Expansive fire in Mojave Desert shrubland reduces abundance and species diversity of small mammals

K.J. Horn, B.R. McMillan, S.B. St. Clair*

Department of Plant and Wildlife Sciences, Brigham Young University, 293 WIDB, Provo, UT 84602, USA

ABSTRACT

Changes in plant community structure and composition of the Mojave Desert in response to greater fire intensity and extent are likely to have strong bottom-up effects on the biological community. The objective of this study was to determine how expansive fire in Mojave Desert impacts small mammal communities across seasons. We sampled small mammals in paired burned (4–5 years post-fire) and unburned areas of Beaver Dam Wash in southwestern Utah. Fire reduced total abundance of small mammals, and species richness and species diversity of the small mammal community. Merriam's kangaroo rat (Dipodomys merriami) responded positively to fire (15% greater in burned areas). Long-tailed pocket mouse (Chaetodipus formosus) and canyon mouse (Peromyscus crinitus) were 91% and 98% less abundant in burned versus unburned areas. The positive response of Merriam's kangaroo rat to fire is most likely correlated with their preference for open foraging microhabitat while other species captured prefer greater and more diverse cover. Because the small mammal community has been dramatically affected by fire, it is likely that top-down control of vegetation structure will be dominated by Merriam's kangaroo rat in burned areas, which may promote more open habitat by limiting the growth of annual and perennial grasses.

1. Introduction

Desert ecosystems tend to experience less fire because water and nutrient limitations to plant growth result in low and discontinuous fuel loads (Kozlowski, 1974). However, recent analysis shows that the Mojave Desert region may be at a “tipping point” between fire regimes of infrequent, patchy, small fires to continuous, large fires (Brooks and Matchett, 2006). For example, fires burned 240,173 ha in the Mojave's mid-elevation shrubland from 1980 to 2004, while in 2005 alone, a few fires burned more than 318,655 ha (Brooks and Matchett, 2006). It is hypothesized that dramatic increases in non-native annual grasses (Bromus and Schismus spp.) under the right climatic conditions produce continuous fuel beds (Brooks, 1999; Brooks et al., 2004; Hunter, 1991) that appear to be driving an invasive plant/fire cycle in the Mojave Desert region (Brooks and Matchett, 2006).

Small mammal communities are influenced directly by fire and also indirectly by burn effects on plant community structure. Research in tallgrass prairies has shown the direct effects of fire on small mammals may include burns, heat stress, asphyxiation, physiological stress, trampling, and predation during escape from fire (Kaufman et al., 1990). Some species that have aboveground nests, such as Neotoma spp., may perish directly from fire (Simons, 1989, 1991). However, burrowing rodents such as Dipodomys spp., Perognathus spp., and Chaetodipus spp. are more likely to survive with greater burrow depth (Howard et al., 1959). Emigration can occur as small mammals flee their burrows/nest during the fire and do not return (Kaufman et al., 1990). Physiological stress induced by fire can impact small mammal populations through abortion of litters or abandonment of young. However, the primary influences fire has on small mammal communities are often indirect effects through changes in vegetation composition and structure via bottom-up effects (Price, 1978). These changes in the plant community can alter the quantity or quality of food, availability of nest sites, alterations in predator–prey interactions and incidence of parasitism and disease (Kaufman et al., 1990).

Heteromyid rodents in the Mojave Desert possess unique attributes that cause them to interact with plant communities differently. For example, Kangaroo rats obtain the majority of their water through metabolism of carbohydrates leading to preferences for seeds high in carbohydrates (Zeng and Brown, 1987). Both pocket mice and kangaroo rats have fur lined cheek pouches in which they transport preferred seeds to scatter and larger hordes (Beck and Vander Wall, 2010; Pyare and Longland, 2000) which is

* Corresponding author. Tel.: +1 801 422 5725; fax: +1 801 422 0008.
E-mail address: stclair@byu.edu (S.B. St. Clair).
a dispersal mechanism for plant propagules. Rodent species differ in foraging patterns based on microhabitat structure (Hallett, 1982; Price, 1978; Rosenzweig and Winakur, 1969). Changes in the structure of the small mammal community following fire can therefore alter top-down controls that small mammals have on plant community structure (Brown and Heske, 1990a; Kerley and Whitford, 2009).

Because of the strong interactions and feedbacks between plant and small mammal communities, understanding how recent expansive fires in the Mojave Desert impacts small mammal communities is an important step in predicting how changing fire dynamics will alter the composition and function of Mojave Desert ecosystems. The objective of this study was to identify how recent fires in Mojave Desert mid-elevation shrubland, impacts the small mammal community. The following predictions were tested: 1) fire reduces small mammal abundance; and 2) small mammal species show differential sensitivity to fire-altered landscapes resulting in changes in small mammal community species richness and diversity.

2. Methods

2.1. Study location

The study area is located in the Beaver Dam Wash in southwest Utah (Fig. 1). Vegetation present is typical of mid-elevation (850–1080 m) Mojave Desert shrubland dominated by blackbrush (Coleogyne ramosissima), creosote bush (Larrea tridentata), white bursage (Ambrosia dumosa), and Joshua tree (Yucca brevifolia). Much of the area is covered with exotic plant species such as, flarree (Erodium cicutarium) and the winter annual red brome (Bromus rubens). The soil is a young alluvium with sandy loam surface soils. The landscape has been altered by extensive fires. From summer 2009 to spring 2010 we sampled small mammals in existing burned areas caused by three separate fires that occurred in the spring/summer of 2005: Westside (June, 27,059 ha), Duzak (July, 7065 ha – within Utah), and Burgess 2 (July, 712 ha) (Utah BLM On-line Data, 2011).

2.2. Rodent survey

Four 1 km long transects were established within previously burned areas and each transect was paired with an adjacent transect in an unburned area (Fig. 1). Using digital elevation models, transects were selected to generally follow ridge tops to minimize topographical variations between burned and control sites. We sampled near burn boundaries to minimize spatial effects on small mammal communities. Therefore differences that we observed were likely due to fire. Burned sites were chosen based on adequate distance to comparable unburned control sites as dictated by existing fire boundaries. Live-traps were geographically distributed at 20 m intervals along eight 1 km long transects and baited with commercially available wild birdseed mix. Traps were at minimum 50 m with an average of 211 m from any burn boundary, road or other distinct landscape transition.

One trapping session was conducted in each of the four seasons. A trapping session consisted of two consecutive nights of trapping the same site. Trapping sessions were held in August (summer) and October (fall) of 2009 and February (winter) and May (spring) of 2010. Sherman live-traps were baited and set at dusk, and then checked after dawn. Small mammals were identified to species, weighed to the nearest 0.5 g, checked for reproductive status, tagged with a small numbered ear tag and then released. Capture and handling procedures were approved by BYU Institutional Animal Care and Use Committee (Protocol # 09-0302).

2.3. Statistics

Mean abundance of small mammals was calculated for the number of unique individuals of all species and for each individual species by site and by season from the trapping data obtained in August 2009 to May 2010. Tagged individuals that were captured in subsequent trapping seasons were counted as a unique individual for that season. We used species richness and Shannon’s Diversity Index (SDI = −∑ pi ln (pi) where pi is the proportion of the ith species) to describe the small mammal community. Statistical significance for abundances, species diversity (SDI), and species richness was analyzed using Proc Mixed Repeated Measures model in SAS (SAS Institute, Cary North Carolina). Season was the repeated measure and data were grouped into 4 blocks of paired sites.

Information criterion methods (Akaike, 1974; Burnham and Anderson, 2002) were used to analyze five hypothetical models based on the effects of fire (fire) and two-way interactions of fire with different seasons, and species (Table 1). Model 1 in Table 1 was used in the repeated measures ANOVA analysis.

3. Results

3.1. Capture rate

We captured 383 individuals in 3136 trap-nights between August 2009 and May 2010. 105 individuals were captured both first and second nights of trapping. 70 individuals were captured in more than one season. No individuals were recaptured on a different transect than where they were initially captured. Species captured included long-tailed pocket mouse (Chaetodipus formosus), Merriam’s kangaroo rat (Dipodomys merriami), chisel-toothed kangaroo rat (Dipodomys microps), Ord’s kangaroo rat (Dipodomys ordii), desert wood rat (Neotoma lepida), grasshopper mouse (Onychomys leucogaster), canyon mouse (Peromyscus cleromys), and deer mouse (Peromyscus maniculatus) (Fig. 2). White-
tailed antelope squirrels (*Ammospermophilus leucurus*) were also common in Beaver Dam Wash but were excluded from analysis since over-night trapping did not provide an accurate measure of the abundance of this diurnally active small mammal.

### 3.2. Relative abundance of individuals by species

Merriam’s kangaroo rat was the most frequently captured rodent averaging 10.8 ± 0.4 unique individuals per site per season (Fig. 2). The number of captures of long-tailed pocket mice and deer mice averaged 1.6 ± 0.4 and 1.3 ± 0.4 unique individuals per site per season, respectively. All other species cumulatively averaged fewer than 0.3 unique individuals per site per season.

### 3.3. Fire and seasonal effects on small mammal abundance

The mean number of unique small mammals captured along burned transects was less than unburned transects according to information theoretic analysis (Table 1). Unburned sites averaged 15.9 ± 1.6 unique individuals per season while burned sites averaged 12.1 ± 1.6 unique individuals per season. The presence of fire, season, and their interaction term in model 1, which had the lowest AICc value, which emphasizes their important role in small mammal responses in our study (Table 1). In the ANOVA analysis season was significant (*p* < 0.0001) while fire (*p* = 0.086) and the interaction term (*p* = 0.14) were not. The Δ of 8.9 between models 2 and 1 indicates that seasonal fluctuation in small mammal activity was affected by fire (see Section 3.5). Small mammal abundance ranged from 21.5 to 5.9 individuals per site and was greatest during the summer and winter periods (Fig. 3). In relation to unburned control sites, burned sites had lower small mammal abundance during summer and fall but not during the winter and spring periods (Fig. 3). Reproductive condition and sex ratios of small mammals were not significantly affected by fire (*p* = 0.5 and *p* = 0.6 respectively).

### 3.4. Fire effects on species richness and diversity

Species richness and diversity were significantly lower along burned transect compared to unburned controls (*p* < 0.001). Grasshopper mice, deer mice, chisel-toothed kangaroo rats, and Ord’s kangaroo rats were never captured within the burned zones.

![Fig. 2. Number of small mammals captured along unburned (white bars) and burned (gray bars) transects differentiated by species. Statistical significant defined as: *p* < 0.05; **p* < 0.01; ***p* < 0.001.](image)

![Fig. 3. Average abundance of small mammals (top) and difference in the number of small mammals between burned and unburned transects (bottom) for all species. Merriam’s kangaroo rat, long-tailed pocket mouse, and canyon mouse for all four trapping sessions. Average values below ‘0’ in bottom graph indicate fewer number of small mammals in burned vs. unburned areas. Error bars are ±1 standard error.](image)
The few desert wood rats that were caught within the burned sites were found near deadfall. Merriam's kangaroo rat, the most abundant small mammal year round, was dominant on both burned and unburned sites, and was often the only species captured on burned sites. This resulted in the average species richness for burned sites of 1.31 ± 0.15 species per site per season. Species richness for unburned sites averaged 2.4 ± 0.15 species per site per season. Shannon's diversity index (SDI) averaged 0.62 ± 0.06 for unburned sites and 0.13 ± 0.06 for burned sites.

3.5. Fire and seasonal effects on individual species

Small mammal species varied in their response to fire (p < 0.01, Table 2). More specifically, Merriam's kangaroo rat had greater abundances along burn transects (p = 0.05), whereas all other species had negative (e.g., long-tailed pocket mouse and canyon mouse) or undetectable responses to fire (Fig. 2). Long-tailed pocket mouse abundance was significantly lower in burned areas in the summer with captures too infrequent to demonstrate a response during other seasons (Fig. 3). Fire had a strongly negative effect on canyon mouse abundance in summer and fall but captures were too infrequent in winter and spring periods to document responses. Merriam's kangaroo rat abundance was positively affected by fire in the summer and winter seasons, showed negative fire responses in fall and no significant effect of fire in the spring.

4. Discussion

4.1. Fire influences on abundance of small mammal

Consistent with our first prediction, burned sites had fewer small mammals than adjacent undisturbed sites. Reduction in total abundance of small mammals in burned sites was most strongly influenced by losses of long-tailed pocket mice and canyon mice. For heteromyid rodents, different species have been observed to specialize in different foraging microhabitats (i.e. large open spaces, small open spaces, large bushes, and trees) and interspecies competition increases heteromyid preferences to particular foraging microhabitats (Price, 1978). The elimination of shrub-covered microhabitats by fire in Beaver Dam Wash likely had negative effects on persistence of long-tailed pocket mice which prefer shrub cover (Price, 1978).

All species captured had negative or undetectable responses to fire with the exception of Merriam's kangaroo rat. Merriam's kangaroo rat dominated small mammal captures (>70%) and was the only species that was more abundant in the burned sites than the unburned controls (see Fig. 2). Merriam's kangaroo rat increase at burned sites is likely related to its foraging preference for open spaces (Price, 1978; Simons, 1991; Vamstad and Rotenberry, 2010). Bailey’s pocket mouse (Chaetodipus baileyi) (similar to long-tailed pocket mouse in our study) has previously been observed to decrease in numbers after controlled fire in the Sonoran Desert (Simons, 1991). Consistent with our findings canyon mice have also been observed to prefer unburned sites and old burned sites with greater vegetation cover than recently burned sites (Vamstad and Rotenberry, 2010). Decreases in individuals of some species at burned sites has not previously been observed to decrease total small mammal numbers as increases in Merriam's kangaroo rat numbers at burned sites compensated for reductions of other species (Vamstad and Rotenberry, 2010). In contrast, we found that the positive response of Merriam's kangaroo rat to burned habitat was not sufficient to compensate for the severe losses of long-tailed pocket mice and canyon mice in burned sites.

The diet of Merriam's kangaroo rat includes up to 30% green vegetation by volume between February to May and again in August (Bradley and Mauer, 1971). Limited green annual vegetation can limit reproduction of Merriam's kangaroo rat and effectively reduce the population (Beatley, 1969, 1976). However, we found Merriam's kangaroo rat from burned sites in reproductive conditions throughout the trapping sessions except in October (see Section 3.3). Either Merriam's kangaroo rat is able to find sufficient green tissue for water from surviving native plants or exotic annuals in burn zones or they are capable of sustaining themselves on metabolic water (Soholt, 1975; Walsberg, 2000). A reliable food source is also necessary to maintain or increase Merriam's kangaroo rat populations whose diet consists primarily of seeds (Bradley and Mauer, 1971). Merriam's kangaroo rat has been shown to be the primary consumers of creosote bush (L. tridentata) seeds (Boyd and Brum, 1983). However, creosote bush mortality along our burned transects was greater than 90% (unpublished data). Merriam's kangaroo rat has been found to be capable of consuming 90% of the total filaree production (Soholt, 1973). Invasive vegetation like redstem filaree (Erodium cicutarium) is prevalent throughout the burned sites. Given the lack of native vegetation and the abundance of invasive annuals we hypothesize that Merriam's kangaroo rats are meeting their food and water needs by consuming exotic plant tissues and seeds.

4.2. Fire reduced species richness and diversity

Burned sites had lower species richness and species diversity (SDI) than in adjacent undisturbed sites as outlined in our second prediction. A study in Joshua Tree National Park (Vamstad and Rotenberry, 2010) also reported that fire decreased small mammal species diversity but not species richness. Rosenzweig and Winakur (1969) observed that granivorous desert rodent diversity increased with environmental heterogeneity. Lower species diversity and richness in burned areas in our study may be linked to increased interspecies competition among rodents as fire homogenizes the landscape (Rosenzweig and Winakur, 1969). Our data are consistent with the idea that more expansive and numerous open spaces left from large fires have provided Merriam's kangaroo rat with its preferred foraging habitat. All other granivorous species in burned sites deal with loss of preferred habitat (which is likely linked with predator evasion strategies) and increased competition from Merriam's kangaroo rat.

4.3. Fire effects vary by season

Seasonal variances in small mammal populations (particularly for Merriam's kangaroo rat) have been observed (Zeng and Brown, 1987) and are linked with precipitation through plant primary production (Beatley, 1976; Thibault et al., 2010). However, we observed that seasonal fluctuations in small mammal captures between burned and unburned areas (see Fig. 3 and Table 1 models 1 and 3). The reductions in Merriam's kangaroo rat captures for
autumn 2009 along burned transect compared to unburned controls may have been associated with exposure to low temperature (0 °C) and high winds (personal observation). Temperature and wind effects are likely greatest at burned sites which lack vegetation cover resulting in temperature extremes to which rodents are sensitive (Reynolds, 1958).

4.4. Implications for plant communities

Fire effects on small mammal community structure can have feedbacks on the plant community via top-down effects that includes consumption of primary production, seed predation and dispersal, and soil disturbance (Stapp, 2010; Titus et al., 2002; Vander Wall et al., 2005). Our data show that burned Mojave Desert landscapes experience drastic changes in small mammal community structure characterized by increases in Merriam’s kangaroo rat and losses of other species. A few studies provide insight on how a more dominant influence by Dipodomys spp. may feedback on the re-establishment of plant communities following fire. Kerley and Whitford (2009) found that Dipodomys spp. can promote shrub establishment by reducing the amount of tall grasses present through the consumption of grass tillers. In the Chihuahuan Desert, experimental exclusion of Dipodomys spp. resulted in an increase in tall perennial and annual grasses (Brown and Heske, 1990b; Curtis et al., 2000).

The interplay between plant and small mammal communities are strongly influenced by climate conditions (Beatley, 1976). The disturbance to the small mammal community may affect their ability to limit the establishment of annual grasses which would result in higher fuel loads. Future studies should focus on identifying how patterns of future climate will influence small mammal—plant interactions particularly as it relates to shorter fire return intervals associated with invasive grass—fire cycles (Agnew, 1997; Beatley, 1966).

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