Research Article

Grazing and Wildfire Effects on Small Mammals Inhabiting Montane Meadows

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ABSTRACT Livestock grazing and fire can intensively modify montane meadows. Understanding how these factors affect habitat, species richness, and diversity of small mammals can inform management decisions. Few studies have investigated the independent and synergistic effects of grazing and wildfire on vegetation and small-mammal communities, and none have focused on montane meadows in the southwestern United States. In 2012 and 2013, we captured small mammals at 105 sites to contrast occupancy, species richness, and diversity among livestock grazing levels (present, absent), wildfire severity (unburned, low, or moderate), and meadow classifications (small or large, wet or dry) in Arizona, USA. During 13,741 trap nights, we captured 1,885 rodents of 8 species. Two species represented 88% of captures: deer mouse (*Peromyscus maniculatus*) and Arizona montane vole (*Microtus montanus arizonensis*). Deer mice, Navajo Mogollon voles (*Microtus mogollonensis navaho*), and thirteen-lined ground squirrels (*Ictidomys tridecemlineatus monticola*; a subspecies endemic to the White Mountains, AZ) had higher occupancy in large, ungrazed meadows compared to small, grazed meadows. Species richness was greater in unburned than burned sites and small meadows than large. However, higher diversity occurred in ungrazed and dry compared to grazed and wet meadows. Three species demonstrated weak relationships between wildfire and occupancy, suggesting short-term (<2 yrs) effects of low to moderate burn severity for these species or their habitat. Livestock grazing had a greater effect than wildfire on the small-mammal community by altering vegetation or other habitat elements and thus decreasing population sizes. Reducing livestock grazing would benefit small-mammal species and increase diversity and abundance of the small-mammal community in montane meadows. © 2019 The Wildlife Society.

KEY WORDS *Ictidomys tridecemlineatus*, livestock grazing, meadow size, *Microtus*, occupancy modeling, *Peromyscus*, White Mountains, wildfire.

Montane meadows in western North America are diverse systems of forbs and grasses that serve many ecological roles; they control flooding, protect water quality, and support high biodiversity and productivity (Brown 1994, Roche et al. 2014, Pope et al. 2015). In the southwestern United States, montane meadows vary in size (e.g., <1 to >1,000 ha) within coniferous forests. At elevations from 1,600 m to 3,400 m, these meadows occur on gentle slopes, broad ridges, or along streams, rivers, or other water sources (Brown 1994). The high vegetative diversity and herbage production in montane meadows make them of value for wildlife because of the quality of food and cover they provide. For example, Arnold (1954) indicated a 0.41-ha meadow produced the same amount of herbage as a 1.6-ha pine (*Pinus* spp.)-bunchgrass (Poaceae) opening.

Montane meadows may experience intensive modification by seasonal or continuous livestock grazing (Dobkin et al. 1998, Herbst et al. 2012, Kalinowski et al. 2014). Cattle and elk (*Cervus elaphus*) often concentrate in these areas (Platts and Nelson 1985) and can increase soil compaction, change plant species composition, vegetation structure, biomass, sediment movement, and streambank stability (Medin and Clary 1989, Kie et al. 1996, McEldowney et al. 2002, Austin et al. 2007). Livestock can also reduce food resources for wildlife or physically interfere with habitat features (e.g., trample the burrows of small mammals).

Wildfire has become a dominant factor that can influence plant and animal communities in montane meadows. In the western United States, the frequency of high-severity fire has increased over the past 40 years (Westerling et al. 2006) and high-severity fires are often outside the natural range of variability (Cooper 1960, Covington and Moore 1994).

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These fires can alter heterogeneity in vegetation structure and composition, thereby affecting wildlife (Westerling et al. 2006). Fire-induced changes in vegetation structure and composition will largely influence species presence and abundance (Rosenzweig and Winakur 1969, Fox 1990) and may lead to declines in some populations. For example, Kern (1981) and Kaufman et al. (1990) documented decreased richness or diversity in small-mammal communities inhabiting burned areas.

Small-mammal communities comprise an important component of the overall vertebrate biomass and biodiversity of meadows. They can influence vegetation structure through consumption and dispersal of seeds (Price and Jenkins 1986) and serve as prey for predators (Block et al. 2005, Cocimano et al. 2011, U.S. Fish and Wildlife Service 2012). However, we found only 1 study on small-mammal communities in wet meadows in Idaho (Austin and Pyle 2004). Other studies focused on the role of small mammals as predators (Cain et al. 2006, Cocimano et al. 2011), prey (Kalinowski et al. 2014), or habitat relationships of individual species (Chambers and Doucett 2008, Frey 2015).

Although studies have examined the effect of fire events on small mammals (e.g., Krefting and Ahlgren 1974, Converse et al. 2006, Lawes et al. 2015), few investigated the independent and synergistic effects of grazing and wildfire on vegetation and associated small-mammal communities, and none focused on montane meadows in the southwestern United States. Thus, we evaluated the effects of grazing and wildfire on small-mammal communities inhabiting wet and dry montane meadows. Specifically, our objectives were to describe the small-mammal community using high elevation montane meadows, estimate annual occupancy and detection probabilities for the most frequently captured species, relate these parameters to habitat or detection covariates, and estimate and compare small-mammal community parameters (i.e., diversity and richness) among grazing levels, fire severity, and meadow classifications (small or large size, wet or dry). We predicted negative effects of grazing on small-mammal occupancy. For wildfire, we predicted positive responses by generalist omnivores but negative effects by herbivores. We expected to find lower species diversity and richness in large meadows.

STUDY AREA

We conducted our study in 2012 and 2013 on the Apache-Sitgreaves National Forests, which encompass 1.05 million ha along the Mogollon Rim and the White Mountains in east-central Arizona. Elevations ranged from 1,060 m to 3,500 m. Annual precipitation averaged 50.6 cm with an additional 99.3 cm in annual snowfall from December to March (Strom 2005). The maximum and minimum temperatures from June to August averaged $24.9 \pm 0.4°C$ and $5.3 \pm 1.5°C$, respectively (Cooperative Climatological Data Summaries 2015). The Mogollon Rim has a limestone bed with soil types varying from clay substrates to sandy loams with alluvial gravels in drainages. Forests surrounding meadows at mid-elevation were dominated by ponderosa pine (Pinus ponderosa) with Gambel oak (Quercus gambelii),

alligator juniper (Juniperus deppeana), New Mexico locust (Robinia neomexicana), and pointleaf manzanita (Arctostaphylos pungens). Higher-elevation areas were dominated by white fir (Abies concolor) and Douglas-fir (Pseudotsuga menziesii) with scattered Engelmann spruce (Picea engelmannii) and blue spruce (Picea pungens; U.S. Forest Service 2011).

We selected trap sites that were within or close to the perimeter of the largest wildfire in Arizona history (Wallow Fire, 217,742 ha burned in 2011; Fig. 1), and surveyed sites during the 2 years following this fire, allowing us to make inferences about short-term effects of large-scale wildfire on small mammals (Veraverbeke et al. 2014). Trap sites were within montane meadows at elevations >2,590 m that we categorized as wet or dry; these differed in flooding, depth to water table, and soil characteristics (Judd 1972, Dwire et al. 2006). Wet meadows along riparian systems were typically dominated by sedges (Carex spp.), rushes (Juncus spp.), muttongrass (Poa fendleriana), big bluegrass (Poa secunda), and western yarrow (Achillea millefolium var. occidentalis; Patton and Judd 1970). Dry meadows without active stream or river systems contained fescues (Festuca spp.), muhly (Muhlenbergia spp.), oatgrasses (Danthonia spp.), tufted hairgrass (Deschampsia spp.), pine dropseed (Blepharoneuron spp.), junegrass (Koeleria spp.), and bluegrass (Poa spp.). Dominant fauna associated in this area included voles (Microtus spp.), pocket gopher (Thomomys bottae), pronghorn
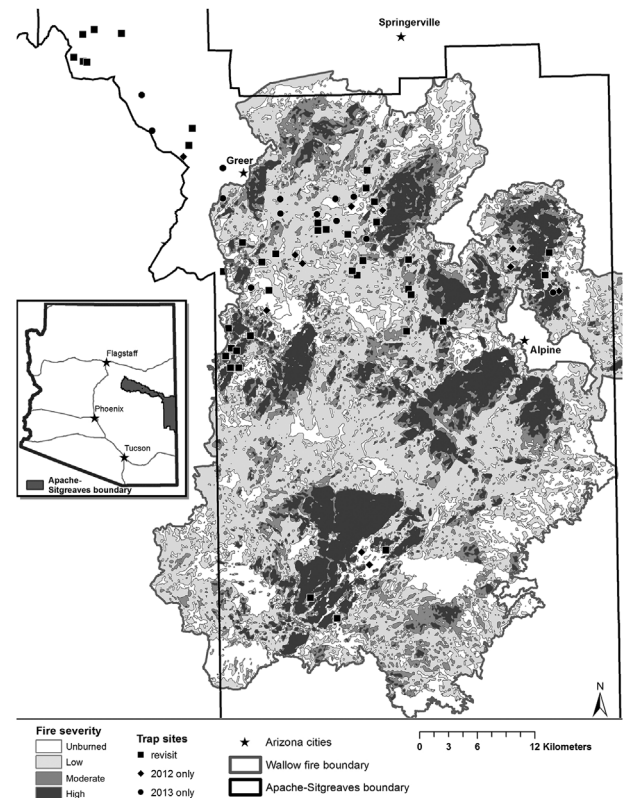

Figure 1. Location of trap sites across the Apache-Sitgreaves National Forests, Arizona, USA, summers 2012 and 2013. Some sites were sampled in both years for a sample size of 105 sites. Inset highlights the boundary of the National Forests; Wallow Fire boundary is in the central portion.

(*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and elk (Brown 1994). Livestock grazing is a primary use of montane meadows (Brown 1994).

METHODS

We sampled small mammals and vegetation in montane meadows from June to August 2012 and 2013. We used a geographic information system (GIS; ArcGIS 9.1, ESRI, Redlands, CA, USA) to determine which meadows and areas within meadows to sample based on our criteria for elevation, size, distance to roads, and meadow type (wet vs. dry). We removed all meadows <2,590 m elevation and those too small (<0.54) to fit our trapping grid. We placed a 50-m buffer from forest edge and major roads to minimize influence of these features. We set a maximum distance from roads of 1,500 m for feasibility of access by field crews, and a minimum distance from minor roads of 25 m. Trap sites were >200 m apart to maintain independence between sites (i.e., avoid capturing the same animal on different sites; Ganey and Chambers 2011). We stratified sites based on the size (large, small) and moisture level (wet, dry) of the meadow. Large meadows averaged $2,866 \pm 997$ ha (mean $\pm$ SD) and contained >800 ha of contiguous open area. Small meadows averaged 168 ± 243 ha. We categorized meadows as wet or dry based on vegetation (percent cover of rushes and sedges) and presence of water. Following stratification, we randomly selected trap sites. We used Burned Area Reflectance Classification (BARC) data (U.S. Forest Service 2017) to determine fire severity levels (high, moderate, low, or unburned) at each site and verified these in the field. High severity indicated all or almost all pre-fire ground cover (litter, duff, fine roots) was consumed with charring visible on larger roots. Moderate severity indicated that fire consumed up to 80% of pre-fire ground cover with some scorching of fine roots (0.25 cm diameter) and low severity indicated surface organic layers were not completely consumed and still recognizable (Parson et al. 2010). Unburned sites were unaffected by the fire.

We sampled 64 unique sites: 51 in 2012 and 13 in 2013 (Fig. 1). To compare captures between years, we resampled 41 sites in 2013 that we surveyed in 2012 ($n = 54$ sites in 2013), providing 105 sites for analysis. Sites were distributed among small ($n = 34$), large ($n = 29$), dry ($n = 29$), wet ($n = 34$), unburned ($n = 34$), and burned ($n = 29$) meadows. Burn severity ranged from low to moderate; no burned sites were categorized as high severity.

We conducted trapping from June to mid-August when sites were accessible (roads open, no snow) and to minimize mortality due to cold nighttime temperatures. At each site, we placed 33 Sherman traps on a 3×8 grid using 15-m spacing. At each grid point, we placed 1 small ($8 \times 9 \times 23$ cm) trap ($n = 24$) and at every third grid point we also placed a large ($10 \times 11 \times 38$ cm) trap ($n = 9$). We baited traps with a mixture of oats, peanut butter, walnuts, and apples. We used polyester batting in each trap to provide insulation, and covered traps with a wooden shingle to provide cover from rain and solar insolation. We opened traps for 4 consecutive nights at each site, checked them each morning, closed them during the day, and reopened them each evening. We identified captured animals to species but did not mark them because we were concerned with presence rather than recapture rate (MacKenzie et al. 2006). We handled animals under guidelines of the American Society of Mammalogists (Sikes et al. 2011) and with approval of Northern Arizona University Institutional Animal Care and Use Committee (protocol 11-006).

We collected habitat data at each trap location using Daubenmire (1959) cover classes in a 20×50-cm quadrat ($n = 33$ quadrats/site). We categorized data into 7 groups: grass, forb, sedge and rush, litter, woody debris, bare ground, and other. This allowed us to calculate percent cover, species composition, and frequency for each category at each trap location. We also measured height of vegetation (base of plant to tip of leaves when extended). We recorded presence (fresh pellets, visual sightings, and trampled vegetation) or lack of evidence of elk, mule deer, pronghorn, and cattle to indicate whether grazing occurred during the trapping season. If we observed trampled vegetation, we searched for additional sign (pellets or presence) to confirm cause (wildlife or livestock). We grouped wildlife (elk, mule deer, pronghorn) but had too few observations to model. We thus categorized intensity based on frequency of livestock grazing: both years if a site sampled in 2012 and 2013 was grazed both years, 1 year, or no grazing (Table 1).

Statistical Analyses

We used occupancy modeling to estimate the proportion of sites occupied by species (MacKenzie et al. 2003, 2004, 2006; Guillera-Arroita et al. 2014). For each species with >40 detections among all sites (i.e., number required for analysis) and based on site-level detection histories, we used either the multi-season or single-season occupancy estimation feature in Program PRESENCE (version 4.1; Hines 2006). For species with too few detections for a multi-season analysis, we used the single-season occupancy estimation feature in Program PRESENCE but pooled detections for both years. Because we hypothesized that fire, grazing, meadow size, and moisture levels (indicated by percent cover of rushes and sedges) affected small-mammal occupancy, model sets included these covariates. We included additional covariates (e.g., vegetation height, elevation, percent grass and forbs) for each species based on known habitat associations.

Prior to modeling, we standardized all covariates by calculating z scores ($\bar{x} = 0$ and SD $= 1$), and then computed a Spearman correlation coefficient to determine if univariate correlations between continuous covariates were present or problematic (Spearman's rho >0.70). Distance to forest edge and meadow size were correlated (0.78) and slope and elevation were correlated (1.0) so we removed distance to forest edge and slope from the analysis. Additionally, we removed percent cover of litter and bare ground because they appeared to be related to other covariates (i.e., as bare ground increases, grasses and forbs decrease) even though values for Spearman's rho were <0.7. Our detection covariates included year (to account for annual variation) and survey

Table 1. Description of response covariates used in the occupancy analysis of small-mammal data collected during summer 2012 and 2013, from the Apache-Sitgreaves National Forests, Arizona, USA.

Variable	Type of variable	Variable description
Year[a]	Discrete	Year that data were collected (2012–2013).
Survey week[a]	Continuous	Indicates whether we trapped the site at the beginning or end of the field season (sites trapped in the early weeks may have occurred before the start of the monsoon season). 1 = week 1, 2 = week 2....
Cattle grazing	Continuous	Indicates whether the trap site had presence or fresh sign of cattle during the trapping season. 0 = none, 1 = grazed in 1 year, 2 = grazed in both years (for sites sampled 2 years).
Fire	Continuous	Indicates whether the trap site was located in an unburned, low, or moderate burn severity grassland. 0 = unburned, 1 = low severity, and 2 = moderate burn severity.
Meadow size (ha)	Continuous	Estimated size of meadow where trapping grid was located. We derived estimates using zonal statistics within a geographic information system.
Vegetation height (cm)	Continuous	The average vegetation height of all species occurring at the trap site across all years.
Rush + sedge (% cover)	Continuous	Average percent cover of rushes and sedges at a trap site across all years. Indicates whether a trapping grid occurred within a wet or dry meadow.
Grass + forb (% cover)	Continuous	Average percent cover of grasses and forbs at a trap site across all years.
Elevation (m)	Continuous	Elevation where trapping grid was located.

[a] Covariates only included as detection covariates in analysis.

week. We included survey week because weather patterns changed from the beginning of the field season (warmer, drier) to the end of the field season (cooler, wetter), which could affect number of animals or species captured. Our final list of occupancy covariates included vegetation height, percent grass plus forb, percent rush plus sedge, meadow size, cattle grazing, fire, and elevation (Table 1).

We considered candidate models with difference values for Akaike's Information Criterion (ΔAIC) <4.0 as those that best approximated the data (Anderson 2008). We also included null models of occupancy and detection probability within each candidate set to evaluate the performance and fit of the candidate models (Anderson 2008). These null models held occupancy and detectability constant across sites and surveys. We calculated and summed the AIC weights across all models in our candidate set in which a given covariate occurred and used cumulative weights (w_{ij}) to rank relative covariate importance for each species (Burnham and Anderson 2002). We considered $w_{ij} \geq 0.50$ indicative of a relatively strong species response to a given covariate, $0.50 \geq w_{ij} \geq 0.30$ a moderate response, and $w_{ij} \leq 0.30$ a weak response. We computed a model-averaged regression coefficient, unconditional standard error, and confidence intervals for each variable (Burnham and Anderson 2002).

To characterize small-mammal community membership, we used EstimateS (Colwell 2006) to calculate diversity and richness estimators for small and large meadows, wet and dry

meadows, burned and unburned sites, grazed and ungrazed sites, and year. For simplicity, we only reported results for Simpson diversity (Magurran and McGill 2011) and the jackknife (Jack1) richness estimator (Burnham and Overton 1978, 1979; Palmer 1990, Hellmann and Fowler 1999, Gotelli and Colwell 2011). We used a paired *t*-test (alpha = 0.05) to compare richness and diversity between burned (low and moderate combined) and unburned sites, grazing presence (2 categories: grazed or ungrazed), meadow size (large or small), and meadow type (wet or dry).

RESULTS

During 13,741 trap nights, we captured 1,885 rodents representing 8 species. Deer mouse (*Peromyscus maniculatus*) and Arizona montane vole (*Microtus montanus arizonensis*) were the most frequently captured species (Table 2).

We analyzed 3 species using multi-season occupancy models: deer mouse, Navajo Mogollon vole (*Microtus mogollonensis navajo*), and Arizona montane vole. Detection probabilities for these species varied between years (Fig. 2) with detection probability for the Arizona montane vole higher in 2012 than 2013 and for the deer mouse lower in 2012 than 2013. The Navajo Mogollon vole had similar detection probability for both years. Detection probabilities ranged from 0.52 to 0.86, which are considered adequate for occupancy analysis (MacKenzie and Royle 2005). We compared 42 models for the deer mouse (Table 3). Deer

Table 2. Small mammals captured during summer 2012 and 2013 in high elevation meadows, Apache-Sitgreaves National Forests, Arizona, USA.

| Species	Common name	2012	2013	% Total captures
Peromyscus maniculatus	Deer mouse	251	856	58.7
Microtus montanus arizonensis	Arizona montane vole	394	162	29.5
Microtus mogollonensis navaho	Navajo Mogollon vole	30	125	8.2
Ictidomys tridecemlineatus	Thirteen-lined ground squirrel	16	31	2.5
Microtus longicaudus	Long-tailed vole	12	1	0.7
Reithrodontomys megalotis	Western harvest mouse	3	0	0.2
Neotoma mexicana	Mexican woodrat	0	2	0.1
Callospermophilus lateralis	Golden-mantled ground squirrel	1	1	0.1
	Total	707	1,178	100
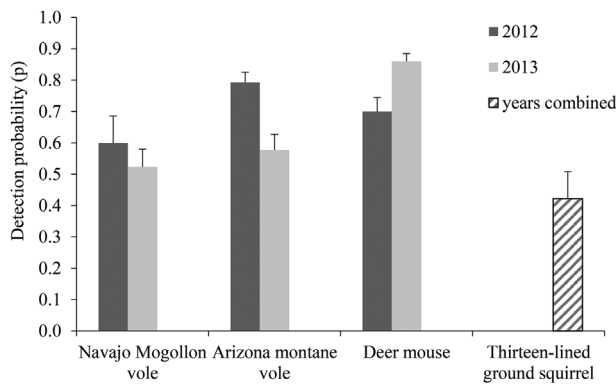
Figure 2. Detection probabilities ($\bar{x}$ and SE) for 4 species of small mammals, Apache-Sitgreaves National Forests, Arizona, USA, summers 2012 and 2013. Each model used the most parsimonious model of occupancy for each species. Because the thirteen-lined ground squirrel had fewer captures, we combined years and used a single-season occupancy model.

mice were strongly and negatively associated with percent cover of forbs and grasses ($w_{ij} = 0.99$), percent cover of rushes and sedges (wet meadow conditions, 0.87), and cattle grazing (0.86) but strongly and positively associated with large meadows (0.58; Table 4). The Navajo Mogollon vole was strongly negatively associated with cattle grazing (0.99) and rushes and sedges (0.70), and strongly positively associated with meadow size (0.90), and elevation (0.63) (44 models; Table 3). This species had greater occupancy in ungrazed, large, dry meadows at higher elevations (Table 4) with a capture rate 7 times higher in these compared to grazed, wet meadows. We compared 23 models for the Arizona montane vole. The top model was no different from the null model, indicating that the covariates we used were uninformative for this species. We captured twice as many Arizona montane voles in ungrazed compared to grazed sites

Table 3. Multi-season occupancy (Ψ) model selection results for 3 species of small mammals detected in Apache-Sitgreaves National Forests, Arizona, USA, 2012–2013. We present candidate models with Akaike's Information Criterion (AIC) difference (ΔAIC) values <4.0, those that best approximated the data, and the null model (.). Modeled effects included cattle grazing (grazing), fire (fire), meadow size (size), vegetation height (height), % rushes (rush), % grasses and forbs (grass), elevation (elev), year (year), and survey week (week). We do not present models that did not converge and did not use them for inference.

Model	$-2l$[a]	K[b]	ΔAIC[c]	w_i[d]
Navajo Mogollon vole[e]				
Ψ(grazing, rush, size)	261.97	10	0.00	0.199
Ψ(grazing, elev, size, rush)	260.90	11	0.93	0.125
Ψ(grazing, size)	265.10	9	1.13	0.113
Ψ(grazing, elev, size, rush, height)	259.29	12	1.32	0.103
Ψ(grazing, elev, size)	263.71	10	1.74	0.084
Ψ(grazing, elev, size, rush, fire)	259.97	12	2.00	0.073
Ψ(grazing, elev, rush, grass, height)	260.61	12	2.64	0.053
Ψ(grazing, elev, rush, size, fire, height)	258.71	13	2.74	0.051
Ψ(grazing, fire, size)	264.74	10	2.77	0.050
Ψ(grazing, elev, size, rush, grass, height)	259.00	13	3.03	0.044
Ψ(grazing, fire, size, elev)	263.45	11	3.48	0.035
Ψ(grazing, elev, fire, rush, height)	261.65	12	3.68	0.032
Ψ(.)	286.75	7	18.78	0.000
Deer mouse[f]				
Ψ(grazing, rush, grass, size)	360.87	11	0.00	0.241
Ψ(grazing, rush, grass)	363.35	10	0.48	0.189
Ψ(grazing, rush, grass, size, height)	360.21	12	1.34	0.123
Ψ(grazing, rush, grass, height)	362.64	11	1.77	0.099
Ψ(grazing, grass, size)	365.22	10	2.35	0.074
Ψ(grazing, rush, grass, size, height, elev)	359.52	13	2.65	0.064
Ψ(rush, grass, elev)	366.46	10	3.59	0.040
Ψ(.)	382.59	7	13.72	0.001
Arizona montane vole[g]				
Ψ(height)	426.01	7	0.00	0.183
Ψ(height, grazing)	424.99	8	0.98	0.112
Ψ(.)	429.38	6	1.37	0.092
Ψ(height, size)	425.42	8	1.41	0.091
Ψ(grazing)	427.87	7	1.86	0.072
Ψ(height, grazing, elev)	423.91	9	1.90	0.071
Ψ(height, grazing, size)	424.11	9	2.10	0.064
Ψ(height, size, elev)	424.73	9	2.72	0.047
Ψ(size)	428.77	7	2.76	0.046
Ψ(height, size, rush)	424.99	9	2.98	0.041
Ψ(height, grass, elev)	425.12	9	3.11	0.039
Ψ(height, grass, size)	424.09	9	3.41	0.033

[a] Twice the negative log-likelihood value.
[b] Total number of model parameters.
[c] AIC difference value.
[d] AIC model weight.
[e] γ(CG)ε(.)p(Y,SW) where γ_i is the probability of an unoccupied site being colonized between seasons i and $i+1$, ε_i is the probability of a species at an occupied site going extinct between seasons i and $i+1$, and p_i is the probability of detecting a species in survey i, given presence.
[f] γ(GF)ε(.)p(Y,SW).
[g] γ(.)ε(.)p(Y,SW).

Table 4. Standardized model-averaged regression coefficients ($\hat{\bar{\beta}}$), cumulative Akaike's Information Criterion (AIC) weights (w_{ij}), and 95% confidence intervals (CI) for variables included in the top models of occupancy for 3 small-mammal species in Apache-Sitgreaves National Forests, Arizona, USA, 2012–2013. We ranked variables only for species whose top models were >4 AIC units from the null model, indicating that these variables were approximating the data well. Cumulative AIC weights ≥0.50 indicate strong evidence for a species response to the habitat covariate. We calculated confidence intervals from unconditional standard errors.

Variable	Deer mouse $\hat{\bar{\beta}}$	w_{ij}	95% CI		Navajo Mogollon vole $\hat{\bar{\beta}}$	w_{ij}	95% CI		Thirteen-lined ground squirrel $\hat{\bar{\beta}}$	w_{ij}	95% CI	
Cattle grazing	−0.94	0.86	−1.86	−0.02	−2.72	0.99	−5.21	−0.23	−1.54	0.85	−3.23	0.15
Meadow size	0.68	0.58	−0.20	1.56	1.41	0.90	0.06	2.76	1.77	0.99	0.56	2.99
% rush + sedge	−0.85	0.87	−1.69	−0.01	−2.24	0.70	−4.93	0.45				
% grass + forb	−1.31	0.99	−2.27	−0.35	−0.44	0.12	−1.52	0.64	−0.82	0.54	−1.96	0.32
Elevation	0.31	0.19	−0.30	0.918	0.70	0.63	−0.48	1.88	0.05	0.24	−1.20	1.30
Vegetation height	−0.32	0.40	−1.08	0.44	−1.23	0.30	−3.21	0.75	−0.03	0.25	−1.40	1.34
Fire severity	−0.01	0.05	−1.18	1.07	0.59	0.25	−1.06	2.24	−0.46	0.21	−2.19	1.27

and 3 times as many Arizona montane voles in small compared to large meadows.

We captured thirteen-lined ground squirrels (*Ictidomys tridecemlineatus monticola*; formerly *Spermophilus tridecemlineatus monticola*; 40 models, Table 5) only in large meadows. This was the only species with enough detections to produce reliable estimates of occupancy using the single-season analysis. Detection probability over 2 years was 0.42 (Fig. 2). This species was strongly positively associated with meadow size (0.99), and strongly negatively associated with cattle grazing (0.85) and grass and forb cover (0.54; Table 4). Greater occupancy occurred in large, ungrazed meadows with lower cover of grasses and forbs. Number of captures was 3 times more likely in dry versus wet meadows and 8 times greater in ungrazed compared to grazed meadows.

Richness was greater in unburned than burned sites ($t = -2.54$, $P < 0.05$) and in small compared to large meadows ($t = -3.35$, $P < 0.05$; Fig. 3). Diversity was greater at ungrazed compared to grazed sites ($t = -3.31$, $P < 0.05$)

Table 5. Single-season occupancy (Ψ) model selection results for thirteen-lined ground squirrels in Apache-Sitgreaves National Forests, Arizona, USA, 2012–2013. We present candidate models with Akaike's Information Criterion (AIC) difference (ΔAIC) values <4.0, those that best approximated the data, and the null model (.). Model effects included cattle grazing ($n = 3$; grazing), fire ($n = 3$; fire), meadow size (size), vegetation height (height), % rushes and sedges (rush), % grasses and forbs (grass), and elevation (elev). The best model for detection included trap day. We do not present models that did not converge and did not used them for inference.

Model	−2*l*[a]	*K*[b]	ΔAIC[c]	w_i[d]
Thirteen-lined ground squirrel				
Ψ(grazing, size, grass)	97.96	8	0.00	0.217
Ψ(grazing, size)	100.44	7	0.48	0.170
Ψ(grazing, size, grass, fire)	97.60	9	1.64	0.095
Ψ(grazing, size, grass, height)	97.94	9	1.98	0.080
Ψ(grazing, size, grass, elev)	97.96	9	2.00	0.080
Ψ(grazing, size, height)	100.43	8	2.47	0.063
Ψ(grazing, size, elev)	100.44	8	2.48	0.063
Ψ(size)	104.73	6	2.77	0.054
Ψ(grazing, size, height, fire)	99.95	9	3.99	0.029
Ψ(.)	122.91	5	18.95	0.000

[a] Twice the negative log-likelihood value.
[b] Total number of model parameters.
[c] AIC difference value.
[d] AIC model weight.

and dry compared to wet sites ($t = 2.84$, $P < 0.05$; Fig. 3). We did not detect differences for other comparisons (Fig. 3), nor did we detect differences in richness or diversity between years.

DISCUSSION

Consistent with other small-mammal communities using structurally simple ecosystems such as grasslands (Rose and Birney 1985, Torre et al. 2007), 2 species (deer mouse and Arizona montane vole) dominated the montane meadows in our study. However, 11% of our captures included 3 additional species, representing higher richness than recorded for 2 large montane meadows in northern Arizona (Ganey and Chambers 2011). We captured Navajo Mogollon voles, thirteen-lined ground squirrels, and long-tailed
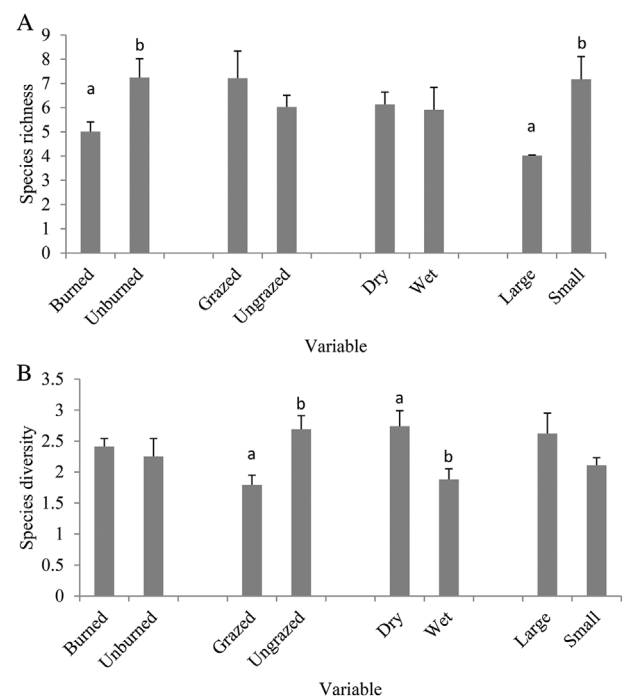

Figure 3. Small-mammal species richness (A) and diversity (B) estimates ($\bar{x}$ and SD) for burned versus unburned sites, grazing, meadow type, and meadow size during summers 2012 and 2013 in the Apache-Sitgreaves National Forests, Arizona, USA. Letters indicate differences between comparisons.

voles (*Microtus longicaudus*) at 45%, 19%, and 6% of sites, indicating that these species were distributed across our study area. The large sizes (e.g., 10 × 15 km) of montane meadows within our study area likely contributed to this diversity.

The deer mouse, a habitat generalist, occurs in large, open areas (Snyder and Best 1988, Kaufman et al. 1989, 1990). Because we found deer mice negatively associated with higher cover of forbs and grasses, we expected higher occupancy of deer mice in grazed and burned meadows because these disturbances decreased litter and vegetation (Bock and Bock 1978, Bock et al. 2011, Litt and Steidl 2011). However, for deer mice we found the opposite, although grazing had a stronger negative effect. Previous studies provided contradictory results for deer mice responses to grazing (Schieltz and Rubenstein 2016). Grant et al. (1982) and Matlack et al. (2001) noted positive responses; Johnston and Anthony (2008) and Medin and Clary (1989) found negative responses. These differences could depend on vegetation type; for example, deer mice in the Great Basin responded positively to grazing in moist vegetation types with abundant herbaceous cover but negatively in dry vegetation types with sparse vegetative cover (Hanley and Page 1982).

The herbivorous Navajo Mogollon vole selects grassy areas in ponderosa pine and mixed conifer forests with greater grass cover, taller vegetation, and dense bunch grasses dominated by C_3 plants (Hoffmeister 1986, Amar and Redpath 2005, Chambers and Doucett 2008). We found higher occupancy for this species in ungrazed meadows, indicating that cattle grazing may have reduced occupancy for Navajo Mogollon voles by reducing cover and food availability. Yarborough and Chambers (2007) also captured fewer Navajo Mogollon voles in grazed meadows compared to meadows with low or no grazing. In other regions, cattle grazing negatively affected abundance of other vole species by reducing vegetation height and volume or trampling burrows (Schmidt et al. 2005, Kalinowski et al. 2014, Schieltz and Rubenstein 2016). Schieltz and Rubenstein (2016) noted consistent negative responses by voles to grazing in an evidence-based review. Reducing levels of livestock grazing in our study area could benefit the habitat attributes that support occupancy by Navajo Mogollon voles.

In our study, we captured thirteen-lined ground squirrels, a subspecies endemic to the White Mountains in Arizona, only in large meadows with little or no livestock grazing. This burrowing omnivore selects open areas with short grasses (Phillips 1936, Streubel and Fitzgerald 1978, Arizona Game and Fish Department 2004). However, in Oklahoma, USA, heavy overgrazing decreased the number of thirteen-lined ground squirrels, although moderate grazing did not (Phillips 1936, Streubel and Fitzgerald 1978, Schieltz and Rubenstein 2016). The higher occupancy we found for this species when grass and forb cover was lower could be an indication of selection for both cover and wide field of visibility. The negative effect of grazing that we found could indicate that livestock trampled burrows, compacted soil, and caused a reduction of grass and forb cover by grazing.

The Arizona montane vole selects habitat with high soil moisture, vertical cover, and litter depth (Frey 2005). Because canopy cover and vertical structure of plants can be reduced in areas grazed by cattle (Kie et al. 1996, Rosenstock 1996), we expected lower abundance of montane voles in grazed meadows. Although we could not identify covariates that affected occupancy for the Arizona montane vole, we noted differences in abundance between grazing and sizes of meadows, with this species captured more frequently in small, ungrazed meadows. Adjacent ponderosa pine and mixed conifer forests provided additional habitat for this species.

In our study, livestock grazing decreased diversity but did not affect richness. Grant et al. (1982), Kauffman et al. (1982), and Keesing (1998) also found grazing reduced diversity of small mammals. In a meta-analysis of published literature from arid environments, Jones (2000) noted a negative overall impact of grazing on rodents because of the effects that grazers had on soils or vegetation. Schieltz and Rubenstein (2016) reviewed 807 sources that assessed effects of grazing livestock on wildlife and reported that abundance of small mammals declined with grazing. Richness declined or remained the same because of changes in species composition. Species adapted to open areas (e.g., ground squirrels, rabbits [*Sylvilagus* spp.]) often were unaffected or positively affected by grazing (Fa et al. 1992, Powers et al. 2011). In contrast, voles responded negatively and deer mice responses varied to livestock grazing. Effects of livestock grazing will be more pronounced if wildlife species are specialists, have small home range sizes and dispersal distances, or rely on habitat features such as forage biomass that are limiting when grazers are present (Szaro and Rinne 1988, Kie et al. 1996, Schieltz and Rubenstein 2016). Other studies also reported that diversity, evenness, and overall abundance of small mammals were greater in ungrazed compared to grazed areas in North American grasslands (Grant et al. 1982) and southwestern United States desert wetlands (Hayward et al. 1997). Livestock may negatively affect burrowing animals through trampling and soil compaction and other species through changes in structure and composition of vegetation (Rosenstock 1996, Hayward et al. 1997, Powers et al. 2011).

Despite starting our project just 1 year after a large wildfire, we found little effect of wildfire on diversity or individual species. Small mammals can survive immediate effects of fire by sheltering in refugia (Yarnell et al. 2007). In addition, rate of recovery of vegetation following fire influences how quickly habitat was again available (Cheeseman and Delany 1979). Vegetation recovered to similar levels as unburned areas just 6 months after fire in a tallgrass blackland prairie in Texas, and relative abundances of some species of rodents returned to preburn (prescribed fire) levels in 8 months (Yarnell et al. 2007, Kirchner et al. 2011). Based on our results, vegetation in montane meadows likely recovered rapidly to conditions that supported small mammals 1 to 2 years post-wildfire.

Although fire did not affect occupancy of the 3 most frequently detected species in our study, capture of a few

uncommon species in unburned meadows compared to burned meadows positively influenced species richness. Detection of the golden-mantled ground squirrel (*Callospermophilus lateralis*), long-tailed vole, and Mexican woodrat (*Neotoma mexicana*) in unburned plots occurred infrequently (≤4 captures each). There was, however, no difference in diversity between burned and unburned meadows because of low evenness in unburned meadows. In addition, the Simpson index might have contributed to a lower diversity value in unburned meadows because it was heavily weighted toward the most abundant species in our sample and less sensitive to species richness.

MANAGEMENT IMPLICATIONS

Despite the size and severity of the wildfire that affected our sites, our results indicated that fire had little effect on small-mammal communities in montane meadows. However, a reduction in livestock grazing in these meadows would likely benefit small-mammal species and increase diversity and abundance of the small-mammal community. Because the distribution and occurrence of thirteen-lined ground squirrels was limited to large meadows (>800 ha), this specialized habitat should not be degraded. Because different grazing systems can result in differential effects on the land, we suggest that future studies incorporate stocking rates, intensity, and timing of grazing to determine at what levels (or thresholds) grazing intensity decreases diversity or occupancy of individual species.

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