SMALL MAMMAL ABUNDANCE IN MOUNTAIN BIG SAGEBRUSH COMMUNITIES AFTER FIRE AND VEGETATION RECOVERY

Aaron L. Holmes[1] and W. Douglas Robinson[1,2]

ABSTRACT.—Managing fire for the conservation of biodiversity is a widespread challenge. An important disturbance mechanism in big sagebrush (*Artemisia tridentata*) communities, fire has well-known effects on vegetation structure but poorly described consequences for sagebrush wildlife communities. We estimated the abundance of small mammals in relation to fire history in mountain big sagebrush (*A. t.* ssp. *vaseyana*) communities by way of a chronosequence approach that included 3 wildfires and adjacent unburned areas. We compared patterns of mammal community succession with expectations of the habitat accommodation model by associating responses of mammals to change over time in vegetation structure. Burned study sites were at various stages of vegetation succession from 7 to 19 years following fire. Shrub canopy cover ranged from 9% to 36% and was not fully recovered on the plots at 19 years after fire. Only Belding's ground squirrel (*Urocitellus beldingi*) demonstrated a measurable response to fire that was consistent across all 3 burned study areas. Its density was approximately 10 times greater in burned areas relative to adjacent unburned habitat irrespective of the number of years since a burn occurred. Deer mouse (*Peromyscus maniculatus*) was more abundant on sites more recently burned than at sites closer to full vegetation recovery. Overall, effects of fire on small mammal abundance in this landscape were relatively small, did not closely match the expectations of the habitat accommodation model, and suggest that conservation of small mammal communities in fire-affected sagebrush landscapes can be influenced by habitat management at large spatial scales.

RESUMEN.—El manejo de incendios en la conservación de la biodiversidad es un gran desafío. Como un importante mecanismo de perturbación en las grandes comunidades de artemisia (*Artemisia tridentata*), el fuego también ha tenido efectos en la estructura de la vegetación, pero las consecuencias sobre las comunidades de artemisas silvestres han sido pobremente documentadas. Estimamos la abundancia de mamíferos pequeños en relación al historial de incendios, que afectaron a las comunidades de artemisas de montañas (*A. t.* ssp. *vaseyana*), por medio del método de cronosecuencias que incluyó tres incendios forestales y áreas adyacentes no quemadas. Comparamos los patrones de sucesión de las comunidades de mamíferos con las expectativas del modelo de ajuste al hábitat mediante la asociación de las respuestas de los mamíferos a los cambios en la estructura de la vegetación a lo largo del tiempo. Las zonas quemadas utilizadas en el estudio se encontraban en varias fases de sucesión vegetal, desde 7 a 19 años tras el incendio. La cobertura de arbustos oscilaron entre un 9% y un 36%, y no se habían recuperado por completo las parcelas en las que el incendio había ocurrido 19 años antes. Sólo la ardilla de tierra de Belding (*Urocitellus beldingi*) mostró una respuesta medible al fuego, la cual fue consistente en las tres áreas quemadas del estudio. Su densidad fue, aproximadamente, 10 veces mayor en las zonas quemadas con respecto al hábitat adyacente no quemado, independientemente del número de años que hubiesen pasado desde el incendio. El ratón (*Peromyscus maniculatus*) fue más abundante en áreas quemadas recientemente que en las zonas más cercanas a la recuperación total de vegetación. En general, los efectos del fuego en la abundancia de mamíferos pequeños en este paisaje fueron relativamente escasos, y no corresponden a las expectativas del modelo de ajuste al hábitat. Esto sugiere que la conservación de las comunidades de mamíferos pequeños en los paisajes de artemisa afectados por los incendios puede estar influenciada por el manejo del hábitat a escalas espaciales grandes.

Fire alters characteristics of plant communities, which in turn influence the species composition, richness, and abundance patterns of many vertebrate species (Fox 1981). With an increasing interest in the occurrence, severity, and extent of fires in the modern era of a dynamic climate, conservation biologists are interested in understanding responses of vertebrates to fire (Clarke 2008). Among the responses of interest is the time since fire. In particular, we need to better understand the responses of vertebrates to vegetation structure as it recovers after fire because managers can actively influence vegetation structure.

A long-standing hypothesis, the habitat accommodation model (Fox 1981), proposes that time since fire is simply a correlate of changing vegetation characteristics that occur with time as succession proceeds. Small mammals, for example, recolonized burned Australian heath at different times depending on the preferences for specific habitat

---

[1]Oak Creek Lab of Biology, Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331.
[2]Corresponding author. E-mail: douglas.robinson@oregonstate.edu

structure by each species (Monamy and Fox 2000). Experimentally setting back the stage of vegetation succession in Australian coastal heath burned long ago attracted rodents that normally appear soon after fire (Monamy and Fox 2010). In the Brazilian Cerrado, mammal richness and diversity peaked within 2 years after fire then declined as late-seral species returned after sufficient time for vegetation recovery (Briani et al. 2004). Similar responses occurred in mammal communities of Mediterranean shrublands (Torre and Diaz 2004). Even across reptiles and birds, animal community succession maps onto changes in vegetation communities and provides general support for the habitat accommodation model of animal responses to burned ecosystems (Arthur et al. 2012, Nimmo et al. 2012, Watson et al. 2012).

Many arid systems are particularly vulnerable to effects of fire because recovery can take decades or centuries depending on availability of moisture and other environmental factors. Within many arid ecosystems, small mammal abundance and diversity have been correlated with vegetation structure and complexity (Rosenzweig and Winakur 1969, Kerley 1992, Monamy and Fox 2000). In shrublands of western North America, the relative dominance of shrub over herbaceous vegetation and the occurrence of related vegetation heterogeneity has been suggested as a determining factor for small mammal abundance and diversity (Germano and Lawhead 1986). Shrub cover may be important as a source of refuge from predators and could influence population density for some species by reducing home range size through the addition of vertical structure provided by shrubs (Zou et al. 1989, Torre and Diaz 2004).

Despite lasting influences of fire on vegetation structure in big sagebrush (*Artemisia tridentata*) communities, few empirical data exist to describe long-term dynamics of small mammal abundances as they relate to habitat succession after fire. Unlike Australian heath communities, experimental work involving manipulation of shrub cover in sagebrush communities has generally failed to demonstrate a clear relationship between shrub structure and small mammal abundance (Parmenter and MacMahon 1983, Zou et al. 1989, Borchgrevink et al. 2010). Conversion of lower-elevation sagebrush communities to exotic annual grasslands has reduced small mammal abundance and species richness (Ostoja 2009), yet this type of conversion is not just a loss of shrub cover and corresponding structural heterogeneity, but a fundamental shift in ecological state that likely affects availability of resources such as arthropods and seed banks.

Small mammal populations in arid environments are highly variable, with variation driven partly by seasonal rainfall and seed production (Shenbrot et al. 2010, Thibault et al. 2010). A chronosequence approach that substitutes space for time can provide insight into how postfire habitat succession shapes small mammal communities (Fox 1990). A chronosequence should minimize variation due to climatic patterns that might otherwise overshadow more subtle effects related to habitat structure. Here we take advantage of multiple fires at various stages of recovery to investigate the longevity of fire effects on small mammals, while furthering our understanding of how vegetation structure correlates with abundance and how management of vegetation can influence conservation of small mammal communities.

Our objectives were to (1) estimate abundance of small mammal species in mountain big sagebrush communities across a fire chronosequence and (2) quantify influence of fire on small mammal abundance in association with vegetation recovery after fire. We compared our results with the predicted outcomes of the habitat accommodation model (Fox 1981) and interpret the resulting patterns in the context of recommendations for conservation of small mammals in burned sagebrush landscapes.

METHODS

Study Area

We quantified vegetation structure and small mammal abundances within mountain big sagebrush communities on Bald and Badger Mountains within the Sheldon National Wildlife Refuge (SNWR) in northwestern Great Basin, USA. The SNWR includes 232,694 ha, most of which occurs as a mosaic of low sagebrush (*Artemisia arbuscula*) and big sagebrush, with the higher elevations supporting mountain big sagebrush. Each of those mountains has expanses of unburned sagebrush and burned areas.

The burned areas vary in size and age. Refuge records indicate aggressive control of natural fires, which were ignited from lightning strikes between June and September, from 1935 into the early 1980s. Most lightning-induced fires were restricted to small extents during this period because of effective suppression and a lack of fine fuels due to livestock grazing. Between 1984 and 2001, the area burned annually by wildland fires was variable, with few to no hectares burned in most years and large fires (>500 ha) in only several years. Excluding prescribed fires, the median size of the 27 fires that occurred during those years was 45 ha.

To evaluate correlates of small mammal abundance in mountain big sagebrush habitats as a function of time since fire, we selected landscapes with similar elevation, slopes, and plant community composition that had experienced sufficiently large fires to include sites for estimating small mammal abundances. Landscapes that met these criteria included Bald Mountain and Badger Mountain. At Bald Mountain, a 915-ha fire burned in 1988 and was surrounded by similar vegetation communities that had not burned since at least the 1930s. Badger Mountain, approximately 32 km southeast of Bald Mountain, had 2 larger burns suitable for study: a 15,380-ha wildfire that occurred in 1999 and a 2792-ha wildfire that occurred in 1994.

Within Bald and Badger Mountain landscape areas, we selected study sites using a geographic information system (GIS) that detailed habitat type and fire boundaries (1984–2001). Our goal was to select several 600 × 600-m (36-ha) study plots within each of these 2 landscapes. We generated 2 random numbers between 1 and 1000 that corresponded to the last 4 digits of a UTM coordinate. From this seed location we extended a 1000-m grid across the landscapes. The centers of these 1-km^2 grid cells corresponded to centers of potential 600 × 600-m (36-ha) study plots. This approach ensured that plot boundaries would be no closer than 400 m to each other in the event that 2 adjacent plots were selected by chance. All potential plots were then evaluated to ensure that >70% of the area was either mountain big sagebrush or mountain big sagebrush–bitterbrush, with the remainder being inclusions of low sagebrush, small meadows, or mountain shrub communities with a sagebrush component. Twenty-four potential plots meeting this criterion were identified at Badger Mountain (7 in the 1994 burn, 8 in the unburned area, and 9 in the 1999 burn). From those, we randomly selected 3 plots in each of the 1994 and 1999 burns and the unburned area. At Bald Mountain, the 1988 burned area was large enough to accommodate 3 plots, so we used all 3 of those plots. We randomly selected 3 of the possible 10 plots in unburned sagebrush on Bald Mountain. The total number of plots selected was 15, with 6 at Bald Mountain and 9 at Badger Mountain. Average elevation ranged from 1875 to 1960 m for plots at Bald Mountain and from 1910 to 2075 m for plots at Badger Mountain.

Mammal Abundance

To estimate abundances of nocturnal small mammals we established 200-m diameter trapping webs following protocols outlined in Parmenter et al. (2003). Trapping webs consisted of 12 radial lines of 100 m each. Each line had 12 trap stations corresponding to 5, 10, 15, 20, 30, 40, 50, 60, 70, 80, 90, and 100 m from the center. Four additional traps were placed approximately 1 m from the center of the web for a total of 148 traps within a circular area of 3.14 ha in the middle of each 36 ha plot. In 2006 we placed webs in the center of each plot. In 2007, to reduce chances of trap shyness across years, we relocated webs at least 200 m away by randomly selecting one of the other eight 200 × 200-m sections within each 36-ha plot (Fig. 1). Thus, a total of 30 webs were run within the 15 plots over the 2 years of trapping.

We used small Sherman live traps (7.5 × 9.5 × 25.5 cm; H.B. Sherman, Tallahassee, FL), which we baited every evening with peanut butter and rolled oats and checked each morning between 05:30 and 08:00. Cotton batting was provided as nesting material and replaced following captures. Captured mammals were identified to species and weighed to the closest 0.5 g using a Pesola scale, or 0.1 g with a digital scale. Deer mice (*Peromyscus maniculatus*) were marked with a uniquely numbered tag (Monel #1, National Band and Tag Co., Lexington, KY) in one ear, with a nontoxic permanent ink on their other ear, and with a stripe down their backs. All other species were marked only with ink. Animals
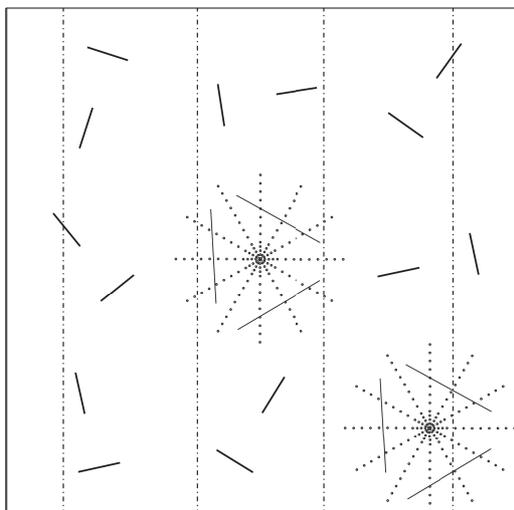
Fig. 1. Small mammal sampling layout for a 36-ha plot. Dots represent live traps in trapping webs, dot-dash lines indicate walking transects for diurnal mammals, and solid lines represent 50-m vegetation transects (outside of trapping webs) and 100-m vegetation transects (inside of trapping webs). Each set of 2 vegetation transects is placed in one of the 9 subsampling areas, 2 of which also contain trapping webs.

were classified as juvenile or adult based on weight and reproductive condition. We left traps closed during the day and opened traps on each web for 5 consecutive nights. To minimize variation in trapping rates among webs due to weather and moon phase (Price et al. 1984), we ran webs simultaneously on each of the 5 treatments (one plot per treatment per week for 3 consecutive weeks in each year). We ran trapping webs between 10 June and 2 July in 2006, and again between 9 June and 27 June in 2007.

To estimate abundances of diurnal small mammals we surveyed 4 parallel 600-m transects on each 36-ha plot. Transects ran north to south and were spaced 150 m apart from each other with 75 m between the outer transects and the sides of the plots (Fig. 1). We completed surveys between the hours of 07:00 and 10:00 during 29 May through 17 June in 2006, 2007, and 2008. We used a handheld GPS unit to follow the transect line and walked slowly while scanning continuously from side to side. To minimize any bias from seasonal trends in detection probability we rotated through the plots such that each mountain-by-burn history combination had one

plot surveyed during the first 5 days, a second plot surveyed during the next 5 days, and the third plot surveyed in the final 5 days. We used a laser rangefinder with a 7× monocular (Leica LRF900) to estimate the perpendicular distance to each animal detected. In addition to species, we recorded how the detection was made (visual or aural) and group size when multiple animals were observed with one detection cue. All surveys were conducted by a single observer (ALH).

Vegetation Sampling

At each trapping web we measured vegetation along three 100-m transects (Fig. 1). We recorded the species, height, and intercept of each shrub canopy along transects (Canfield 1941). We excluded from cover estimates any discrete gaps in the shrub canopy that were >20 cm. Herbaceous vegetation and ground cover was measured every 5 m along these transects using a 0.2-m^2 frame (40 × 50 cm). This approach is a modification of Daubenmire (1959) in several ways. First, cover is estimated on a continuous scale to the nearest whole percentage value rather than in cover classes, and second, cover estimates are made of total horizontal coverage when viewed from above as opposed to several discrete strata. Within each frame we estimated cover of bare ground, litter, cryptobiotic soil crust, annual grasses, perennial grasses, and forbs. We conducted all vegetation sampling associated with the trapping webs during July of the same year in which trapping occurred.

To identify potential correlates of diurnal mammal abundance, we also measured vegetation within each of the additional seven 4-ha subsampling areas and averaged the subsamples to obtain plot-level estimates that corresponded spatially to the extent of the survey transects. We completed two 50-m vegetation transects within each of the other 7 subsampling areas. For these, the compass bearing of the first transect was randomly selected and began 20 m from the middle point of the 4-ha cell. The second transect was oriented perpendicular to the first and was centered 65 m away from the beginning of the first transect (Fig. 1). In total we completed 1300 m of line intercept sampling to measure shrub cover and sampled ground cover using 260 cover frames within each of the fifteen 36-ha plots. We conducted vegetation sampling at the 7 subsampling

points not associated with trapping webs during 2008. All vegetation sampling was conducted by 4 personnel.

Statistical Analysis

We used program DISTANCE to estimate density at trapping webs (excluding juveniles) for species with sufficient data (Thomas et al. 2010). We established distance intervals primarily by the midpoints between traps along the radial lines of the webs, although we grouped some traps into distance intervals to improve fit. We did not truncate data and only included new captures in analyses. Trapping webs, unlike traditional trapping grids, carry no assumption of population closure.

To estimate densities of diurnal small mammals along our walking transects, we used program DISTANCE when sufficient data were available. However, data was fairly sparse even for the most abundant diurnal species. Since the same transects were surveyed in all 3 years, with approximately the same number of detections annually (suggesting no year effect), we combined all surveys for analyses. Resulting models thus ignored year and included a divisor in the density estimator to account for the repeat surveys. Truncation distances (w) for the transect data were selected based approximately at the point where detection probability dropped below 20% (Buckland et al. 2001).

In all DISTANCE analyses, we used half-normal, hazard rate, and negative exponential key functions to model both global and stratum-specific detection functions. One or more adjustment terms were also evaluated and included in models where they reduced AIC relative to models without adjustment terms. Half-normal key functions were paired with cosine adjustment terms, whereas the other key functions used simple polynomial adjustment terms. The key function with the lowest AIC was selected for a given model structure. To reduce potential bias in density estimates due to variation in detection probability associated with vegetation structure, or driven by year-to-year variation in demographic parameters, we also evaluated models with a global detection function that included one or more covariates (burn history, year, shrub cover), including detection cue type (visual or aural), for the diurnal surveys. Models with covariates were developed following guidelines from Marques et al. (2004, 2007) and were only estimated with the hazard rate and half-normal key functions. Model sets were ranked based on the lowest AIC scores, and density estimates were generated from the highest-ranked model for each species.

Patterns of abundance were related to fire histories and vegetation structure using ANOVA and linear regression. Where ANOVA showed an effect of fire, we further explored the relationship with linear comparisons between burned and unburned portions of each mountain. To relate density estimates to habitat variables measured on the trapping webs and survey plots, we first looked for univariate correlations with habitat variables and then estimated one or more candidate models including correlates that were significant at $P \leq 0.1$. Final models accounted for design effects (multiple webs per plot and stratified random design) and included only terms that were significant within the model at $P \leq 0.05$. We examined residual plots and formally tested their distribution (sktest and hettest: STATAcorp, College Station, Texas, USA) to ensure that assumptions of heteroscedasticity and normality were not violated.

Differences in environmental variables that may be related to fire and postfire succession (shrub cover and height) were estimated using linear regression followed by pairwise linear comparisons between each burn and the adjacent unburned areas. We used data from the 9 vegetation subsampling plots within each of the fifteen 36-ha plots ($n = 135$) so variance was calculated using a 2-stage stratified random design.

Results

Abundance of Small Mammals

We captured 1398 individuals representing 8 species of nocturnal mammals during 22,200 trap nights (150 web nights). Of these individuals, 1031 were classified as adults or subadults of breeding age based on mass and/or breeding condition. Deer mice (*Peromyscus maniculatus*) were the most abundant ($n = 598$ adults), followed by Great Basin pocket mouse (*Perognathus parvus; n = 281*), sagebrush vole (*Lemmiscus curtatus; n = 103*), montane vole (*Microtus montanus; n = 17*), northern grasshopper mouse (*Onychomys leucogaster; n = 16*), vagrant shrew (*Sorex vagrans; n = 7*),

TABLE 1. Density estimates (*D*, individuals · ha^{-1}), including 95% confidence intervals and coefficients of variation for small mammals in fires of different vintage during 2 years of trapping (*Peromyscus, Perognathus,* and *Lemmiscus*) and transect counts (*Tamias* and *Urocitellus*) on Badger and Bald Mountains, Sheldon National Wildlife Refuge, Nevada.

Species	Mountain	Fire year	Year	*D*	%CV	95% CI LL	95% CI UL
Peromyscus maniculatus	Badger	1999	2006	58.7	19	39.1	88.1
			2007	31.1	33	11.6	83.5
	Badger	1994	2006	44.9	24	24.8	81.2
			2007	32.6	21	19.9	53.4
	Bald	1988	2006	63.0	16	45.5	87.3
			2007	27.5	33	10.1	75.3
	Badger	—	2006	32.6	28	15.2	69.8
			2007	16.7	32	6.4	43.5
	Bald	—	2006	71.0	16	51.2	98.3
			2007	55.0	50	9.4	320.7
Perognathus parvus	Badger	1999	2006	42.4	47	9.9	182.7
			2007	36.9	31	17.2	78.7
	Badger	1994	2006	44.7	36	16.6	119.9
			2007	19.0	55	3.2	112.3
	Bald	1988	2006	22.3	60	3.1	160.0
			2007	5.6	75	0.4	70.5
	Badger	—	2006	46.9	57	7.1	307.0
			2007	38.0	39	12.6	114.7
	Bald	—	2006	32.4	39	10.7	98.0
			2007	25.7	31	12.0	55.1
Lemmiscus curtatus	Badger	1999	2006	9.5	58	1.6	55.9
			2007	7.6	103	0.3	212.8
	Badger	1994	2006	22.8	103	0.8	638.4
			2007	1.9	103	0.1	53.2
	Bald	1988	2006	51.3	30	27.0	97.5
			2007	30.4	56	5.5	167.5
	Badger	—	2006	0.0	—	0.0	0.0
			2007	0.0	—	0.0	0.0
	Bald	—	2006	45.6	44	13.4	155.0
			2007	32.1	52	7.7	168.7
Tamias minimus	Badger	1999	2006–2008	0.21	56	0.04	1.12
	Badger	1994	2006–2008	0.31	32.8	0.13	0.72
	Bald	1988	2006–2008	0.18	56	0.03	0.92
	Badger	—	2006–2008	0.42	42	0.12	1.60
	Bald	—	2006–2008	0.13	45	0.04	0.37
Urocitellus beldingi	Badger	1999	2006–2008	0.28	52	0.04	2.06
	Badger	1994	2006–2008	0.30	34	0.09	1.00
	Bald	1988	2006–2008	0.27	28	0.10	0.71
	Badger	—	2006–2008	0.02	54	0.01	0.09
	Bald	—	2006–2008	0.04	61	0.01	0.21

and one each of Ord's Kangaroo rat (*Dipodomys ordii*) and bushy-tailed woodrat (*Neotoma cinera*). Capture totals for each trapping web are provided in Supplementary Material 1.

We estimated density using program DISTANCE for only the 3 most abundant of these species at the resolution of stratum by year (Table 1). The coefficients of variation for most estimates were too large to allow for meaningful investigation of differences. In no case was there support, based on AIC, for modeling separate detection functions by stratum (Supplementary Material 2). For all 3 species, the best model estimated detection probability using a negative exponential key function with 2 simple polynomial adjustment terms of the second and fourth order. This key function is seldom recommended for use in program DISTANCE (Thomas et al. 2010), primarily because it lacks a shoulder but also because of known biases if the true detection function is something other than negative exponential. In this study, with multiple traps placed near the web centers and closer trap spacing for the first 20 m of each web spoke, capture probability declined precipitously in the first 20 m,

TABLE 2. Factors affecting small mammal densities in mountain big sagebrush habitats on Bald and Badger Mountains, Sheldon National Wildlife Refuge, Nevada. ANOVA was conducted only for species captured on greater than half of the trapping webs in 2006 and 2007 (nocturnal, $n = 30$ webs), or detected on greater than half of the transect survey plots in 2006–2008 (diurnal, $n = 15$ plots).

Species	Model terms	R^2_{adj}	F	P
Peromyscus maniculatus	Model	0.41	4.39	0.0043
	Mountain		9.58	0.0051
	Burn		0.00	0.9753
	Year		10.23	0.0040
	Mountain * Burn		6.68	0.0166
	Year * Burn		0.63	0.4369
	Mountain * Year		0.46	0.5064
Perognathus parvus	Model	0.07	1.38	0.2633
	Mountain		4.24	0.0510
	Burn		1.63	0.2151
	Year		1.98	0.1731
	Mountain * Burn		0.24	0.6286
	Year * Burn		0.23	0.6349
	Mountain * Year		0.00	0.9851
Lemmiscus curtatus	Model	0.38	3.98	0.0071
	Mountain		21.03	0.0001
	Burn		0.45	0.5079
	Year		1.85	0.1873
	Mountain * Burn		0.45	0.5080
	Year * Burn		0.55	0.4660
	Mountain * Year		0.38	0.5428
Tamias minimus	Model	0.14	1.73	0.2185
	Mountain		4.11	0.0675
	Burn		0.41	0.5370
	Mountain * Burn		1.41	0.2607
Urocitellus beldingi	Model	0.37	3.72	0.0455
	Mountain		0.00	0.9750
	Burn		10.20	0.0086
	Mountain * Burn		0.09	0.7732

resulting in no shoulder in the detection function, which is represented best by the negative exponential. The selected function was qualitatively similar for all 3 species and was characterized by a rapid decline of capture probability from the center of the web until about 25 m before it stabilized and appeared constant at greater distances.

Deer mouse was ubiquitous, occurring on all 30 trapping webs. Estimated deer mouse densities ranged among burn histories and mountains from a low of about 17 individuals per hectare to a high of 63 individuals per hectare (Table 1). Densities were greater in 2006 than in 2007 (Table 1) and there was a significant Burn * Mountain interaction (Table 2). Further exploration of that interaction revealed higher densities in burned areas than in unburned areas for the more recent fires on Badger Mountain, but not for Bald Mountain. Great Basin pocket mouse was nearly ubiquitous, occurring on 28 of 30 trapping webs with densities ranging from 5.7 to 46.9

individuals per hectare (Table 1). Densities did not differ between burned and unburned portions of the mountains, or by year, but tended to be higher on Badger Mountain than on Bald Mountain. Sagebrush voles were more abundant on Bald Mountain (11 of the 12 trapping webs) than on Badger Mountain (5 of the 18 webs). Estimated densities for burn history and mountain stratum ranged from 0 to 51.3 individuals per hectare; there was no significant effect of fire or year. Northern grasshopper mouse was captured rarely, and only on Badger Mountain (6 of 18 webs), whereas montane vole was captured on 4 of 12 webs at Bald Mountain and only on 1 of 18 webs at Badger Mountain.

Diurnal surveys totaling 108 km of walking transects resulted in 380 detections of 6 species. The most numerous was Belding's ground squirrel (*Urocitellus beldingi*) with 203 detections, followed by least chipmunk (*Tamias minimus; n* = 89), Townsend's ground squirrel (*Urocitellus townsendii; n* = 35),

yellow-bellied marmot (*Marmota flaviventris; n* = 25), golden-mantled ground squirrel (*Callospermophilus lateralis; n* = 25), and cottontail rabbits (*Sylvilagus nuttallii; n* = 10). Detection summaries are provided in Supplementary Material 3. Additional species of small and medium-sized mammals observed on the plots but not during surveys included short-tailed weasel (*Mustela erminea*), long-tailed weasel (*Mustela frenata*), American badger (*Taxidea taxus*), and black-tailed jackrabbit (*Lepus californicus*). We developed density models in program DISTANCE only for the 2 most abundant species due to insufficient observations for the others. For both species, the best model used a hazard rate key function and included a covariate for detection type (call or visual; Supplementary Material 2). Detection probabilities remained very high for aural detections out the to the truncation points (80 m for Belding's ground squirrel, 35 m for least chipmunk) but declined rapidly with distance from the observer for visual detections.

Estimated densities of least chipmunk varied from 0.13 to 0.42 individuals per hectare among strata, and there were no significant differences associated with burn history or mountain (Tables 1, 2). Belding's ground squirrel was patchily distributed. Densities were extremely low in unburned portions of both mountains (0.02–0.04 per ha), and greater in all 3 burned strata (0.27 to 0.30 per ha; Table 1). There was a strong effect of burn history, with no significant interaction with mountain (Table 2).

Townsend's ground squirrel was detected on all 3 of the plots that had burned in 1994, 2 of the 3 plots burned in 1999, and one of the plots burned in 1988, but it was not detected on the unburned plots of either mountain. Golden-mantled ground squirrel (detected on 9 of 15 plots) and yellow-bellied marmot (detected on 7 of 15 plots) showed no pattern in relation to burn history, with detections of both generally occurring on rocky outcrops. Rock cover was a significant predictor of marmot abundance (detections = $-0.29 + 0.22 *$ rock cover, P = 0.027, R^2 = 0.32), but not for the golden-mantled ground squirrel. Cottontails were detected on 2 of 3 unburned plots on each mountain, but only on a single plot in the 1994 burn and a single plot in the 1988 burn.

For the 2 species that showed significant effects of fire (deer mouse and Belding's ground squirrel) we conducted additional regression analyses and linear comparisons. The deer mouse was more abundant in the unburned habitat than in the 1994 burn at Badger Mountain by 14.2 animals per ha (95% CI: -1.7 to 30, P = 0.075), and the 1999 burn by 20.3 per ha (95% CI: 4.9 to 35.7, P = 0.015). Its estimated abundance was also greater in the 1994 burn than in the 1999 burn by 6.1 animals per ha, although this difference was not statistically significant (95% CI: -14.08 to 26.39, P = 0.51). There was no relationship with fire for the deer mouse at Bald Mountain.

Belding's ground squirrel was more consistent in patterns of abundance in relation to fire history. It was significantly more abundant at plots within the 1988 burn than on adjacent unburned plots of Bald Mountain (by 0.22 per ha; 95% CI: 0.05 to 0.40, P = 0.018). At Badger Mountain they occurred at greater densities in both the 1994 burn (by 0.28 per ha; 95% CI: 0.06 to 0.50, P = 0.017) and 1999 burns (by 0.26 per ha; 95% CI: 0.07 to 0.59; P = 0.108). The 2 burns on Badger Mountain did not differ in estimated ground squirrel abundance (estimated difference of 0.02 per ha; 95% CI: -0.37 to 0.42, P = 0.902).

Habitat Variables

Shrub cover, big sagebrush cover, and average shrub height differed among mountains and burn histories, but other variables did not show clear-cut patterns related to fire (Table 3). Even after approximately 20 years of recovery at Bald Mountain, percent cover of shrubs was greater on the unburned study sites (mean difference in percent cover [$\bar{x}$] = 9 percentage points [pp], 95% CI: 0.04 to 17.9, P = 0.049). Cover of big sagebrush was not significantly greater ($\bar{x}$ = 1.2 pp, 95% CI: -9.03 to 11.56, P = 0.79), but the average height of big sagebrush shrubs was 11.5 cm taller outside of the fire perimeter (95% CI: 5.32 to 17.64, P = 0.002). At Badger Mountain, the unburned study areas had greater percent shrub cover than the 1994 burn ($\bar{x}$ = 15.3 pp, 95% CI: 9.3 to 21.3, P < 0.001) as well as the 1999 burn ($\bar{x}$ = 24.2 pp, 95% CI: 12.4 to 36.0, P = 0.001). The same pattern held true for big sagebrush cover where the unburned study sites had greater cover than the 1994 burn ($\bar{x}$ = 5.4 pp, 95% CI: 0.9 to 9.9, P = 0.024) and the 1999 burn ($\bar{x}$ = 12.4 pp, 95% CI: 7.9 to 16.9, P < 0.001). In addition, the 1994 burn

TABLE 3. Mean vegetation and ground cover measurements (SE) for each mountain and burn history. Estimates are derived from a stratified sampling design with 9 subsampling locations within each of three 36-ha plots for each of the 5 strata.

	Badger Mountain			Bald Mountain	
Cover	1999	1994	Unburned	1988	Unburned
Shrub cover (%)	9.0 (1.0)	13.9 (0.8)	29.2 (2.5)	27.0 (0.9)	36.0 (3.9)
Artemisia tridentata (%)	1.1 (0.2)	8.1 (0.2)	13.5 (2.0)	13.0 (4.0)	14.2 (2.3)
A. tridentata height (cm)	32.2 (3.3)	49.2 (3.9)	56.5 (4.1)	59.7 (1.6)	71.1 (2.2)
Bunchgrass cover (%)	13.4 (1.4)	15.1 (1.7)	12.4 (1.0)	23.5 (2.8)	20.6 (1.2)
Poa sandbergii (%)	3.0 (0.6)	2.1 (0.1)	5.5 (5.5)	3.7 (1.2)	2.9 (0.9)
Bromus tectorum (%)	8.1 (3.5)	1.5 (0.5)	3.2 (1.0)	2.2 (1.2)	3.4 (1.4)
Forb (%)	10.9 (0.9)	3.4 (0.5)	5.6 (1.9)	9.8 (1.1)	9.4 (2.3)
Bare ground (%)	41.1 (5.6)	53.0 (3.3)	35.8 (3.8)	35.6 (0.4)	29.0 (2.6)
Rock (%)	12.1 (4.7)	9.0 (4.2)	8.9 (0.5)	3.4 (0.9)	4.0 (0.5)
Litter (%)	11.3 (1.0)	15.5 (1.3)	26.9 (1.9)	21.6 (0.9)	29.2 (1.9)

had higher percent sagebrush cover than the 1999 burn ($\bar{x}$ = 7.0 pp, 95% CI: 6.3 to 7.6, $P < 0.001$). Average sagebrush height was not significantly greater in the unburned sites than the 1994 burn (mean difference in height = 7.3 cm, 95% CI: –5.3 to 19.9, $P = 0.228$), but was greater relative to the 1999 burn (mean difference in height = 24.2 cm, 95% CI: 12.4 to 36.0, $P = 0.001$). Sagebrush height was on average 17.0 cm (95% CI: 5.6 to 28.3, $P = 0.007$) greater in the 1994 fire area than in the 1999 burn.

Litter cover followed a similar pattern to shrub cover but was not analyzed further because it was highly correlated with shrub cover across all study areas ($r = 0.96$) since most litter was located under shrubs. Percent cover of grasses and forbs on study plots was not related to burn history, although bunchgrass cover tended to be higher at Bald Mountain than at Badger Mountain, and Badger Mountain was rockier than Bald Mountain, reflecting differences in soils and overall productivity.

Habitat Correlates and Predictive Models

Univariate correlations between density estimates and habitat variables for Belding's ground squirrel included a positive relationship with bare ground and bunchgrass cover and a negative correlation with shrub cover. The final linear regression model was D = 0.152 − 0.012 ∗ shrub cover + 0.185 ∗ bunchgrass cover ($R^2 = 0.46$, $F_{2,9} = 12.49$, $P = 0.0025$). Univariate correlations between least chipmunk density and habitat variables included a positive correlation with rock cover and negative correlations with bunchgrass and forb cover. The final model, which did not include bunchgrass

cover due to covariation with rock cover, was D = 0.283 + 0.0190 ∗ rock cover − 0.022 ∗ forb cover ($R^2 = 0.53$, $F_{2,9} = 15.84$, $P = 0.0011$).

There were no significant habitat correlates with deer mouse density, even after controlling statistically for the strong year effect revealed through ANOVA. Great Basin pocket mouse density was weakly and negatively correlated with bunchgrass cover and positively correlated with rock cover. The linear regression model estimated for pocket mouse density at trapping webs was D = 21.0 + 1.29 ∗ rock cover ($R^2 = 0.23$, $F_{1,10} = 9.42$, $P = 0.0119$). Sagebrush vole density was weakly and positively correlated with total shrub and bunchgrass cover, as well as the average height of big sagebrush, but only sagebrush height was included in the final model (D = −24.71 + 0.76 ∗ mean sagebrush height; $R^2 = 0.17$, $F_{1,10} = 5.17$, $P = 0.0463$).

DISCUSSION

Fire regimes in most sagebrush ecosystems are believed to have changed during the past century because of invasion of exotic plant species, shifts in land-use practices altering composition and configuration of habitats, and fire suppression (D'Antonio and Vitousek 1992, Miller et al. 2011). Prior to the introduction of livestock in the late 1800s, spatial and temporal variation in recurrent fires likely resulted in a mosaic of sagebrush communities in different stages of community succession (Young et al. 1979). Even during protracted periods without fire, mature stands of sagebrush likely varied in vegetation structure as a result of climatic patterns and insect outbreaks (Baker 2011). Historical fire regimes in big

sagebrush communities have been altered with either an increased frequency related to invasions of exotic grasses, primarily at lower elevations and in communities dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis;* Peters and Bunting 1994, Whisenant 1990), or lengthened fire-return intervals resulting from a number of factors, notably livestock grazing and active fire suppression (Miller and Rose 1999, Miller and Wigand 1994). This reduction of fire, which has occurred primarily in mid- and high-elevation mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities, has led to increases in the density of pinyon and juniper woodlands in portions of the North American Great Basin (Miller and Tausch 2001). Our study area is at the edge of the range of western juniper and has not transitioned towards juniper woodland communities, but the mechanisms, primarily livestock grazing and active suppression, have likely contributed to reduced fire frequency relative to the historic average. Growing concern about woodland expansion has catalyzed efforts to reintroduce fire or to use fire surrogate management activities in mountain big sagebrush ecosystems, elevating the importance of understanding wildlife responses to fire and habitat dynamics after fire.

In the 2 landscapes we studied, vegetation showed clear and expected changes after fire. Shrub cover and average shrub height was lowest on sites burned most recently and highest in the unburned study sites. All 3 burns investigated appeared to be on a similar trajectory of canopy recovery, with ratios of shrub cover between burned and unburned areas progressing in a linear fashion with time since fire from 0.3 (approximately 7 years postfire), to 0.48 (approximately 13 years postfire) to 0.75 (approximately 19 years postfire). If this linear relationship is extrapolated, it suggests that shrub canopies would recover after approximately 25 years, which is within the range of recovery periods documented elsewhere for mountain big sagebrush (Harniss and Murray 1973, Nelle et al. 2000, Lesica et al. 2007, Ziegenhagen and Miller 2009). Other habitat variables such as bunchgrass and forb cover did not vary as a function of burn history.

Only Belding's ground squirrel demonstrated consistent long-term differences in abundance in relation to wildfire. It was approximately 10 times more abundant on

burned plots than unburned plots regardless of the number of years since burning. Deer mice showed a variable response with increased densities occurring on the more recent burns on Badger Mountain relative to adjacent unburned areas, but not at the older burn on Bald Mountain. Densities of sagebrush vole, great basin pocket mouse, and least chipmunk varied independently of fire history, but were weakly correlated with habitat variables measured at the scale of the study plots. These findings suggest that, at least in relatively intact high-elevation sagebrush steppe communities where shrub recruitment facilitates rapid canopy development, the effects of fire on most species of small mammals are not long lived. Variation in shrub recovery rates related to shrub recruitment in the years immediately following a fire or, in cases where initial recruitment fails, related to fire size and distance from edge may influence the longevity of effects on Belding's ground squirrel and sagebrush vole—the 2 species whose abundances were correlated with shrub canopy variables.

The relatively weak correlations between habitat variables and density estimates found in our study may reflect weak responses of mammals to habitat changes after fire or could also be influenced by the scales at which we made our measurements. Most of the small mammal species we studied experience population fluctuations sufficiently large across time and space to mask all but the strongest and most extensive effects of habitat change. Although the 36-ha study plots were large compared to typical home ranges of the small mammals we studied, they may have been too small to detect moderate to weak effects of changes in habitat structure. In addition, by averaging habitat measurements across subsampling areas, the within-plot heterogeneity in both habitat features and mammal use was ignored. Because habitat measurements were not directly linked at a spatial scale relevant to individual trapping sites, we cannot further evaluate how habitat heterogeneity at very small spatial scales may influence small mammals. Nonetheless, the scale of study is appropriate from a management perspective because conservation of small mammal habitat is typically conducted by habitat management across larger extents of sagebrush landscapes.

We found weak effects overall in responses of abundance to time since fire, and we found community responses that provided only a moderate fit with expectations of the habitat accommodation model of mammal community succession. Most species were found in all plots regardless of time since fire. Only Belding's ground-squirrel was commonest primarily in the younger burns. Deer mice are often an early colonizer after disturbance, so we expected them to appear and be most numerous in the younger burned sites. We found that deer mice were more abundant on plots that had burned between 6 and 14 years prior than in the older burn (18–19 years) and nearby communities outside those burn boundaries. Yet, deer mouse densities were not correlated with shrub cover, which is expected to be the primary habitat driver of abundance under the habitat accommodation model (Monamy and Fox 2000, 2010). Most other research in sagebrush communities also failed to find effects of shrub removal on deer mouse abundance, or correlations with shrub cover (Parmenter and MacMahon 1983, Zou et al. 1989, Borchgrevink et al. 2010). Olson et al. (2003) used a chronosequence approach similar to ours by examining paired burned and unburned plots in Wyoming big sagebrush shrublands that had burned at various times and as much as 12 years prior to study. They found that deer mice occurred in greater numbers at burned sites than unburned sites, especially in the early years after a fire. McGee (1982) found no effects of either spring or fall burns on deer mice in mountain big sagebrush. In our study, it is possible that we missed the initial early spike in abundance of deer mice soon after a fire because our youngest burn was already 7 years old. Research in other habitats has established that deer mice can rapidly colonize and take advantage of the increased grass and forb seed production provided in some postfire vegetation communities (Tevis 1956, Stout et al. 1971, McGee 1982).

The chronosequence approach carries with it several key assumptions that are seldom evaluated, and as such it has been criticized as a means of understanding long-term patterns of succession (Johnson and Miyanishi 2008). Most importantly, the approach requires that biotic and abiotic conditions have been similar over the time span of the successional stage being investigated and, in this case, that inherent site differences did not influence the probability of fire. Rocky areas, for example, with low fuel loadings and poor horizontal connectivity of fuels can inhibit the spread of fire. In our case, bare ground and rock cover were similar between burned and unburned portions of the different mountains and study areas, suggesting that boundaries were not determined by preexisting environmental differences. In addition, fires we studied were actively suppressed, and boundaries between burned and unburned areas included lines of suppression. In the absence of suppression, we expect the adjoining unburned areas would have burned as well. Walker et al. (2010) examined potential limitations and pitfalls of using chronosequence approaches and concluded that when there are demonstrable linkages between stages (i.e., when successional trajectories are predictable) that the approach is useful in studies dealing with temporal change across time frames of <100 years. Our data on shrub cover among strata indicate the presence of a more or less linear relationship among sites in terms of secondary vegetation succession, suggesting that the approach is reasonable for this data set.

The degree to which our results can be generalized to other sagebrush landscapes depends on characteristics of vegetation recovery trajectories. Recovery rates of shrub canopy cover are related to recruitment in the initial years following a fire (Baker 2011), which suggests that our results may not appropriately extend to fires that are on different recovery trajectories due to poor initial recruitment. Nevertheless, we hypothesize that, as long as fires are not excessive in severity or extent, the small mammal communities in mountain big sagebrush communities are resilient to the effects of fire, such that their conservation will largely be determined by managing the severity and extent of fires. Additional research on demographic parameters such as reproductive success and survival would promote better understanding of the influence of disturbance and succession on sagebrush small mammal communities.

SUPPLEMENTARY MATERIAL

Three online-only supplementary files accompany this article (scholarsarchive.byu.edu/wnan/vol76/iss3/8).

SUPPLEMENTARY MATERIAL 1. Detection function model sets for each mammal species.

SUPPLEMENTARY MATERIAL 2. Trapping web capture totals for nocturnal mammals in mountain big sagebrush communities on Badger Mountain, Sheldon National Wildlife Refuge, June 2006 and June 2007.

SUPPLEMENTARY MATERIAL 3. Total number of detections of diurnal small mammals on Bald and Badger Mountains, Sheldon National Wildlife Refuge, June in 2006–2008.

ACKNOWLEDGMENTS

LITERATURE CITED

ARTHUR, A.D., P.C. CATLING, AND A. REID. 2012. Relative influence of habitat structure, species interactions and rainfall on the post-fire population dynamics of ground-dwelling vertebrates. Austral Ecology 37:958–970.

BAKER, W.L. 2011. Pre-Euroamerican and recent fire in sagebrush ecosystems. Pages 185–201 in S.T. Knick, and J.W. Connelly, editors, Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

BORCHGREVINK, M.B., J.D. DERNER, T.R WESTON, R.A. OLSON, G.E. SCHUMAN, AND B.W. HESS. 2010. Small mammal and plant community responses to mechanical disturbance and rest in Wyoming big sagebrush grassland. Arid Land Research and Management 24:57–67.

BRIANI, D.C., A.R.T. PALMA, E.M. VIEIRA, AND R.P.B. HENRIQUES. 2004. Post-fire succession of small mammals in the Cerrado of central Brazil. Biodiversity and Conservation 13:1023–1037.

BUCKLAND, S.T., D.R. ANDERSON, K.P. BURNHAM, J.L. LAAKE, D.L. BORCHERS, AND L. THOMAS. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press. 448 pp.

CANFIELD, R.H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388–394.

CLARKE, M.F. 2008. Catering for the needs of fauna in fire management: science or just wishful thinking? Wildlife Research 35:385–394.

D'ANTONIO, C.M., AND P.M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–63.

FOX, B.J. 1981. Fire and mammalian secondary succession in an Australian coastal heath. Ecology 62:1415–1425.

FOX, B.J. 1990. Changes in the structure of small mammal communities over successional time scales. Oikos 59:321–329.

GERMANO, D.J., AND D.N. LAWHEAD. 1986. Species diversity and habitat complexity: does vegetation organize vertebrate communities in the Great Basin? Great Basin Naturalist 46:711–720.

HARNISS, R.O., AND R.B. MURRAY. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. Journal of Range Management 26:322–325.

JOHNSON, E.A., AND K. MIYANISHI. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11:419–431.

KERLEY, G.I.H. 1992. Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. Journal of Zoology 227:17–27.

LESICA, P., S.V. COOPER, AND G. KUDRAY. 2007. Recovery of big sagebrush following fire in southwest Montana. Rangeland Ecology and Management 60:261–269.

MARQUES, F.F.C., AND S.T. BUCKLAND. 2004. Covariate models for the detection function. Pages 31–47 in S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas, editors, Advanced distance sampling. Oxford University Press.

MARQUES, T.A., L. THOMAS, S.G. FANCY, AND S.T. BUCKLAND. 2007. Improving estimates of bird density using multiple covariate distance sampling. Auk 124:1229–1243.

McGEE, J.M. 1982. Small mammal populations in an unburned and early fire successional sagebrush community. Journal of Range Management 35:177–180.

MILLER, R.F., S.T. KNICK, D.A. PYKE, C.W. MEINKE, S.E. HANSER, M.J. WISDOM, AND A.L. HILD. 2011. Characteristics of sagebrush habitats and limitations for long-term conservation. Pages 145–184 in S.T. Knick and J.W. Connelly, editors, Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

MILLER, R.F., AND J.A. ROSE. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

MILLER, R.F., AND R.J. TAUSCH. 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. Tall Timbers Research Station Miscellaneous Publication No. 11:15–30.

MILLER, R.F., AND P.F. WIGAND. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465–474.

MONAMY, V., AND B.J. FOX. 2000. Small mammal succession is determined by vegetation density rather than time since disturbance. Austral Ecology 25:580–587.

MONAMY, V., AND B.J. FOX. 2010. Responses of two species of heathland rodents to habitat manipulation: vegetation density thresholds and the habitat accommodation model. Austral Ecology 35:334–347.

NELLE, P.J., K.P. REESE, AND J.W. CONNELLY. 2000. Long-term effects of fire on sage grouse habitat. Journal of Range Management 53:586–591.

NIMMO, D.G., L.T. KELLY, L.M. SPENCE-BAILEY, S.J. WATSON, A. HASLEM, J.G. WHITE, M.F. CLARKE, AND A.F. BENNETT. 2012. Predicting the century-long post-fire responses of reptiles. Global Ecology and Biogeography 21:1062–1073.

OLSON, R.A., B.L. PERRYMAN, S. PETERSBURG, AND T. NAUMANN. 2003. Fire effects on small mammal communities in Dinosaur National Monument. Western North American Naturalist 63:50–55.

OSTOJA, S.M. 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. Diversity and Distributions 15:863–870.

PARMENTER, R.R., AND J.A. MacMAHON. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. Oecologia 59:145–156.

PARMENTER, R.R., T.L. YATES, D.R. ANDERSON, K.P. BURNHAM, J.L. DUNNUM, A.B. FRANKLIN, M.T. FRIGGENS, B.C. LUBOW, M. MILLER, G.S. OLSON, ET AL. 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. Ecological Monographs 73:1–26.

PETERS, E.F., AND S.C. BUNTING. 1994. Fire conditions pre- and post-occurrence of annual grasses on the Snake River Plain. Pages 31–36 in S.B. Monsen and S.G. Kitchen, editors, Proceedings—ecology and management of annual grasslands. General Technical Report INT-GTR-313, USDA Forest Service, Intermountain Research Station, Ogden, UT.

PRICE, M.V., N.M. WASER, AND T.A. BASS. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65:353–356.

ROSENZWEIG, M.L., AND J. WINAKUR. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50:558–572.

SHENBROT, G., B. KRASNOV, AND S. BURDELOV. 2010. Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. Journal of Mammalogy 91:776–786.

STOUT, J., A.L. FARRIS, AND V.L. WRIGHT. 1971. Small mammal populations of an area in northern Idaho severely burned in 1967. Northwest Science 45:219–226.

TEVIS, L., JR. 1956. Effect of a slash burn on forest mice. Journal of Wildlife Management 20:405–409.

THIBAULT, K.M., S.K. ERNEST, E.P. WHITE, J.H. BROWN, AND J.R. GOHEEN. 2010. Long-term insights into the influence of precipitation on community dynamics in desert rodents. Journal of Mammalogy 91:787–797.

THOMAS, L., S.T. BUCKLAND, E.A. REXSTAD, J.L. LAAKE, AND S. STRINDBERG. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

TORRE, I., AND M. DIAZ. 2004. Small mammal abundance in Mediterranean post-fire habitats: a role for predators? Acta Oecologica 25:137–142.

WALKER, L.R., D.A. WARDLE, R.D. BARGETT, AND B.D. CLARCKSON. 2010. The use of chronosequence in studies of ecological succession and soil development. Journal of Ecology 98:725–736.

WATSON, S.J., R.S. TAYLOR, D.G. NIMMO, L.T. KELLY, A. HASLEM, M.F. CLARKE, AND A.F. BENNETT. 2012. Effects of times since fire on birds: how informative are generalized fire response curves for conservation management? Ecological Applications 22:685–696.

WHISENANT, S.G. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. Pages 4–10 in E.D. McArthur, E.M. Romney, S.D. Smith, and P.T. Tueller, editors, Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. GTR INT-276, USDA Forest Service, Intermountain Research Station, Ogden, UT.

YOUNG, J.A., R.E. ECKERT, AND R.A. EVANS. 1979. Historical perspectives regarding the sagebrush ecosystem. Pages 1–13 in The sagebrush ecosystem: a symposium. Utah State University, College of Natural Resources, Logan, UT.

ZIEGENHAGEN, L.L., AND R.F. MILLER. 2009. Postfire recovery of two shrubs in the interiors of large burns in the Intermountain West, USA. Western North American Naturalist 69:195–205.

ZOU, J., J.T. FLINDERS, H.L. BLACK, AND S.G. WHISENANT. 1989. Influence of experimental habitat manipulations on a desert rodent population in southern Utah. Great Basin Naturalist 48:435–448.