

THESIS

SMALL MAMMAL POPULATIONS AND PLANT COMMUNITY SUCCESSION AT
ARTESIAN WELL SITES IN GREAT SAND DUNES NATIONAL PARK, COLORADO

Submitted by

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In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2013

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ABSTRACT

SMALL MAMMAL POPULATIONS AND PLANT COMMUNITY SUCCESSION AT ARTESIAN WELL SITES IN GREAT SAND DUNES NATIONAL PARK, COLORADO

For more than 100 years, artificial artesian wells in the San Luis Valley of south-central Colorado have been a steady source of water for livestock and wildlife on lands administered by Great Sand Dunes National Park and The Nature Conservancy. In summer 2011, a study was established to examine the effects of capping these wells on the local biota. In Chapter 1, I focused on the short-term effects to the population dynamics and species diversity of small mammals. In 2011 and 2012, I compared newly capped well sites, wells with water (open well sites), and reference sites by estimating density (Program DISTANCE), survival (Cormack-Jolly-Seber Model in Program MARK), species occupancy (Robust Occupancy Model in Program MARK), and measures of species diversity (species richness, Shannon-Weiner index, and species evenness) of small mammals. I modeled small mammal density and survival as a function of well site type, percent plant cover, disturbance level intensity from ungulates, and year of study using an information theoretic approach to rank models and estimate the relative importance of the independent variables. Over the two years, I captured 1,150 individuals of 6 rodent species; however, only two species, Ord's kangaroo rat (*Dipodomys ordii*) and Apache or plains pocket mice (*Perognathus* sp.), had sufficient numbers for density and survival analyses. There was no significant difference in density and survival estimates of these species at the different well site types; however species occupancy estimates varied such that open well and reference sites had the greatest occupancy probability of the deer mouse (*Peromyscus maniculatus*), and reference sites had the greatest occupancy probability of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). For the kangaroo rat, the plant cover and year

of study were the highest importance variables for density and survival respectively. For pocket mice, the disturbance level by ungulates and year of study were important predictors for density and survival; density was negatively correlated with amount of disturbance and survival nearly doubled from 2011 to 2012. Estimates of species diversity were greatest at reference sites.

Results suggest that in the short-term, small mammal density and survival does not increase after a well is capped, species occupancy is variable, and diversity does not change. Additional studies are needed to provide a better understanding of the long-term changes in small mammal population dynamics and biodiversity as capped well sites continue to revert to habitats similar to reference sites.

In Chapter 2, I concentrated on the short-term effects of capping wells on the plant community with a focus on secondary ecological succession. I characterized the habitats at sampled sites by identifying plant species (native and exotic) and examining potential sources of variation by modeling plant cover and frequency as a function of variables such as well site type, the ungulate disturbance level, distance from well heads, and the year of study. I used an information theoretic approach to rank models and estimate the relative importance of the independent variables. I also estimated indices of native species diversity including richness, Shannon-Weiner diversity index, Simpson's index, community evenness, and compared patterns of plant form cover (i.e., shrubs, forbs, and grasses) at increasing distances from well heads. There was no significant difference in plant cover at different well sites; year of study and distance from well heads were the most important predictors for native plant cover and exotic plant cover, respectively. Well site type, year of study, and distance from well head were significant predictor variables for native species frequency whereas for exotic species frequency, only well site type was important. Estimated species diversity values tended to be highest at the

reference sites with the exception of higher community evenness values at capped well sites. Capped well sites also had varying distance patterns across different plant forms whereas all plant cover was highest at the farthest distances from open well heads. Overall, this study suggested that while plant communities at well sites are not significantly different after capping the well head, the abundant exotics may need additional control efforts for the community to return to a species composition typical of the sand sheet ecosystem.

ACKNOWLEDGEMENTS

The study was primarily funded by a cooperative effort between the U.S. Geological Survey, Colorado State University, and the National Park Service. For that I am extremely grateful. I am also thankful for the additional funds provided by the Alliance for Graduate Education and the Professoriate and the Department of Fish, Wildlife, and Conservation Biology at Colorado State University. Specifically, I thank my advisors K. Wilson and G. Bowser, and my committee members P. Doherty and M. Paschke for all of their support. I appreciate the patience you showed and the effort you urged onto me to grow as a scientist. I also thank J. Kershner with the Northern Rocky Mountain Science Center of the U.S. Geological Survey for his project guidance, and K. Schoenecker with the Fort Collins Science Center who was instrumental in inspiring the project and always had good sound advice.

Many other individuals must also be thanked. J. Harte of the National Park Service provided valuable insight into the legal history of groundwater rights in the San Luis Valley. J. Stevens of the Colorado Natural Heritage Program provided information on plant inventories. I also thank D. Lewis, A. Craig, and L. Zeigenfuss for invaluable field assistance and R. Reich of the Department of Forest and Rangeland Stewardship who gave sound spatial statistics advice. P. Chapman and J. zumBrunnen of the Mathematics Department provided statistical consulting, and A. Green, J. Dertien, and M. Peterson of the Wagar 113 Lab provided feedback and constructive criticism on early drafts of this thesis. I also thank Great Sand Dunes National Park superintendents A. Hutchinson and L. Carrico for being very accommodating and Park employees A. Valdez, F. Bunch, and P. Bovin-Pineda for all their project support and hauling my truck out of sand. Last, but not least, I thank my family back in Texas; for their support, their unconditional love, and for believing in me while I completed this adventure.

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CHAPTER 1: SMALL MAMMAL POPULATION DYNAMICS AT ARTESIAN WELL SITES IN GREAT SAND DUNES NATIONAL PARK, COLORADO

Concentrations of ungulates around artificial watering sources is a worldwide phenomenon, with strong impacts on ecosystem functioning. For example, increasing water availability in desert ecosystems of southwestern North America from the building of artificial water catchments causes a decrease in the local forage abundance and in the structural diversity of plant cover (Krausman and Czech 1997, Brooks et al. 2006, Marshal et al. 2006), while in Africa, effects to ecosystem processes around artificial waterholes include changes in vegetation growth dynamics in the Kalahari Desert (Dean et al. 1997) and increases in litter and bare ground in the semi-arid rangelands of Namibia, South Africa (Nangula and Oba 2004). The resulting combination of trampling, grazing, and high densities of ungulates, along with periodic drought, can produce dramatic habitat changes in the structure of desert ecosystems (Buffington and Herbel 1965, Nash et al. 1999). One major effect is the development of radial grazing and disturbance patterns called a piosphere (Lange 1969, Andrew 1988, Brooks et al. 2006) that are characterized by high herbivore (wild and domestic) densities (Lange 1969; Andrew and Lange 1986, Brooks et al. 2006), low plant coverage (Fusco et al. 1995), and high disturbance levels (Thrash et al. 1993). The focus of this study was on understanding the changes to small mammal communities around recently closed artesian wells in the Great Sand Dunes National Park and Preserve in south-central Colorado.

Great Sand Dunes National Park and Preserve (GRSA) is a high-elevation desert ecosystem and contains some of the tallest sand dunes in North America (Rupert and Plummer 2004). The 63-km² main dune field, rising 215 m above the surrounding valley floor, is estimated to be 2,000 to 12,000 years old when Pleistocene glaciers began to retreat (Chatman et al. 1997,

Janke 2002). One purpose of the GRSA is to preserve these sand dunes and their high elevation watersheds and "to perpetuate the entire system for the benefit and enjoyment of present and future generations" (National Park Service [NPS], <http://www.nps.gov/grsa/index.htm> accessed 24 October 2012). Prevailing winds transport sand across the San Luis Valley (SLV) northeastward towards the Sangre de Cristo Mountains into the dune field. Two mountain streams outline this dune field, Sand Creek on the northwestern edge and Medano Creek on the southeastern edge. The creeks deposit sand around the perimeter of the dunes on the upwind side, where prevailing winds transport it northeastward towards the mountains again (Rupert and Plummer 2004). The water in the Medano and Sand Creeks infiltrates a two-layered confined and unconfined aquifer, which extends more than 1,500 m below the surface (Rupert and Plummer 2004). The existence of the dune field relies upon this aquifer system, because if groundwater levels are lowered, the distance the creeks flow before infiltrating the shallow unconfined aquifer would likely decrease and sand maintenance would slow, threatening the viability of the dunes (NPS, <http://www.nps.gov/grsa/index.htm> accessed 3 February 2013).

In the late 1800s, 24 artificial artesian wells were drilled into the confined aquifer as part of the development of grazing lands and ranching operations within the SLV. Allowing water from the confined aquifer to infiltrate the unconfined aquifer disrupts the natural hydrological regime (Rupert and Plummer 2004). This could lower the pressure in the confined aquifer, and potentially lower the water table in the unconfined aquifer, leading to reduced flows or complete drying of surface water such as natural springs (e.g., Medano Creek), water table-fed streams (e.g., Big and Little Spring Creeks), and interdunal ponds. These well sites augmented available surface water (GRSA General Management Plan 2006), but the NPS is charged with protecting water-dependent resources within the park, and so all artesian well sites on NPS lands (10) were

capped in April 2010. The remaining 14 uncapped well sites are on adjacent lands belonging to The Nature Conservancy (TNC). The NPS is interested in maintaining the natural hydrological system, eliminating the piosphere effects around artificial water sources, and restoring the ecosystem to a more natural state. In addition, Colorado Parks and Wildlife (CPW) is interested in whether capping well heads will redistribute ungulates, in particular elk (*Cervus elaphus*), away from wells within the park's boundary making them more accessible for harvest (James Harte, NPS, pers. comm.).

A major fauna within the GRSA is the small mammal community. Changes in small mammal population dynamics can serve as an ecological indicator of recovery in ecosystem structure and function (Carey and Harrington 2001). Different indices of species diversity of a small mammal community such as number of species present (species richness), proportion of species present (Shannon-Weiner index), and the distribution of individuals among the species present (species evenness; Krebs 1989) are also considered gauges of ecosystem processes. Small mammal species richness was not altered at watering sites in semi-arid mixed scrub, grassland, and pinyon-juniper communities of southern New Mexico (Burkett and Thompson 1994) nor in the Chihuahuah desert grassland (Eldridge and Whitford 2009) where density was also unchanged. Others have documented decreases in small mammal abundances near watering sources in the arid grasslands of Australia (James et al. 1997) and in the sagebrush steppe of Karoo, South Africa (Eccar et al. 2000). When grazing effect on small mammal communities in arid ecosystems has been isolated, Jones and Longland (1999) found that Merriam's kangaroo rat (*Dipodomys merriami*) was significantly more abundant in heavily grazed areas of the Great Basin Desert, whereas Germano et al. (2011) found Heermann's kangaroo rat (*D. heermanni*)

more abundant on ungrazed control plots, protected from disturbance by cattle in California's arid San Joaquin Valley.

My primary objective was to evaluate the short-term effects (recovery) of capping artesian well sites on small mammal population dynamics and species diversity. In the absence of long-term data sets and information on the historic ecosystems (Knapp 1992, Morris et al. 2011), "recovery" will be measured by comparison of well sites to reference sites with no influence of well heads. I compared density, survival, occupancy, and species diversity across 3 site types (capped well sites, wells with water [open well sites], and reference sites) in the GRSA. I also measured percent total plant cover and disturbance levels by ungulates across all sites to relate to small mammal responses. Based on ungulate distributions around artificial water sources (Thrash et al. 1993, Smit et al. 2001) and habitat suitability for small mammals in arid ecosystems (Bich et al. 1995, Davidson et al. 2010, Germano et al. 2011), I predicted that small mammal population dynamics would be related to disturbance intensity levels such that capping of artesian wells reduced disturbance, which subsequently improved habitat, and resulted in the following patterns of density, survival, occupancy, and species diversity indices: Capped well sites > Reference sites > Open well sites. In addition to providing a characterization of small mammal communities at capped well sites in the GRSA, my study provides resource managers a picture of the short-term effect of capping wells on small mammal communities in the GRSA sand sheet ecosystem.

STUDY AREA

The study occurred from May-August in 2011 and 2012 within Great Sand Dunes National Park and the adjacent Zapata Ranch, owned by TNC. The entire area is within the high-elevation region of the SLV in south-central Colorado (Figure 1.1), a closed basin valley in

Colorado and New Mexico covering approximately 21,000 km² at an average elevation of 2,300 m above sea level. The valley is drained by the Rio Grande River, which passes through the San Juan Mountains, and then flows south into New Mexico (Winger and Winger 2003, Rupert and Plummer 2004). Annual precipitation averages 28 cm, mostly in July through September with an average annual snowfall of 104 cm, primarily from October through March. Average daytime temperatures on the valley floor in summer range from 26.5 °C to 29.5 °C and from -9.5 °C to 1.5 °C in winter (Western Regional Climate Center, <http://www.wrcc.dri.edu/> accessed 20 March 2013).

My research was conducted on the southern and southwestern sides of the main dune field, an area known as the sand sheet. The plant community in this region varies from wet meadows to grassy prairies to desert shrub lands, depending on proximity to groundwater (NPS, <http://www.nps.gov/grsa/index.htm> accessed 24 October 2012). Rocky Mountain iris (*Iris missouriensis*) and inland saltgrass (*Distichlis spicata*) are found in the wet meadows and around ephemeral wetlands (NPS, <http://www.nps.gov/grsa/index.htm> accessed 24 October 2012). The grassy prairies include blue grama (*Bouteloua gracilis*), Indian rice grass (*Oryzopsis hymenoides*), needle and thread grass (*Hesperostipa comata*), and false buffalo grass (*Monroa squarrosa*). Shrubs commonly found include rubber rabbitbrush (*Ericameria nauseosus*), sagebrush (*Artemisia* sp.), and yucca (*Yucca glauca*). Non-indigenous plants (exotics) include Russian thistle (*Salsola tragus*), Russian knapweed (*Acroptilon repens*), and cheatgrass (*Bromus tectorum*) (Spackman Panjabi et al. 2004). Bison (*Bison bison*), elk, mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) grazed this area until about 1840 when bison, pronghorn, and elk were extirpated as ranching developed (Swift 1945, Schoenecker 2012). Currently, all but bison can be found in the GRSA.

The 24 artificial artesian well sites were in place by the late 1800s, scattered throughout these new ranchlands. Livestock, including sheep (*Ovis aries*) and cattle (*Bos taurus*), were grazed throughout the study area, especially in the sand sheet that now comprises part of the national park (Schoenecker et al. 2006; NPS, <http://www.nps.gov/grsa/parkmgmt/index.htm> accessed 17 March 2013). The former Luis Marie “Baca” Ranch, which makes up the northern part of the GRSA and all of the Baca National Wildlife Refuge, was grazed by cattle until 2004 (Schoenecker 2012). Approximately 2,800 bison were reintroduced on the Zapata Ranch in 1989, and in 1999, TNC purchased the 40,500-ha Zapata ranch and converted part of the area to a preserve (The Zapata Ranch, <http://www.zranch.org> accessed 17 March 2013).

METHODS

Study Design

Two capped well sites, open well sites, and reference sites, with one reference site near each well type, were selected for this study (Figure 1.1). Open well sites had a 5-cm steel pipe inserted into the ground that filled a watering tank, surrounded by a denuded piosphere zone where vegetation was generally lacking (Figure 1.2). Capped well sites were similar, but lacked water in the tank (Figure 1.3). All sites were at least 2,000 m apart to avoid capture of small mammals between sites. Criteria for selection of well sites included accessibility and similarity of habitat surrounding the sites. Elk, mule deer, and pronghorn inhabit and moved freely across the ~125,000-ha study area, while the bison were fenced within 20,000 ha of the Zapata Ranch (Figure 1.1, Zapata Ranch, <http://www.zranch.org> accessed 25 February 2013). Thus, all sites were accessible to ungulates, but only the open well sites and the nearby reference site were accessible to bison. To determine if conditions were historically similar, the well site appearance and visible piosphere conditions for each of the selected well sites was compared using Google

Earth® and past photographs. The estimated numbers of elk, mule deer and pronghorn within the study period were 4,500 (K. Schoenecker, unpublished data), 5,800 (Colorado Parks and Wildlife [CPW] 2011a), and 1,010 (CPW 2011b), respectively. Precipitation and temperature data were obtained from the Great Sand Dunes Colorado Remote Automated Weather Station (Western Regional Climate Center, <http://www.wrcc.dri.edu/cgi-bin/rawMAIN.pl?coCSDU> accessed 4 June 2012) and were used to compare differences between years.

Sampling

I used a “quasi” robust design (Pollock et al. 1990) that included 3 to 4 primary sampling periods in 2011 and 2012 between late May and late August of each year. Each primary period included 4 secondary sampling periods (4 consecutive trapping nights, Figure 1.4). In Pollock’s robust design, survival is estimated between primary sampling periods using open capture-recapture (CR) models (Pollock et al. 1990, White and Burnham 1999). Population size (abundance) or density is estimated within the secondary periods using closed CR models (Otis et al. 1978, White 2008).

Small mammals were sampled using a trapping web design (Anderson et al. 1983) with 12 equally spaced lines of 7 Sherman live traps (23 x 8 x 9 cm) spaced at 10-m intervals, radiating from a central point; 12 additional traps were placed between each transect line at the 20-m mark. The trapping web allows for density estimation using distance sampling methodology with program DISTANCE (Buckland et al. 1993); this eliminates the need to estimate the effective grid-trapping area (see Otis et al. 1978, Wilson and Anderson 1985). The center of each trapping web was offset 10 m north of the well head to avoid tank structures (for example, see Figures 1.2 and 1.3). If trap placement was directly on a road or on top of an obstruction, e.g., metal or wood remaining from previous cattle ranching operations, then the trap was moved as close as possible to its original location, but still along the transect line. The new

distance was then recorded. Trap locations were staked, flagged, and labeled with distance from center and transect number.

Between late May and late August of each year, each site was sampled during primary periods (Figure 1.4) with trapping occurring at paired sites. Traps were provided with insulating material (polyester bedding), baited in the evening with rolled oats and peanut butter, and checked in the morning. On initial capture, individuals were uniquely marked by hair clipping and unique ink marks (species < 15 g) or with 2 Monel size-one ear tags (#2001-1 Monel, National Band and Tag Company, Newport, KY), identified to species, weighed, sexed, assessed for reproductive condition, and released at the capture sites. Mass and pelage color were used to age individuals as juveniles or adults (Valdez 2003, Reid 2006). Animals with only one tag or no tags and torn ears were considered to be recaptures. In these cases, new tags were applied and during data analyses an attempt was made to assign the tag numbers of the most likely candidates based on species, sex, weight, and the nearest individuals that were previously captured, but not recaptured (Anderson et al. 1983). Reference sources for identifying small mammals included taxonomic guides based on a *List of Mammal, Reptile, Amphibian, and Fish Species* (NPS, <http://www.nps.gov/grsa> accessed 11 March 2011), the *Mammal inventory of Great Sand Dunes and Florissant Fossil Beds National Monuments* (Valdez 2003), and Peterson's Guide to Mammals of North America (Reid 2006). The two potential species of pocket mice in the study area, Apache pocket mouse (*Perognathus apache*) and Plains pocket mouse (*Perognathus flavus*) (Valdez 2003) were difficult to identify without examining skulls and teeth, therefore pocket mice were only identified to genus and treated as one species. Animal handling procedures were approved by Colorado State University's Institutional Animal Care and Use Committee

(Protocol 11-2629A) and followed the American Society of Mammalogists guidelines (Sikes and Gannon 2011).

Habitat variables were measured each month using a 1-m² polyvinyl chloride (PVC) sampling frame placed at 10-m intervals along each transect line at 5-100 m from the trapping web center. Recorded habitat variables included: 1) percent plant species cover (0-100%, native and exotic), 2) number of individual plants (frequency), 3) disturbance intensity level (0-3, see explanation below), and 4) percent cover of woody debris and/or water (0-100%). Evidence of disturbance by ungulates included trampling (e.g., lack of plant cover, compacted sand), presence of tracks, and flattened shrubs (Howe and Baker 2003). Four disturbance levels were defined based on intensity within the sampling frame: 0) none, 1) mild (bare ground was < 25% of quadrat and presence of ungulate tracks), 2) intermediate (bare ground was ~50% of quadrat and presence of ungulate tracks), and 3) extreme (bare ground was > 50% of quadrat and presence of ungulate tracks). The 10 sampling frames per transect line resulted in 120 samples per site and these were averaged for each primary sampling period to compute an overall estimate of plant cover and disturbance intensity level.

DATA ANALYSES

Density

I estimated species-specific density at each sampled site (n = 6) for each primary occasion by treating the trapping webs as point estimates. Initial captures of individuals were grouped by intervals, defined as distance to center of the web (i.e., 10-70 m), and inputted into Program DISTANCE (Distance 6.0, Release 1; Thomas et al. 2010) to estimate density (Anderson et al. 1983). I used Akaike's Information Criterion (AIC; Akaike 1973, Buckland et al. 1993) in program DISTANCE to select the most appropriate detection probability model based on the standard detection functions (i.e., uniform, negative exponential, half-normal, and

hazard rate) and adjustment functions (i.e., cosine, simple polynomial, and hermite polynomial). When appropriate (see Buckland et al. 1993), I used interval adjustments and truncation to improve model fit, and log-based confidence intervals are reported.

Based on a review of the literature, I decided *a priori* that well site type (capped, open, and reference), disturbance level by ungulates (0-3), percentage total plant cover (native and exotic), and annual variation, i.e., year of study, could influence the density and survival of small mammal. I created linear regression models (Proc GENMOD, identity link function, SAS software, Version 9.1.3, SAS Institute Inc. 2005) where average density by species for each primary period varied as a function of the type of well, the habitat variables (percent total plant cover and disturbance intensity level), or year of study (2011 or 2012). I also considered additive and interactive effects of these factors, except either well type or disturbance were modeled, i.e., not both together, because both captured the effect of well type. Density estimates were averaged by well type ($n = 2$ per well type) for each primary period and a \log_{10} transformation was used to normalize variance of density estimates. Models were ranked based on AIC_C , the small-sample size adjustment for AIC (AIC_C ; Hurvich and Tsai 1989); I also reported ΔAIC_C (difference in AIC_C value between each model and the best model), AIC_C weights (strength of evidence for each model; Burnham and Anderson 2002), and the number of parameters in the model (K). The lowest AIC_C score indicates the model with the most parsimonious fit to the density data. Models with $\Delta AIC_C < 2$ were considered to have relatively strong support (Burnham et al. 2011). I also computed relative importance values (sum of the weights over all models in a balanced model set that include the given variable) for each variable (Burnham and Anderson 2002, Converse et al. 2006). A relative importance value > 0.50 , indicates that a variable is influential to the process of interest (Burnham and Anderson 2002, Doherty et al. 2012). By using this method, I utilized

multi-model inference (the use of more than one model when models are closely ranked) rather than just the single best model. Multi-model inference accounts for model uncertainty and improves bias and precision measures (Burnham et al. 2011, Doherty et al. 2012).

Survival

Survival was modeled and estimated separately for each species using the mark-recapture data in program MARK (White and Burnham 1999) as a function of well site type, capture occasion, and the variables (percent total plant cover and disturbance intensity level). Low between-year recapture rates did not allow estimation of survival, therefore I estimated monthly apparent survival (ϕ) and detection probabilities (p) by scaling the time intervals between the primary trapping periods (4 weeks) using Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965, White and Burnham 1999). Apparent survival is the probability that an animal is alive at $t + 1$, given that it was alive at t and has not emigrated (White and Burnham 1999). Since the focus was on difference between well types and recovery time since capping, I structured the mark-recapture data into six groups representing the sampled sites (capped, open, reference) for each year of study (2011 or 2012); these were inputted as attribute groups in the CJS model with different survival and detection rates. As with the density analyses, I developed a set of CJS models in program MARK to explain survival and probability of detection, computed AIC_C statistics, and used multi-model inference to calculate weighted averages for survival and detection according to the AIC_C weight of each competing model (Burnham and Anderson 2002). Models ranged from the simple intercept-only model to the most general model where survival varied by well site type (closed, reference, open), capture occasion (t , i.e. May-August), and the variables.

Occupancy

The probability of occupying a well site for small mammal species with insufficient capture rates for density or survival estimates was calculated using the multiple-season occupancy model (MacKenzie et al. 2005). The approach is similar to Pollock's robust design model (Pollock et al. 1990) in that there are primary sampling periods with longer time intervals, such that occupancy status can change, and then there are secondary sampling periods, where occupancy status is expected to be static (closed). In this case, well sites were sampled using the same primary and secondary sampling periods (Figure 1.4). Using the Robust Design Occupancy models in Program MARK, I utilized a simplified multi-modeling approach whereby the occupancy (ψ), vital rates (ϵ and γ), and detection (p) were modeled as either site-specific, month-specific (June-August), or constant. Monthly precipitation and temperature varied; with precipitation declining from May through August, therefore I similarly allowed parameter estimates to vary by month. I assumed probability of detection was constant within each secondary sampling period but could vary across primary periods. AIC_C statistics were used for model selection and ranking.

Species Diversity

To make inferences on the species diversity at the different well sites, I estimated species richness using the jackknife estimator in Program SPECRICH (Hines 1996). Here, N is the number of species in the community rather than the population size. The jackknife estimator is appropriate for use in the typical small-mammal study and is more reliable than the naïve counts of species captured, which does not account for detection probability of a species. The jackknife estimator also allows for the more realistic assumption of heterogeneity in detection of individual species (Burnham and Overton 1979). In SPECRICH, the basic data are the capture frequencies

(f_i) for each species, where f_i = the number species encountered exactly i times in the various samples.

I also computed the Shannon-Weiner diversity index (H') and community evenness index or dispersion measure (E'). The Shannon-Weiner diversity index is based on proportional abundance of each species in a community:

$$H' = - \sum P_i \log_2 P_i$$

where P_i is the proportion of the total sample belonging to the i th species (Krebs 1989). Density estimates were used for the proportional abundances. The community evenness value is the Shannon-Weiner value (H') divided by the natural log of the number of sites samples ($E' = H'/\ln S$). This mathematically incorporates the sites sampled that had no individuals (Payne et al. 2005). Maximum evenness (1.0) is when all species are equally abundant; the more the relative abundances of species differ, the lower the evenness value is. E' approaches zero as one species becomes increasingly dominant in number, thus the higher E' values indicate a greater evenness in number of species per sampled site.

RESULTS

Sampling

There were 168 trap nights and 1,150 individuals captured in 2011 and 2012 of six potential species of rodent (Table 1.1). At capped well sites, open well sites, and reference sites, 441, 342, and 367 individuals were captured, respectively. Kangaroo rats and pocket mice were captured most frequently, accounting for 66% (757) and 21% (246) of individuals captured, respectively, while ground squirrel (58), grasshopper mouse (51), deer mouse (30), and least chipmunk (3) each accounted for 5% or less. All species were captured at the reference sites and capped well sites, but the least chipmunk was not captured at open well sites (Table 1.1).

Across sites and years ($n = 12$), capped well sites had the greatest average plant cover ($\bar{x} = 57\%$, $SE = 1.53\%$; note SEs in parentheses unless otherwise indicated), open well sites had lowest cover ($\bar{x} = 38\%$, $SE = 1.51\%$), while reference sites had intermediate values ($\bar{x} = 49\%$, $SE = 1.47\%$); of these percentages, 5%, 4%, and 1% were exotics, respectively. Average percent bare ground was 39% (1.58%), 59% (1.57%), and 50% (1.50%) and average disturbance intensity levels were 1.28 (0.06), 2.06 (0.06), and 0.67 (0.06) at capped, open, and reference sites, respectively. Average monthly temperature and precipitation from May to August were 17°C (1.23) and 21 mm (5.52) in 2011 and 18°C (0.82), and 30 mm (4.14) mm in 2012 (Western Regional Climate Center, <http://www.wrcc.dri.edu/> accessed 20 March 2013).

Density

The pattern of average monthly density by year for kangaroo rats was capped well sites > reference sites > open well sites, while the pattern for pocket mice was reference sites > capped well sites > open well sites. However, the 95% asymmetrical, log-based confidence intervals of monthly averages for both species overlapped considerably across well sites (Figures 1.5 and 1.6). The regression models that best explained kangaroo rat density included plant cover or well sites ($\Delta AIC_C < 2$); while for the pocket mice there were 5 top models with very similar AIC_C weights (Table 1.2). The variable with the greatest relative importance value for kangaroo rat density was total plant cover (Table 1.3). Kangaroo rat density tended to increase with increasing plant cover, and confidence intervals did not overlap zero ($\hat{\beta} = 0.02$; 95% CI = 0.01-0.04). All other variables had importance values < 0.50 (Table 1.3), and confidence intervals of regression coefficients overlapped zero. For pocket mice density, the variable with the greatest importance was disturbance intensity level ($\hat{\beta} = -0.50$; [-1.03-0.04]) with a negative relationship to density

and confidence intervals slightly overlapped zero. All other variables had importance values < 0.50

Survival

Estimates of apparent survival (φ) for kangaroo rats averaged over the 2 years of the study ranged from 0.30 (95% CI = 0.14-0.53) at open well sites to 0.48 (0.28-0.69) at capped well sites (Table 1.4), however confidence intervals greatly overlapped. Of the 450 models evaluated, > 50% of the top ranked models (Table 1.5) included well sites (capped wells: $\hat{\beta} = 0.37$, 95% CI = [-0.05-0.79]; open wells: $\hat{\beta} = -0.37$, [-0.84-0.10]; reference sites: $\hat{\beta} = -0.64$, [-1.06-{-0.21}]), with the top model having the year of study variable ($\hat{\beta} = 2.93$, [0.42-5.45]). Indeed, year of study had the greatest importance value ($w_+ = 0.59$; Table 1.6). Well sites were also highly ranked ($w_+ = 0.49$), but had an importance value < 0.50.

For the pocket mice, model-averaged estimates of survival ranged from 0.55 (0.33-0.75) at capped well sites to 0.79 (0.46-0.93) at reference sites (Table 1.4), but again, confidence intervals overlapped considerably. Of the 450 models evaluated, year of study appeared in all top models ($\hat{\beta} = 1.89$, [-2.54-6.33]; Table 1.5) and had the greatest relative importance (Table 1.6). Estimates of survival in 2012 were nearly twice that of 2011 for all sites. All other variables ranked < 0.50 (Table 1.6) and regression coefficient confidence intervals overlapped zero.

Occupancy

For the other small mammal species captured in 2011 and 2012, the ground squirrel, deer mouse, and grasshopper mouse species had enough captures for probability of occupancy estimation. I applied a suite of simple models ($n = 25$) where occupancy, vital rates, and detection probabilities were either well site type specific, month specific, or constant. For the ground squirrel, models with occupancy varying across well sites were among the best with

model-averaged occupancy being greatest at reference sites (Table 1.7). For the grasshopper mouse, models with constant occupancy ranked highest in the model selection criterion, suggesting little variation in occupancy across well sites (Table 1.7). For the deer mouse, the model with variation of occupancy by time (i.e., month of sampling) ranked highest and probability of occupancy was similar at open well sites and reference sites (Table 1.7).

Species Diversity

In 2012, all species richness estimates were equal across the sampled sites (7, SE = 1.41) however in 2011, estimates ranged from 5 (0.49) at open well sites to 7 (1.41) at reference sites (Table 1.8). Estimates of richness were slightly higher than the total number of recorded species. The pattern of Shannon-Weiner diversity index and community evenness values in 2011 was reference sites > open well sites > capped well sites while in 2012 it was reference sites > capped well sites > open well sites (Table 1.8).

DISCUSSION

This study evaluated the small mammal population dynamics at artesian well sites in the sand sheet ecosystem of the GRSA. I found no support for my hypothesis that capping artesian well sites increases small mammal densities; changes in density estimates of kangaroo rat and pocket mice at different well sites were not significant. Despite other observations that kangaroo rats prefer open, sandy grassland habitats (Kerley et al. 1997, Price et al. 2000, Lightfoot et al. 2012), my findings suggest that Ord's kangaroo rat chose sites of greater plant cover versus sites with more open habitat (i.e., open well sites). Plant cover had the greatest relative importance in explaining kangaroo rat density (positive relationship), and well sites with higher plant cover possibly provide the kangaroo rat with more seeds during foraging (Rosenzweig and Sterner 1970, Veech and Jenkins 2005, Reid 2006). In particular, Indian rice grass (*Oryzopsis*

hymenoides), an important component to the kangaroo rat diet (Rosenzweig and Sterner 1970, Veech and Jenkins 2005, Ward 2009) had greater cover on sites with greater kangaroo rat density. Similarly, other studies have reported that densities of small mammals can be negatively affected by ungulate disturbance, which decreased food availability through trampling of vegetation (Jones et al. 2003, Torre et al. 2007). After the exclusion of ungulates from high-elevation riparian zones, Parsons et al. (2013) detected an increase in relative abundances of small mammals, due to an increase in plant cover and habitat quality. Increased disturbance intensity levels reduced the abundance of all plant cover at open well sites; including grass species (see Chapter 2).

Pocket mice densities were not significantly different at well sites; however, a trend of increasing density with decreased disturbance by ungulates was evident. The less-disturbed reference sites possibly provided more suitable habitat for pocket mice by offering increased cover for hiding (Leaver and Daly 2003), increased resource availability (Kotler et al. 1994), and a greater diversity of seeds for consumption (Veech 2001). Pocket mice are often associated with less-disturbed sites, (Jones et al. 2003) and have greater abundances in areas of greater plant cover (Rosenzweig 1973, Schorr et al. 2007, Tietje et al. 2008, Thompson and Gese 2013). In a study of disturbances and density-dependent population dynamics of spiny pocket mice (*Chaetodipus spinatus*), Klinger (2007) found that decreased densities were strongly related to consistent disturbance events such as floods and rains. Areas of greater plant cover (i.e., capped sites and reference sites in my study) are typically characterized by small, seed-eating mice such as the pocket mice (Schorr et al. 2007, Thompson and Gese 2013). Furthermore, the apparent lower density of the kangaroo rat at reference sites may have positively influenced pocket mice densities as other studies have shown these species compete for habitat and seeds (Heske et al.

1994, Price et al. 2000, Upham and Hafner 2013). In the GRSA, resource availability and interspecific competition should be considered when making predictions on the pocket mice species response to artesian well site closures.

Kangaroo rat survival was not significantly greater at capped well sites, refuting my hypothesis that reduced disturbance intensity by ungulates would increase survival rates. This is contradictory to other studies that have documented higher kangaroo rat survival in areas that are structurally open and slightly disturbed (Waser and Ayers 2003, Kelt et al. 2005, Schorr et al. 2007), but the amount of disturbance at the well sites might be considered more severe in comparison to these studies. Since kangaroo rats consume the seeds of grasses, succulents, and certain shrub species (Reid 2006, Davidson et al. 2010, Germano et al. 2011), the additional plant cover at capped well sites and reference sites could increase survival of the kangaroo rat, however kangaroo rat survival varied more by year in my study. Some of this variation may be linked to annual variation in precipitation. Rain and snowfall levels were lower than expected during both years of the study with rain levels in 2011 being 7 cm below average (Western Regional Climate Center, <http://www.wrcc.dri.edu/> accessed 20 March 2013). Seeds of various desert plant species require different amounts of rain for germination and seedling establishment (Gutterman and Gozlan 1998). After insufficient rainfall, seedlings may suffer irreversible damage from dehydration stress, resulting in decreased seed availability for rodents. Average survival estimates of kangaroo rat at well sites all increased from 2011 to 2012 whereas average mass of individuals captured decreased, suggesting that in these times of decreased resources, the rodents may have reduced energy expenditure directly through a decrease in mass, and reduced resource requirements (McNab 1994). Understanding how climate variation and changes in

habitat structure affect yearly small mammal survival has important implications for future classifications of the capped artesian well sites in terms of ecological succession.

Survival rates of pocket mice were not higher at capped well sites, the rates varied more by year than by well sites. Pocket mice survival can be sensitive to yearly changes in vegetation community composition and diversity (Thompson and Gese 2013). Plant species in arid regions vary considerably in their ability to utilize annual pulses of rain, and a shift to drier growing season conditions could affect plant growth and competition, causing changes in plant community composition (Knapp et al. 2002, Chimner and Cooper 2004, Elmore et al. 2006). In a rainfall manipulation experiment, Kray et al. (2012) found that reduced rainfall in the SLV decreased native grass species (*Sporobolus airoides* and *Distichlis spicata*), but had little effect on more deeply-rooted shrubs such as greasewood (*Sarcobatus vermiculatus*) and rubber rabbitbrush because shrubs can use a combination of groundwater and precipitation recharged soil water (Chimner and Cooper 2004). Other studies have reported greater survival of pocket mice in areas of greater shrub cover (Tietje et al. 2008, Thompson and Gese 2013), therefore shrub cover at all well sites from 2011 and 2012 may have increased pocket mice survival by providing protection from predation (Upham and Hafner 2013), increasing food resources (Kotler et al. 1994), and/or discouraging greater abundances of kangaroo rat (Rosenzweig 1973, Price et al. 2000). Pocket mice may also be responding to release from kangaroo rat foraging competition (Reichman and Price 1993).

There was no evidence to suggest that the probability of small mammal occupancy was highest at capped well sites. For example, ground squirrel occupancy was greatest at the reference sites. Ground squirrel abundance is higher in areas of shrub cover rather than open areas dominated by grass (Steenhof et al. 2006, Ordenana et al. 2012), and the greater shrub

abundance at reference sites may have provided food, escape cover, and trapped sand to maintain hummocks where the ground squirrel burrows (Ball et al. 2005). Occupancy rates for the grasshopper mouse did not vary among sampled sites. Stapp (1997) investigated the presence of northern grasshopper mouse in shortgrass prairie and found that grasshopper mice concentrate in areas with slight disturbance due to terrestrial arthropods being more accessible and frequent. Whether the concentration and accessibility of prey will eventually explain the occupancy rates at well sites by the grasshopper mouse is an area for future investigation. The deer mouse had similar occupancy rates at open well sites and reference sites and much lower occupancy rates at capped well sites. As a generalist species, the deer mouse is more often found in areas of less cover (Hadley and Wilson 2004), and often in areas with greater disturbance (Leis et al. 2008) which may explain their higher occupancy at open well sites. Additionally, the deer mouse and Ord's kangaroo rat live sympatrically in dry grasslands and have many of the same resource requirements (Koehler and Anderson 1991). Falkenberg and Clarke (1998) observed aggressive attacks (active chasing and locking fights) by kangaroo rats towards deer mice that caused deer mice to shift towards a narrower plant cover habitat selection. The reference sites may be areas where the deer mouse is able to better forage while evading aggression from the kangaroo rat.

Contrary to my hypothesis, the species diversity indices (species richness, Shannon-Weiner diversity index, and community evenness) were greatest at reference sites rather than the capped well sites. Species diversity can be influenced by a variety of environmental factors, including changes in land use, nutrient availability, and disturbance regimes (Hooper et al. 2005). There are several studies in arid/semi-arid regions where decreased plant composition and cover due to ungulates resulted in loss of small mammal diversity. In arid Utah grasslands, small mammal richness was 50% higher in ungrazed, control areas compared to grazed plots

(Rosenstock 1996). In South Africa, small mammal species diversity was lower in more-heavily disturbed, communal semi-arid rangelands due to lack of plant cover for predator avoidance (Joubert and Ryan 1999). Other studies have suggested that the presence or absence of large herbivorous mammals commonly influences the species diversity values of small mammals through engineering effects on their habitat (Jones et al. 2003, Parsons et al. 2013, Thompson and Gese 2013). The main determinant of small mammal diversity appears to be plant cover, particularly of shrub species, therefore the expectation is that small mammal diversity at capped well sites will continue to increase and eventually reflect reference site values as ecological succession continues. In addition, two species, the bushy-tailed wood rat (*Neotoma cinerea*) and the plains harvest mouse (*Reithrodontomys montanus*) are known to inhabit sand sheet ecosystems, but were not captured in my study. Their absence could reflect low probability of capture, and/or simple absence from my study sites. Time of year and lower plant/seed abundance due to drought could also be factors, but the May through August trapping overlapped periods when these species should have been active (Carey 1991; Moses and Millar 1992; CPW, <http://wildlife.state.co.us/WildlifeSpecies/Mammals/HarvestMice.aspx> accessed 27 April 2013). The footprint of the well sites is small relative to the surrounding natural habitats, thus restoration of these well sites is probably not necessary to ensure that small mammal biodiversity is maintained within the GRSA.

Although my data suggests capping well sites does not significantly affect small mammal communities, the ecosystem changes may have implications for local plant community composition. Recovery of arid grasslands can take decades (Daubenmire 1975, Rickard and Sauer 1982), because initial plant colonizers strongly influence future community composition (Hoelzle et al. 2012). Despite apparent increase of native plant cover at capped well sites,

intensive management may be needed due to the concurrent increase in exotic plants (see Chapter 2). Additionally, the continued sightings of elk and the observed intermediate disturbance intensity levels suggested that elk were still returning to the capped well sites, and therefore have not completely redistributed outside of the GRSA. Based on my findings, capping of artesian wells has very little impact on small mammal population dynamics in the short-term, therefore TNC should focus on their goal of protecting ecologically important lands and waters for nature and people (TNC, <http://www.nature.org/about-us/vision-mission/index.htm> accessed 27 April 2013) when considering whether to cap the remaining open wells. Further study can ultimately provide a better understanding of the long-term recovery of these well sites and promote sound management decisions for the conservation, not only of the small mammal populations, but also of the groundwater in this unique, arid ecosystem.

Table 1.1 Number of individual captured per small mammal species by year at capped well sites (capped since 2010), open well sites (flowing water), and reference sites in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Two species of *Perognathus* sp were potentially captured.

Species	Capped Well Sites		Open Well Sites		Reference Sites	
	2011	2012	2011	2012	2011	2012
<i>Dipodomys ordii</i>	183	179	170	78	90	57
<i>Perognathus</i> sp. ¹	27	30	10	52	33	94
<i>Spermophilus tridecemlineatus</i>	1	3	2	15	17	23
<i>Onychomys leucogaster</i>	5	6	3	3	28	8
<i>Peromyscus maniculatus</i>	0	6	2	7	3	12
<i>Tamias minimus</i>	0	1	0	0	1	1
Total Individuals	216	225	187	155	172	195
Total Species	4	6	5	5	6	6

¹Two species of pocket mouse, *Perognathus apache* and *P. flavus*, were potentially captured but were difficult to identify without examining skulls and teeth, therefore pocket mice were only identified to genus (Valdez 2003).

Table 1.2 Model selection results of top regression models (Proc GENMOD, identity link, SAS Institute Inc. 2005) comparing well sites and habitat characteristic effects on monthly densities of kangaroo rats (*Dipodomys ordii*) and pocket mice (*Perognathus* sp.) in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Headings are Akaike's information criterion for small sample size (AIC_C), difference in AIC_C and top ranked model (ΔAIC_C), model weight (AIC_C weight), and number of parameters (K) for the most supported models. The 4 variables modeled included: well sites (capped, open, reference); disturbance intensity level (0-3); average plant cover (%); and year (2011, 2012).

Model	AIC_C	ΔAIC_C	AIC_C weight	K
Kangaroo rat				
Plant Cover	48.85	0	0.34	2
Well Sites	50.01	1.16	0.19	2
Intercept	51.49	2.64	0.09	1
Pocket mice				
Disturbance	50.23	0	0.19	2
Well Sites	50.36	0.13	0.18	2
Intercept	50.51	0.28	0.17	1
Year + Disturbance	51.47	1.24	0.10	3
Plant Cover + Disturbance	51.76	1.53	0.09	3
Year	52.95	2.72	0.05	2

Table 1.3 Relative importance values (w_+) of variables influencing density of kangaroo rat (*D. ordii*) and pocket mice (*Perognathus* sp.) in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Variables are defined in Table 1.2.

Variable	Kangaroo rat	Pocket mice
Well Sites	0.26	0.26
Year	0.22	0.27
Plant Cover	0.62	0.25
Disturbance	0.15	0.57

Table 1.4 Model-averaged estimates of 4-week apparent survival (ϕ and 95% CIs) for Ord's kangaroo rat (*D. ordii*) and pocket mice (*Perognathus* sp.) at well sites in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. The smaller confidence intervals at capped well sites may be due to greater relative abundance values compared to the other sampled sites for both years of the study.

Species	2011	2012
Kangaroo rat		
Capped Well Sites	0.41 (0.23-0.61)	0.48 (0.28-0.69)
Open Well Sites	0.30 (0.14-0.53)	0.37 (0.13-0.70)
Reference Sites	0.33 (0.19-0.51)	0.40 (0.19-0.65)
Pocket mice		
Capped Well Sites	0.55 (0.33-0.75)	0.78 (0.47-0.93)
Open Well Sites	0.56 (0.34-0.76)	0.78 (0.46-0.94)
Reference Sites	0.56 (0.34-0.74)	0.79 (0.46-0.93)

Table 1.5 Model selection results for apparent survival (ϕ) and detection probabilities (p ; program MARK [White and Burnham 1999]) of Ord's kangaroo rat (*Dipodomys ordii*) and pocket mice (*Perognathus* sp.) populations as a function of well sites, disturbance level, plant cover, and year in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Headings are Akaike's information criterion for small sample size (AIC_C), change in AIC_C (ΔAIC_C), model weight (AIC_C weight), and number of parameters (K) for the most parsimonious models. Variables are defined in Table 1.2.

Model	AIC_C	ΔAIC_C	AIC_C weight	K
Kangaroo rat ϕ (Year) p (Year + Well Sites)	1368.07	0	0.04	6
ϕ (Well Sites + Plant Cover) p (Year)	1368.46	0.39	0.03	6
ϕ (Year + Well Sites) p (Year + Well Sites)	1368.48	0.41	0.03	8
ϕ (Year + Plant Cover + Disturbance) p (Year + Disturbance)	1368.53	0.47	0.03	7
ϕ (Year + Month) p (Year + Well Sites + Month+ Plant Cover)	1368.72	0.65	0.03	11
ϕ (Well Sites + Plant Cover) p (Year + Plant Cover)	1369.09	1.02	0.02	7
ϕ (Year + Plant Cover) p (.)	1369.22	1.16	0.02	5
ϕ (Year) p (Year + Well Sites + Plant Cover)	1369.24	1.18	0.02	7
ϕ (Well Sites) p (.)	1369.34	1.28	0.02	4
ϕ (Well Sites + Plant Cover) p (Year + Well Sites)	1369.50	1.43	0.02	8
ϕ (Year + Month) p (Year + Well Sites + Month)	1369.57	1.50	0.02	10
ϕ (Year) p (Year + Well Sites + Month)	1369.59	1.53	0.02	8
ϕ (Year + Disturbance) p (Year + Disturbance)	1369.82	1.75	0.02	6
ϕ (Year + Well Sites + Plant Cover) p (Year)	1369.87	1.80	0.02	7

	ϕ (Year + Plant Cover) p (Year + Well Sites)	1369.93	1.86	0.02	7
	ϕ (Year + Well Sites + Plant Cover)				
	p (Year + Well Sites)	1370.06	2.00	0.01	9
Pocket mice	ϕ (Year) p (Year)	373.19	0	0.06	3
	ϕ (Year) p (Year + Disturbance)	373.62	0.43	0.05	4
	ϕ (Year) p (Year + Month)	373.68	0.49	0.05	5
	ϕ (Year) p (Year+ Disturbance + Month)	374.07	0.88	0.04	6
	ϕ (Year + Disturbance) p (Year)	374.32	1.13	0.04	4
	ϕ (Year) p (Year + Plant Cover)	374.44	1.25	0.03	4
	ϕ (Year + Disturbance) p (Year + Month)	374.83	1.64	0.03	6
	ϕ (Year + Plant Cover) p (Year)	375.09	1.90	0.02	4

Table 1.6 Relative importance values (w_+) of variables affecting survival for kangaroo rat (*D. ordii*) and pocket mice (*Perognathus* sp.) in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Variables are defined in Table 1.2.

Variable	Kangaroo rat	Pocket mice
Well Sites	0.49	0.09
Year	0.59	0.84
Plant Cover	0.48	0.29
Disturbance	0.16	0.26

Table 1.7 Model-averaged estimates for site occupancy (Ψ and 95% CIs) with vital rates of colonization and extinction (ε and γ), and detection probability (p) in the top-ranking models ($\Delta AIC_C < 2$) of three of the least common species of small mammals at sampled sites during primary sampling periods in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Blank lines represent models where occupancy varied by month of sampling and therefore did not have occupancy values by well site.

Species	Model	ΔAIC_C	ψ (Capped)	ψ (Open)	ψ (Reference)
Ground Squirrel	Ψ (Well Sites) ε (.) γ (Well Sites) p (.)	0	1.39E-09	0.25	0.51
	Ψ (t) ε (.) γ (t) p (.)	0.45			
	Ψ (.) ε (.) γ (Well Sites) p (.)	0.77	0.25	0.25	0.25
	Ψ (Well Sites) ε (.) γ (.) p (.)	0.92	4.86E-09	0.25	0.51
	Ψ (Well Sites) ε (.) γ (Well Sites) p (Well Sites)	1.00	7.60E-11	0.25	0.50
	Ψ (.) ε (.) γ (Well Sites) p (Well Sites)	1.34	0.25	0.25	0.25
	Ψ (Well Sites) ε (.) γ (.) p (Well Sites)	1.45	4.51E-09	0.25	0.50
	Ψ (t) ε (.) γ (.) p (.)	1.89			
	Ψ (.) ε (.) γ (.) p (Well Sites)	2.00	0.25	0.25	0.25
	Model Averaged ψ			0.11	0.25
95% Confidence Intervals			(0.04-0.24)	(0.06-0.67)	(0.11-0.74)
Grasshopper Mouse	Ψ (.) ε (.) γ (Well Sites) p (Well Sites)	0	0.51	0.51	0.51
	Ψ (.) ε (.) γ (.) p (Well Sites)	1.78	0.49	0.49	0.49
	Ψ (.) ε (.) γ (Well Sites) p (.)	6.14	0.44	0.44	0.44
	Model Averaged ψ			0.52	0.39
95% Confidence Intervals			(0.15-0.85)	(0.10-0.82)	(0.15-0.84)
Deer Mouse					

$\Psi(t) \varepsilon(\cdot) \gamma(\cdot) p(\cdot)$	0			
$\Psi(\text{Well Sites}) \varepsilon(\cdot) \gamma(\cdot) p(\cdot)$	0.55	5.75E-09	0.29	0.33
$\Psi(t) \varepsilon(\cdot) \gamma(t) p(\cdot)$	2.38			
Model Averaged ψ		0.08	0.26	0.27
95% Confidence Intervals		(0.02-0.38)	(0.04-0.71)	(0.04-0.72)

Table 1.8 Species richness, Shannon-Weiner diversity index (H'), and community evenness (E') for the sand sheet small mammal community at sampled well sites and reference sites in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. SEs are in parentheses.

Index	2011			2012		
	Capped	Open	Reference	Capped	Open	Reference
Species richness	5 (1.41)	5 (0.49)	7 (1.41)	7 (1.41)	7 (1.41)	7 (1.41)
H'	0.78 (0.10)	0.88 (0.08)	0.96 (0.05)	0.97 (0.04)	0.96 (0.05)	0.99 (0.01)
E'	0.44	0.49	0.54	0.54	0.53	0.56

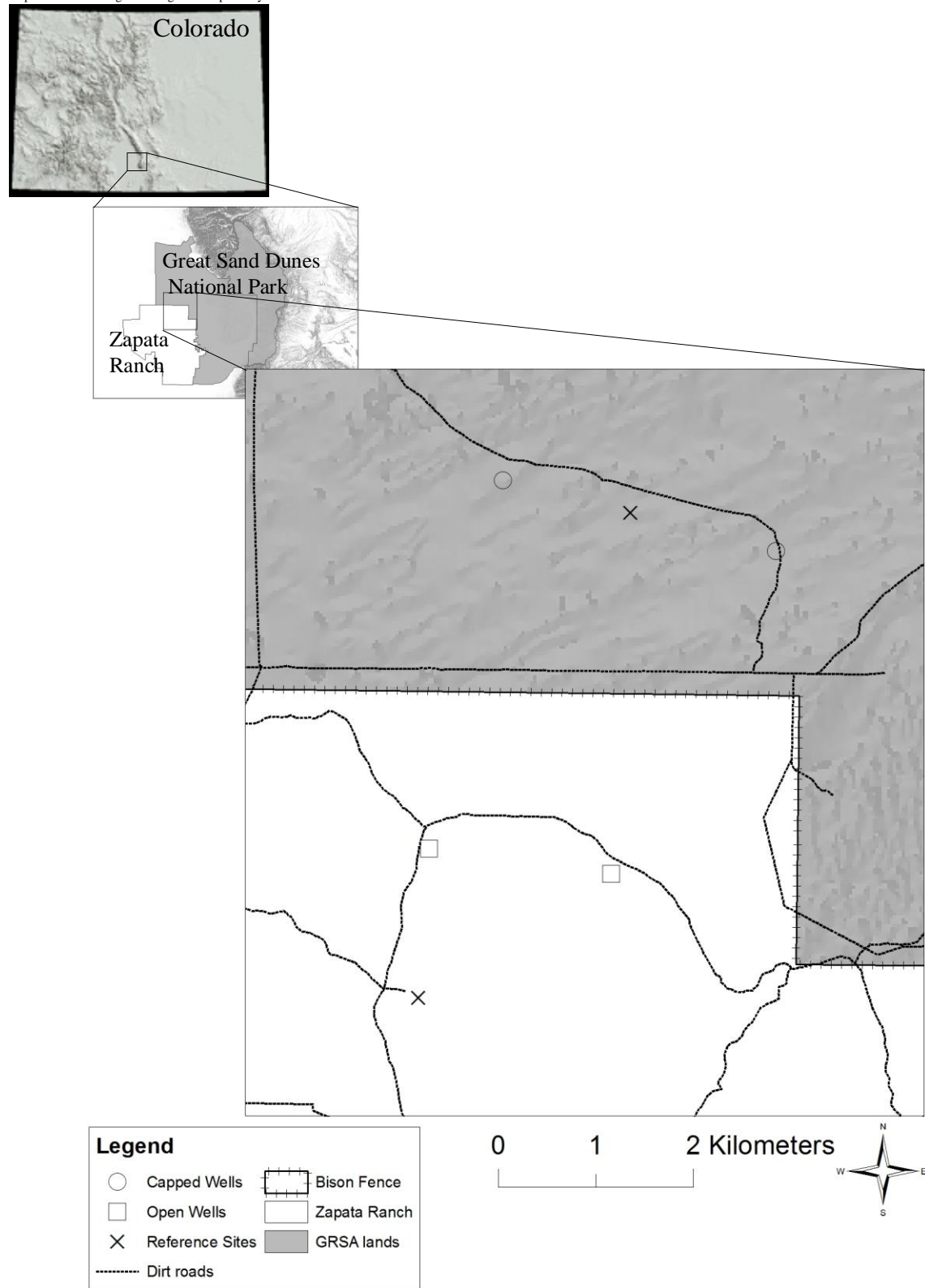


Figure 1.1 Location of artesian well sites and reference sites studied in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, south-central Colorado, 2011-2012.



Figure 1.2 Bison drinking at a typical open artesian well site comprised of a 5-cm steel pipe that fills a tank in TNC's Zapata Ranch, adjacent to the Great Sand Dunes National Park, Colorado, 2011. Note the piosphere effect around the tank (Photo by Sarah J. Garza).



Figure 1.3 A typical capped artesian well site comprised of a 5-cm steel pipe and the now empty water tank in the Great Sand Dunes National Park, Colorado, 2011 (Photo by Sarah J. Garza).

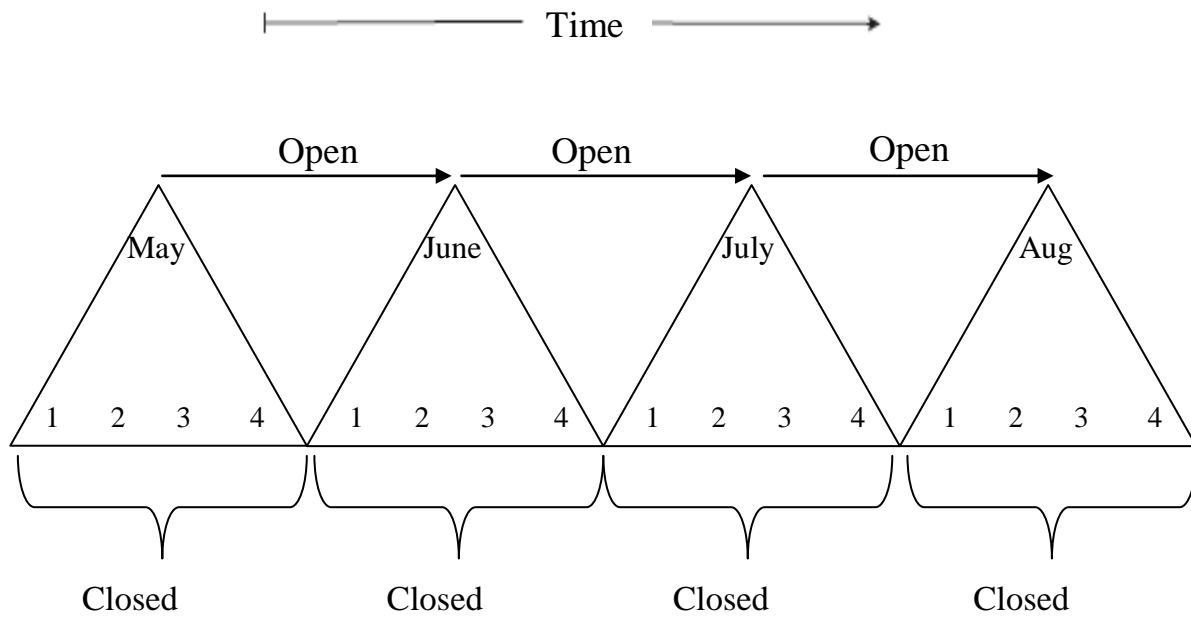


Figure 1.4 Quasi-robust design of primary (month) and secondary (4 trap nights) sampling periods.

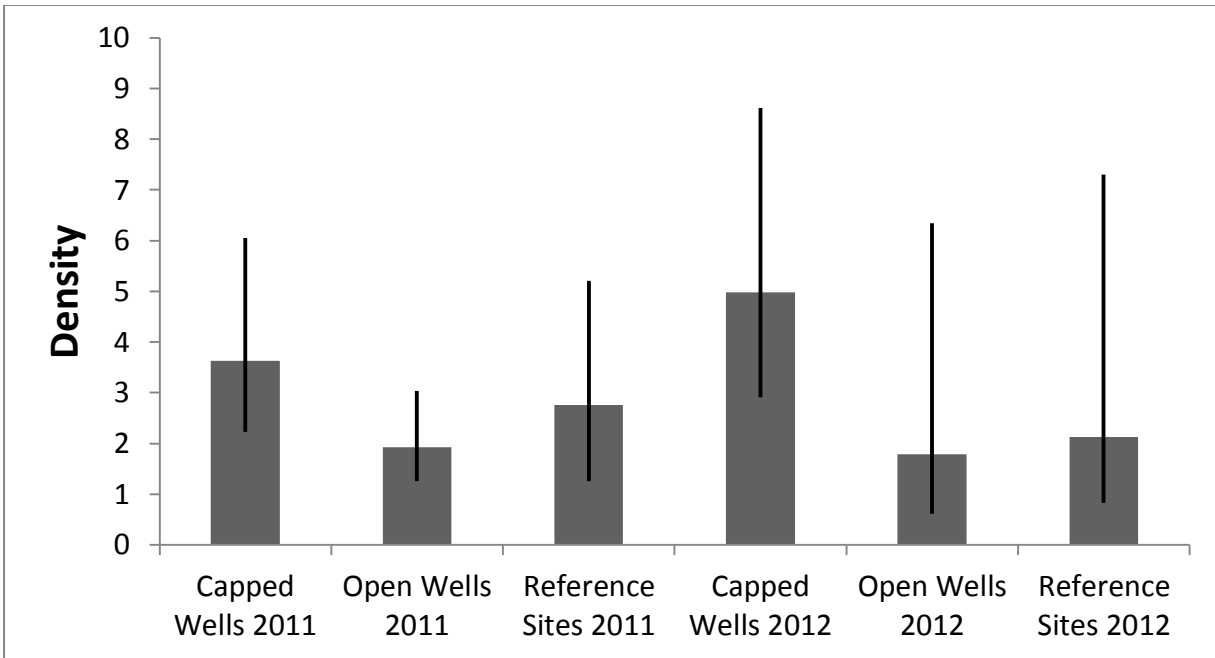


Figure 1.5 Average density ($\hat{D} \pm$ log-based 95% CIs, $n = 6$ in 2011 and $n = 8$ in 2012) of Ord's kangaroo rat (*Dipodomys ordii*) by year and well site type from May to August in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Log-based 95% confidence intervals of \hat{D} were calculated in program DISTANCE.

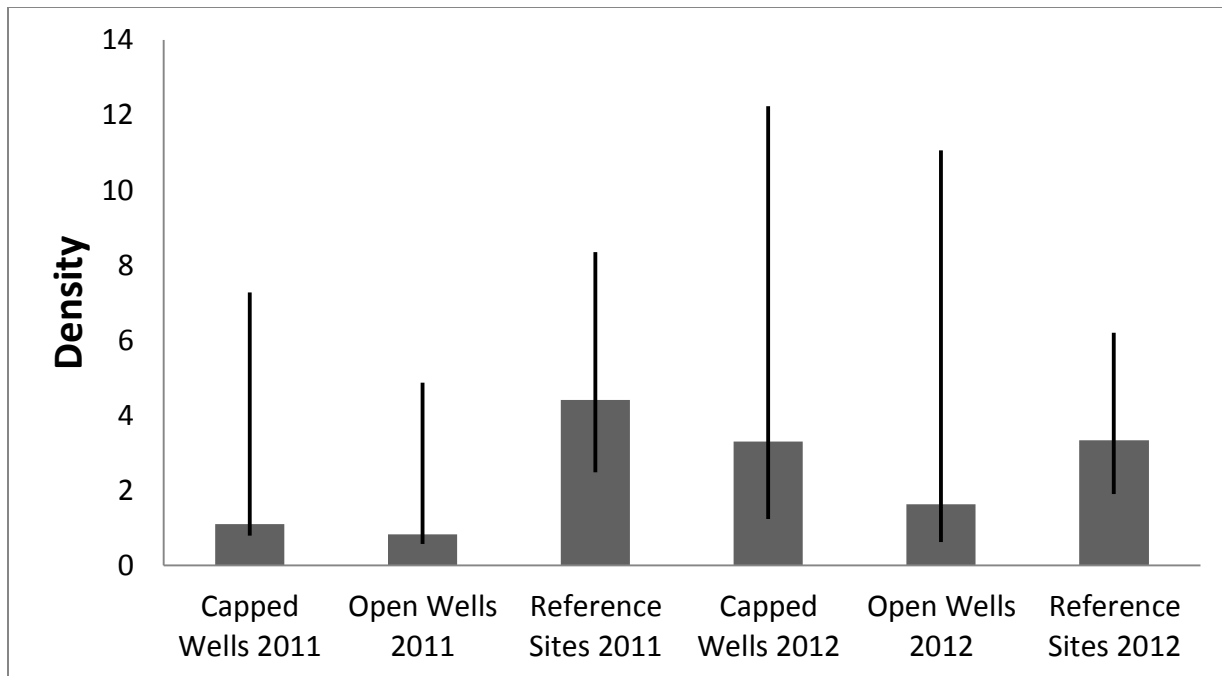


Figure 1.6 Average density ($\hat{D} \pm$ log-based 95% $n = 6$ in 2011 and $n = 8$ in 2012) of pocket mice (*Perognathus* sp.) by year and well site type from May to August in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Log-based 95% confidence intervals of \hat{D} were calculated in program DISTANCE

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CHAPTER 2: SAND SHEET PLANT COMMUNITY DEVELOPMENT FOLLOWING CAPPING OF ARTESIAN WELL SITES IN GREAT SAND DUNES NATIONAL PARK, COLORADO.

Plant community development, ecological succession, and recovery of lands on former agricultural and ranching operations are a critical part of ecological restoration throughout the United States. Recovery of these lands after development is important for ecosystem services and can be characterized by sequential stages of community assembly (Hoelzle et al. 2012). Studies of ecological succession examine these sequential community stages to try and explain plant community development following disturbance (Paschke et al. 2003, Hoelzle et al. 2012). However, native plant species reestablishment after changes in land use can take up to decades (Daubenmire 1975, Rickard and Sauer 1982), because initial colonizers strongly influence future community composition (Hoelzle et al. 2012). The time needed for an area to recover may also be a result of ongoing disturbance to the ecosystem (Coffin et al. 1996, Cramer et al. 2008). Land use and ecosystems recovery have been studied in many arid North American ecosystems including the sagebrush steppe (Morris et al. 2011, Hoelzle et al. 2012), the Sonoran Desert (Banerjee et al. 2006), and the eastern sand plains (Motzkin et al. 1996).

Great Sand Dunes National Park and Preserve (GRSA) is located in south-central Colorado along the eastern edge of the San Luis Valley (SLV). This area was ranched during the early 20th century (Stewart 1938, Emery et al. 1969). When the first cattle ranches were established, 24 artesian wells were drilled to support these livestock operations (GRSA General Management Plan 2006). Cattle ranching operations ceased in 2004, and in 2010, the NPS capped all artesian wells located within the park boundaries (n = 10), and all of the remaining uncapped wells (n = 14) are currently within The Nature Conservancy (TNC) Zapata ranch

boundaries. Today, the TNC well sites continue to operate, creating open water access points for wildlife and changing the surrounding vegetation communities.

Artificial watering sites can become focal points of grazing by domestic and wild ungulates in rangelands (Eldridge and Whiteford 2009). Livestock use areas more heavily around well sites compared to areas away from water (Fusco et al. 1995, Brooks 2000). Wild ungulates, such as mule deer (*Odocoileus hemionus*), will change distributions and movements relative to water catchments (Hervert and Krausman 1986). For free-ranging bison (*Bison bison*), density is related to water availability during the summer (Fortin and Andruskiw 2003), and distance to water influences habitat choice of elk (*Cervus elaphus*) populations (Beck et al. 2006). When large numbers of grazers concentrate at a water site, the impact can lead to changes in plant species and a gradient of disturbance known as a piosphere (Lange 1969, Andrew 1988). These gradients are characterized by high herbivore activity (Thrash et al. 1995), densities (Lange 1969, Andrew and Lange 1986, Brooks et al. 2006) and disturbance (Thrash et al. 1993), which can result in loss of soil microtopography (Nash et al. 2003) and low plant cover (Fusco et al. 1995).

Piosphere plant communities are characterized by early stages of ecological succession, e.g., large areas devoid of plant cover (Andrew and Lange 1986, Fusco et al. 1995), decreased plant species composition (Tolsma et al. 1987, Fernandez-Gimenez and Allen-Diaz 2001), and decreased plant reproductive output (Riginos and Hoffman 2003). In desert ecosystems, the types of emerging plant species related to ecological succession at artificial watering sites varies greatly (Andrew 1988, Fusco et al. 1995, Nangula and Oba 2004, Landsberg et al. 2003). For example, in the Mojave Desert, California, the earliest stage of succession at watering sites was characterized by exotic plant species on bare ground (Brooks et al. 2006). In the Chihuahuan

Desert, New Mexico, livestock created nutrient-rich patches near water that supported species of native annual plants that were rare or absent in other areas (Nash et al. 1999). The goal of my study was to characterize the ecological succession and possible recovery of the plant communities at capped well sites in the GRSA sand sheet ecosystem. In the absence of long-term data sets and information on the historic ecosystem (Knapp 1992, Morris et al. 2011), "recovery" was defined as well site similarity to adjacent reference sites with no well heads. Specifically, I focused on the following objectives: 1) to determine the short-term effects of capping artesian well sites on local plant community recovery and 2) to examine some of the factors that may influence vegetation recovery in these well sites. To do this, I compared plant species percent cover and frequency, across 3 well types (capped wells, wells with water [open wells], and reference areas) in the GRSA. These responses were then related to distance from the well head, disturbance levels by ungulates, and annual variation using a multi-model approach (Burnham and Anderson 2002, Johnson and Omland 2004). I also compared plant species diversity (richness and evenness) as a function of well type and patterns of plant form cover at different distances from well heads to determine vegetation responses within these sites following the capping of an artesian well.

Several studies have shown that succession of key plant species on disturbance zones in previously cultivated lands can be influenced by abiotic factors such as soil recovery, elevation, and local climate (Walker et al. 2004, Brunson et al. 2010, Hacker et al. 2011). In addition, succession and recovery may vary depending on certain biotic factors such as seed availability, land-use legacies, and available browsers (Paschke et al. 2003, Wong et al. 2010, Scott and Morgan 2012). Therefore, I hypothesized that well sites would affect plant cover, frequency, and species diversity, because differences in ungulate use between capped and open well sites creates

differences in disturbance intensity (Lange 1969) that can influence plant community development (Leicht-Young et al. 2009). Specifically, I expected native plant cover and frequency to be greatest at the capped well sites due to less disturbance by ungulates (Stohlgren 2007). Furthermore, I hypothesized that exotic plant cover and frequency would be greatest at open well sites due to higher tolerance to disturbance and decreased competition for resources (Pegman and Rapson 2005). I also hypothesized that native species would have greater species diversity at capped well sites compared to reference sites and open well sites, because intermediate grazing reduces plant biomass and competition and can increase available nutrient and water resources (Stohlgren 2007). Finally, I expected plant cover as a function of plant form, i.e., shrub, forb, or grass, to increase linearly as a function of distance from open wells based on native plant cover decreasing with proximity to water sites (Brooks et al. 2006). Based on the intermediate disturbance hypothesis, I also expected plant form cover at capped wells to increase with distance, peak at an intermediate distances from the well head, and then decrease (Fox 1979).

STUDY AREA

This study was conducted on the eastern edge of the SLV of south-central Colorado in Great Sand Dunes National Park and the adjacent Zapata Ranch, owned by The Nature Conservancy (Figure 2.1). The SLV is an arid, high elevation (2,300 m) closed basin valley just west of the Sangre de Cristo Mountains. Water entering the southern portion of the valley forms the headwaters of the Rio Grande River, while in the north, water collects in numerous small playa lakes in the hydrologically closed portion of the valley (Rupert and Plummer 2004, Schoenecker 2012). Precipitation averages 28 cm annually, mostly in July through September, and average annual snowfall is 104 cm, primarily from October through March (Western

Regional Climate Center, <http://www.wrcc.dri.edu/> accessed 20 March 2013). Average daytime temperatures on the valley floor in summer range from 26.5 °C to 29.5 °C and from -9.5 °C to 1.5 °C in winter.

My research was conducted on the southern and southwestern sides of the main dune field, an area known as the sand sheet. The plant community in this region varies from wet meadows to grassy prairies to desert shrub lands, depending on proximity to groundwater (NPS, <http://www.nps.gov/grsa/index.htm> accessed 24 October 2012). Rocky Mountain iris (*Iris missouriensis*) and inland saltgrass (*Distichlis spicata*) are found in the wet meadows and around ephemeral wetlands (NPS, <http://www.nps.gov/grsa/index.htm> accessed 24 October 2012). The grassy prairies include blue grama (*Bouteloua gracilis*), Indian rice grass (*Oryzopsis hymenoides*), needle and thread grass (*Hesperostipa comata*), and false buffalo grass (*Monroa squarrosa*). Shrubs commonly found include rubber rabbitbrush (*Ericameria nauseosus*), sagebrush (*Artemisia* sp.), and yucca (*Yucca glauca*). Some wetland species present at the open well sites included leafy pondweed (*Potamogeton foliosus*), duckweed (*Lemna minor*) and water sedge (*Carex aquatilis*). Cottonwoods and willows (coyote willow, *Salix exigua*; mountain willow, *S. monticola*; interior willow, *S. interior*; and narrowleaf cottonwood, *Populus angustifolia*) grow on top of dunes along Sand Creek, and near other fresh water springs in the park (Schoenecker et al. 2006, Salas et al. 2010). Non-indigenous plants (exotics) include Russian thistle (*Salsola tragus*), Russian knapweed (*Acroptilon repens*), and cheatgrass (*Bromus tectorum*) (Spackman Panjabi et al. 2004).

Bison, elk, mule deer, and pronghorn (*Antilocapra americana*) grazed this area until about 1840 when bison, pronghorn, and elk were extirpated as ranching developed (Swift 1945,

Schoenecker 2012). Currently, all but bison can be found in the GRSA. Livestock, including sheep (*Ovis aries*) and cattle (*Bos taurus*), were grazed throughout the study area, especially in the sand sheet that now comprises part of the national park (Schoenecker et al. 2006; NPS, <http://www.nps.gov/grsa/parkmgmt/index.htm> accessed 17 March 2013). The former Luis Marie “Baca” Ranch, which makes up the northern part of the GRSA and all of the Baca National Wildlife Refuge, was grazed by cattle until 2004 (Schoenecker 2012). Approximately 2,800 bison were reintroduced on the Zapata Ranch in 1989, and in 1999, TNC purchased the 40,500-ha Zapata ranch and converted part of the area to a preserve (The Zapata Ranch, <http://www.zranch.org> accessed 17 March 2013).

METHODS

Study Design

Two capped wells on NPS lands (Figure 2.2), 2 open (uncapped) wells on TNC lands (Figure 2.3), and 2 reference sites, one in each land area, were selected for this study (Figure 2.1). All sites were accessible to elk, mule deer, and pronghorn, but only the open well sites and the nearby reference site on TNC lands were accessible to bison. To determine if different well type conditions were historically similar, the site appearance and visible piosphere conditions for each of the selected well sites was compared using Google Earth® and past photographs. Site conditions were similar at capped and open wells prior to this study; therefore, I considered any differences found at the capped well sites during the study to be evidence of ecological succession since the NPS sites were not in better condition prior to the start of this study than the TNC sites.

Sampling

Each site was sampled between late May through August in 2011 and in 2012. At each location, twelve 100-m transect lines were arranged in a web originating 10 m north of the well heads. The web design was used because it could accommodate a small mammal population dynamics study (see Chapter 1) and this study. The first transect was oriented at 0° and the others at intervals of 30° to complete the web. Sampling points were established at 10-m intervals along each line (n =120 per site). If placement was directly on a road or an obstruction, e.g., metal, old tires or wooden structures, then it was moved as close as possible to its original location, but still along the transect line. Sampling locations were staked, flagged, and labeled with distance from web center and transect number. At each sampling point, I measured habitat within a 1-m² quadrat frame that was placed 2 m to the right of the transect line to avoid disturbance by the researcher. Recorded habitat variables included: 1) percent native and exotic plant species cover (0-100%), 2) number of individual native and exotic plants (frequency), 3) disturbance intensity level (0-3, see explanation below), and 4) percent cover of woody debris and/or water (0-100%). Evidence of disturbance by ungulates included trampling, e.g., lack of plant cover, compacted sand, presence of tracks, and flattened shrubs (Howe and Baker 2003). Disturbance was recorded at 4 levels based on degree of intensity: 0) none, 1) mild (bare ground was < 25%), 2) intermediate (bare ground was ~50%), and 3) extreme (bare ground was > 50%). Unknown plants were collected on-site, placed in a plant press, and later identified. Species were categorized as native or exotic species using the *List of Plant Species for Great Sand Dunes National Park and Preserve* found on the National Park Service (NPS) website (<http://www.nps.gov/grsa> accessed 11 March 2011), personal communication with Phyllis Bovin-Pineda (Biologist NPS), the 2003 vascular plant inventory (Spackman Panjabi et al. 2004), and *Weeds of the West* (Whitson 2000).

DATA ANALYSES

Species Cover and Frequency

Data from monthly surveys for all quadrats at each well type ($n = 240$; i.e., 2 plots per well type \times 120 samples per plot) were pooled across sites and years to generate summary statistics of percent plant species cover and frequency. All statistical analyses were performed using SAS (SAS Institute Inc. 2005). Based on a review of the literature, *I a priori* felt that well type (capped, open, and reference), disturbance level by ungulates (0-3), distance from well head (0-100 m), and annual variation, i.e., year of study, could influence percent plant species cover and frequency. The data was first square-root transformed to reduce non-normality prior to the following analyses. I separately modeled percent species cover and frequency as a function of well type, disturbance level by ungulates, distance from well head, and year of study (2011 or 2012) using general linear models in PROC GENMOD (identity link function, SAS Institute Inc. 2005). All combinations including intercept, additive, and interactive effects were considered except either well type or disturbance were modeled, i.e., not both together, because both captured the effect of well type. For model selection, I ranked the models based on Akaike's Information Criterion with the small-sample size adjustment (AIC_C ; Akaike 1973). The lowest AIC_C value indicates the most parsimonious model. I also reported ΔAIC_C (difference in AIC_C value between each model and the best model), AIC_C weight (strength of evidence for each model), and the number of parameters in the model (K). Models with $\Delta AIC_C < 2$ were considered to have similar support. I also computed the relative importance values (w_+) by summing the model weights over all models that include a given variable. A relative importance value > 0.50 , indicates that a variable is influential to the process of interest (Burnham and Anderson 2002, Doherty et al. 2012).

Species Diversity

To characterize the species diversity of a sampled well site I computed species richness, Shannon-Weiner diversity, Simpson diversity, and a modified Hill's ratio. The estimators were calculated using the monthly plant survey data sets. Native plant species richness, N = number of plant species per 1-m² quadrat, was estimated using the jackknife estimator in Program SPECRICH (Hines 1996), which accounts for probability of detection (Burnham and Overton 1979). The basic input data for SPECRICH are the frequencies (f_i) for each species, where f_i = the number plant species encountered exactly i times in the sampled quadrats ($n = 120$) at each sampled site ($n = 6$) within each month of survey (2011: $n = 3$; 2012: $n = 4$). These richness values were then averaged and SEs calculated. Shannon-Weiner diversity index (H') was estimated using the average monthly cover (%) as a measure of the relative abundance of species in the sample (Stohlgren 2007) and calculated as:

$$H' = - \sum P_i \log_2 P_i$$

where P_i is the proportion of cover of the species at each sampled site ($n = 6$) within each monthly survey (2011: $n = 3$; 2012: $n = 4$). A low H' suggests a site with few dominant species, while a high H' value suggests more species, usually many species of low cover. Simpson's diversity index (D') is a diversity index more weighted towards the most abundant species in the sample and less sensitive to species richness (Smith and Wilson 1996, Stohlgren 2007). The Simpson's diversity index was calculated as:

$$D' = 1 - \sum P_i^2$$

The value of this index ranges between 0 and 1 and the greater the value of D' , the greater the sample diversity. Finally, I used a modified Hill's ratio (E') as an index of plant species evenness:

$$E' = \frac{(1/D')^{-1}}{e^{H'} - 1}$$

where H' and D' are the previously mentioned diversity indices (Hill 1973, Stohlgren 2007). All diversity values were averaged across well types and monthly surveys.

Distance Patterns

Plant species responses to disturbance gradients at artificial water sites have been analyzed in previous studies using response curves along transects (Landsberg et al. 2003, Brooks et al. 2006). I tested the hypothesized patterns of different plant forms (shrub, grass, forb) cover as a function of distance from well head by developing linear regression models in Program R (Version 2.14, R Development Core Team 2011). Additionally, to further determine how plant forms were affected by variable distances from well heads, I identified a set of hypothetical trends to test for alternative plant form distance patterns. I used statistical models to fit regressions describing the trends of plant forms and tested nonlinear regressions (e.g. quadratic, logarithmic, and exponential) with the transformed plant cover (%) as the dependent variable and distance from well head (m) as the independent variable. Graphs showing fitted models for all plant forms were generated and used to determine whether the trend of the best-fitting model was increasing, decreasing or constant. AIC_C model selection was used and I pooled quadrat data by years for each well type because patterns of cover by distance were similar for transect lines within.

RESULTS

Species Cover and Frequency

Forty-six plant species were identified at the study site (APPENDIX A). Across sites and years, capped well sites had the highest average plant cover ($\bar{x} = 57\%$, $n = 12$), open well sites

had lowest cover ($\bar{x} = 38\%$), and reference sites were intermediate ($\bar{x} = 49\%$); of these percentages, 5%, 4%, and 1% were exotics. The plant cover types at the capped well consisted of 25% sedge, followed by 12% shrub, 10% grass, 6% cactus species, and 4% forb. Plant cover at open well sites was also primarily sedge (14%), followed by 11% shrubs, 8% grass, 4% forb, and < 1% cactus species. Finally, reference sites were primarily shrub (27%), followed by 10% grass, 8% cactus species, and 4% forb. Percent bare ground was 39%, 59%, and 50% for capped wells, open wells, and reference sites, respectively. Average disturbance intensity levels (0-3) were 1.28 2.06 and 0.67 at capped, open, and reference sites, respectively. The frequencies of native species tended to be greatest at reference sites, whereas for exotic species, frequency was greatest at capped well sites (Table 2.1).

For native and exotic plant cover, regression models were considered separately (including the intercept-only model). For native plant cover, the top model with 40% of the weight included only the year effect (Table 2.2). The next models with strong support, i.e., $\Delta AIC_C < 2$, included year plus distance from well head and disturbance level for the 2nd and 3rd most supported models, respectively. For native plant cover, the highest relative importance variable ($w_+ = 0.99$) was year of study (Estimates from the top models; year of study: $\hat{\beta} = -0.85$, [SE = 0.22]; distance: $\hat{\beta} = -0.003$, [0.004]; disturbance: $\hat{\beta} = -0.09$, [0.17]) (Table 2.2). All other variables had an importance value < 0.50. For exotic plant cover, the most supported model included distance from well head, followed by year and distance effects (Table 2.2). Distance had the highest relative importance value (Table 2.3), and the 95% confidence interval of the top model parameter estimate for distance ($\hat{\beta} = -0.008$, [0.004]) did not overlap zero. All other variables had low importance values (< 0.50) with little support for influence of well site type

(capped wells: $\hat{\beta} = -0.05$ [0.27]; open wells: $\hat{\beta} = -0.08$, [0.26]; reference sites: $\hat{\beta} = 3.34$, [0.19]) or year of study ($\hat{\beta} = -0.21$, [0.25]) on exotics (Table 2.3).

The top model for native plant frequency with 59% of the weight included well site, year of study, and distance effect (Table 2.4). The highest relative importance variable was the well site variable ($w_+ = 0.99$; capped wells: $\hat{\beta} = -1.37$ [$SE = 0.34$], open wells: $\hat{\beta} = -1.88$, [0.33], reference sites: $\hat{\beta} = 6.2$, [0.26]). Year of study ($w_+ = 0.98$; $\hat{\beta} = 1.65$, [0.27]) and distance to well head ($w_+ = 0.59$; $\hat{\beta} = 0.007$, [0.005]) were also influential and the remaining variable had importance values < 0.50 . For exotic plant frequency, the top model with 41% of the weight included only a well site effect and the next model with support, i.e., $\Delta AIC_C < 2$ also included distance. For exotic species plant frequency, the most influential variable was also well site ($w_+ = 0.99$; capped wells: $\hat{\beta} = 1.20$ [0.28], open wells: $\hat{\beta} = 1.18$, [0.28], reference sites: $\hat{\beta} = 1.19$, [0.19]; all other variables had importance values < 0.50 (Table 2.5).

Species Diversity

Estimates of native species richness was essentially equal in 2011, but in 2012 richness was greatest at reference sites, followed by capped and open well sites (Table 2.6). Shannon-Weiner index values for native plants ranged from 3.24 (0.04) at capped well sites in 2011 to 4.41 (0.02) at reference sites in 2012, and the highest values were at reference sites for both years of the study (Table 2.6). Simpson's index values also had highest values at reference sites for both years of the study. Hill's ratio values for native plant species ranged from 0.02 at the open well sites in 2011 to 0.13 at the capped well sites in 2011 and the highest values were at capped well sites for each year of the study (Table 2.6).

Distance Patterns

At capped well sites, native shrub cover increased with distance from the well head, peaked at 55 m, and then decreased (Figure 2.4a). Native shrub cover at open well sites increased linearly with distance from the well head (Figure 2.4b), and there was no pattern with distance from the center of reference sites transects (Figure 2.4c). Forb species at all site types showed a linear pattern of decreasing cover when distances were closer to the well head or center of reference sites (Figures 2.5a, 2.5b, and 2.5c). Grass species at capped well sites and reference sites showed a nonlinear pattern with cover decreasing and then increasing with distance (Figure 2.6a and 2.6c), whereas grass cover increased linearly with distance from open wells (Figure 2.6b).

DISCUSSION

Native plant cover was not significantly different at capped well sites compared to open well sites or reference sites, refuting my first hypothesis. Native cover varied more by year of the study and variation in annual precipitation may have played a more important role than well site types in these two years. For the past 4 years, the GRSA has been in a drought (Western Regional Climate Center, <http://www.wrcc.dri.edu/> accessed 20 March 2013) and the area experienced lower than average precipitation, rain and snowfall in both years of this study. The seeds of various desert plant species require varying amounts of rain for germination and seedling establishment (Gutterman and Gozlan 1998), and after insufficient rainfall, seedlings can suffer irreversible damage from dehydration stress, resulting in lower seed availability. I did note increased cover of scurf pea, skeleton weed, and blowout grass at the capped well sites, plants that are key components of the dune maintenance (Gadgil and Ede 1998). These species are sensitive to environmental changes such as trampling and grazing (Acosta et al. 2000) and may be ecological indicators of recovery at capped well sites.

My hypothesis of greater cover and frequency of exotic plants at open well sites was not supported; instead both parameters were greatest at capped well sites. Exotics are known to be resilient to drought conditions and can dominate water-stressed, arid ecosystems (Kotanen 1997, Marushia et al. 2012, Perry et al. 2013). Several studies have shown an increased abundance of exotics at artificial water sites (Andrew and Lange 1986, James et al. 1997, Nangula and Oba 2004, Todd 2006). For example, in piospheres among sagebrush communities in Idaho, the exotic cheatgrass overwhelmed the local ecosystems (Hosten and West 1996) and in Australian rangelands, exotic plant cover increased with proximity to water sites (Landsberg et al. 2003). If exotic plants are growing at capped well sites, focused eradication efforts on noxious weeds found only at the open well sites (e.g., Russian knapweed) may be important. Even the establishment of a diverse native plant community at previously disturbed sites does not limit the distribution of exotic species (Lonsdale 1999, Stohlgren 2007). These findings are somewhat contrary to Hoelzle et al. (2012), where ecosystem recovery in a formerly cultivated sagebrush steppe resulted in a vegetation community dominated by both perennial grasses and mid-seral shrubs. My observations suggest that the cover and frequency of exotics at capped well sites may be a relic effect from the previous high numbers of cattle gathering at the wells and more time is needed for well site recovery and ecological succession.

Native species frequencies and the majority of the species diversity indices were greatest at the reference sites, not the capped well sites as predicted. Rubber rabbitbrush, a dominant shrub species at capped well sites, may be a factor due to its ability to inhibit the establishment of other species (Ward 2009, Mata-Gonzalez et al. 2012); this may have contributed to the intermediate diversity levels compared to higher levels at reference sites. Furthermore, I found that levels of disturbance by ungulates at the capped well sites were greater than at reference

sites. Ungulates tend to selectively graze on forbs and grasses (Damhoureyeh and Hartnett 1997) and increased grazing can decrease root size and inhibit plant growth (Shahriary et al. 2012). Other studies have shown decreases in species richness and diversity on grazed sites in arid ecosystems (Reynolds and Trost 1980, Brooks et al. 2006), conversely, there can also be a subsequent increase of shrub or tree abundance (Skarpe 1990, Perkins and Thomas 1993, Ward 2009). One possible successional stage at capped well sites after the water is removed is the encroachment of shrub species rather than an increase in the native species frequency and biodiversity of the plant community.

As hypothesized, I did detect cover increasing linearly as a function of distance from open well heads for all plant forms, but only the shrubs followed the hypothesized distance pattern at capped well heads. Following disturbance, rapid encroachment of shrub species can preclude the establishment of competitors such as palatable forbs and grasses (Scholes and Archer 1997, West 1999, Ward 2009), and the increase in shrub species at the capped wells may be at the expense of more palatable and less disturbance-tolerant species. For example, forb species at capped well sites tended to cover less area per quadrat and grass species exhibited a distance pattern that was opposite to shrubs. Shrub species, such as rabbitbrush and sagebrush, are often not subjected to herbivory because they are thorny or have high fiber content (Ward 2009). Most other studies that have reported on plant species cover in relation to watering points describe increasing cover with increasing distances (James et al. 1997, Nangula and Oba 2004, Todd 2006). In this study, overall plant cover did tend to increase further away from well heads, suggesting a selective removal by the grazing ungulates (Thrash et al. 1993, James et al 1997, Fernandez-Giminez and Allen-Diaz 2001, Shahriary et al. 2012) or disturbance from trampling limiting growth near the well head (Nash et al. 1999, Landsberg et al. 2003, Eldridge and

Whitford 2009). Overall, these results indicate changes in plant community composition that are possibly related to the short-term impacts of capping artesian well sites.

One confounding variable in my study was the presence of bison. Capped well sites were only found in the GRSAs where no bison exist, whereas open well sites were only found in TNC areas with bison. However, after comparing historical well site conditions using Google Earth® and photographs taken at the time of capping (April 2010), it appeared that all sites had similar piosphere conditions pre-capping (APPENDIX B). Therefore, I considered any site differences found at the capped well sites to be evidence of ecological succession and recovery process that occurs after a well head has been capped. Because there is no significant variation in cover between open well sites and capped well sites it appears that not enough time has passed since closure of the wells for a noticeable ecosystem recovery. However, several plant species, e.g., Indian rice grass, needle-and-thread grass, and blue grama were found in greater frequencies at capped well sites and can be significant sources of food for wildlife; the restoration of these plants at newly capped well sites may be important in the management of grazers and browsers like elk, mule deer, and pronghorn (Singer and Norland 1994, Hamr et al. 1999, Schoenecker et al. 2006) in the GRSAs. Conversely, the establishment of exotic annuals at capped well sites is a concern, because these species have the ability to outcompete native species for space and resources. Exotic plants should be prioritized for control based on their potential to spread, with particular concern for those species known to be highly invasive and a significant management problem, e.g., Canada thistle, field bindweed (*Convolvulus arvensis*), leafy spurge (*Euphorbia esula*), yellow sweetclover (*Melilotus officinalis*), and cheatgrass (*Bromus tectorum*) (Whitson 2000, Colorado Department of Agriculture, <http://www.ag.state.co.us/DPI/weeds/statutes/weedrules.pdf> accessed 23 April 2013). Control

efforts should focus primarily on the areas within 30 m of the capped well heads, since this area had the greatest amount of exotic cover. Because this study only reflects a two-year period since the capping of wells, additional research will be important to better understand long-term recovery of artesian well sites and ultimately help to promote sound management decisions for the conservation, not only of the groundwater, but of the recovering plant communities in the GRSA sand sheet ecosystem.

Table 2.1 Characteristics of plants (average percent cover and frequency per quadrat) within 1-m² plots in Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Sites are capped well sites (capped since 2010), open well sites (artesian well sites still containing water), and reference sites (no artesian well influence).

Year	Study Site	Native		Exotic	
		Percent cover (SE)	Frequency (SE)	Percent Cover (SE)	Frequency (SE)
2011					
	Capped Well Sites	15.58 (0.59)	9.15 (0.97)	5.01(0.73)	1.07 (0.33)
	Open Well Sites	14.13 (0.77)	8.43 (1.18)	3.93 (0.32)	0.69 (0.26)
	Reference Sites	14.95 (0.82)	16.73 (0.76)	3.00 (0.58)	0.02 (0.01)
2012					
	Capped Well Sites	9.53 (0.36)	9.84 (0.19)	4.95 (0.47)	1.30 (0.07)
	Open Well Sites	9.08 (0.27)	8.37 (0.34)	2.80 (0.29)	1.01 (0.06)
	Reference Sites	9.21 (0.39)	16.61 (0.23)	1.67 (0.13)	0.31 (0.08)

Table 2.2 Model selection results from regression analyses of well sites and habitat variables on native and exotic plant cover in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Headings are Akaike's information criterion for small sample size (AIC_C), change in AIC_C (ΔAIC_C), model weight (AIC_C weight), and number of parameters (K) for the most parsimonious models. Habitat variables modeled were: well site (capped, open, reference); disturbance by ungulates level (0-3); distance from well head (m); and year of study (2011, 2012).

Model	AIC_C	ΔAIC_C	AIC_C weight	K
Native Cover				
Year	951.37	0.00	0.40	2
Year + Distance	952.84	1.47	0.19	3
Year + Disturbance	953.09	1.72	0.17	3
Year + Distance + Year*Distance	954.47	3.1	0.07	4
Exotic Cover				
Distance	388.42	0.00	0.30	2
Year + Distance	390.00	1.58	0.13	3
Distance + Disturbance	390.46	2.04	0.11	3

Table 2.3 Relative importance of variable (w_+) influencing native and exotic plant cover based on regression modeling in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012.

Variable	Native Cover	Exotic Cover
Well Sites	0.09	0.10
Disturbance by ungulates	0.33	0.29
Distance from well head	0.45	0.77
Year of study	0.99	0.36

Table 2.4 Model selection results from regression analyses of well sites and habitat characteristic effects on frequency of native and exotic plant species in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Heading include Akaike's information criterion for small sample size (AIC_C), change in AIC_C (ΔAIC_C), model weight (AIC_C weight), and number of parameters (K) for the most parsimonious models. Variables defined in Table 2.2.

Model	AIC_C	ΔAIC_C	AIC_C weight	K
Native Frequency				
Well Sites + Year + Distance	1084.27	0	0.59	4
Well Sites + Year	1085	0.73	0.41	4
Disturbance + Year	1105.1	20.83	1.77E-05	3
Exotic Frequency				
Well Sites	410.19	0	0.41	2
Well Sites + Distance	410.87	0.68	0.29	3
Well Sites + Year	412.25	2.06	0.15	3

Table 2.5 Relative importance of variable (w_+) influencing frequency of native and exotic plant species based on regression modeling in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012.

Variable	Native Frequency	Exotic Frequency
Well Sites	0.99	0.99
Disturbance by ungulates	0.02	0.01
Distance from well head	0.59	0.44
Year of study	0.98	0.29

Table 2.6 Species richness (Program SPECRICH), Shannon-Weiner diversity index (H'), Simpson diversity index (D'), and modified Hill's ratio (E') for native plant species at capped well sites, open well sites, and reference sites at Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. Standard errors are in parentheses.

Year	Study Site	Species Richness	H'	D'	E'
2011	Capped Well Sites	11 (0)	3.24 (0.04)	0.86 (0.004)	0.13
	Open Well Sites	11 (0)	3.66 (0.03)	0.89 (0.002)	0.02
	Reference Sites	11.5 (0.71)	3.69 (0.03)	0.96 (0.001)	0.09
2012	Capped Well Sites	27 (1.71)	4.08 (0.02)	0.92 (0.001)	0.08
	Open Well Sites	26 (1.23)	4.12 (0.02)	0.93 (0.001)	0.06
	Reference Sites	31.5 (1.71)	4.41 (0.02)	0.95 (0.0004)	0.04

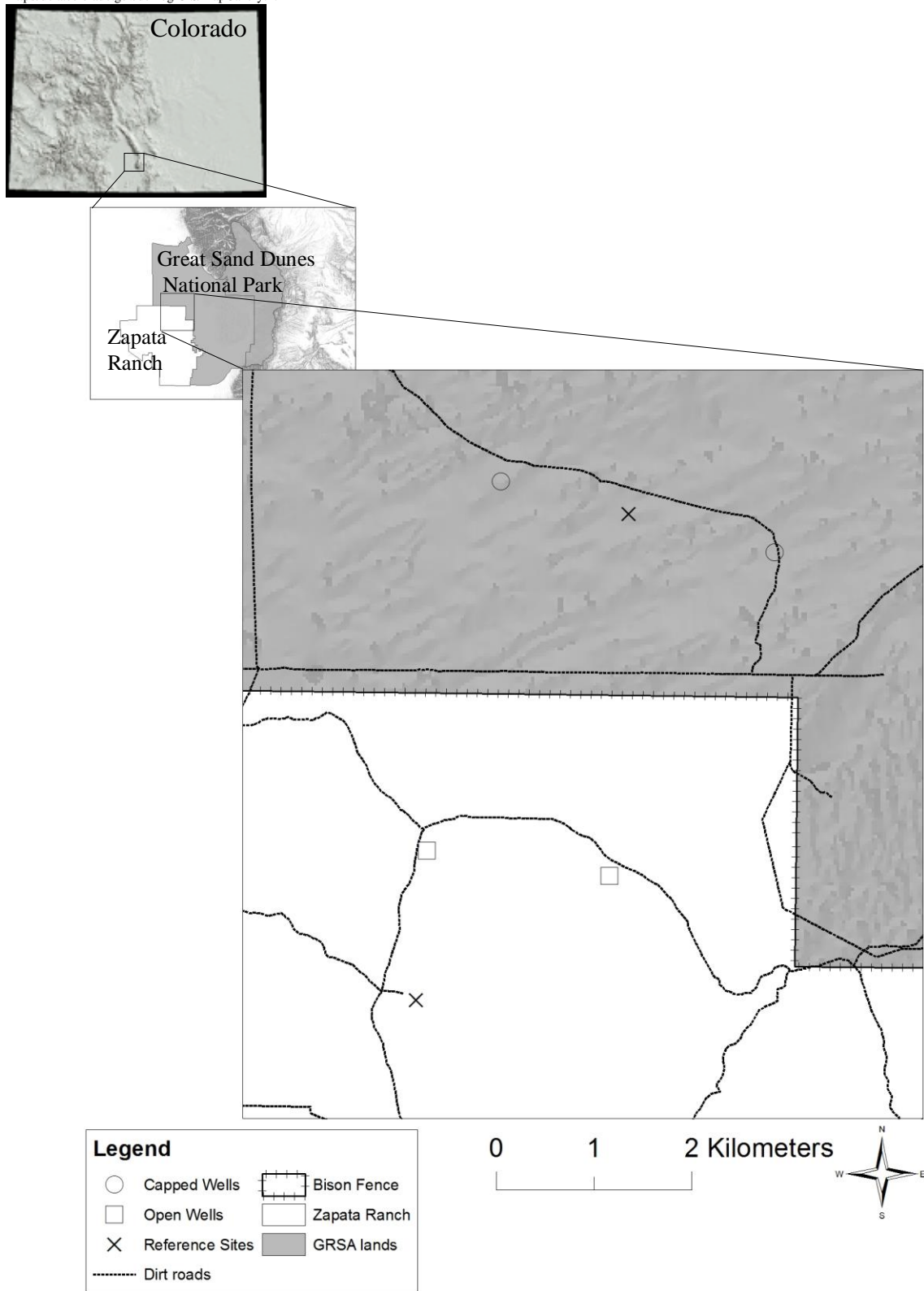


Figure 2.1 Location of artesian well sites and reference sites studied in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, south-central Colorado, 2011-2012.



Figure 2.2 A capped artesian well site, prior to the study, comprised of a 5-cm steel pipe and the now empty water tank in the Great Sand Dunes National Park, Colorado, April 2010 (Photo by James Harte, NPS). Note the piosphere around the tank.



Figure 2.3 Bison drinking at a typical open artesian well site comprised of a 5-cm steel pipe that fills a tank in TNC's Zapata Ranch, adjacent to the Great Sand Dunes National Park, Colorado, 2011. Note the piosphere around the tank (Photo by Sarah J. Garza).

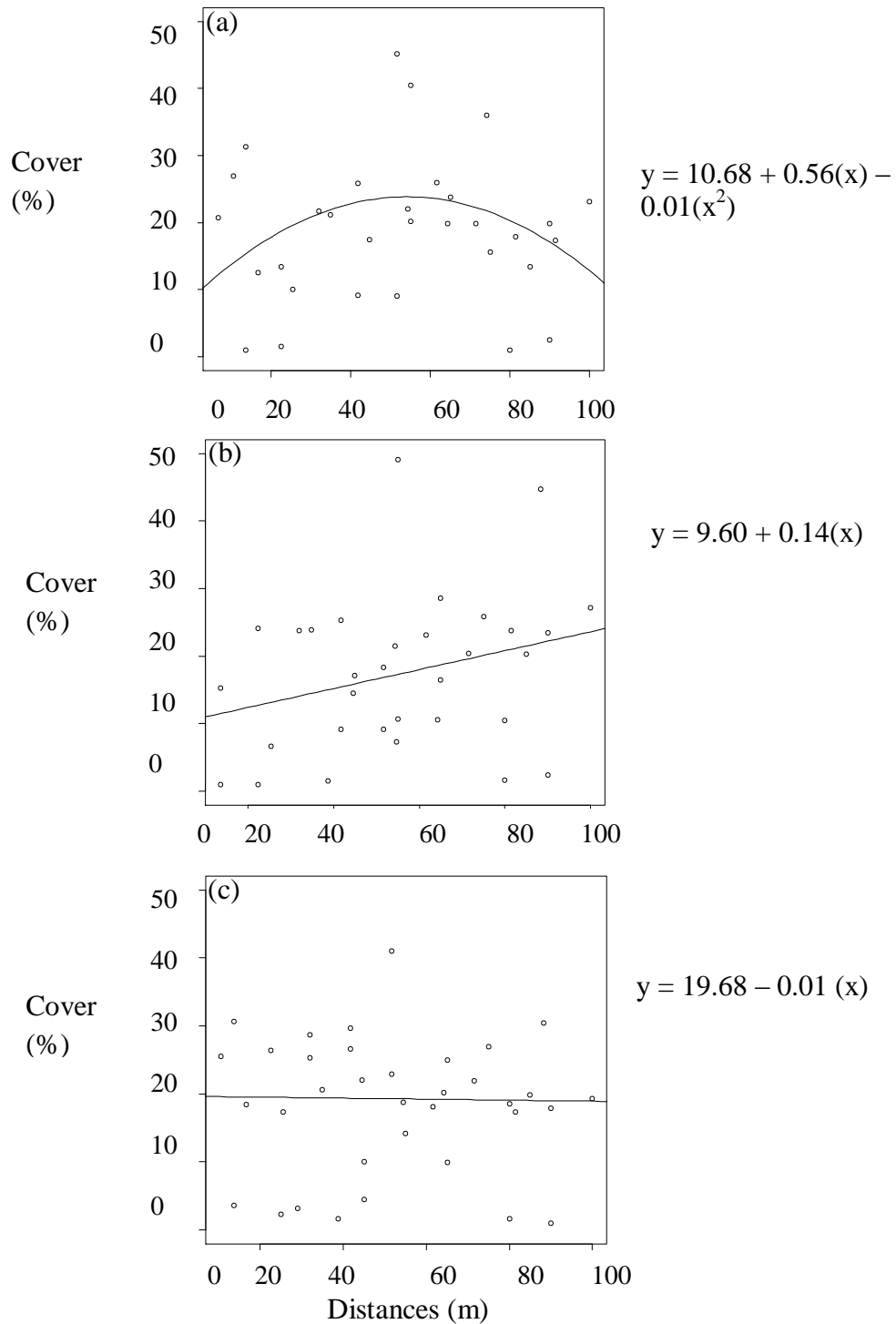


Figure 2.4 Patterns of shrub cover with proximity to well heads at (a) capped well sites and (b) open well sites, and from center of site for (c) reference sites during summers of 2011 and 2012 in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado. Lines represent the fitted regression models where y = plant cover percentage and x = distance from well head or center of site.

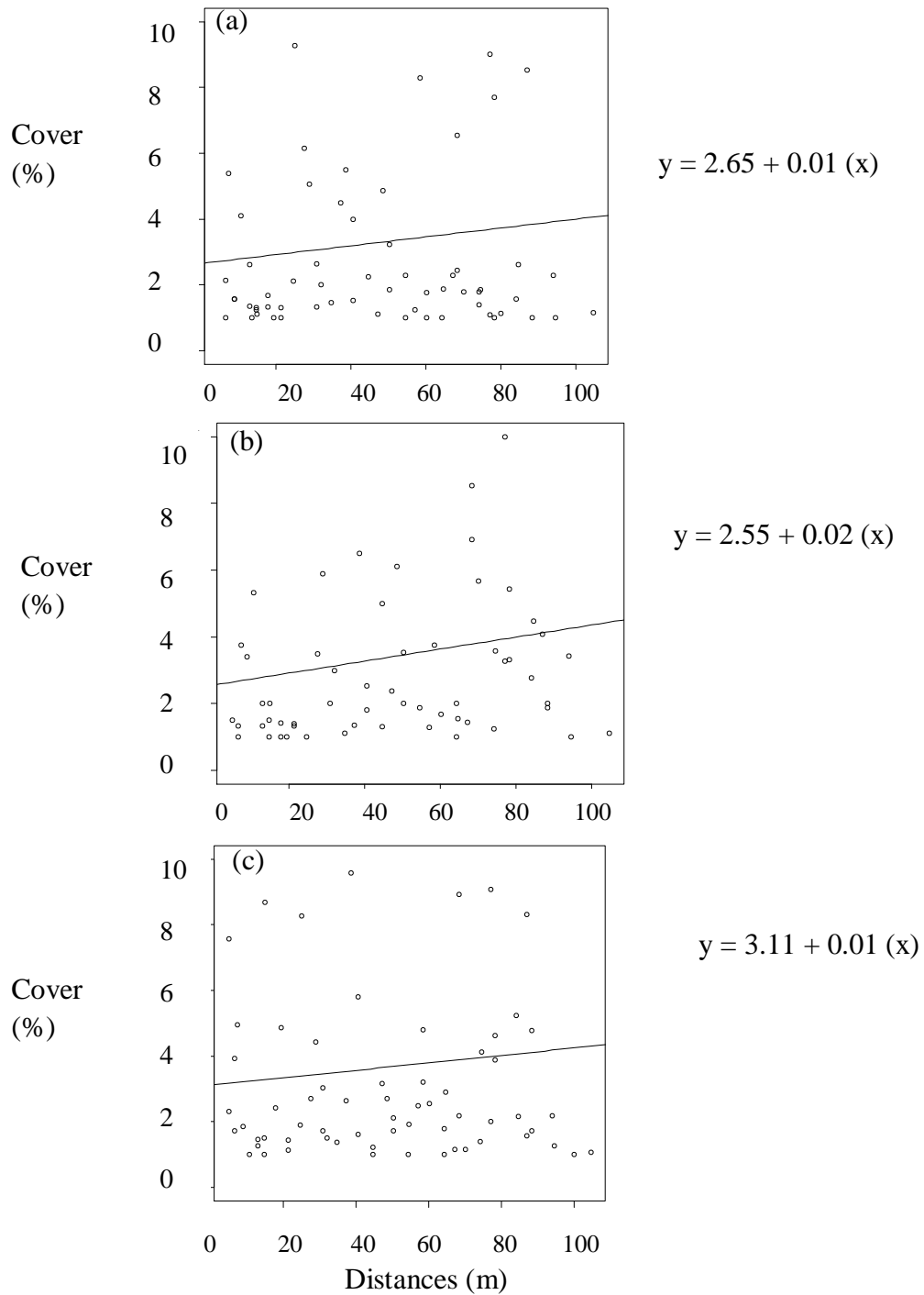


Figure 2.5 Patterns of forb cover with proximity to well heads at (a) capped well sites and (b) open well sites, and from center of site for (c) reference sites during summers of 2011 and 2012 in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado. Lines represent the fitted regression models where y = plant cover percentage and x = distance from well head or center of site.

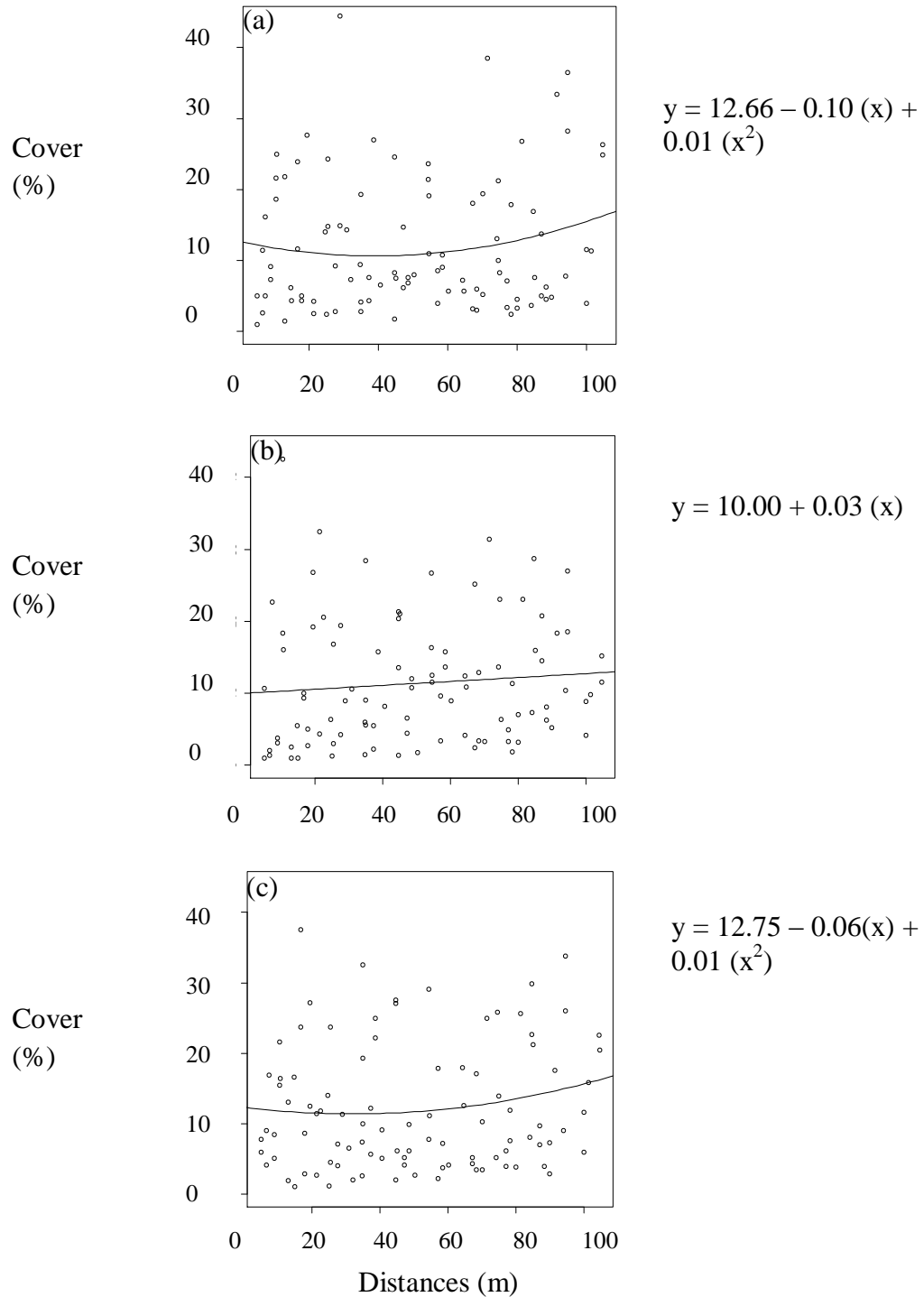


Figure 2.6 Patterns of grass cover with proximity to well heads at (a) capped well sites and (b) open well sites, and from center of site for (c) reference sites during summers of 2011 and 2012 in the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado. Lines represent the fitted regression models where y = plant cover percentage and x = distance from well head or center of site.

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APPENDIX A

List of plant species detected at capped and open well sites and reference sites (n = 6) within the Great Sand Dunes National Park and The Nature Conservancy's Zapata Ranch, Colorado, 2011-2012. See methods for descriptions of each study site.

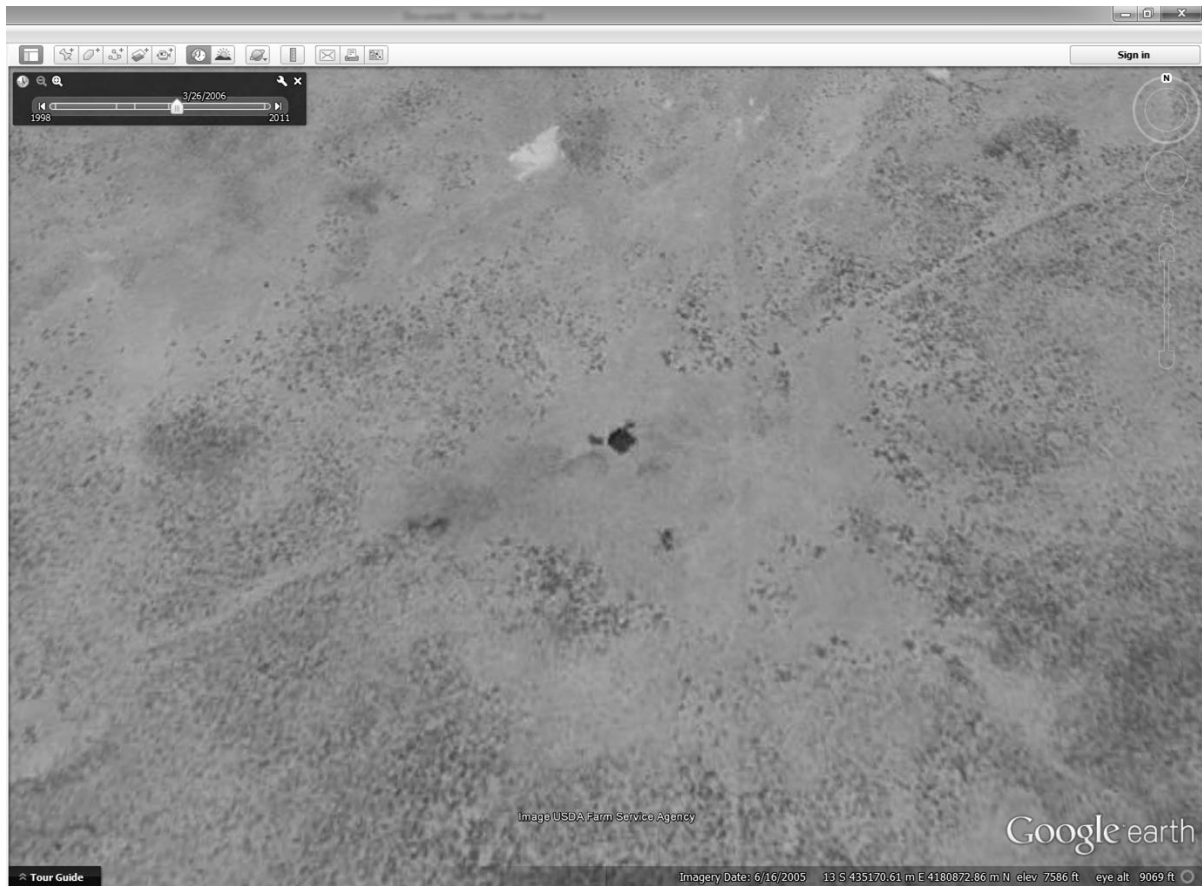
Species	Common name	Occurrence	Sites present
Shrubs			
<i>Artemisia ludoviciana</i>	White sagebrush	Perennial	Capped, Reference
<i>Artemisia frigid</i>	Prairie sagewort	Perennial	All
<i>Ericameria nauseosa</i>	Rubber rabbitbrush	Perennial	All
Forbs			
<i>Allium geeyeri</i>	Geyer's onion	Perennial	Reference
<i>Amaranthus retroflexus</i>	Rough pigweed	Annual	All
<i>Amaranthus palmeri</i>	Careless weed	Annual	All
<i>Ambrosia acanthicarpa</i>	Bur ragweed	Annual	All
<i>Artemisia scopulorum</i>	Alpine sagebrush	Perennial	All
<i>Carex</i> sp.	Sedge	N/A	Capped, Open
<i>Chenopodium desiccatum</i>	Lamb's quarter	Annual	All
<i>Cleome serrulata</i>	Rocky mountain bee plant	Annual	All
<i>Erysimum capitatum</i>	Sand dune wall flower	Perennial	Capped, Open
<i>Gilia leptomeria</i>	Sand gilia	Annual	Open, Reference
<i>Helianthus petiolaris</i>	Sunflower	Annual	All
<i>Hutchinsia procumbens</i>	Prostrate hutchinsia	Annual	All
<i>Ipomopsis longiflora</i>	Blue gilia	Annual	All
<i>Krascheninnikovia lanata</i>	Winterfat	Perennial	Capped, Reference
<i>Packera tridenticulat</i>	Three-toothed ragwort	Perennial	Reference
<i>Oenothera</i> sp.	Primrose	Perennial	Capped, Reference
<i>Lygodesmia juncea</i>	Rush skeletonweed	Perennial	All
<i>Polygonum</i> sp.	Knotweed	N/A	All
<i>Polygonum amphibium</i>	Water knotweed	Perennial	Open
<i>Psoralea lanceolata</i>	Scurf pea	Perennial	All
<i>Solanum triflorum</i>	Cut-leaf nightshade	Annual	Capped, Open
<i>Caltha leptosepala</i>	White water marigold	Perennial	Open
<i>Tripterocalyx microanthus</i>	Sand verbena	Annual	Capped, Reference
Grasses			
<i>Bouteloua gracilis</i>	Blue grama	Perennial	All
<i>Catabrosa aquatic</i>	Water whorlgrass	Perennial	Open
<i>Distichlis spicata</i>	Salt grass	Perennial	All
<i>Elymus elymoides</i>	Squirreltail grass	Perennial	Capped, Reference

<i>Elymus glaucus</i>	Blue wildrye	Perennial	All
<i>Elymus trachycaulus</i>	Slender wheat grass	Perennial	All
<i>Hesperostipa comata</i>	Needle and thread grass	Perennial	All
<i>Heteropogon contortus</i>	Tanglehead	Perennial	Capped, Reference
<i>Monroa squarrosa</i>	False buffalo grass	Annual	All
<i>Muhlenbergia andina</i>	Foxtail grass	Perennial	All
<i>Muhlenbergia sp.</i>	Muhly grass	Perennial	Capped, Reference
<i>Panicum capillare</i>	Witch grass	Annual	All
<i>Oryzopsis hymenoides</i>	Indian rice grass	Perennial	All
<i>Redfieldia flexuosa</i>	Blowout grass	Perennial	All
<i>Sporobolus cryptandrus</i>	Sand dropseed	Perennial	All
Cactus			
<i>Opuntia polyacantha</i>	Prickly pear cactus	Perennial	Capped, Reference
Exotics			
<i>Acroptilon repens</i>	Russian knapweed	Perennial	Open
<i>Amaranthus blitoides</i>	Mat amaranth	Annual	All
<i>Cirsium arvense</i>	Canadian thistle	Perennial	Open
<i>Salsola tragus</i>	Russian thistle	Annual	All

APPENDIX B



Capped well #2 on July 3 2009. This well site piosphere is outside of the Zapata ranch boundaries and was subject to disturbance by elk, mule deer, and pronghorn. It was capped on April 10 2010.



Open well #1 on March 26 2006. This well site piosphere is inside of the Zapata ranch boundaries and was subject to disturbance by bison, elk, mule deer, and pronghorn. It has not been capped as of this study.