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The influence of wildlife water developments and vegetation on rodent abundance in the Great Basin Desert

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Rodent communities have multiple functions including comprising a majority of the mammalian diversity within an ecosystem, providing a significant portion of the available biomass consumed by predators, and contributing to ecosystem services. Despite the importance of rodent communities, few investigations have explored the effects of increasing anthropogenic modifications to the landscape on rodents. Throughout the western United States, the construction of artificial water developments to benefit game species is commonplace. While benefits for certain species have been documented, several researchers recently hypothesized that these developments may cause unintentional negative effects to desert-adapted species and communities. To test this idea, we sampled rodents near to and distant from wildlife water developments over 4 consecutive summers. We employed an asymmetrical before-after-control-impact (BACI) design with sampling over 4 summers to determine if water developments influenced total rodent abundance. We performed an additional exploratory analysis to determine if factors other than free water influenced rodent abundance. We found no evidence that water developments impacted rodent abundance. Rodent abundance was primarily driven by vegetation type and year of sampling. Our findings suggested that water developments on our study area do not represent a significant disturbance to rodent abundance and that rodent abundance was influenced by the vegetative community and temporal factors linked to precipitation and primary plant production. Our findings represent one of the 1st efforts to determine the effects of an anthropogenic activity on the rodent community utilizing a manipulation design.

Key words: arid, guzzlers, indirect effect, precipitation, small mammal, total abundance, vegetation cover

Rodents comprise a majority of the mammalian diversity within most ecosystems (Merritt 2010; Jones and Safi 2011; Feldhamer et al. 2015), provide a significant portion of the available biomass consumed by predators (Andersson and Erlinge 1977; Sieg 1987), and can influence the structure and composition of vegetation communities (Sieg 1987; McMurray et al. 1997). In addition, recent investigations have found that rodent assemblages contribute to ecosystem services such as encouraging groundwater recharge, decreasing soil erosion, promoting soil productivity potential, and promoting soil carbon storage (Longland and Ostaja 2013; Martinez-Estevez et al. 2013). Factors reported to influence rodent communities include predation (Stapp 1997; Henke and Bryant 1999; Shenbrot 2014), competition (Heske et al. 1994; Stokes et al. 2009; Shenbrot 2014), precipitation and primary productivity (Ernest et al. 2000; Thibault et al. 2010; Shenbrot 2014), vegetation characteristics (Whitford and Steinberger 1989; Hernandez et al. 2005; Thompson and Gese 2013), and both natural and anthropogenic disturbances (Ramirez and Hornocker 1981; Medin and Clary 1989; Kutiel et al. 2000). Of these factors, anthropogenic disturbances are receiving ever-increasing attention due to their growing pervasiveness on many natural landscapes.

Many investigations have revealed negative effects on rodent communities from a host of anthropogenic disturbances, including urbanization (e.g., Umetsu and Pardini 2007; Shenko et al. 2012), livestock grazing (e.g., Medin and Clary 1989), predator removal (e.g., Henke and Bryant 1999), and military training activities (e.g., Shenko et al. 2012). Conversely, disturbances such as wind farm construction (e.g., de Lucas et al. 2005) and roads and road traffic have been shown to have benign or positive effects (e.g., Bissonette and Rosa 2009; Rotholz and Mandelik 2013), but see Mallick et al. (1998) and Ashley

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and Robinson (1996) for examples of negative road effects on rodents. The variability of the effects of anthropogenic disturbance on rodent communities suggests that a myriad of ecological processes are likely at play, disturbances may have direct or indirect effects on communities, species comprising a community may be effected differently, and similar types of disturbances may not have an effect on communities occurring in different areas in the same fashion. For example, Shenko et al. (2012) found military training to have negatives effects, while Thompson and Gese (2013) found benign and positive effects. Hence, there may be a need to limit inference outside the scope of site-specific investigations and address the role of specific anthropogenic disturbances on rodent communities on a case-by-case basis, and when possible, incorporate sampling designs that allow studies to go beyond a purely observational nature. One type of anthropogenic modification to the landscape that has been suggested as a possible disturbance in arid environments is artificial water developments (hereafter water developments) that were constructed to benefit certain wildlife species.

Free water has been reported as a key limiting factor on individual species and communities (Leopold 1933), especially in arid systems (Rosenstock et al. 1999; Krausman et al. 2006). As a result, the construction and maintenance of water developments in arid regions of the United States is a common practice. The intent of such developments is the addition of free water on a landscape to increase populations, influence animal movements, redistribute wildlife species, and facilitate livestock grazing (Simpson et al. 2011; Larsen et al. 2012). Water developments aimed at benefiting wildlife almost exclusively target game species (e.g., game birds, ungulates—Simpson et al. 2011; Larsen et al. 2012). At the end of the last century, 10 of 11 western United States state wildlife agencies reported ongoing water development programs with combined annual expenditures > $1,000,000 US dollars (Rosenstock et al. 1999), and as of 2012, nearly 7,000 water developments had been constructed in the western United States (Larsen et al. 2012). Furthermore, water developments have been utilized as a mitigation technique to offset the effect of military activities (Broyles 1995). Larsen et al. (2012) forecasted the importance of water developments will increase as a conservation and management tool in the western United States. Though water developments are unique in that they are explicitly constructed to benefit certain targeted species, they also represent a potential disturbance on the landscape.

Positive or benign effects of water developments have been reported for populations of several game species (see Simpson et al. 2011; Larsen et al. 2012 for reviews) but in recent years, researchers have hypothesized that water developments may negatively influence communities indirectly. Proposed indirect negative effects include spreading disease, encouraging exotic species, or negatively influencing nongame populations not dependent on free water by increased predation or predation risk (Broyles 1995; DeStefano et al. 2000; Rosenstock et al. 2004; Simpson et al. 2011). This notion that the addition of free water on arid landscapes negatively affects desert-adapted species is known as the indirect effect of water hypothesis (Hall et al. 2013). Investigations testing the indirect effect of water hypothesis are rare, especially at the community level. DeStefano et al. (2000) suggested the leporid community was negatively influenced in areas near water developments due to increased presence of mammalian and avian carnivores. Indeed, carnivorous mammal and avian species known to regularly prey upon rodents have been documented to regularly visit water developments during the summer months in arid environments (Rosenstock et al. 2004; O'Brien et al. 2006; Hall et al. 2013). Conversely, Cutler and Morrison (1998) found no evidence water developments affected the relative abundance of rodents or reptiles.

To date, no investigations have tested the indirect effect of water hypothesis on rodent communities using either long-term monitoring (i.e., > 2 years) or an experimental/manipulative study design. Whether rodent communities are indirectly affected by water developments may help guide future management decisions for wildlife management agencies and conservation organizations, especially in arid areas where communities include rare or imperiled species, or when rodents comprise the primary food source for rare or imperiled carnivores. The overall objective of our study was to elucidate the indirect effects of water developments on the rodent community in a cold desert ecosystem. Specifically, we used both an observational and before-after-control-impact (BACI) design to determine 1) whether total abundance of rodents is different near to or away from active water developments and 2) whether removal of water developments affects the total abundance of rodents.

Materials and Methods

Study area.—We conducted our research on 879 km^2 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, United States. Elevations ranged from 1,302 m to 2,137 m. The study site was in the Great Basin and was characterized as a cold desert (Arjo et al. 2007). Winters were cold, summers were hot and dry, with the majority of precipitation occurring in the spring.

Annual weather, derived from daily averages, consisted of mean air temperatures of 12.69°C (range: −20.02°C to 40.58°C) and mean precipitation of 20.99 cm (range: 14.71 to 29.38; U.S. Army Dugway Proving Ground, Meteorological Division). The study area consisted of predominately flat playa punctuated with steep mountain ranges. The lowest areas consisted of sparsely vegetated salt playa flats. Slightly higher elevation areas supported a cold desert chenopod shrub community. At similar elevations, shrub communities dominated by greasewood (*Sarcobatus vermiculatus*) were found. Mid elevations consisted of vegetated sand dunes. Near the bases of the higher steep mountains were shrub steppe communities of sagebrush (*Artemisia* sp.). The highest elevations consisted of Utah juniper (*Juniperus osteosperma*) community including black sagebrush (*Artemisia nova*) and bluebunch wheatgrass (*Pseudoroegneria spicatus*). Where wildfires had occurred along the foothills, cheatgrass (*Bromus tectorum*), tall tumble-mustard (*Sisymbrium altissimum*), and Russian thistle (*Salsola kali*) had invaded

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communities of sagebrush, rabbitbrush (*Chrysothamnus* sp.), and juniper (Arjo et al. 2007).

The study area contained 8 artificial water developments installed during 1970–1990. Impacts to vegetation near these water developments were minimal due to fencing that excluded livestock and feral horses (Beever and Brussard 2004; Evans et al. 2016) and a high volume capacity tank (e.g., 10,000 gallons) that prohibited water runoff (Balciauskas et al. 2012) given the low annual precipitation associated with the study area. Resident predators that preyed on rodent species and regularly visited DPG water developments included coyotes (*Canis latrans*), bobcats (*Lynx rufus*), red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), and great horned owls (*Bubo virginianus*—Hall et al. 2013; Hall et al. 2014). The small mammal fauna consisted of granivores, folivores, omnivores, and carnivores, and included Ord's kangaroo rats (*Dipodomys ordi*), chisel-toothed kangaroo rats (*D. microps*), Great Basin pocket mice (*Perognathus mollipilosus*), little pocket mice (*P. longimembris*), long-tailed pocket mice (*Chaetodipus formosus*), deer mice (*Peromyscus maniculatus*), Piňon mice (*P. truei*), western harvest mice (*Reithrodontomys megalotis*), northern grasshopper mice (*Onychomys leucogaster*), white-tailed antelope squirrels (*Ammospermophilus leucurus*), Townsend's ground squirrels (*Spermophilus mollis*), desert woodrats (*Neotoma lepida*), montane voles (*Microtus montanus*), sagebrush voles (*Lemmiscus curtatus*), and desert shrews (*Notiosorex crawfordi*—Arjo et al. 2007).

Design and sampling.—We used stratified random sampling to establish 16 total 50×50 m trapping grids. Eight trapping grids were placed in areas near to (hereafter proximate grids) and 8 were placed away from (hereafter distant grids) water developments. For proximate grids, we randomly established a sampling grid centroid at a distance between 75 and 100 m from the edge of a water development's infrastructure. We did not center trapping grids on water developments because each development consisted of an 8×3 m storage tank and a 10×30 m rubber collection apron. The tank and apron resulted in large patches void of rodent habitat (e.g., burrowing substrate, cover, and food), so we opted for a spacing that was both spatially affiliated with a water development but did not contain a large patch of nonhabitat. For distant grids, we randomly established a sampling grid centroid between 1 and 1.1 km from the water developments. We selected this distance to reduce potential overlap among grids associated with other water developments; the minimum distance between developments was 2.3 km. Dispersal capabilities of our target species appeared to be less than the minimum distance between trapping grids. Hayssen (1991) reported 428 m as the maximum dispersal distance for chisel-toothed kangaroo rats and Kissner (2009) found that 270 m exceeded the natural dispersal capabilities of Ord's kangaroo rat. The maximum dispersal distance for other species of kangaroo rats did not exceed 500 m (Jones 1989; Price et al. 1994). Dispersal distances for deer mice can exceed 1 km, but such events are rare (Rehmeier et al. 2004). During the course of our study, no individual rodents were captured at multiple trapping grids. As such, we feel confident that dispersal capabilities of species investigated did not bias our findings. Because vegetation type can influence rodent abundance in arid environments (Decher and Bahian 1999; Brehme et al. 2011), available locations for distant grids were further constrained to be located in the same type of existing vegetation type using the LANDFIRE existing vegetation type spatial geospatial database (LANDFIRE 2012) as their respective paired proximate grid. Established trapping grids were sampled repeatedly over the course of the study; new grids were not established every trapping session or year.

We sampled rodents in grids using a 7×7 configuration (49 traps [2×2.5×9″; H.B. Sherman Traps, Inc., Tallahassee, Florida], 8.3 m spacing) for 4 consecutive nights (i.e., 4 capture occasions). We were more interested in obtaining estimates of small mammal abundance at the scale of specific grids rather than an inventory of species at the landscape level. Thus, we followed the recommendations of Conrad et al. (2008) and used high-density Sherman live trap grids (≤ 11 m spacing) and a moderate sampling duration (4 nights). We did not use species accumulation curves to assess how completely the 4-night duration sampled the local rodent fauna. Each 4-night sampling period was considered an individual trapping session. We conducted trapping sessions on each grid in early (1 May to 30 June) and late (1 August to 30 September) summer. Traps were baited with a mixture of black sunflower and mixed bird seed. All rodents captured were identified to species, ear tagged, and measured (e.g., mass, tail length, hind foot length). 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). Permits to capture and handle rodents were obtained from the Utah Division of Wildlife Resources (COR #4COLL8322). In order to reduce potential sampling bias among distant and proximate grids paired with each water development, both grids were sampled on the same nights, and the order that paired grids were sampled across sessions was randomized. All capture and handling procedures were in accordance with guidelines endorsed by the American Society of Mammalogists (Sikes et al. 2011).

We evaluated vegetation structure at each grid using seven 60-m line transects following the axis of the grid and spaced 10 m apart. 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), we measured vegetation structure at 1-m intervals. We sampled vegetation on plots twice per summer on the day prior to the onset of rodent sampling. Parameters estimated from transects were percent bare ground, percent litter cover, percent grass cover, percent shrub cover, percent ground cover, percent forb cover, and vegetation height. In April 2012, we drained 4 wildlife guzzlers, each associated with a proximate trapping grid, using a generator and submersible pump. Drinking portals were covered with plywood and water levels were checked monthly and we re-drained them if they reached > 2/3 capacity. To summarize our design, we repeatedly sampled 16 spatially fixed trapping grids over the course of 8 trapping sessions (e.g., 2 sessions per year for 4 years). Eight of these grids were close

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to water and 8 were away from water, and we drained 4 of the close-to-water grids between the 4th and 5th trapping session.

Data analyses.—We employed a BACI design (Underwood 1994; Morrison et al. 2001; Smith 2002) where we sampled all grids prior to (i.e., before period) and after (i.e., after period) eliminating water availability at 4 water developments. We considered the 8 distant and 4 proximate grids not associated with our manipulation (e.g., water removal) as reference grids. Grids associated with the water manipulation were considered impact grids. This allowed us to implement an asymmetrical BACI design where our reference locations outnumbered our treatment locations; this framework is recommended for investigations aiming to detect environmental disturbances on populations (Underwood 1994). We used the lme4 package (Bates et al. 2014) in R (R Development Core Team 2013) to employ generalized linear mixed models (GLMMs). We calculated 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 Ernest 2014). Rodent abundance, a measure of the productivity of a community (i.e., the sum of abundances across all species), is a commonly utilized metric in community ecology in general and is often used when investigating the impacts of disturbances on rodent communities (Ernest et al. 2000; Supp and Ernest 2014). We tested the categorical main effects of period (before and after) and grid type (impact and reference) on the continuous response variable rodent abundance. Following recommendations of Morrison et al. (2001) and Smith (2002), we only included variables explicitly associated with our BACI design (e.g., period and grid type) in our initial analysis. Specifically, we tested the effect of the water manipulation by including a period by grid type interaction in our model (Underwood 1992). Within the framework of a BACI design, such an interaction tests for a differential change (i.e., nonparallelism) between impact and reference sampling units following some type of manipulation (Underwood 1992). Inspection of capture data revealed nonnormality. As a result, we fit the following model families: lognormal, Poisson, quasi-Poisson, and negative binomial. Models that did not converge were eliminated and we assessed remaining models based on the generalized chi-square fit statistic (Stroup 2012). We chose negative binomial as the most appropriate model family in the BACI analysis. Because the same 16 plots were sampled over time, plot was fit as a random effect in all GLMMs. We evaluated the influence of main effects by examining *P*-values in terms of relative evidence of differences (Ramsey and Schafer 2013).

Following our BACI analysis, we performed a secondary analysis to test the effects of predictor variables (i.e., vegetation type, vegetation structure metrics, sampling year) on rodent abundance. If the initial BACI analysis revealed a water effect, we would remove from the secondary analysis all observations associated with impact and proximate grids; observations associated with water (e.g., an established disturbance) would be biased. Alternatively, if the BACI design revealed no water effect, we deemed it appropriate to include observations from all grids and sampling sessions in the secondary analysis. Our initial list of predictor variables included the 2 categorical variables (i.e., vegetation type and year) and 7 continuous vegetation structure variables (i.e., percent shrub cover, grass cover, bare ground cover, forb cover, litter cover, plant height [cm], and plant species richness). Mean plant height, percent shrub cover, and percent litter cover were arcsine square-root transformed to improve normality. We checked continuous variables for collinearity using correlational analysis (we eliminated any one of a pair of variables with Pearson *r* indicating more than 30% correlation—Ramsey and Schafer 2013). As with the BACI analysis, we fit several model families: the lognormal, Poisson, quasi-Poisson, and negative binomial and compared model fit using the generalized chi-square fit statistic (Stroup 2012). We then used the MuMIn package in R (Barton 2014) to run all possible additive model combinations based on a global model (Doherty et al. 2012). By doing so, our hypotheses (i.e., candidate models) were incorporated during the variable selection stage, not at the level of model specification (Arnold 2010). We used Akaike's Information Criteria corrected (AICc) for small sample size to select the best performing models, based on delta AIC < 3 and model weights (Anderson 2008).

Results

Between May 2010 and September 2013, we conducted 8 summer trapping sessions (2 sessions per year) for a total of 128 sampling occasions. We accumulated 25,088 trap nights, 5,086 captures, and captured 2,145 individual rodents. Abundance averaged 18.6 rodents ($SD = 15.61$) per grid/session and ranged from 0 to 59. Ord's kangaroo rat was the most commonly captured species and comprised 68.9% of all captures and 66.3% of all individuals captured (Table 1). Trapping grids occurred in exotic grassland (32 sampling occasions), mixed sagebrush shrubland (32 sampling occasions), and Great Basin mixed salt desert scrub (64 sampling occasions). We detected 119 unique plant species during vegetation sampling. Average percentage of grass, shrubs, litter, forbs, and bare ground at trapping grids was 21.37% ($SD = 25.78$), 8.93% ($SD = 11.89$), 40.7% ($SD = 30.34$), 4.2% ($SD = 5.76$), and 20.69% ($SD = 13.29$), respectively. Plant height averaged 24.5 cm ($SD = 12.31$) and median plant richness was 9 (range: 2–19).

We found no evidence that elimination of water at developments influenced rodent abundance (period × transect type interaction: $t = -1.15$, $P = 0.25$, $d.f. = 108$; Fig. 1). Rodent abundance was not influenced by period ($t = 0.406$, $P = 0.68$, $d.f. = 108$), but there was slight evidence that grid type (i.e., reference or impact) was an influential factor ($t = 1.54$, $P = 0.12$, $d.f. = 108$; Fig. 1). Rodent abundance at reference grids during the before period was 5.50 ($SE = 1.77$) and 6.35 ($SE = 1.66$) during the after period (Fig. 1). Rodent abundance at impact grids during the before period was 17.27 ($SE = 2.79$) and 19.9 ($SE = 2.83$) during the after period (Fig. 1). For the exploratory analysis, percent litter and bare ground were removed from models due to collinearity with

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Table 1.—Summarized rodent capture results across all trapping grids and sessions at Dugway Proving Ground, Utah, 2010–2013. Total number of trap nights was 25,088.

Species	Number of captures	Percentage of captures	Number of individuals captured	Percentage of individuals captured
Dipodomys ordi	3,507	68.95	1,423	66.34
Peromyscus maniculatus	798	15.69	374	17.44
Dipodomys microps	306	6.02	133	6.20
Chaetodipus formosus	171	3.36	62	2.89
Onychomys leucogaster	95	1.87	61	2.84
Reithrodontomys megalotis	81	1.59	49	2.28
Perognathus mollipilosus	40	0.79	16	0.75
Neotoma lepida	14	0.28	9	0.42
Peromyscus truei	12	0.24	6	0.28
Ammospermophilus leucurus	8	0.16	7	0.33
Lemmiscus curtatus	4	0.08	1	0.05
Perognathus longimembris	1	0.02	1	0.05

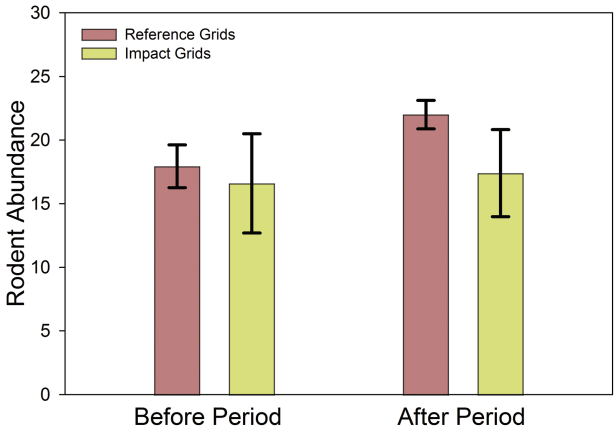

Fig. 1.—Mean rodent abundance (average nightly captures/trapping session/grid; ± *SE*) observed within rodent trapping grids before and after removal of water availability near a subset of trapping girds (impact grids) on the U.S. Army Dugway Proving Ground, Utah, United States, 2010–2013 (n = 128 sampling occasions).

percent grass. The best performing models (Table 2) included combinations of the variables year, vegetation class, percent shrub, percent forb, and plant richness (Table 1). Vegetation type (Fig. 2) and year (Fig. 3) appeared to have the strongest influence on rodent abundance, as models containing these individual variables or the additive combination accounted for 48% of model weight and all top models included vegetation type or year (Table 2).

Discussion

We found no evidence that water developments impacted rodent abundance (Fig. 1). Rodent abundance appeared to vary with the type of vegetation class (Fig. 2) and year (Fig. 3), whereas vegetation measurements at and near trapping grids did not appear to have a strong influence (Table 2). We observed a general trend of mixed desert shrubs containing the highest levels of rodent abundance, exotic grasslands containing moderate numbers, and sagebrush areas containing the least. There appeared to be a positive relationship between rodent abundance and previous years' precipitation (Fig. 4).

Researchers have posited that water developments represent a disturbance by negatively effecting individual species or communities indirectly (Broyles 1995; Larsen et al. 2012). Rodents occurring in the Great Basin Desert are reportedly independent of free water (Merritt 2010; Feldhamer et al. 2015). During the summers of 2010–2012, summer rodent use of our study guzzlers totaled 33 visits in 2,880 camera days (L. Hall, Brigham Young University, pers. comm.). Because of the aforementioned, our investigation was focused on the specific hypothesis of indirect effects prompted by increased levels of predation, predation risk, or competition (Hall et al. 2013). Our results did not support this premise, which we speculate was due to several factors.

First, numbers or proportions of preyed upon rodents may simply not differ in respect to proximity to water sites. In west Texas, Atwood et al. (2011) reported mammalian carnivores partitioned use of water resources both spatially and temporally in an attempt to reduce interspecific interactions. Investigations focused on antagonistic interactions at water sites for raptor species are lacking, but behavioral modifications, including temporal segregation, have been noted as mechanisms to reduce antagonistic interactions among a host of competing raptor species (Sergio and Hiraldo 2008). Thus, species visiting water developments that regularly prey upon rodents may face a trade-off between timely maintenance of basic physiological needs (i.e., hydration, thermoregulation) and the cost of interspecific and intraspecific interactions (Atwood et al. 2011). Such a trade-off could facilitate such predators to forego foraging in areas in proximity of water developments prior to and/or following visitations. Alternatively, increased predation rates on rodents may have occurred near water developments but been compensatory; mortality that did not impact abundance because succumbed individuals would have been otherwise removed from the population by other mortality agents (Hastings 1996). Predation-driven mortality has been found to be both compensatory (Mihok 1988) and additive (Meserve et al. 1993) for rodent populations. We did not monitor rodent predation rates, thus we cannot make any firm conclusions in relation to this topic. Rodents may also have mitigated increased predation risk by changing their behavior,

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Table 2.—Top 8 models and null model in AICc model selection used to determine factors influencing rodent abundance in the U.S. Army Dugway Proving Ground, Utah, 2010–2013. Models shown are those that exhibited delta AICc < 4 in original model set containing all possible additive combinations of predictor variables and the null model. *K* refers to the number of parameters (including intercept) in a model plus 1 for the error term. Vegetation type included exotic grassland, mixed desert scrub, sagebrush as derived from LANDFIRE 2011. Shrub = % shrub cover, Grass = % grass cover, Forb = % forb cover (all % cover derived from line-point intercept method). AICc = Akaike's Information Criteria corrected.

Model	AICc	*K*	Delta AIC	Model weight
Vegetation Type, Year	1,164.50	6	0	0.212
Vegetation Type	1,164.38	4	0.152	0.179
Year	1,162.76	5	1.622	0.089
Vegetation Type, Year, Shrub	1,161.05	8	1.671	0.087
Vegetation Type, Year, Forb	1,158.37	8	2.718	0.052
Vegetation Type, Shrub	1,155.26	4	3.111	0.042
Year, Forbs, Shrub	1,151.86	6	3.365	0.031
Vegetation Type, Year, Grass	1,148.08	8	3.773	0.022
Null	1,141.77	2	6.321	< 0.001

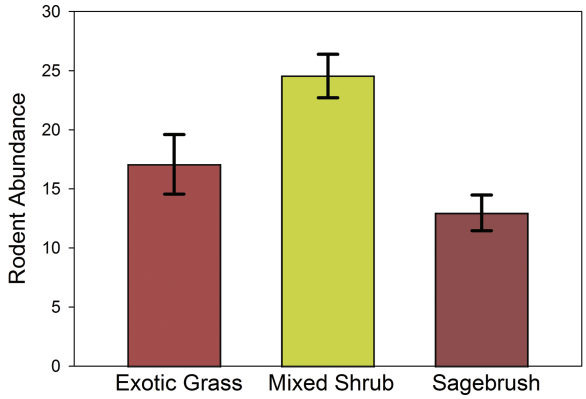

Fig. 2.—Mean rodent abundance (average nightly captures/trapping session/grid; ± *SE*) observed within rodent trapping grids in 3 vegetation classes (exotic grassland, mixed desert scrub, sagebrush) on the U.S. Army Dugway Proving Ground, Utah, United States, 2010–2013 (*n* = 128 sampling occasions).

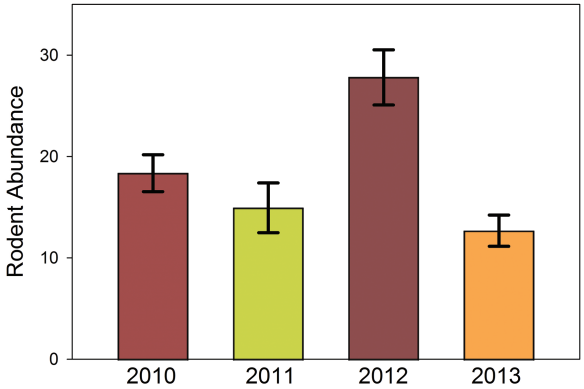

Fig. 3.—Mean rodent abundance (average nightly captures/trapping session/grid; ± *SE*) observed within rodent trapping grids for 4 consecutive summers on the U.S. Army Dugway Proving Ground, Utah, United States, 2010–2013 (*n* = 128 sampling occasions).

as behavioral strategies have been observed as mechanisms to mitigate predation risk within a host of rodent species and communities (Brown et al. 1994; Kotler et al. 1994; Shenbrot 2014), and the magnitude of behavioral responses has been shown to be correlated to the magnitude of predation risk for some species (Orrock and Danielson 2004). Our study was not designed to measure rodent behavioral response to predation risk.

Rodent abundance was influenced by vegetation cover class. In general, this finding is not novel, as rodent abundance and density can differ in hardwood versus softwood forests (Degraaf et al. 1991), upland versus riparian woodlands (Doyle 1990), agricultural versus wildland areas (Decher and Bahian 1999), native versus exotic dominance (Longland 2012), and by Great Basin Desert vegetation communities (O'Farrell and Clark 1986). Similar to our findings, Hernandez et al. (2005) observed that rodent abundance was higher in a mixed shrubland when compared to grassland; they speculated that the shrubland areas exhibited higher productivity and biomass stability. Our finding of exotic grasslands containing more rodents than sagebrush areas was unexpected because several investigations have reported that exotic grasslands, which are predominantly dominated by cheatgrass in the Great Basin Desert, are detrimental to rodent abundance and diversity in this biome (Hall 2012; Freeman et al. 2014). To our knowledge, previous rodent investigations have not compared rodent community abundance in sagebrush versus exotic grassland cover types. As such, determining if our findings are unique or ubiquitous across the Great Basin Desert is not currently possible.

In our study area, the dominant rodent species occurring in sagebrush were chisel-toothed kangaroo rats (i.e., > 70% of individuals captured), while exotic grasslands and mixed shrublands primarily consisted of Ord's kangaroo rats (i.e., > 80% of individuals captured). Chisel-toothed kangaroo rats in our study area were on average 30% larger than Ord's kangaroo rats (B. M. Kluever, pers. obs.). As such, chisel-toothed kangaroo rats likely require more resources than Ord's, which could ultimately result in lower abundance of chisel-toothed kangaroo rats driven by spacing/territorial mechanisms. Reported density estimates for the Ord's and chisel-toothed kangaroo rats range from 9.9 to 53.0 (Garrison and Best 1990) and 6.72 to 34.0 animals per ha (Hayssen 1991), respectively. These broad ranges make density comparisons between the 2 species difficult. O'Farrell (1978) observed similar home range sizes for Ord's (e.g., 0.43 ha) and Chisel-toothed kangaroo rats (e.g., 0.45 ha) in the same sagebrush community and also observed

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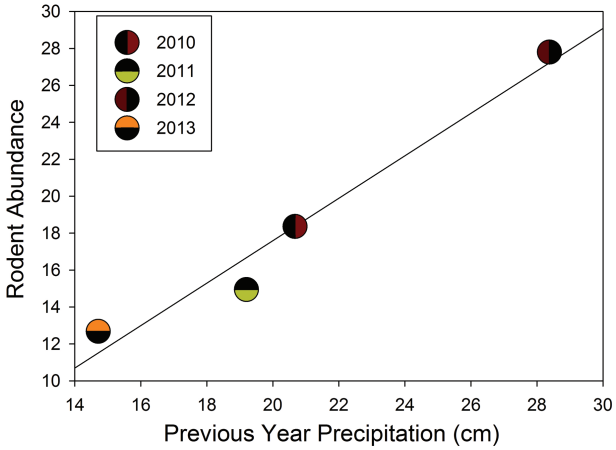

Fig. 4.—Scatterplot and trendline exhibiting relationship between annual rodent abundance and previous year's precipitation (cm) on the U.S. Army Dugway Proving Ground, Utah, United States, 2010–2013 (n = 128 sampling occasions).

that home range size, which is often tied to density, was not strongly correlated with body size across all species investigated. This suggests factors beyond body size may have influenced densities of the species we investigated, but we cannot rule out the influence of differential densities on our findings.

Findings from Clark and Kaufman (1991) and Thompson and Gese (2013) suggested that measures of vegetation structure (e.g., percent bare ground, average shrub height) may more suitably explain/predict rodent abundance than more coarse-grained classifications of vegetation (e.g., remote sensing–based vegetation cover types). Our findings suggest that dominant vegetation cover was a better indicator of rodent abundance than vegetation structure data collected at the sampling plot extent. One explanation is that, to our knowledge, previous rodent investigations have incorporated either vegetation structure measurements or coarse-grained classifications of vegetation rather than both. As a result, we cannot compare our findings with other published works. Second, though our sampling encompassed 4 years, and was extensive in comparison to the majority of published rodent investigations, sampling occurred repeatedly on a limited number of plots which reduced the variability of vegetation structure measurements. Our rationale for this design was tied to our central research question of determining the effect of previously constructed water developments on rodents. Study designs that incorporate a higher degree of spatial replication than ours may be better suited to determine the role of vegetation structure on rodent communities. In addition, increased replication of sampling units, number of traps per grid, and number of sampling nights could bolster number of captures, thus allowing investigators to examine the effects of water developments, or other potential disturbances, on individual species rather than needing to pool across species.

Rodent abundance was partially driven by temporal factors, as we observed the highest estimates of rodent abundance in the year following the highest amount of annual precipitation (Fig. 4). This finding was likely a result of a time lag effect between precipitation, plant productivity, and subsequent rodent abundance (Fig. 4). Ernest et al. (2000) reported a positive correlation among precipitation, plant productivity, and rodent abundance in the Chihuahuan Desert, with plant productivity responding to precipitation during the same growing season, and rodent populations lagging at least one season behind. A similar time lag correlation between precipitation and rodent abundance was observed for rodent communities in Chihuahuan Desert shrublands (Hernandez et al. 2005). Annual precipitation rates at DPG during 2011 were the highest observed during our study, with the majority of precipitation taking place in the spring (U.S. Army Dugway Proving Ground, West Desert Test Center Meteorological Division, pers. comm.). Thus, a general trend of increased plant productivity during the growing season prior to 2012 may have resulted in increased rodent vital rates, facilitating an increase in overall rodent abundance (Fig. 4). Similarly, the dry conditions of 2012 (Fig. 4) likely resulted in decreased plant productivity, which negatively influenced vital rates and subsequently rodent abundance.

Our study was the first to incorporate a resource manipulation design to evaluate the potential indirect effects of water developments on a rodent community. Our findings suggested that water developments do not constitute a deleterious disturbance to rodent community abundance. It is important to note that our inference is limited to areas associated with water developments on DPG, and that factors not relevant to our study (i.e., livestock or feral horse visitation to water developments) may promote negative effects at water developments for rodent and other communities. Further, it is important to note that there are a suite of rodent metrics (e.g., species richness, diversity indices, biomass, sex ratios, etc.) that were not examined as response variables in our investigation. We encourage future field investigations on water developments, and other potential disturbances, to incorporate study designs that include a manipulation component. BACI designs in particular should be incorporated into field investigations more frequently. Such investigations will be more feasible when disturbances are discrete points on a landscape (i.e., water developments) and can thus be readily identified and manipulated. Our other findings, especially those suggesting that exotic grasslands contain more rodents than sagebrush shrublands, warrant further investigation.

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