Habitat preference and species interactions of the desert woodrat (*Neotoma lepida*) in the Mojave Desert

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ABSTRACT

Ecosystem engineers often have cascading impacts on the ecosystems in which they occur. Understanding the factors that contribute to their habitat selection can provide valuable information on how ecosystems function. Our study investigates the habitat distribution of desert woodrats (*Neotoma lepida*) in the Eastern Mojave Desert. We show that there is a difference in desert woodrat abundance among habitats, and found that specific aspects of these environments are associated with woodrats. These aspects include grass cover, shrub richness, and especially substrate architecture. Our findings indicate that woodrats may facilitate plant productivity within this arid environment.

INTRODUCTION

Preferential habitat selection is one of the driving factors that allow species to coexist (Rosenzweig 1981). Habitat quality, determined by resource availability, is a primary driver of habitat selection (Orians and Wittenberger 1991). A greater understanding of what leads an organism to choose a specific habitat can uncover ecological dynamics and interactions between species. This is especially the case for ecosystem engineers that modify their environment and in turn support biodiversity. For example, American pikas (*Ochotona princeps*) are ecosystem engineers in alpine environments because their burrows increase the levels of nutrients available to plants (Aho et al. 1998). Thus, the places that pikas prefer to live would therefore be associated with the distribution of alpine vegetation. In other words, understanding what determines the habitat preference of a single organism can reveal what drives habitat selection of other species. This
in turn can lend greater understanding of the spatial distribution of species and resource availability within that habitat.

Abiotically extreme environments that contain limited resources, such as deserts, can provide insight into the greater ecological impacts associated with habitat selection of key organisms. Ecosystem engineers play major roles in the distribution of patchy and limited resources. Rodents that create soil disturbances in arid regions, such as the desert woodrat (*Neotoma lepida*), are often classified as ecosystem engineers because collected organic materials and fecal detritus surrounding desert woodrat middens promote nitrogen mineralization that in turn promotes local biodiversity (Whitford and Steinberger 2010). Reciprocally, desert woodrats are also heavily reliant on their habitat. For example, desert woodrat survivorship was found to be heavily correlated with the success or failure of desert annual and perennial plant production (Smith 1995). When Mojave yucca (*Yucca schidigera*) failed to set seed during drought years, desert woodrats also failed to reproduce (Smith 1995). Thus, vegetation can influence woodrat survivorship, and the fact that woodrats have been cited as ecosystem engineers indicates that woodrats may also be responsible for the composition of their surrounding vegetation. Nevertheless, the specific composition of these surrounding plant communities has yet to be documented. In this study, we investigated how woodrat habitat preference correlates with differences in their communities.

In order to examine the reciprocal relationship between woodrat habitat preference and the associated surrounding vegetation, we investigated whether (1) woodrats prefer specific habitats and microhabitats, (2) midden substrate vegetation differed from non-midden vegetation, and (3) woodrat presence drives changes in surrounding vegetation. Together, our study helps contribute to a better understanding of the underlying mechanisms driving habitat preference of desert woodrats, and in turn, the potentially large impact of desert woodrats on desert vegetation. Furthering our knowledge of this relationship will allow us to better understand the dynamics of desert ecosystems at large, and what enables desert natives to persist in this harsh, resource limited environments.

**METHODS**

**Study site**

We conducted our study in three separate sites in the University of California Sweeney Granite Mountains Desert Research Center (UCGMR) in the Eastern Mojave Desert (24°47’ N, 115°43’ W). This area is a transition zone and contains flora and fauna characteristic of the Great Basin, Sonoran, and Mojave Deserts. There are 14 species of rodents in the area and 502 species of plants. At roughly 1200 m elevation, our study sites did not breach dusky-footed woodrat (*Neotoma fuscipes*) territory and instead featured only desert woodrat middens. Among three sites, we characterized each according to their predominant
vegetation. “Mixed Cholla/Yucca Scrub” was abundant in Mojave yucca (*Yucca schidigera*) and buckhorn cholla (*Cylindropuntia acanthocarpa*). “Mixed Yucca Scrub,” was abundant in yucca but had fewer buckhorn cholla. “Mixed Acacia Scrub” had few to no yucca and cholla, but was abundant in cat-claw acacia (*Senegalia greggii*). All three sites had a varying number of creosote bush (*Larrea tridentata*).

**Shrub richness**

To test whether desert woodrat densities correlated with richness of surrounding shrubs we used five 50 m² macro-plots within each site. To reduce bias, we randomly determined the distance between macro-plots. Each macro-plot was divided into four transects to give five 10 m x 50 m bands and within three bands we counted the total number of yucca, cholla, creosote, and acacia individuals. We used this data to estimate the abundance of each plant species. Additionally, a belt transect was performed along the x-axis of each macro-plot in order to measure species richness of all plants in addition to the previously surveyed yucca, cholla, creosote, and acacia individuals.

**Midden data**

To assess woodrat habitat preference, we surveyed every woodrat midden within each macro-plot. For each midden we encountered within macro-plots, we recorded its position, the plant species that hosted the midden (hereafter referred to as substrate), and the midden construction material. In order to test if woodrat presence was associated with shrub richness, we measured the following variables for every substrate: surrounding plant species richness, percent grass cover under shrubs, and plant architecture (as number of clones). We defined an individual yucca clone as a new rhizomatous growth and an individual cholla clone as a main branch at the base. Then, we chose the next closest non-midden substrate of the same species of similar height, and measured the same variables.

**Statistical analyses**

We used a one-way ANOVA to test differences in midden abundance among sites, followed by Tukey’s HSD post-hoc test to distinguish specific differences among sites. To determine what habitat characteristics were associated with woodrat abundance, we used linear regressions to examine relationships between midden abundance and shrub species richness, shrub density, proportion of cholla, and proportion of creosote.

We conducted two way ANOVAs to test the relationships of midden presence and substrate species on surrounding shrub richness, percent grass cover, and shrub architecture. To determine specific difference among the effects of substrate species on surrounding shrub richness, understory percent grass cover, and substrate architecture we used Tukey HSD post-hoc tests. Acacia was excluded from the ANOVA analysis of number of clones because acacia does not exhibit the same growth patterns as yucca and cholla.
Lastly we used ANCOVA to compare number of yucca clones and surrounding species richness by midden presence. All statistical analyses were conducted using JMP 13.0.0.

RESULTS

Mixed cholla scrub predominantly consisted of Mojave yucca (30%), buckhorn cholla (60%), and desert creosote bush (10%). Mixed yucca scrub was composed of Mojave yucca (41%), buckhorn cholla (6%), and desert creosote bush (53%). Mixed acacia scrub consisted of desert creosote bush (57%) and catclaw acacia (43%).

There were significantly more middens in the mixed cholla scrub than any other habitat (p < 0.001; Figure 1). Mixed cholla scrub also had higher shrub richness and total shrub density than the other two habitats. Midden density was positively correlated with shrub richness (p < 0.01; R^2 = 0.8; Figure 2A) and shrub density (p < 0.001; R^2 = 0.85; Figure 2B). Midden abundance increased as proportion of cholla increased (p < 0.0001; R2 = 0.8; Figure 2C) but decreased as proportion of creosote increased (p < 0.001, R^2 = 0.99; Figure 2D). Also, 76% of middens contained cholla as midden material.

Midden presence was positively correlated with shrub richness of surrounding vegetation (p < 0.002; Figure 3A). Shrub richness was significantly higher in yucca than in cholla, but acacia shrub richness did not significantly differ from either yucca or cholla (p < 0.04; Figure 3B). Midden substrates also had greater percent grass cover than non-midden substrates (p < 0.03; Figure 3C). Grass percent cover was highest under acacia, followed by cholla, then yucca. Acacia was significantly different from cholla and yucca, and cholla and yucca were not significantly different from each other (p < 0.0001; Figure 3D). Number of clones had the strongest correlation with midden presence (p < 0.0001; Figure 3E). The number of clones was significantly higher in yucca than in cholla (p < 0.0001; Figure 3F).

Woodrat presence is more strongly associated with a high number of clones in yucca than in cholla (p < .001; Figure 4). Yuccas with woodrat middens had almost double the number of clones than yuccas without woodrat middens.

In yucca with middens, as number of clones increased, shrub richness slightly increased. In yucca without middens, as number of clones increased, shrub richness slightly decreased. However, these results were not significant (P(midden presence) = 0.09, P(midden presence*no. of clones) = 0.15, P(no. of clones) = 0.76. R2 = 0.045. Linear regression R2 pres = 0.02, R2 abs = 0.02; Figure 5.)
Figure 2. The relationship between habitat characteristics and midden density. Graphs demonstrate response of midden density to shrub richness (A), shrub density (B), proportion of cholla (C), and proportion of creosote (D).

Figure 3. Mean vegetation characteristics ±1 S.E by midden presence (A, C, E) and midden substrate species (B, D, F). Bars not connected by the same letters were significantly different after Tukey’s HSD post-hoc tests.

Figure 4. Relationship of midden presence and substrate species with substrate architecture. Dark and light bars represent midden presence and absence, respectively. Bars represent means ± 1 S.E. Bars not connected by the same letters were significantly different after Tukey’s HSD post-hoc tests.
DISCUSSION

Our research suggests that woodrat habitat preference influences the distribution of desert vegetation by promoting growth around middens. We found higher woodrat midden densities in areas with the highest proportion of cholla, demonstrating that woodrats exhibit habitat preference. This finding complements the fact that woodrat survivorship is greater in cholla middens because it confers more protection against predators (Smith 1995). This cholla-woodrat relationship is further underscored by the high proportion of cholla used as midden construction material. The fact that the species richness and the percent cover of grass around middens were higher than in areas that lacked middens indicates that there is clear relationship between desert woodrats and desert vegetation. We suggest a manipulation study to confirm a cause-and-effect relationship, but these findings nevertheless endorse the desert woodrat’s position as an ecosystem engineer.

There were also habitats that desert woodrats selected against. For example, midden density was negatively correlated with proportion of creosote. Habitats with a greater proportion of creosote were also less dense and had lower diversity. This relationship may be due to the fact that creosote has allelopathic effects on surrounding vegetation and avoids growing around competing root systems (Brisson and Reynolds 1994). Since woodrats prefer dense areas that provide ample cover, it is appropriate that a woodrat would avoid this habitat (Bonaccorso and Brown 1972).

There were strong differences in the biotic communities around middens when compared to non-midden substrates. Midden presence was strongly linked with greater diversity of surrounding shrubs, grass cover, and architectural complexity, most notably in yucca. Since woodrats promote nitrogen mineralization, it is quite possible that midden presence is responsible for the correspondingly higher diversity and density of surrounding vegetation. Nevertheless, the association of woodrat middens with greater shrub diversity and percent grass cover could be confounded by inherent differences in the three habitats we surveyed. It is also unclear whether woodrat presence allows yucca to live longer and thus generate more clones, or whether woodrats simply prefer to build their middens in yuccas that are more architecturally complex. Yet the relationship between woodrats
and yucca shows promise because woodrats pass down their middens for several generations (Dial 1988) and the number of clones in yucca increases with age (LaPre 1979).

Desert woodrats exhibited clear habitat preference and there were differences between the vegetation around middens versus non-middens. This demonstrates that desert woodrat habitat preference is biotically driven and there are strong interspecific relationships between woodrats and desert vegetation. Desert woodrat habitat preference was associated with shrub density and diversity, but this preference was driven by the proportion cholla. Our findings further illustrate the complexity of desert woodrat habitat selection in a resource-deficient environment. There are likely other species interactions that we have not accounted for, but this study portrays a baseline understanding of the dynamic relationship woodrats have with desert vegetation. Our results indicate that shrub diversity and abundance may drive midden presence which in turn can have ecosystem level consequences. These findings further clarify what drives habitat selection, and what enables these organisms to survive in arid environments.

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REFERENCES


