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Group effects of a non-native plant invasion on rodent abundance

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Abstract. Cheatgrass (*Bromus tectorum*) is the most prolific invading plant in western North America. Investigations determining the impact of this invasion on population state variables and community dynamics of rodents have largely occurred at the community or species level, creating a knowledge gap as to whether rodents affiliated by a shared taxonomy or other grouping are differentially affected by cheatgrass invasion. We examined rodent abundance along a gradient of cheatgrass cover using various groupings of two nocturnal rodent taxa comprising the majority of the rodent community in the Great Basin Desert. In the summers of 2010–2013, rodents were sampled and vegetation was measured on the U.S. Army Dugway Proving Ground in the Great Basin Desert of Utah, USA. We separately examined estimates of rodent abundance for all combined species within the Cricetidae and Heteromyidae families, the most numerically dominant species, and uncommon species pooled in relation to cheatgrass invasion severity. We detected an expected negative linear relationship between invasion severity and abundance for all cricetid groupings, including the most numerically dominant species, the deer mouse (*Peromyscus maniculatus*). Unexpectedly, heteromyid abundance exhibited an initial positive relationship, reached a threshold, and then exhibited a negative relationship, a phenomenon driven by Ord's kangaroo rats (*Dipodomys ordii*), the most numerically dominant species. We speculate this non-linear finding was caused by a combination of trophic and non-trophic pathways. Our findings provide new insight as to the potential for differential effects of cheatgrass on rodents in arid portions of the western United States. We suggest that future investigations on cheatgrass, and plant invader effects in general, consider parsing animal communities of interest by various taxonomic and/or ecological groupings rather than focusing exclusively on individual species or entire communities.

Key words: *Bromus tectorum*; cheatgrass; Cricetidae; habitat; Heteromyidae; non-native vegetation; small mammal.

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INTRODUCTION

Plant invasions have been identified as one of the greatest threats to ecological processes and functions (D'Antonio and Flory 2017). For example, herbaceous plant invasions can alter plant community composition and structure by decreasing plant species richness and diversity (Knapp 1996, Hejda et al. 2009, Freeman et al.

2014), increasing plant biomass and litter (Steidl et al. 2013), and reducing functional plant diversity (Hejda et al. 2009). More contemporary investigations have examined how plant invasions alter ecosystem processes (Grebner et al. 2014, Peh et al. 2015, Sladonja et al. 2015), economics (Pimentel 2011) and fauna at both the community and individual species levels (Martin and Murray 2011, Hayes and Holzmüller 2012,

Litt and Pearson 2013). Gaining a better understanding of the effects of plant invasions on fauna is paramount because invasions are expanding throughout many portions of the globe (Rai 2013), and there is a paucity of studies exploring this topic in relation to the number of communities, species, and landscapes potentially affected.

Non-native plant invasions can have negative, positive, non-linear, or neutral effects on terrestrial animal species and communities (French and Zubovic 1997, Hayes and Holzmueller 2012, Litt and Pearson 2013, Steidl et al. 2013, Smith et al. 2017). The degree to which non-native induced structural changes influence vertebrate species richness and abundance depends largely on the magnitude of alteration to native vegetation communities (Pimentel 2011, Litt and Pearson 2013). These changes can increase or decrease food resources for the vertebrate community (i.e., a trophic pathway) and create unique habitat characteristics (i.e., a non-trophic pathway). An example of a non-trophic pathway was put forth by Ehlers Smith et al. (2015) when they observed that despite mango orchards having greater vertical height structure than areas dominated by native plants, the absence of low-scrub woody cover in orchards caused an absence of avian species with life-history traits associated with this structural component. The impact to these pathways can depend largely on the physiological limitations, behavioral characteristics, and habitat requirements of the groups of animals being investigated (i.e., shared functional traits, and taxonomy or guild-based associations; French and Zubovic 1997).

The majority of investigations on non-native plants and vertebrates have analyzed the effects of invading plant species on either individual species or entire communities (Ostoja and Schupp 2009, Litt and Steidl 2011, Hall 2012, Horn et al. 2012, Malick et al. 2012, Litt and Pearson 2013, Freeman et al. 2014, Ceradini and Chalfoun 2017a, Smith et al. 2017). Though several of the above investigations have reported on non-native plant effects on rodent families (Litt and Steidl 2011, Smith et al. 2017), not all have done so by analyzing data at the actual group level. For example, though Litt and Steidl (2011) reported that presence and abundance of heteromyids decreased with increasing dominance of

Lehmann lovegrass (*Eragrostis lehmanniana*), whereas abundance of murids decreased, their analytical framework was individual species based. A recent exception to the pattern of examining plant invader effects on rodents at the species or community level was put forth by Ceradini and Chalfoun (2017b), where authors examined cheatgrass (*Bromus tectorum*) effects on rodent occupancy based on species' natural history traits, such as habitat associations (i.e., open vs. closed).

In the western United States, cheatgrass (*B. tectorum*) is the most dominant non-native plant species on the landscape (Young et al. 1987, Billings 1990, Link et al. 2006). This species transforms habitat by replacing native plant communities with homogeneous grass cover (Knapp 1996); the continuous grass cover increases the probability and extent of wildfires, which favors cheatgrass over native species, thus creating a positive feedback loop (Balch et al. 2013).

The majority of investigations on the effects of cheatgrass on animals have focused on rodents; notable exceptions include works focused on ant (Ostoja et al. 2009) and avian (Earnst et al. 2009) assemblages. The majority of cheatgrass-rodent investigations exhibit two key similarities: a focus on individual species or entire communities, and concluding that abundance and other metrics (i.e., species richness, diversity indexes) steadily decreased with increasing cheatgrass dominance (Gitzen et al. 2001, Ostoja and Schupp 2009, Hall 2012, Freeman et al. 2014). However, more contemporary cheatgrass-rodent investigations have deviated from this pattern. For example, using vegetation cover classes, Kluever et al. (2016) examined rodent abundance and found areas classified as exotic herbaceous vegetation (primarily cheatgrass) had higher rodent abundance than native sagebrush areas. Smith et al. (2017) examined rodent abundance in relation to fine-scale vegetation measurements and found rodent abundance was highest at intermediate levels of cheatgrass dominance; the authors speculated this finding was primarily driven by Heteromyids flourishing in areas where cheatgrass became established but did not dominate the vegetative community.

This recent finding by Smith et al. (2017), in concert with a scarcity of works examining

cheatgrass effects on rodents at groupings intermediate to entire communities or individual species, creates a clear need for investigation. Such research could reveal the need and relevancy of parsing rodent groupings by disparate physiological, behavioral, functional, or other traits when examining non-native plant effects. In addition, because rodents often have significant effects on other trophic levels (e.g., primary producers and predators) and ecosystem processes (e.g., seed dispersal/consumption and soil disturbance), furthering our understanding of cheatgrass invasion, and invading plants in general, on rodent communities is needed to gain a more comprehensive understanding of ecosystem structure and function. This could also help prioritize native vegetation restoration efforts in the face of limited resources. Finally, such findings would differ from the bulk of prior rodent-cheatgrass investigations. Because these works vary widely in terms of study area size and geographic location, revealing incongruent findings for impacts of cheatgrass on rodents would also underscore the importance of exercising caution when extrapolating inference of study finding beyond the spatial extent of specific study areas.

Here, we describe a 4-yr investigation on the effects of cheatgrass encroachment on rodents, as categorized by different taxa, in the Great Basin Desert of the United States. We tested the hypothesis that cheatgrass effects on rodents are negative and linear across the major rodent groups in our study system. To make this assessment, we determined abundance of rodents and tested for cheatgrass effects for the two families comprising the rodent community, the most numerically dominant species from each rodent family, and across the less dominant species of each family.

METHODS

Study area

Our study area comprised 366 km² of the eastern portion of the U.S. Army Dugway Proving Ground (DPG) located approximately 128 km southwest of Salt Lake City, in Tooele County, Utah, USA (Fig. 1). Elevations ranged from 1349 to 2021 m. The area was characterized as a cold desert, and average maximum temperatures ranged from 3.3°C in January to 34.7°C in July (Arjo

et al. 2007). Mean annual precipitation was 20.07 cm. The study area consisted of a predominantly flat playa punctuated with steep mountain ranges. Non-native herbaceous vegetation, primarily cheatgrass (*B. tectorum*), had replaced approximately 40% of historical juniper woodland and shrub communities (Emrick and Hill 1999). These non-native plant species were also interspersed within communities of sagebrush, rabbitbrush (*Chrysothamnus* sp.) and greasewood (Arjo et al. 2007). Previous rodent investigations revealed that the study area was dominated by nocturnal granivores and folivores from the family Heteromyidae and nocturnal granivores, folivores, and carnivores from the family Cricetidae (Arjo et al. 2007, Kluever et al. 2016).

Data collection

In 2010, we used stratified random sampling (Kluever et al. 2016) to establish sixteen 50 × 50 m sampling plots throughout the study area. From 2010 to 2013, we evaluated the plant community at these plots using seven 60-m line transects following the axis of the plot and spaced 10 m apart (Kluever et al. 2016). The orientation of vegetation transects (e.g., east to west, north or south) was randomly chosen for each sampling event. Using the line-point intercept method (Herrick et al. 2005, Thompson and Gese 2013), we measured plant species and height at 1-m intervals. This sampling provided us with 420 vegetation points (i.e., 60 data points per transect) per sampling effort on each plot and allowed us to characterize or estimate vegetation structure and community parameters, including percent shrub cover, percent bare ground, mean plant height (cm), percent litter cover, percent cheatgrass cover, and plant species richness (Thompson and Gese 2013). We sampled plot vegetation twice per summer, one day prior to the onset of rodent sampling. Sampling vegetation immediately prior to rodent sampling throughout the summer is a commonly employed method to investigate vegetation effects on rodent communities, including the effects of non-native plants (Hall 2012, Thompson and Gese 2013, Freeman et al. 2014). All sampling plots were located in either exotic grassland, mixed desert scrub, or sagebrush vegetation cover classes (Kluever et al. 2016).

We sampled rodents at each site for four consecutive nights (i.e., one trapping session) with at

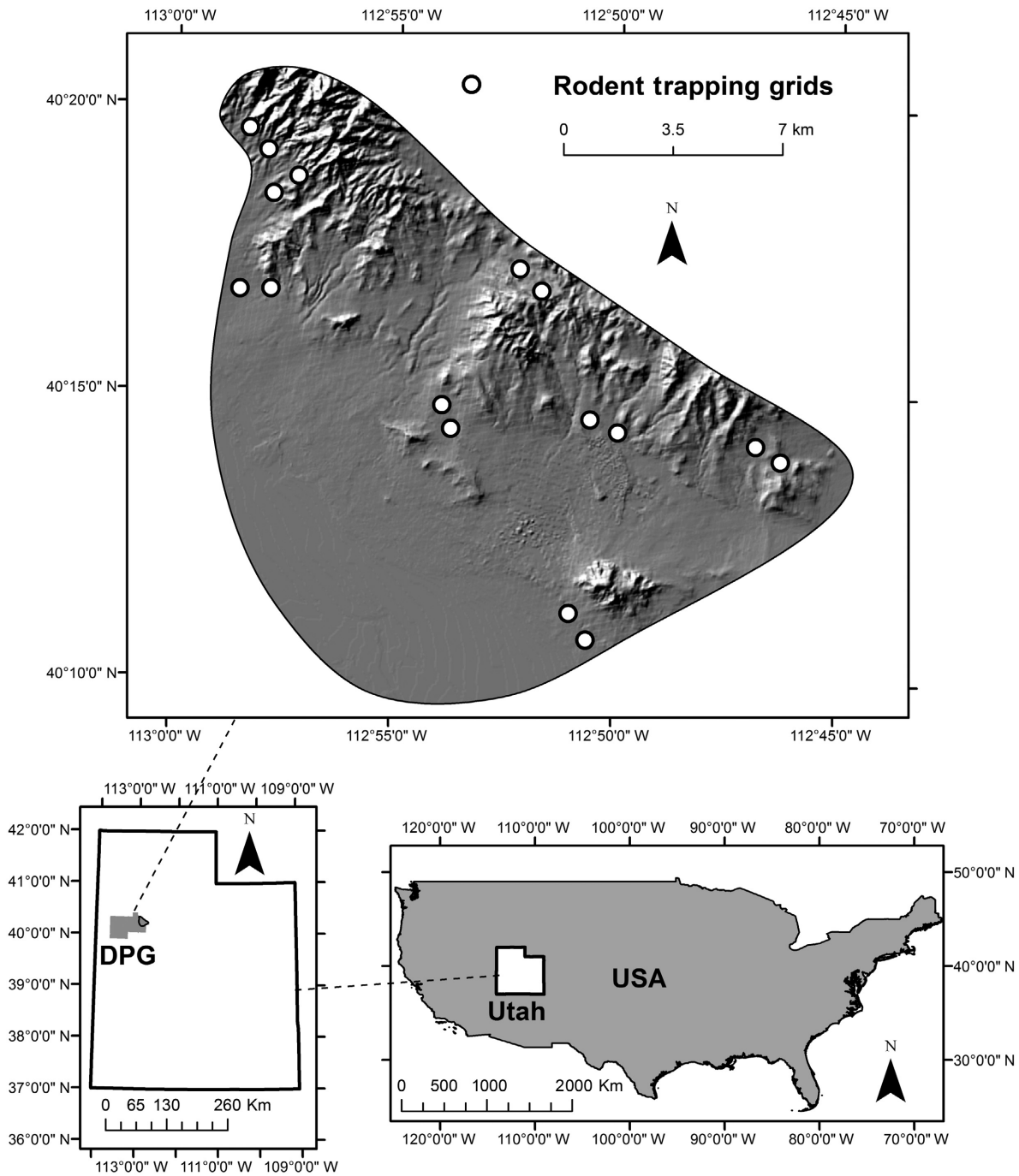


Fig. 1. Map of study area location, 16 rodent trapping grids, and area available for trapping grid selection on the U.S. Army Dugway Proving Ground (DPG), Utah, USA, 2010–2013.

least two trapping session taking place each summer: one in late spring/early summer (May 1–June 30) and the other in late summer/early autumn (August 1–September 30). In 2010 (year

one of the study), three sampling sessions were conducted at each site. We established a 7 × 7 trapping grid (49 traps per grid, 8.3 m spacing per trap) with Sherman live traps (Sherman

Traps, Tallahassee, Florida, USA) at each site. Because we were more interested in obtaining estimates of population state variables (i.e., abundance) at the scale of specific grids rather than an inventory of species at the landscape level, we followed the recommendations of Conrad et al. (2008) and used high-density Sherman livetraps (≤ 11 m spacing) and a moderate sampling duration (4 nights).

We baited traps with a mixture of black sunflower and mixed bird seed and identified and ear tagged each individual captured. Because moon brightness can influence foraging behavior and activity patterns of desert rodents (Kaufman and Kaufman 1982, Kotler et al. 2010, Upham and Hafner 2013), we recorded moon brightness for each trapping session as percent moon illuminated following the methods described by Upham and Hafner (2013). We estimated rodent abundance by calculating the minimum number of rodents known to be alive (MNA; the total number of unique individuals captured) at each trapping grid for each trapping session. MNA is commonly used as a measure of abundance in rodent investigations (Hall 2012, Freeman et al. 2014, Shenbrot 2014, Supp and Morgan Ernest 2014). Rodent abundance, a measure of the productivity of a community (i.e., the sum of abundances across a group of species), taxon, or species, is a commonly utilized metric in community ecology and is often used when investigating the impacts of disturbances on rodent communities (Ernest et al. 2000, Freeman et al. 2014, Supp and Morgan Ernest 2014, Kluever et al. 2016). In addition, for rodents, MNA has been shown to exhibit a strong association with probabilistic population estimators (Graipel et al. 2014).

Fieldwork was approved and sanctioned by the United States Department of Agriculture's National Wildlife Research Center and the United States Army's Dugway Proving Ground. Permission to access land on the Dugway Proving Ground was obtained from the United States Army. Capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees (IACUC) at the United States Department of Agriculture's National Wildlife Research Center (QA-1734) and Utah State University (#1438). All applicable institutional and/or national guidelines for the care and use of animals were followed.

Data analyses

Our data collection efforts resulted in an effective sample size of 144 sampling occasions (9 trapping sessions of 16 permanent sampling plots) available for analysis. We used the lme4 package in R (R Development Core Team 2018) to employ generalized linear mixed models (GLMMs) for the following response variables: total cricetid abundance, deer mouse (*Peromyscus maniculatus*) abundance, non-deer mouse cricetid abundance, heteromyid abundance, Ord's kangaroo rat (*Dipodomys ordii*) abundance, and non-Ord's kangaroo rat heteromyid abundance. We selected these response variables because our lack of capture data for the majority of species, primarily due to the rodent community being numerically dominated by two species (deer mouse and Ord's kangaroo rat), did not allow us to analyze each species individually. Our initial list of predictor variables included six continuous vegetation structure variables (i.e., percent cheatgrass cover, percent shrub cover, percent bare ground, mean plant height [cm], percent litter cover, and plant species richness), the continuous variable percent moon illumination, and the continuous variable Julian date; we included this final variable to account for possible within-year temporal effects. Because we were interested in testing for a non-linear relationship between abundance and non-native plant cover, a quadratic term (cheatgrass cover \times cheatgrass cover; Lind and Mehlum 2010, Zar 2010) was included as an additional predictor variable. Mean plant height, percent shrub cover, and percent litter cover were arcsine-square-root-transformed to improve normality (Zar 2010). We checked continuous variables for collinearity using correlational analysis and eliminated any one of a pair of variables with Pearson r indicating more than 30% correlation (Atwood et al. 2011, Ramsey and Schafer 2013, Kluever et al. 2016, Smith et al. 2017). Because the same 16 plots were sampled over time, plot was fit as a random effect in all GLMMs (Kluever et al. 2016, Smith et al. 2017); this allowed us to include data points that were not completely independent unique samples into our analytical framework. To improve model performance and fit, Julian date was square-root-transformed (Zar 2010) and the cheatgrass cover quadratic term was log-transformed.

Inspection of capture data revealed non-normality for each of the six examined rodent

groups: (1) total cricetid abundance, (2) deer mouse abundance, (3) non-deer mouse abundance, (4) total heteromyid abundance, (5) Ord's kangaroo rat abundance, (6) and non-Ord's kangaroo rat. As a result, we fit the following model families: lognormal, Poisson, quasi-Poisson, and negative binomial for each rodent grouping. Models that did not converge were eliminated, and we assessed remaining models based on the generalized chi-square fit statistic (Stroup 2012). For each rodent group, we then used the MuMIn package in R to run all possible additive model combinations of exploratory variables, based on a global model (Doherty et al. 2012). We used Akaike's information criteria corrected (AIC_c) for small sample size to select the best performing models, based on $\Delta AIC < 2$ and model weights (Anderson 2008) and averaged parameter estimates across them using the zero-method (Burnham and Anderson 2002). The relative importance, defined as the proportion a variable is selected as a predictor in the candidate model set (Beyene et al. 2009) and 95% confidence intervals (CI) were examined for each averaged parameter to determine its influence on our response variable (Grueber et al. 2011). Confidence intervals were derived using the MuMIn package in R. Only predictor variables that had both a relative importance of 1.00 and 95% CI not overlapping zero were considered influential (Sprayberry and Edelman 2018). Percent bare ground cover and litter were removed from all models due to $>30\%$ collinearity with percent cheatgrass cover (Atwood et al. 2011). Reported means, standard deviations (SDs), and standard errors for MNA were derived from the raw data, rather than model-driven estimates.

RESULTS

Captures

Between May 2010 and September 2013, we conducted nine trapping sessions, resulting in 144 total sampling occasions, and captured 2146 unique rodents over 28,224 trap nights. A total of 12 species were captured. Seven antelope ground squirrels (*Ammospermophilus leucurus*) were captured but excluded from analyses because this species is primarily diurnal and our sampling effort was focused on capturing nocturnal rodents. We captured 1637 individual

heteromyids across five species. In decreasing order of prevalence, the following heteromyids were captured: Ord's kangaroo rat ($n = 1423$; 87%), chisel-toothed kangaroo rat (*Dipodomys microps*, $n = 134$; 8%), long-tailed pocket mouse (*Chaetodipus formosus*, $n = 63$; 4%), Great Basin pocket mouse (*Perognathus parvus*, $n = 16$; 1%), and little pocket mouse (*Perognathus longimembris*, $n = 1$; $<1\%$). Abundance of heteromyids averaged 11.36 individuals per plot/session (SD = 9.52) and ranged from 0 to 44. Abundance of Ord's kangaroo rat and other species of heteromyids pooled averaged 9.88 (SD = 9.94, range 0–40) and 1.49 individuals per plot/session (SD = 2.34, range 0–13), respectively.

We captured 502 individual cricetids across six species. In decreasing order of prevalence, the following cricetids were captured: deer mouse ($n = 375$; 75%), northern grasshopper mouse (*Onychomys leucogaster*, $n = 63$; 11%), western harvest mouse (*Reithrodontomys megalotis*, $n = 48$; 10%), desert woodrat (*Neotoma lepida*, $n = 9$; 2%), piñon mouse (*Peromyscus truei*, $n = 6$; 1%), and sagebrush vole (*Lemmiscus curtatus*, $n = 1$; $<1\%$). Abundance of cricetids averaged 3.48 individuals per plot/session (SD = 4.24) and ranged from 0 to 20. Abundance of deer mice and other species of cricetids pooled averaged 2.60 (SD = 3.52, range 0–19) and 0.88 (SD = 1.47, range 0–10), respectively.

Vegetation sampling

We detected 119 unique plant species during vegetation sampling efforts. Cheatgrass cover averaged 41.2% (SD = 26.19) and ranged from 3% to 98%. Moon illumination averaged 52.1% (SD = 33.34) and ranged from 0.20% to 98%. Plant height averaged 24.35 cm (SD = 11.82) and ranged from 5.76 to 69.42 cm. Shrub cover averaged 9.81% (SD = 11.84) and ranged from 0% to 36.93%. In decreasing order of abundance, the following plant species were encountered: cheatgrass (*B. tectorum*, 59.5%), big sagebrush (*Artemisia tridentata*, 7.48%), tall tumble mustard (*Sisymbrium altissimum*, 6.97%), Russian thistle (*Salsola kali*, 5.02%), *Poa* spp. (2.93%), and Indian rice grass (*Achnatherum hymenoides*, 1.90%).

Abundance of heteromyids in relation to predictor variables

The best performing models for heteromyid abundance included up to seven predictor

variables, but only the cheatgrass quadratic term, percent moon illumination, and Julian date had a relative importance of 1.00 and 95% CI that did not span zero (Tables 1, 2). Julian date appeared to have a positive influence on heteromyid abundance, whereas moon illumination appeared to have a negative effect. We found evidence that abundance of heteromyids was negatively influenced by cheatgrass cover in a non-linear fashion (Tables 1, 2, Fig. 2). The best performing models for Ord's kangaroo rat included the same seven predictor variables as the model containing all species (Table 3). Number of shrubs was not included as predictor variable in the other heteromyid species models. For Ord's kangaroo rats, we found that the cheatgrass quadratic term, moon illumination, and Julian date had a relative

importance of 1.00 and 95% CI that did not span zero (Table 4). For the other heteromyid species models, only Julian date and percent moon illumination had both a relative importance of 1.00 and 95% CI that did not span zero (Table 4). As a result, we found evidence that abundance of Ord's kangaroo rats, but not other heteromyids, was negatively influenced by cheatgrass cover in a non-linear fashion (Fig. 2).

Abundance of cricetids in relation to predictor variables

The best performing models for cricetid abundance included a maximum of seven predictor variables, but only cheatgrass cover, plant species richness, and Julian date had a relative importance of 1.00 and 95% CI that did not span

Table 1. Results from best performing generalized linear mixed models in AIC_c model selection used to separately explore factors influencing cricetid and heteromyid abundance at the U.S. Army Dugway Proving Ground, Utah, 2010–2013.

Model	ΔAIC _c	W _i	K	ER
Cricetid abundance				
<i>Cheatgrass, moon, richness, Julian date</i>	0.00	0.17	5	1.00
<i>Cheatgrass, cheatgrass × cheatgrass, moon, richness, Julian date, height</i>	0.11	0.16	7	1.05
<i>Cheatgrass, moon, richness, Julian date, height, shrub</i>	0.31	0.14	7	1.17
<i>Cheatgrass, cheatgrass × cheatgrass, moon, richness, Julian date, shrub, height</i>	1.08	0.09	8	1.72
Heteromyid abundance				
<i>Cheatgrass × cheatgrass, moon, Julian date, cheatgrass</i>	0.00	0.13	5	1.00
<i>Cheatgrass × cheatgrass, moon, Julian date, shrub</i>	1.37	0.07	5	1.98
<i>Cheatgrass × cheatgrass, moon, Julian date, shrub, cheatgrass</i>	1.73	0.06	6	2.37
<i>Cheatgrass × cheatgrass, moon, Julian date, shrub, richness, height</i>	1.97	0.05	7	2.67

Notes: AIC_c, Akaike's information criteria corrected; K, number of parameters (including intercept); W_i, model weight; ER, evidence ratio. Models shown are best performing models based on ΔAIC < 2. Italicized predictor variables are those with a relative importance of 1. The relative importance is the frequency in which the variable occurred in the top models; moon = % moon illumination, richness = plant species richness, date = Julian date for the onset of each trapping session × trapping grid event, shrub = % shrub cover, height = mean plant height (cm; n = 144 sampling occasions).

Table 2. Model averaging results of top linear regression models (ΔAIC < 2) for factors influencing abundance of heteromyids and cricetids at the U.S. Army Dugway Proving Ground, Utah, 2010–2013.

Parameter	Cricetids			Heteromyids		
	Estimate	95% CI	RI	Estimate	95% CI	RI
Cheatgrass	-0.0227	-0.0372, -0.0083	1.00	-0.0085	-0.5768, 0.1702	0.50
Cheatgrass × cheatgrass	0.1445	-0.1342, 0.766	0.50	0.2562	0.0436, 0.6663	1.00
Height	-0.0134	-0.0253, 0.0016	0.75	-0.0004	-0.0080, 0.0041	0.25
Moon	-0.3745	-0.6937, 0.0553	1.00	-0.4505	-0.6292, -0.0017	1.00
Richness	0.0766	0.0326, 0.1207	1.00	0.0108	-0.0121, 0.0034	0.25
Julian date	-0.2966	-0.3829, -0.2102	1.00	0.1045	0.0039, 0.0708	1.00
Shrubs	0.0172	-0.0093, 0.0439	0.50	-0.0228	-0.0439, -0.0020	0.75

Notes: AIC, Akaike's information criteria; CI, confidence interval.

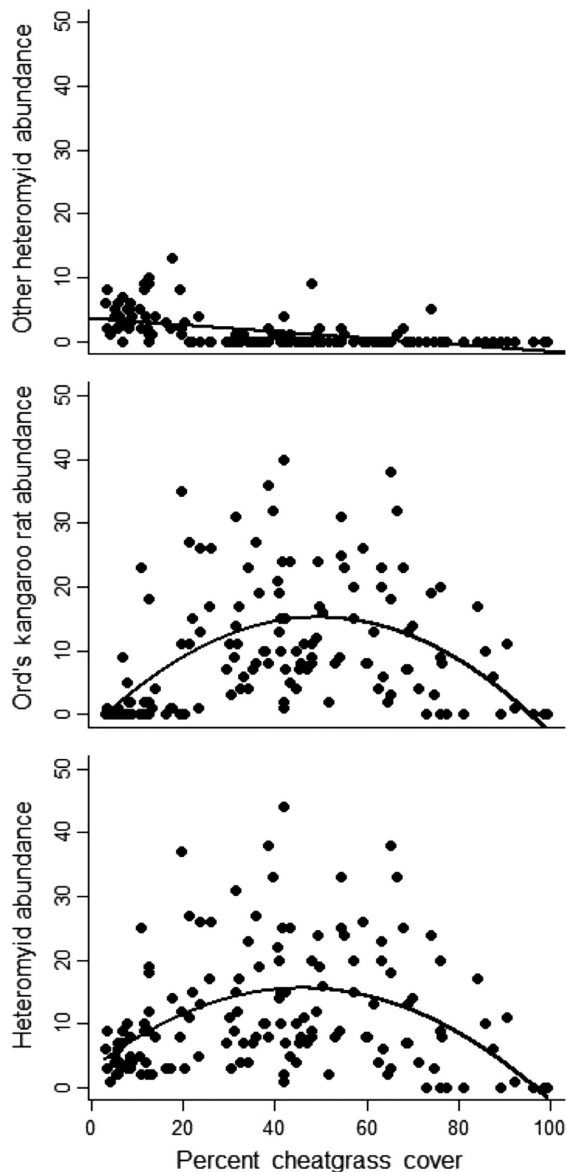


Fig. 2. Scatterplot exhibiting relationship between abundance of all heteromyids, Ord's kangaroo rats (*Dipodomys ordii*), and non-Ord's kangaroo rat heteromyids pooled in relation to percent cheatgrass cover on the U.S. Army Dugway Proving Ground, Utah, USA, 2010–2013 ($n = 144$ data points).

zero (Tables 1, 2). Cheatgrass cover and Julian date appeared to negatively influence cricetid abundance, whereas plant species richness appeared to have a positive influence (Table 2). The best performing models for deer mouse only included the same seven predictor variables as

the model containing all species (Table 5). Plant height was not included as a predictor variable in the other cricetid species models. For deer mice, we found that only cheatgrass cover, plant species richness, and Julian date had a relative importance of 1.00 and 95% CI that did not span zero (Tables 5, 6). Similar to the models for all cricetids, cheatgrass cover and Julian date appeared to have a negative influence on deer mice abundance, whereas plant species richness appeared to have a positive influence (Table 6). For other cricetid species, cheatgrass cover and moon illumination had a relative importance of 1.00 and 95% CI that did not span zero (Tables 5, 6); both of these predictor variables appeared to negatively influence the abundance of this grouping (Table 6). Both deer mice and other cricetid species appeared to be negatively influenced by cheatgrass in a similar manner (Fig. 3).

DISCUSSION

Our study revealed that cheatgrass encroachment did not affect all groupings of rodents in a uniform manner. Abundance of all rodent groups did ultimately become depressed when cheatgrass cover reached high levels, and for all rodent groups and species other than Ord's kangaroo rat, this relationship was negative and linear. We observed a non-linear relationship for heteromyids that was driven by Ord's kangaroo rats, where abundance was positively associated with increases in cheatgrass cover, reached a threshold at intermediate levels of cheatgrass cover, and then exhibited a negative response (Fig. 2).

This finding for Ord's kangaroo rats is not entirely unique for rodents. For example, Cerdini and Chalfoun (2017b) observed that deer mice abundance increased marginally with cheatgrass abundance. In addition, Pearson and Fletcher (2008) and Malick et al. (2012) observed that spotted knapweed (*Centaurea maculosa*) bolstered abundance of rodents by indirectly increasing food resources. Malo et al. (2012) found that an invasive shrub bolstered abundance of wood mice (*Apodemus sylvaticus*) by reducing predation risk from avian predators. Similar patterns with respect to invasive plants have been observed in the avian literature when entire communities (Fischer et al. 2012, MacGregor-Fors et al. 2013) or

Table 3. Results from best performing generalized linear mixed models in AIC_c model selection used to separately explore factors influencing abundance of Ord’s kangaroo rats (*Dipodomys ordii*) and remaining heteromyid species pooled at the U.S. Army Dugway Proving Ground, Utah, 2010–2013.

Model	ΔAIC _c	W _i	K	ER
Ord’s kangaroo rat abundance				
<i>Cheatgrass</i> × <i>cheatgrass</i> , <i>moon</i> , <i>Julian date</i> , <i>shrub</i>	0.00	0.17	5	1.00
<i>Cheatgrass</i> × <i>cheatgrass</i> , <i>cheatgrass</i> <i>Julian date</i> , <i>moon</i> , <i>shrub</i>	0.51	0.14	6	1.29
<i>Cheatgrass</i> × <i>cheatgrass</i> , <i>moon</i> , <i>richness</i> , <i>Julian date</i> , <i>shrub</i> , <i>height</i>	1.33	0.09	7	1.94
<i>Cheatgrass</i> × <i>cheatgrass</i> , <i>cheatgrass</i> , <i>moon</i> , <i>richness</i> , <i>Julian date</i>	1.69	0.07	6	2.33
<i>Cheatgrass</i> × <i>cheatgrass</i> , <i>cheatgrass</i> , <i>moon</i> , <i>richness</i> , <i>Julian date</i> , <i>shrub</i> , <i>height</i>	1.80	0.06	8	2.46
Other heteromyids abundance				
<i>Cheatgrass</i> , <i>moon</i> , <i>Julian date</i>	0.00	0.11	4	1.00
<i>Moon</i> , <i>Julian date</i>	0.11	0.10	3	1.06
<i>Cheatgrass</i> <i>moon</i> , <i>Julian Date</i> , <i>shrub</i>	0.90	0.07	5	1.57
<i>Cheatgrass</i> , <i>cheatgrass</i> × <i>cheatgrass</i> , <i>moon</i> , <i>Julian date</i> , <i>shrub</i>	1.59	0.05	6	2.21
<i>Cheatgrass</i> , <i>cheatgrass</i> × <i>cheatgrass</i> , <i>moon</i> , <i>Julian date</i> , <i>richness</i>	1.87	0.04	6	2.55

Notes: See Table 1 for further detail.

Table 4. Model averaging results of top linear regression models (ΔAIC < 2) for factors influencing abundance of Ord’s kangaroo rat and other heteromyid species pooled at the U.S. Army Dugway Proving Ground, Utah, 2010–2013.

Parameter	Ord’s kangaroo rat			Other heteromyids		
	Estimate	95% CI	RI	Estimate	95% CI	RI
Cheatgrass	-0.0070	-0.0222, 0.0004	0.40	-0.0259	-0.0506, -0.0013	0.80
Cheatgrass × cheatgrass	<i>0.2872</i>	<i>0.0851, 0.4893</i>	<i>1.00</i>	0.2378	-0.0114, 0.4896	0.40
Height	-0.0003	-0.0082, 0.0041	0.40	*	*	*
Moon	-0.4265	-0.6155, -0.2376	1.00	-0.7948	-1.3184, -0.2713	1.00
Richness	0.0036	-0.012, 0.0036	0.60	0.0020	-0.0389, -0.0953	0.20
Julian date	<i>0.0856</i>	<i>0.0504, 0.1209</i>	<i>1.00</i>	<i>0.2924</i>	<i>0.185, 0.4000</i>	<i>1.00</i>
Shrubs	-0.0172	-0.0910, -0.0159	0.80	-0.0228	-0.0452, 0.0163	0.40

Notes: AIC, Akaike’s information criteria corrected. Averaged estimate, 95% confidence interval (CI), and relative importance (RI) for each parameter are shown and parameters deemed as influential to rodent abundance italicized.

*Represents a parameter that was not included in any of the top regression models.

Table 5. Results from best performing generalized linear mixed models in AIC_c model selection used to separately explore factors influencing abundance of deer mice (*Peromyscus maniculatus*) and remaining cricetid species pooled at the U.S. Army Dugway Proving Ground, Utah, 2010–2013.

Model	ΔAIC _c	W _i	K	ER
Deer mouse abundance				
<i>Cheatgrass</i> , <i>cheatgrass</i> × <i>cheatgrass</i> , <i>height</i> , <i>richness</i> , <i>Julian date</i>	0.00	0.21	6	1.00
<i>Cheatgrass</i> , <i>height</i> , <i>richness</i> , <i>Julian date</i>	0.58	0.15	5	1.34
<i>Cheatgrass</i> , <i>height</i> , <i>richness</i> , <i>Julian date</i> , <i>shrub</i>	0.68	0.15	6	1.40
<i>Cheatgrass</i> , <i>cheatgrass</i> × <i>cheatgrass</i> , <i>height</i> , <i>richness</i> , <i>Julian date</i> , <i>shrub</i>	0.92	0.13	7	1.58
<i>Cheatgrass</i> , <i>cheatgrass</i> × <i>cheatgrass</i> , <i>height</i> , <i>richness</i> , <i>Julian date</i> , <i>moon</i>	1.41	0.11	7	2.02
<i>Cheatgrass</i> , <i>height</i> , <i>richness</i> , <i>Julian date</i> , <i>moon</i>	1.82	0.08	6	2.48
<i>Cheatgrass</i> , <i>richness</i> , <i>Julian date</i> , <i>shrub</i> , <i>moon</i>	1.89	0.08	6	2.57
Other cricetids abundance				
<i>Cheatgrass</i> , <i>height</i> , <i>moon</i>	0.00	0.19	4	1.00
<i>Cheatgrass</i> , <i>cheatgrass</i> × <i>cheatgrass</i> , <i>height</i> , <i>moon</i>	1.78	0.08	5	2.45
<i>Cheatgrass</i> , <i>height</i> , <i>moon</i> , <i>shrub</i>	1.80	0.08	5	2.46
<i>Cheatgrass</i> , <i>height</i> , <i>moon</i> , <i>Julian date</i>	1.85	0.07	5	2.53
<i>Cheatgrass</i> , <i>moon</i> , <i>richness</i> , <i>Julian date</i>	1.97	0.05	5	2.67

Note: See Table 1 for further detail.

Table 6. Model averaging results of top linear regression models ($\Delta AIC < 2$) for factors influencing abundance of deer mouse and other cricetid species pooled at the U.S. Army Dugway Proving Ground, Utah, 2010–2013.

Parameter	Deer mouse			Other cricetids		
	Estimate	95% CI	RI	Estimate	95% CI	RI
Cheatgrass	<i>-0.0226</i>	<i>-0.0395, -0.0056</i>	<i>1.00</i>	<i>-0.01923</i>	<i>-1.2211, 1.8292</i>	<i>1.00</i>
Cheatgrass × cheatgrass	0.1934	-0.1029, 0.8995	0.43	0.6567	-0.3006, 1.6140	0.20
Height	-0.0247	-0.0402, 0.0057	0.71	<i>0.0283</i>	<i>0.0105, 0.0460</i>	<i>1.00</i>
Moon	-0.1812	-0.5507, 0.1875	0.43	<i>-1.6278</i>	<i>-2.2755, -0.9080</i>	<i>1.00</i>
Richness	<i>0.0872</i>	<i>0.0355, 0.1389</i>	<i>1.00</i>	0.0234	-0.0567, 0.1036	0.20
Julian date	<i>-0.2710</i>	<i>-0.3496, -0.1923</i>	<i>1.00</i>	-0.0064	-0.1719, 0.0897	0.40
Shrubs	0.0204	-0.0097, 0.0504	0.43	0.0113	-0.0452, 0.0163	0.20

Notes: AIC, Akaike's information criteria corrected. Averaged estimate, 95% confidence interval (CI), and relative importance (RI) for each parameter are shown and parameters deemed as influential to rodent abundance italicized.

foraging guilds (French and Zubovic 1997) are examined. However, with regard to Ord's kangaroo rats in particular, our finding appears to be novel and runs contrary to those of Litt and Steidl (2011), who found that heteromyid abundance decreased in a linear fashion as cover of a non-native grass increased. That investigations on exotic grasses and rodents can clearly affect the same species or groups differently across space (i.e., study areas) underscores the importance to not extrapolate inference beyond study areas.

Our finding of a non-linear association for Ord's kangaroo rat abundance in relation to cheatgrass may be attributed to several factors. First, Ord's kangaroo rats have been shown to both cache and consume cheatgrass seeds (McMurray et al. 1997, Jenkins and Breck 1998). Despite the low quality of this food source (Kelrick et al. 1986, Freeman et al. 2014) and a demonstrated preference by several species of rodents for seeds from native grasses (Kelrick et al. 1986, Lucero et al. 2015), the sheer quantity of cheatgrass seeds may have allowed Ord's kangaroo rats to better engage in both scatter-hoarding and larder-hoarding (White 2008), resulting in increased reproductive output, survival, and/or relaxed competition (Schroder and Rosenzweig 1975), all of which could have promoted higher rodent abundance. Horn et al. (2012) observed areas containing higher levels of invasive grasses contained a greater abundance of Merriam's kangaroo rats (*Dipodomys merriami*) when compared to areas dominated by native vegetation. This pattern however was not detected for the less abundant Ord's kangaroo rat, a sympatric competitor (Lima et al. 2008).

Though the pocket mice species we investigated also engage in scatter-hoarding and can hoard and consume cheatgrass seeds (Schreiber 1978) our findings suggest these species do not benefit from cheatgrass establishment in this system. Chisel-toothed kangaroo rats were likely not able to confer the same benefits of cheatgrass as Ord's kangaroo rats because they are primarily folivores, though this species does possess the ability to supplement their diet with seeds (Hayssen 1991, Jenkins and Breck 1998). Litt and Steidl (2011) found a similar non-linear relationship to ours for heteromyids and an invasive grass, but their response variable was species richness rather than abundance. At moderate levels of cheatgrass invasion, more inter-shrub space can be created without eliminating the entire shrub component as a result of low-intensity wildfires (Young et al. 1987), and these inter-shrub areas can be better exploited by bipedal rodents, such as Ord's and chisel-toothed kangaroo rats, than by quadrupeds (Thompson 1982, Freeman et al. 2014).

It has been long hypothesized that bipedalism in desert rodents developed as a means to better avoid predators (Hafner 1993, Kotler et al. 1994, Degen 1997). Recently, by combining field trials, laboratory experiments, and entropy calculations, Moore et al. (2017) revealed that movement/gait trajectories of bipedal jerboas (family Dipodidae) were more unpredictable than those of sympatric quadrupedal rodents, and as a result, these bipedal rodents could better evade predators that hunt using a pre-calculated intercept course (Moore et al. 2017). It has also been reported that some quadrupedal heteromyid

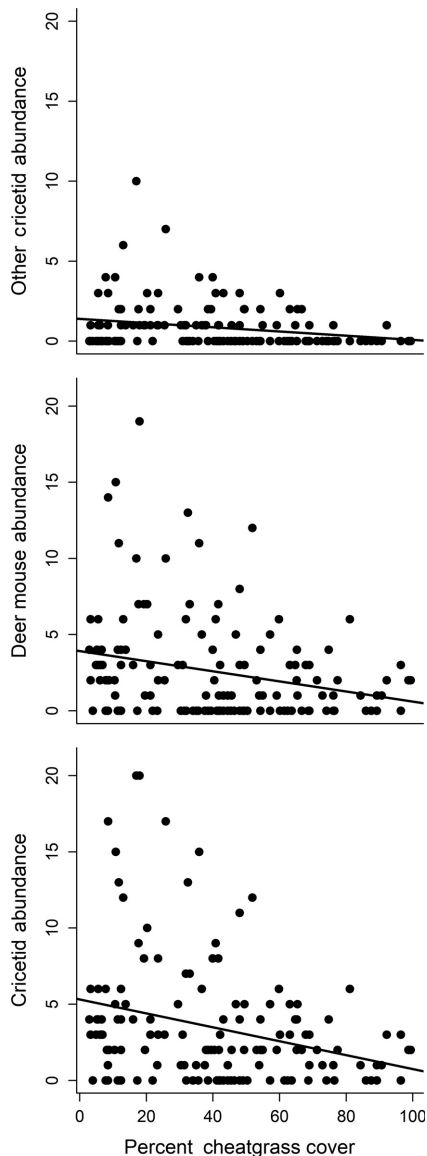


Fig. 3. Scatterplot exhibiting relationship between abundance of all cricetids, deer mice (*Peromyscus maniculatus*), and non-deer mice cricetids pooled in relation to percent cheatgrass cover on the U.S. Army Dugway Proving Ground, Utah, USA, 2010–2013 ($n = 144$ data points).

rodents, including the three species of pocket mice we investigated, more effectively rely on ricochet, erratic jumping as an effective means of escaping predators when compared to other quadrupedal rodents such as deer mice (Degen 1997). In our study area, if the heteromyid rodent

species we investigated were more effective at avoiding predators than sympatric cricetids, it could be expected that heteromyids would suffer less predator-caused mortality, at least initially, if rodent predation risk generally increases as cheatgrass becomes more pervasive. Our findings suggest that, in our study area, Ord's kangaroo rats may be able to escape predation more effectively than other heteromyid species and cricetids.

We speculate the subsequent decrease in abundance of Ord's kangaroo rats following a threshold at intermediate levels of cheatgrass invasion was likely caused by a cumulative effect brought about by decreased forage diversity and quality, obstruction and hindrance of movement, and raised predation risk that this species could not cope with after cheatgrass became the dominant plant feature, changing the affected areas to monocultures with ostensibly no shrub component (Reisner et al. 2013). We speculate that other researchers conducting rodent-cheatgrass investigations in the Great Basin Desert have not observed a similar threshold pattern because these works occurred in areas where deer mice were by far the most abundant species during data collection efforts (Ostoja and Schupp 2009, Freeman et al. 2014). Clearly, a better determination of the biotic and abiotic factors and conditions responsible for whether heteromyids or cricetids numerically dominate a particular rodent population is needed and could be achieved with a more robust experimental design.

Our observation of a negative linear trend for abundance of cricetids in relation to cheatgrass cover is in agreement with the majority of investigations examining effects of cheatgrass on rodents at the individual species (Hall 2012) and community levels (Ostoja and Schupp 2009, Freeman et al. 2014, but see Ceradini and Chalfoun 2017b). The species comprising the family Cricetidae in our study area represented several foraging guilds (e.g., granivores, folivores, and carnivores), but were similar in that they were all relatively small and reliant upon quadrupedal motion. Cheatgrass encroachment likely affects rodents in a host of direct and indirect ways, including reducing quality of available forage (Kelrick et al. 1986), increasing obstruction to mobility (Rieder et al. 2010), and decreasing vegetation structural heterogeneity (Freeman et al.

2014). We suspect that each of these factors, and possibly indirect effects receiving less attention, such as increased predation risk (Mattos and Orrock 2010, Ceradini and Chalfoun 2017b), was responsible for a reduction in abundance of cricetids. For example, it has been speculated that the cricetid species we investigated are more vulnerable to predation because they do not engage in long ricochet, erratic jumping as a means of escaping predators (Degen 1997), though this groups' preference for more closed habitat types likely also influences their locomotor style. Deer mice were by far the most abundant cricetid species we encountered. Previous cheatgrass studies occurring in the Great Basin Desert and focusing entirely on this species (Hall 2012) or communities numerically dominated by this species (Freeman et al. 2014) reported similar findings of a negative linear relationship between cheatgrass prevalence and rodent abundance.

We found that Julian date and plant species richness influenced abundance of cricetids, but that these predictor variables appeared to influence deer mice more so than other species of this family. The role of temporal factors on rodent abundance has been explored across years or seasons (Ernest et al. 2000, Kluever et al. 2016), but to our knowledge, examining and accounting for an intra-seasonal effect is often overlooked or disregarded. We suspect that Julian date negatively influenced abundance of deer mice for several reasons. First, as the calendar year progressed, resources may have become increasingly limited, which in turn impacted reproductive productivity. Second, predation risk may have increased over time, as the number of potential rodent predators on the landscape may have increased toward the end of the summer; this time period coincides with independence of offspring (i.e., increased hunting intensity/predators) and dispersal of both mammalian and avian predators in our study system.

That Julian date appeared to not influence other species of cricetids in a similar manner suggests that in our system temporal variation can influence species population dynamics differently, as has been revealed for rodents in other systems (Rocha et al. 2017).

Moon phase did not appear to influence abundance or activity patterns of cricetids during our study, but this finding appeared to be driven by

deer mice. Although several investigations have revealed moon effects for rodents (see Prugh and Golden 2014 for review), our finding is similar to the conclusion of Upham and Hafner (2013) that activity patterns of cricetids in the Great Basin Desert are not markedly governed by moonlight. Our finding of moon phase having a stronger effect on cricetid species other than deer mice may have been driven by northern grasshopper mice, which has been shown to reduce activity patterns in the presence of pronounced moonlight (Jahoda 1973). Our finding of plant richness positively influencing abundance of deer mice exclusively may be attributed to plant species richness being a good indicator of overall habitat quality for this species, which can take advantage of myriad sources of forage (Johnson 1961).

Our study, like most cheatgrass-rodent investigations to date, was observational in nature, hampering our ability to establish causality or completely parse the underlying mechanisms driving our findings. In addition, our study did not encapsulate all vegetation cover classes that comprise the Great Basin Desert (e.g., greasewood-dominated shrubland). Further, we were unable to explicitly account for capture probability (White 2005) in our analyses due to insufficient captures in relation to the number of exploratory variables we felt necessary to include in our global model; attempts to do so led to model non-convergence. Our models included both Julian date and moon phase, which helped control for climatic and moon variables that can influence capture probability. In addition, our sampling design, which called for sampling the same plots over time, further justified the use of MNA as a surrogate of absolute abundance, as capture probability issues were likely less influential than if plots were spatially unique during each trapping session. Despite these limitations, we feel our study reveals the potential importance of parsing rodents by various groups when examining the effects of disturbance on rodent communities. As such, we recommend future cheatgrass-rodent investigations incorporate a more robust experimental design than employed here and in previous works. For example, tracking rodent population state variables and vital rates prior to and following fluctuations of cheatgrass cover, in both controlled and observational settings, should enhance our understanding of

cheatgrass-rodent dynamics. Further, future investigation could be improved upon by collecting field data in a manner that allows for validation of models generated from cheatgrass-rodent investigations. There is also a clear need to further investigate whether and/or to what extent cheatgrass invasion influences predation on rodents and rodent anti-predator behavior.

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