proximity to each other and therefore with similar habitat characteristics did not prove to be significantly similar.

This type of cluster analysis may be more effective when data with greater species richness is analyzed. However, more descriptive results could also be attained with further categorization of habitat type. For example, the shrub spacing and density of flora species, the density, texture, and pH of soils, the abundance of predator species, the proximity to roads or other structures, and the degree of human interference are all variables that could be analyzed in future cluster dendograms.

The results of this study suggest that while *D. ordii, D. microps,* and *P. maniculatus* are often found with *M. megacephalus*, these species are also present at many sites where *M. megacephalus* is not present. The results also imply that *M. megacephalus* is associated with *Perognathus* species and that these species are found in similar habitats. It is possible that the loss of a strongly associated species like *P. parvus* would coincide with casualties to populations of *M. megacephalus*. However, it is also likely that the presence of *M. megacephalus* does not depend directly on the presence or absence of associated species. If *M. megacephalus* and *P. parvus* begin to disappear from a site concurrently, it may be an indication of changes in habitat rather than a dependence on one another.

Still, the knowledge of these interspecific associations is valuable in a conservation context. For example, the fact that *M. megacephalus* is positively associated with *P. parvus* indicates that there are habitat elements that attract both species and allow for coexistence. Therefore, populations of *P. parvus* at a site may indicate the presence of *M. megacephalus*, or at least that the habitat may be suitable for *M. megacephalus*.

While the results of these interspecific association and cluster analyses cannot fully explain interspecific competition, habitat selection, or community composition and dynamics, they do provide evidence for the argument that assembly rules and constraints exist and are responsible for community structure, particularly in desert rodent communities of the Great Basin Desert. These results add to the current collection of knowledge about the nocturnal granivore guild, and may provide direction for future research on assembly rules, competition, habitat preservation, and the conservation of *M. megacephalus* and its fellow members of the nocturnal granivore guild.

ACKNOWLEDGMENTS

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LITERATURE CITED

Blaustein, A.R., and A.C. Risser, Jr. 1974. Dominance relationships of the dark kangaroo mouse (*Microdipodops megacephalus*) and the little pocket mouse (*Perognathus longimembris*) in captivity. Great Basin Naturalist 34:312–316.

Bowers, M.A. 1982. Foraging behavior of heteromyid rodents: field evidence of resource partitioning. Journal of Mammalogy 63:361–367.

Brown, J.H., B.J. Fox, and D.A. Kelt. 2000. Assembly rules: desert rodent communities are structured at scales from local to continental. The American Naturalist 156:314–321.

Brown, J.H., and G.A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology 54:788–797.

Brown, J.H., and J.C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology 66:1545–1563.

Bureau of Land Management. 2003. Nevada BLM Sensitive Species.

Cole, L.C. 1949. The measurement of interspecific association. Ecology 30:411–424.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities. Pages 460–490 in M.L. Cody, and J.M. Diamond, editors, Ecology and evolution of communities. Harvard University Press, Cambridge, MA.

Davidson, D.W., J.H. Brown, and R.S. Inouye. 1980. Competition and the structure of granivore communities. BioScience 30:233–238.

Diamond, J.M. 1975. Assembly of species communities. Pages 342–444 in M.L. Cody, and J.M. Diamond, editors, Ecology and evolution of communities. Harvard University Press, Cambridge, MA.

Ernest, S.K.M., J.H. Brown, K.M. Thibault, E.P. White, and J.R. Goheen. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. The American Naturalist 172:E258-E269.

Frye, R.J. 1983. Experimental field evidence of interspecific aggression between two species of kangaroo rat (*Dipodomys*). Oecologia 59:74–78.

Hall, E.R., and J.M. Linsdale. 1929. Notes on the life history of the kangaroo mouse (*Microdipodops*). Journal of Mammalogy 10:298–305.

Harris, J.H. 1984. An experimental analysis of desert rodent foraging ecology. Ecology 65:1579–1584.

Hayssen, V. 1991. *Dipodomys microps*. Mammalian species 39**:**1–9.

Krebs, C.J. 1999. Ecological methodology. 2nd edition. Addison-Wesley Educational Publishers, Inc.

Lawhon, D.K. 1984. Spatial and temporal patterns of *Microdipodops megacephalus* in two California rodent communities. Unpublished doctoral dissertation. University of California Irvine.

Lemen, C. 1978. Seed size selection in heteromyids, a second look. Oecologia 35:13-19.

Lemen, C., and P.W. Freeman. 1983. Quantification of competition among coexisting heteromyids in the southwest. The Southwestern Naturalist 28:41–46.

Lemen, C., and P.W. Freeman. 1987. Competition for food and space in a heteromyid community in the Great Basin Desert. The Great Basin Naturalist 47:1–6.

O'Farrell, M.J. 1974. Seasonal activity patterns of rodents in a sagebrush community. Journal of Mammalogy 55:809–823.

Price M.V., N.M. Waser, and S.A. McDonald. 2000. Elevational distributions of kangaroo rats (genus *Dipodomys*): long-term trends at a Mojave Desert site. The American Midland Naturalist 144:352–361.

Reichman, O.J., and M.V. Price. 1993. Ecological aspects of heteromyid foraging. Pages 539-574 in H.H. Genoways and J.H. Brown, editors, Biology of the Heteromyidae. Special Publication No. 10, The American Society of Mammalogists.

Renkonken, O. 1938. Statisch-okologische Untersuchungen uber die terrestiche kaferwelt der finnischen bruchmoore. Ann. Zool. Soc. Bot. Fenn. Vanamo 6:1–231.

Romesburg, H.C. 1984. Cluster analysis for researchers. Lifetime Learning Publications, Belmont, CA.

Schmidly, D.J., K.T. Wilkins, and J.N. Derr. 1993. Biogeography. Pages 319-356 in H.H. Genoways and J.H. Brown, editors, Biology of the Heteromyidae. Special Publication No. 10, The American Society of Mammalogists.

Sneath, P.H., and Sokal, R.R. 1973. Numerical taxonomy. Freeman, San Francisco, CA.

State of Utah Department of Natural Resources: Department of Wildlife Resources. 2007. Utah Sensitive Species List.

SYSTAT. 2004. SYSTAT for Windows, Version 11. WYSTAT Software Inc., Richmond, California.

Thompson, S.D. 1982. Structure and species composition of desert heteromyid rodent species assemblages: effects of a simple habitat manipulation. Ecology 63:1313–1321.

Waltz, R.D. 2005. Habitat characteristics and the species richness and abundance of desert rodents in the Alvord Basin, Oregon. Unpublished doctoral dissertation. Western Washington University.

Wilson, D.E., and S. Ruff. 1999. The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, D.C.

Table 1. Names and GPS coordinates of the 99 sites where nocturnal granivorous rodents were trapped in Utah (2005–2008), Oregon (2001–2002), and California (1983–1984) (Oregon and California sites are designated as such).

Site	Latitude	Longitude
AA	37°56'53.16"N	113°25'39.00"W
AS	37°56'34.50"N	113°26'7.20"W
ATCO-1 (OR)	42°19'34.21"N	118°37'17.85"W
ATCO-2 (OR)	42°19'9.25"N	118°36'41.61"W
AW	37°57'8.94"N	113°26'38.52"W
B1A	37°54'6.78"N	113°32'0.48"W
B1B+B1C	37°54'5.53"N	113°32'15.35"W
B1D	37°53'56.16"N	113°32'22.92"W
B1E+B1F+BC	37°54'10.22"N	113°32'33.14"W
B2A+B2B	37°53'59.24"N	113°39'7.98"W
B2C	37°53'55.92"N	113°39'2.52"W
B2D	37°54'4.44"N	113°39'19.08"W
B2E+BTS	37°53'49.21"N	113°39'3.89"W
BDE	37°56'58.56"N	113°29'24.90"W
BDW	37°56'40.44"N	113°29'59.34"W
BE	37°53'53.52"N	113°31'44.76"W
BENTON (CA)	37°50'17.00"N	118°20'49.00"W
BFW	37°54'8.70"	113°35'1.56"W
BNE	37°54'15.36"N	113°31'38.76"W
BNW	37°55'4.98"N	113°32'56.64"W
BP	37°53'10.98"N	113°28'14.28"W
BSW	37°53'55.44"N	113°33'2.76"W
BTN	37°53'56.52"N	113°39'26.28"W
BW	37°54'17.88"N	113°32'49.26"W
C1A	39° 0'24.54"N	112°37'30.00"W
C1B	39° 0'14.28"N	112°37'38.58"W
C1C	39° 0'21.30"N	112°37'1.74"W
C1D	39° 1'14.28"N	112°35'48.96"W
C1E	38°59'55.50"N	112°37'25.98"W
D1A+D1B	40° 1'39.48"N	112°54'57.23"W
D1C	40° 1'39.30"N	112°55'8.28"W
D1D	40° 1'47.52"N	112°54'56.10"W
DUG1	39°58'14.04"N	112°53'12.18"W
DUG2	39°57'5.66"N	112°54'57.37"W
DUG3	39°57'20.06"N	112°54'12.56"W
DUG4	39°57'57.96"N	112°53'47.81"W
DUNE-N (OR)	42°18'2.66"N	118°36'57.87"W
DUNE-S (OR)	42°17'48.79"N	118°36'10.40"W
DW-1 (OR)	42°18'19.03"N	118°37'22.26"W
ESC1	38° 9'48.60"N	113°11'25.38"W
ESC2	38° 9'15.13"N	113°13'3.14"W
EXP1	38°39'54.48"N	113°40'29.74"W
EXP2	38°35'10.16"N	113°42'40.74"W
F1A+F1B+ F1C+F1D	38°54'43.67"N	113°37'4.81"W
F2A+F2B	38°52'24.06"N	113°33'17.98"W
F2C+F2D	38°51'27.04"N	113°32'15.57"W
FS1+FS2	39°46'25.50"N	113°24'28.40"W
FS4+FS4B	39°37'18.14"N	113°23'58.91"W
FS5+FS6	39°37'57.79"N	113°22'51.79"W
GAN1	39°23'17.94"N	113°58'54.18"W
GAN2	39°22'24.33"N	113°58'12.18"W
L1A	37°55'18.54"N	113°17'29.64"W
L1B	37°55'30.24"N	113°17'23.52"W
LPL	37°55'6.30"N	113°17'35.70"W
LS1A	39°38'43.50"N	112°32'41.10"W
LS1B	39°38'58.50"N	112°32'33.36"W
LS1C	39°38'49.08"N	112°32'43.92"W
MONO (CA)	38° 4'3.64"N	119° 4'46.09"W
MIL	38°27'51.30"N	112°59'9.56"W
O1A+O1B+O1C	39°22'57.55"N	112°22'42.50"W
S1A	40°15'20.40"N	112°44'4.20"W
S1B	40°15'27.84"N	112°44'9.18"W
S1C+S1D	40°19'33.66"N	112°44'45.20"W
SAGE-1 (OR)	42°17'44.20"N	118°37'52.05"W
SAGE-2 (OR)	42°17'39.54"N	118°38'8.31"W
SALT-1 (OR)	42°17'44.28"N	118°36'39.95"W
SALT-2 (OR)	42°18'7.78"N	118°36'37.12"W
SI1	40°55'15.20"N	113°55'11.37"W
SI1A+SI1B	40°52'4.69"N	114° 0'22.07"W
SI1C+SI1D	40°50'3.90"N	114° 0'10.85"W
SI1E	40°48'42.84"N	114° 0'14.46"W
SI1F	40°48'39.66"N	114° 0'2.64"W
SI2	40°54'7.84"N	113°55'13.27"W
SI3	40°53'6.34"N	113°55'47.35"W
SI4	40°58'47.17"N	113°52'37.71"W
SI5	40°58'2.01"N	113°52'50.29"W
SI6+SI7	40°56'48.93"N	113°53'59.85"W
SR	37°52'38.22"N	113°39'16.02"W
SV1A+SV1B+ SV1C	38°51'24.69"N	113°59'3.66"W
SV1D+SV1E	38°51'12.39"N	113°55'25.79"W
T1A+T1B	39°44'27.25"N	113°42'19.39"W
T1C	39°44'21.54"N	113°42'26.58"W
T1D	39°44'15.18"N	113°42'28.68"W
T1E	39°44'25.56"N	113°42'26.46"W
T1F	39°44'29.70"N	113°42'25.56"W
TC1	39°38'1.04"N	113°53'54.32"W
TC2	39°38'47.87"N	113°53'33.45"W
TC3	39°39'25.97"N	113°52'39.83"W
TC4	39°37'51.36"N	113°53'58.65"W
TS1	39°20'39.59"N	113°26'6.62"W
TS2	39°20'59.72"N	113°30'29.74"W
TS3+TS4+TS5	39° 6'34.39"N	113°27'52.45"W
W1A+W1B	38°18'46.02"N	113°23'9.88"W
W1C	38°19'0.00"N	113°23'7.56"W
W1D	38°19'13.20"N	113°23'4.98"W
W1E+W1F	38°18'55.11"N	113°23'19.98"W
WAH1	38°34'17.53"N	113°27'3.70"W
WAH2	38°34'21.12"N	113°28'53.48"W
WAH3	38°32'7.79"N	113°24'55.70"W

Table 2. Key to the 88 study sites in Utah labeled on the map in Figure 1, where nocturnal granivorous rodents were trapped from 2005–2008.

Area Number	Sites in Area
1	SI1, SI1A+SI1B, SI1C+SI1D, SI1E, SI1F, SI2, SI3, SI4, SI5, SI6+SI7
2	S1A, S1B, S1C+S1D
3	D1A+D1B, D1C, D1D, DUG1, DUG2, DUG3, DUG4
4	T1A+T1B, T1C, T1D, T1E, T1F, TC1, TC2, TC3, TC4
5	FS1+FS2, FS4+FS4B, FS5+FS6
6	LS1A, LS1B, LS1C
7	GAN1, GAN2
8	TS1, TS2
9	O1A+O1B+O1C
10	TS3+TS4+TS5
11	C1A, C1B, C1C, C1D, C1E
12	SV1A+SV1B+SV1C, SV1D+SV1E
13	F1A+F1B+F1C+F1D, F2A+F2B, F2C+F2D
14	EXP1, EXP2
15	WAH1, WAH2, WAH3
16	MIL
17	W1A+W1B, W1C, W1D, W1E+W1F
18	ESC1, ESC2
19	AA, AS, AW, B1A, B1B+B1C, B1D, B1E+B1F+BC, B2A+B2B, B2C, B2D, B2E+BTS, BDE, BDW, BE, BFW, BNE, BNW, BP, BSW, BTN, BW, SR
20	L1A, L1B, LPL

Table 3. The template for the 2x2 contingency table described by Cole (1949) for use in interspecific association analysis, where *a* = the number of sites where both species are present; *b* = the number of sites where species A is present and species B is absent; *c* = the number of sites where species B is present and species A is absent; *d* = the number of sites where both species are absent; and *n* = the total number of sites.

		SPECIES B		
		present	absent	
SPECIES A	Number of times present	*a*	*b*	*a*+*b*
	Number of times absent	*c*	*d*	*c*+*d*
		a+*c*	*b*+*d*	*a*+*b*+*c*+*d* = *n*

Table 4. Expected values of *a* (above the diagonal) and observed values of *a* (below the diagonal) according to the analysis developed by Cole (1949) for all pair-wise analyses of interspecific associations for six nocturnal granivorous rodents (*Microdipodops megacephalus, Perognathus longimembris, Perognathus parvus, Dipodomys ordii, Dipodomys microps,* and *Peromyscus maniculatus*) trapped at 99 study sites in the Great Basin (bold values indicate a significant association, and the sign indicates a positive or negative association).

		Species					
		M. megacephalus	***P. longimembris***	***P. parvus***	***D. ordii***	***D. microps***	***P. maniculatus***
Species	***M. megacephalus***		8.83	4.88	20.21	12.55	18.82
	P. longimembris	12		8.06	33.39	20.73	31.09
	P. parvus	**15+**	**15+**		18.45	11.45	17.18
	D. ordii	20	35	17		47.45	71.18
	D. microps	12	**27+**	13	47		44.18
	P. maniculatus	20	**27-**	17	69	**48+**	

Table 5. Chi-square values (above the diagonal) and *p*-values (below the diagonal) for all pair-wise analyses of interspecific associations for six nocturnal granivorous rodents (*Microdipodops megacephalus, Perognathus longimembris, Perognathus parvus, Dipodomys ordii, Dipodomys microps,* and *Peromyscus maniculatus*) trapped at 99 study sites in the Great Basin (significant values are in bold).

		Species					
		M. megacephalus	***P. longimembris***	***P. parvus***	***D. ordii***	***D. microps***	***P. maniculatus***
Species	***M. megacephalus***		2.41	**34.71**	0.024	0.068	0.53
	P. longimembris	0.5		**12.31**	1.034	**6.78**	**4.81**
	P. parvus	**0.01**	**0.01**		1.2	0.58	0.013
	D. ordii	>0.5	0.5	0.5		0.079	3.034
	D. microps	>0.5	**0.01**	0.5	>0.5		**3.99**
	P. maniculatus	0.5	**0.05**	>0.5	0.1	**0.05**	

LIST OF FIGURES

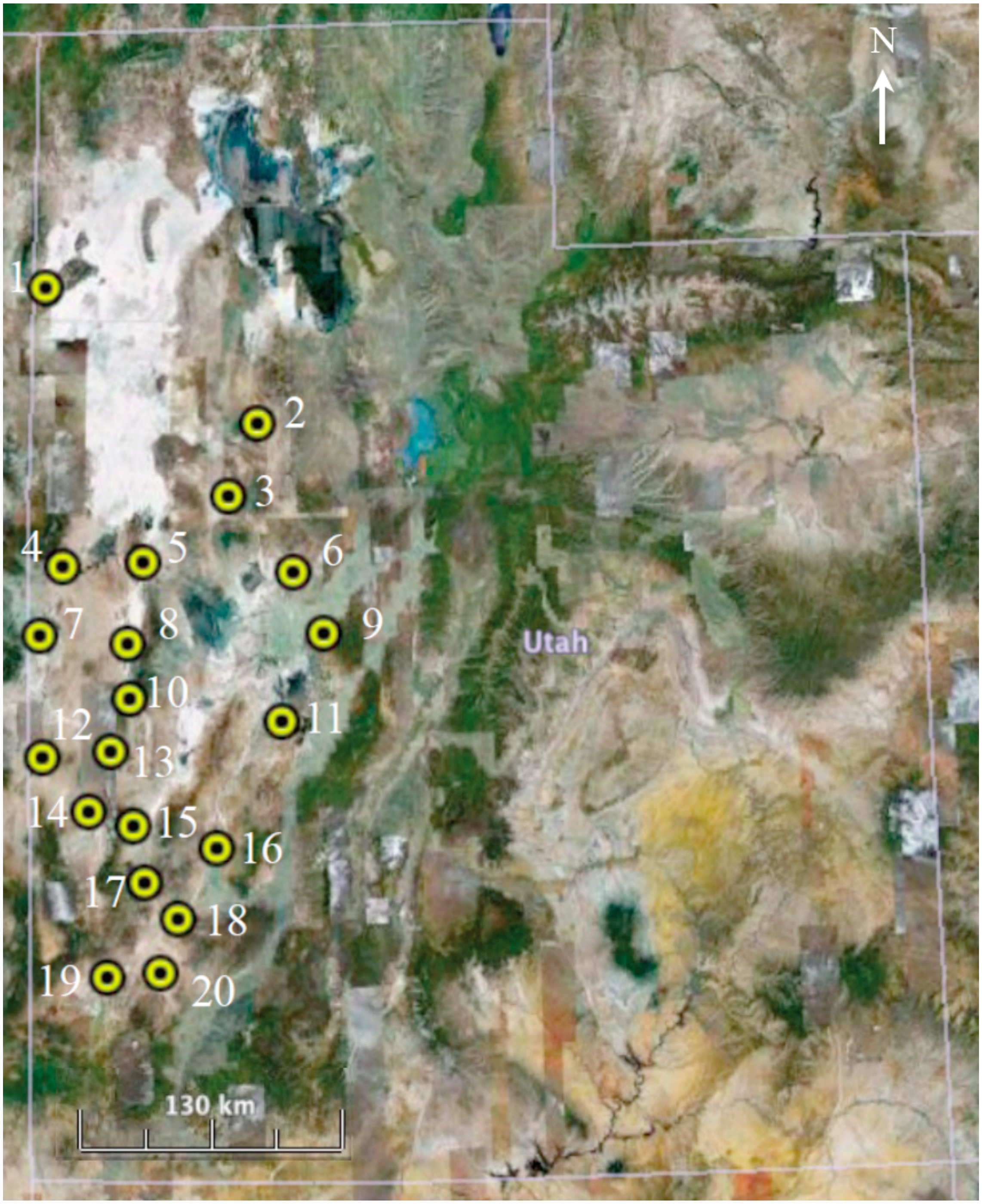
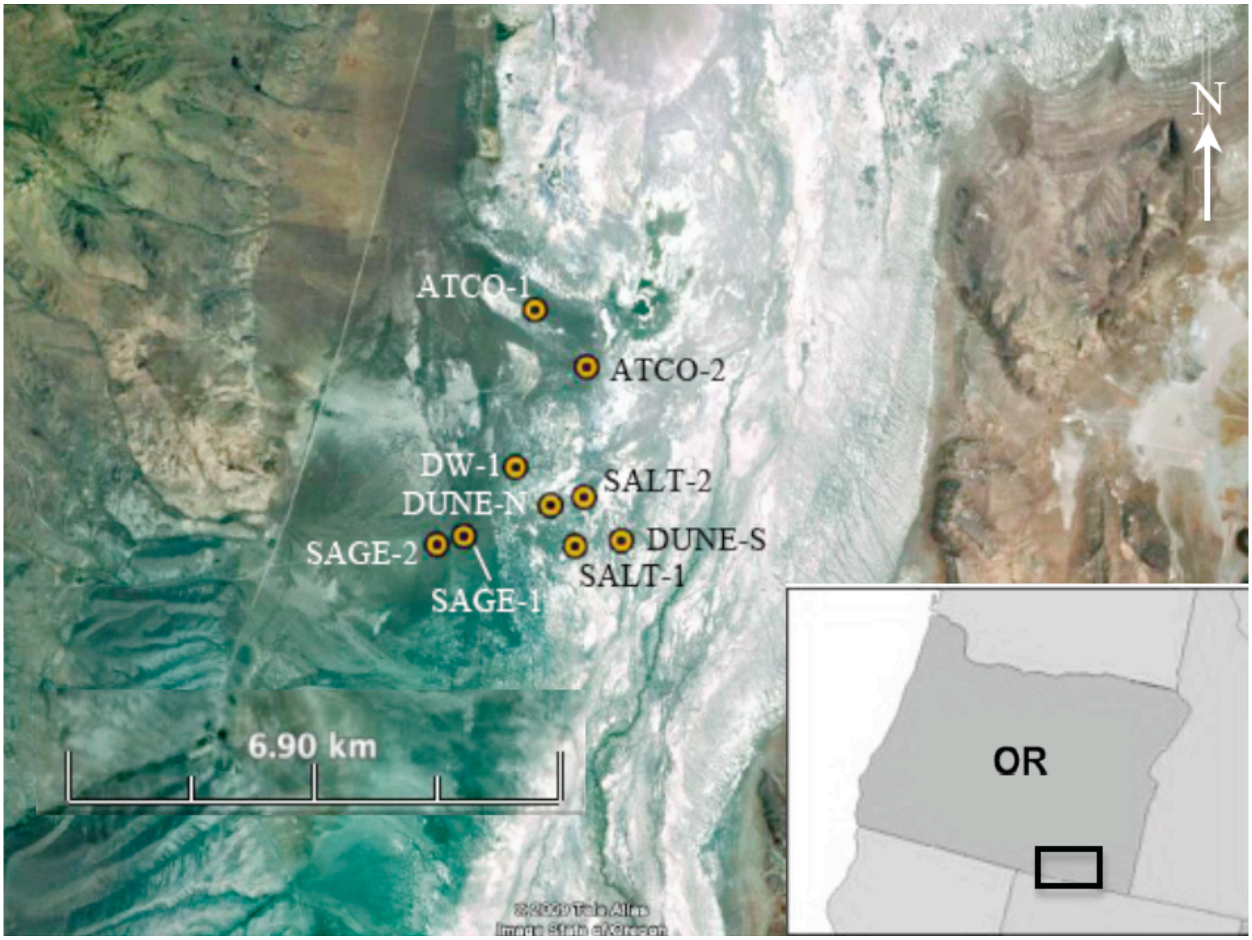


Figure 1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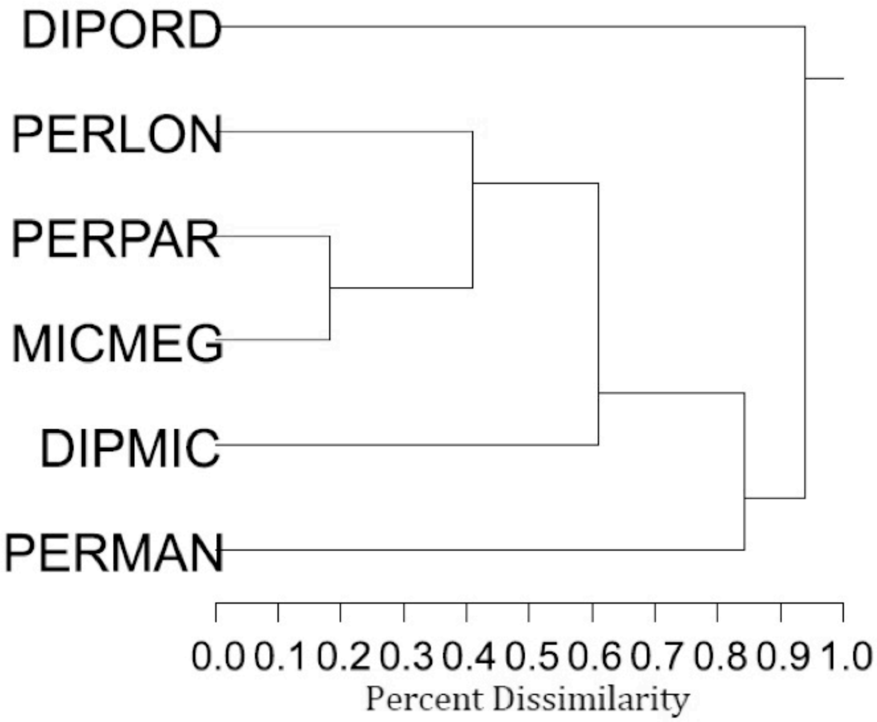
ATCO-2
DW-1
SALT-2
DUNE-N
DUNE-S
SAGE-2
SALT-1
SAGE-1
6.90 km
OR
© 2009 Tele Atlas
Image State of Oregon

Figure 2


N
Nevada
Sacramento
San Francisco
San Jose
MONO
BENTON
California
Fresno
180 km

Figure 3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PERMAN
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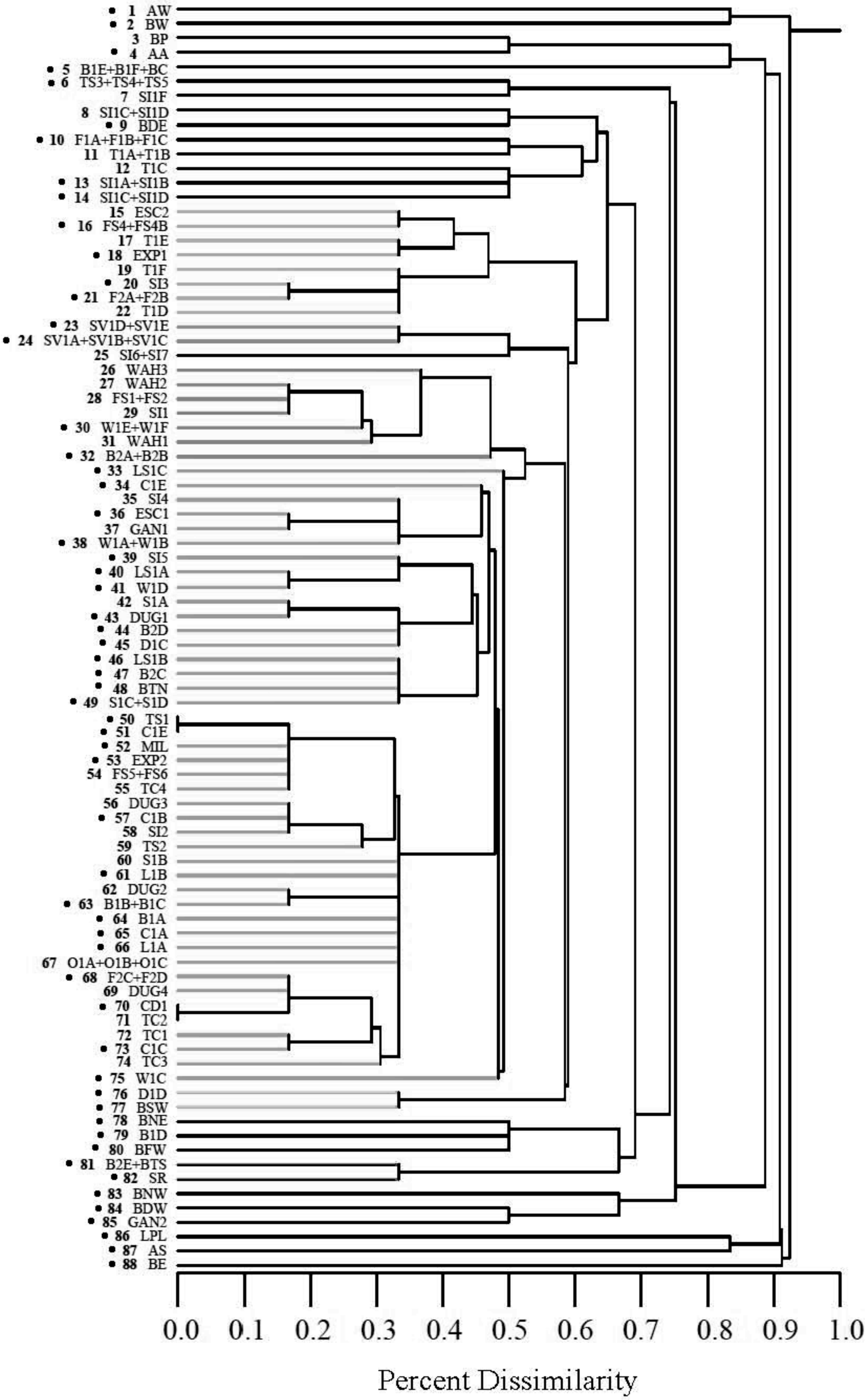
1.0
Percent Dissimilarity

Figure 4


• 1 AW
• 2 BW
3 BP
• 4 AA
• 5 B1E+B1F+BC
• 6 TS3+TS4+TS5
7 SI1F
8 SI1C+SI1D
• 9 BDE
• 10 F1A+F1B+F1C
11 T1A+T1B
12 T1C
• 13 SI1A+SI1B
• 14 SI1C+SI1D
15 ESC2
• 16 FS4+FS4B
17 T1E
• 18 EXP1
19 T1F
• 20 SI3
• 21 F2A+F2B
22 T1D
• 23 SV1D+SV1E
• 24 SV1A+SV1B+SV1C
25 SI6+SI7
26 WAH3
27 WAH2
28 FS1+FS2
29 SI1
• 30 W1E+W1F
31 WAH1
• 32 B2A+B2B
• 33 LS1C
• 34 C1E
35 SI4
• 36 ESC1
37 GAN1
• 38 W1A+W1B
• 39 SI5
• 40 LS1A
• 41 W1D
42 S1A
• 43 DUG1
• 44 B2D
• 45 D1C
• 46 LS1B
• 47 B2C
• 48 BTN
• 49 S1C+S1D
• 50 TS1
• 51 C1E
• 52 MIL
• 53 EXP2
54 FS5+FS6
55 TC4
56 DUG3
• 57 C1B
58 SI2
59 TS2
60 S1B
• 61 L1B
62 DUG2
• 63 B1B+B1C
• 64 B1A
• 65 C1A
• 66 L1A
67 O1A+O1B+O1C
• 68 F2C+F2D
69 DUG4
• 70 CD1
71 TC2
72 TC1
• 73 C1C
74 TC3
• 75 W1C
• 76 D1D
• 77 BSW
• 78 BNE
• 79 B1D
• 80 BFW
• 81 B2E+BTS
• 82 SR
• 83 BNW
• 84 BDW
• 85 GAN2
• 86 LPL
• 87 AS
• 88 BE
0.0
0.1
0.2
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0.6
0.7
0.8
0.9
1.0
Percent Dissimilarity

Figure 5