Carrizo Plain Ecosystem Project
2010 Report

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Summary

Understanding relationships among giant kangaroo rats (GKR), plant dynamics, and cattle grazing is necessary to optimize conservation of upland species in the Carrizo National Monument. We completed the fourth year of the Carrizo Plain Ecosystem Project (CPEP), a long-term study to tease apart these relationships using replicated cattle and GKR exclosures. Because of high precipitation in 2010, vegetation biomass was three times higher than in previous years, and effects of cattle grazing on the dynamics of GKR and other species began to emerge. Cattle grazing positively affected GKR and beetle abundance and negatively affected San Joaquin antelope squirrel and side-blotched lizard abundance. Cattle grazing did not significantly affect native or exotic plant cover, whereas GKR negatively affected overall native plant cover. However, bunchgrasses were positively affected by GKR presence and exotic grasses were negatively affected, suggesting that GKR foraging may limit the dominance of exotics they prefer to eat, such as large-seeded grasses. GKR positively affected the species richness and abundance of invertebrates, especially beetles, crickets, and grasshoppers. Thus, treatment effects from of our cattle and GKR exclosures are beginning to emerge, revealing complex dynamics. Results from 2010 mark a major step towards teasing out relationships among cattle, GKR, plants, and other wildlife in the grasslands of the Carrizo Plain. The high precipitation levels this winter indicate that 2011 will be another "wet" year, allowing us to evaluate the robustness of these findings.

Prepared by Laura Prugh, 2010

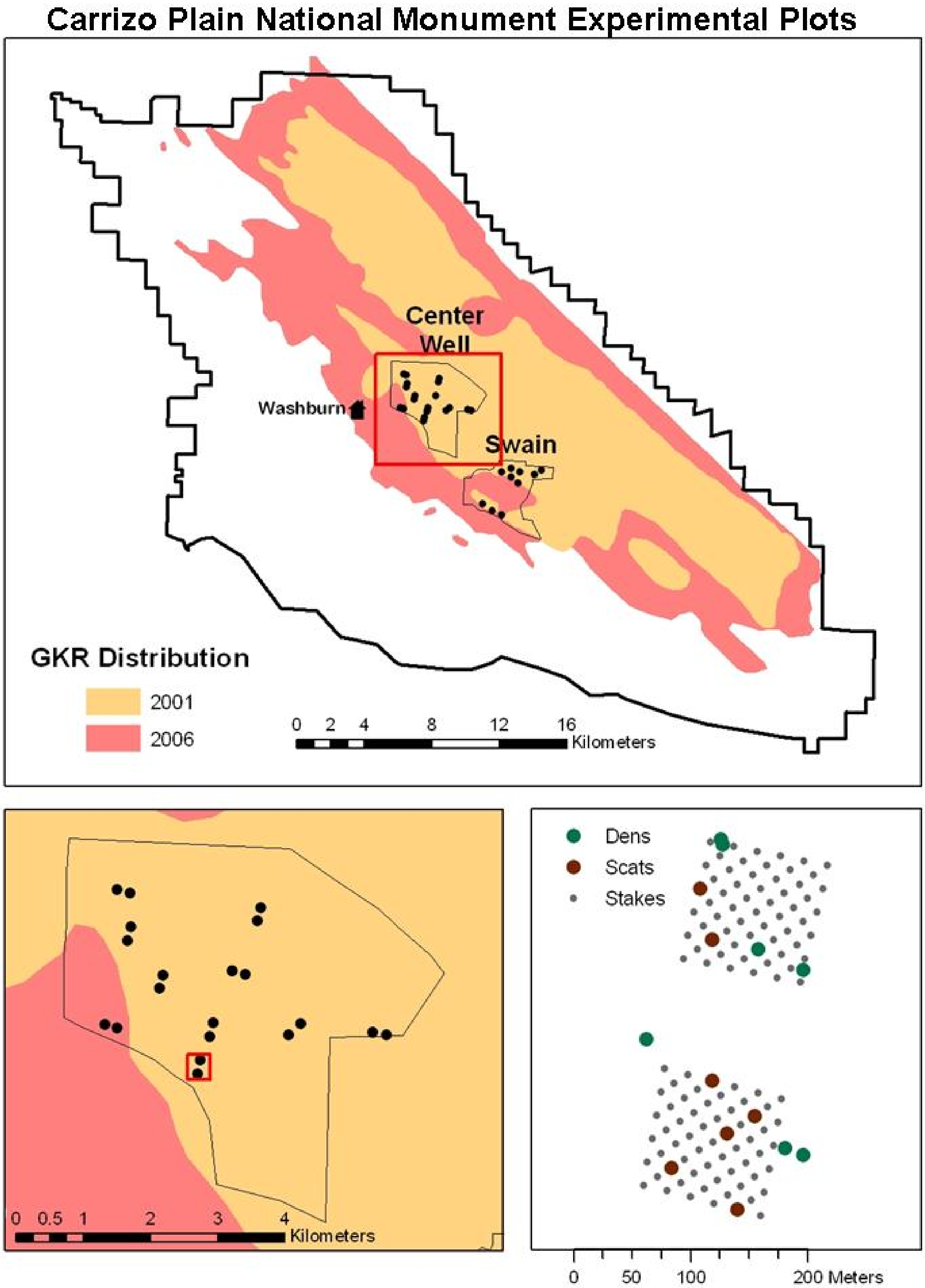

Figure 1. Map of study sites in the Carrizo Plain National Monument. Details are shown for the Center Well pasture and site CW 7. Kit fox dens and scats, as well as trap stakes, are shown for site 7.

Background

The Carrizo Plain National Monument, located in the southern San Joaquin Valley of California, is the largest (810 km^2) of the few remaining San Joaquin grassland ecosystem remnants and is a "hotspot" of species endangerment (Dunn et al. 1997). The federally endangered giant kangaroo rat (*Dipodomys ingens*, hereafter "GKR") is a keystone species in this system; it modifies the soil extensively with burrow systems and is important prey for many predators, such as the federally endangered San Joaquin kit fox (*Vulpes macrotis mutica*). Managing for endangered species conservation is a mandate of the monument (B. Stafford, pers. comm.), and this is a particularly challenging task because endangered species occur at every trophic level in the Carrizo Plain. Additionally, the Carrizo Plain is now dominated by annual grasses from Europe. Thus, sound management in the Carrizo Plain requires an understanding of the interactions between the many endangered and exotic species that occur there.

Previous research in the Carrizo by D. Williams provided basic demographic and life history information for GKR and compared a population in a grazed area to one in an ungrazed area. Additionally, monitoring data for a variety of species (including GKR) in relation to grazing was carried out for nine years and is currently being analyzed by Dr. C. Christian. These studies and others have provided conflicting evidence as to the effect of grazing on upland species and their habitats. Additionally, they cannot establish causal relationships between invasive plant dynamics and factors such as GKR abundance because they were observational rather than experimental.

In 2007, we initiated the Carrizo Plain Ecosystem Project (CPEP) to examine the relationships between cattle, GKR, plants, and other species in the Carrizo Plain using replicated exclosures (Prugh 2007). We gathered baseline data on the flora and fauna on our experimental plots, and we constructed 10 cattle exclosures in the annually-grazed Center Well pasture and 20 kangaroo rat exclosures in the Center Well and Swain (ungrazed) pastures. In 2010, we continued monitoring the flora and fauna on these plots, and three graduate student research projects were initiated.

Long-term project goals

1. To determine how giant kangaroo rats affect the distribution and abundance of native and invasive plants in the Carrizo Plain National Monument
2. To determine how livestock grazing directly and indirectly affects native species in the Carrizo Plain, especially giant kangaroo rats and plants.

Methods

Experimental design

We are using the Before-After-Control-Impact design with Paired sampling (BACIP; Osenberg et al. 1994) to determine the effect of GKR and cattle removal treatments on plant biomass and composition. BACIP is a powerful statistical framework that requires baseline surveys to control for pre-existing differences between control and treatment sites. To determine the effect of GKR on plants, we are using a randomized block split-plot design with three fully-crossed factorial treatments: pasture, GKR presence, and soil disturbance (Figure 2). The effect of cattle on GKR, plants, and other species is added as a partial fourth treatment (Figure 2). Because there is no cattle grazing in the Swain pasture and because it is not feasible to exclude GKR while allowing access to cattle, we were not able to add livestock presence as a fully factorial treatment. Thus, we have used structural equation modeling to estimate the strength of interactions and indirect effects of cattle (Wootton 1994).

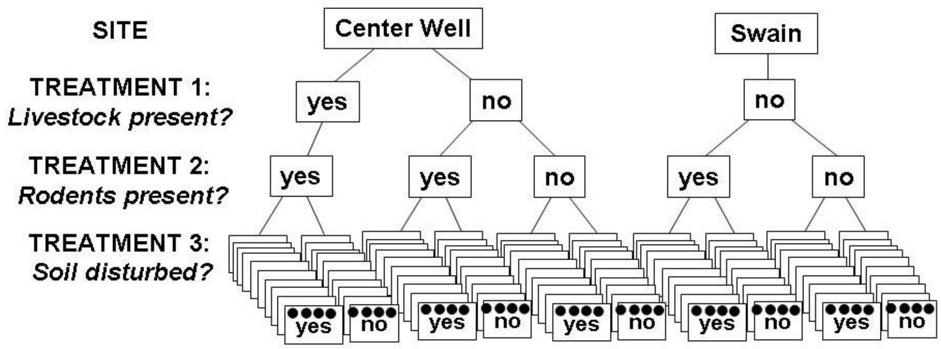

Figure 2. Experimental design of the project. There are ten blocks of each treatment combination and four nested vegetation plots (filled circles) within each block.

Exclosures

We constructed 20 20x20-m GKR exclosures, 10 in Center Well and 10 in Swain. Exclosures were placed in the center of each randomly chosen sub-block. Cattle exclosures were constructed around each GKR exclosure in Center Well. Cattle exclosures are 140x140-m (1.96 ha), large enough to have a population of roughly 20-100 GKR occurring within each exclosure. Paired 1.96-ha control plots are located 60 m from each cattle exclosure in Center Well in a random compass direction. Plants were sampled in each GKR exclosure, in a paired 400-m^2 area 20 m away from the GKR exclosure, and in Center Well, at the center of each paired control plot (Figure 3).

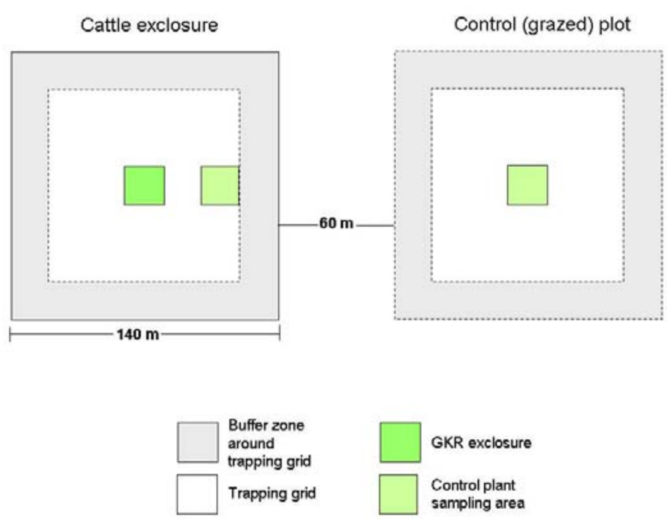

Figure 3. Nested exclosure design to separate livestock and GKR effects on plants, with paired control plot. A buffer zone around each GKR trapping grid ensured that the surveyed population was comprised of individuals living within the plot. This shows the design in Center Well; in Swain each plot is identical to the cattle exclosure but does not have cattle fencing.

Plant and soil sampling

We established 8 1-m^2 permanent plant sampling quadrats in each of the 50 400-m^2 plant sampling areas, for a total of 400 quadrats. Half of the quadrats were placed on GKR precincts and half were placed off precincts. The pinframe sampling method was used to determine plant cover and composition in each 1-m^2 plot, in which all species intercepted by 81 crossing points were recorded (Figure 4; Kimball and Schiffman 2003, Seabloom et al. 2003). Species occurring in the plot but not in the crosshairs were also noted. Biomass samples were obtained from 1/16-m^2 plots adjacent to each 1-m^2 plot to estimate biomass in April, June, and October (peak, post-grazing, and minimum biomass). Clip plots cannot be resurveyed in the same spot and are placed adjacent to the previous clip plot. Plant height was also measured prior to clipping.

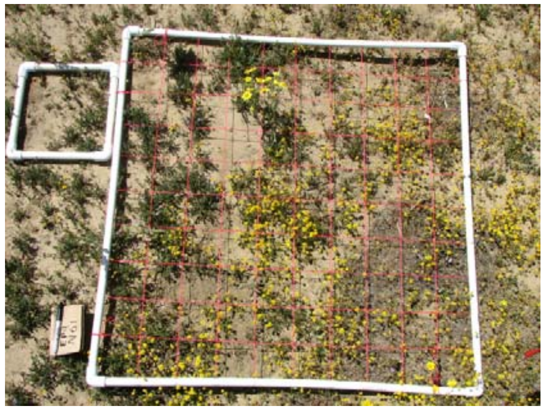

Figure 4. Plant sampling plot in a non-precinct area, showing the 1-m^2 point frame and the 1/16-m^2 clip plot.

GKR surveys

Mark-recapture surveys were conducted on each plot to estimate GKR abundance. Extra-long Sherman traps were placed every 20 meters, with each line offset such that traps were arranged in a checkerboard (Figure 5; n = 60 traps per plot, diagonal trap distance = 14.1 m). Traps were baited with parakeet seed (microwaved to prevent germination) and paper towel, and they were set at dusk and checked approximately 3 hours later. Sessions lasted for 3 nights on each grid in April and August. All captured animals were marked with an ear and PIT tag, weighed, sexed, and released. Trapping occurred from April 12-May 14, 2010 (22 trap nights) and August 1-28, 2010 (21 trap nights).

To obtain mark-recapture estimates, I used the program R (R Development Core Team 2010) package RMark. We obtained population estimates for each trapping session as well as apparent survival estimates for the period between sessions using the robust design model (Pollock 1982). Death cannot be distinguished from dispersal in this model, so the "survival" rate obtained is referred to as "apparent survival."

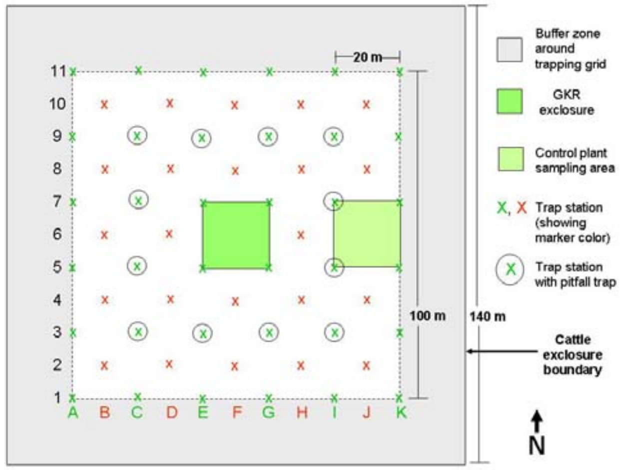

Figure 5. Detailed diagram of a cattle exclosure. Trap stations show trap locations for GKR mark-recapture surveys. Colors correspond to the spray-painted color on the stake marking the location. Letters and numbers identify the grid stakes (A1, B2, etc.).

GKR dietary preferences were determined as part of a UCB student senior thesis project in 2007 (Olney 2008) and were repeated in 2008 and 2009. We did not repeat diet trials in 2010, but we did collect contents of GKR surface pit caches to quantify seed collection by GKR. One cache was collected on each plot (*n* = 30 total), and seeds present in each cache were identified using a seed reference collection.

Graduate student projects

Three graduate student projects focusing on GKR were initiated in 2010:

1) Doctoral student Tim Bean, UC Berkeley (supervisor: Justin Brashares)
Tim completed his masters project modeling the distribution of GKR in 2009, and his doctoral research builds from this project. He is conducting mark-recapture surveys of GKR at sites across the Carrizo Plain and combining this data with remote sensing and habitat variables to develop a habitat suitability model for GKR.

2) Masters student Chris Gurney, UC Berkeley (supervisor: Justin Brashares)
Chris is studying the effect of GKR foraging behavior and soil disturbance on native plant restoration in the Carrizo Plain. Using our exclosures, he conducted an experiment seeding small plots with four native species, two of which were preferred by GKR in diet trials and two of which were avoided. He seeded plots in and out of the GKR exclosures and with and without soil disturbance to see how these factors affect the success of seeding efforts. He also mapped out surface pit caches and haypiles and is monitoring these sites to determine how seed caching affects plant composition.

3) Masters student Steve Etter, CSU Northridge (supervisor: Tim Karels)
Steve is studying adult GKR survival and juvenile GKR survival and dispersal. He radio-collared 50 adult GKR and monitored individuals daily to determine causes and rates of mortality. Individuals were collared on our plots in Swain, and sites with high or low GKR density were chosen in order to determine how density affects survival. Steve plans to collar juveniles in the spring of 2011.

SJAS surveys

San Joaquin antelope squirrel (*Ammospermophilus nelsoni*, hereafter "SJAS") abundance was determined on each plot using mark-recapture surveys. Tomahawk traps were placed every 40 m in checkerboard spacing, for a total of 18 traps per plot. Traps were baited with oats, set at dawn, and checked every two hours until noon or temperatures rose over 90° F. All captured animals were PIT-tagged, weighed, and sexed. Trapping occurred from May 23–June 12, 2010. The RMark package was used to obtain density estimates on each plot each year.

Bird surveys

Point counts were conducted four times on each plot from April 13–May 6, 2010. Concentric rings were demarcated with flags from the center of each 1.96-ha plot, marking 10 m, 25 m, 45 m, and 70 m. Point counts lasted 10 minutes and all birds seen and heard during this time were identified and recorded, along with the time heard/seen and which ring the bird(s) occurred in. Birds detected off plot or flying over the plot were recorded separately. We tried to avoid re-counting the same birds during counts on different plots. Plots were conducted from 6–9 am and the order of plots visited was randomized.

Reptile surveys

Line transect surveys were used to estimate reptile abundance on each 1.96-ha plot. Three surveys were conducted on each plot from May 25–July 1, 2010. Seven 140-m long transects spaced 20 m apart were slowly walked by a single observer, and all reptiles detected within 10 m on either side of the transect were identified and recorded, along with the perpendicular distance from the transect line and age (hatchling or adult). Soil/air temperature, wind speed, and time of day were recorded at the start and end of each survey. We adopted temperature and wind cutoffs recommended in the blunt-nosed leopard lizard (BNLL) protocol. Density estimates of the most common reptile, the side-blotched lizard (*Uta stansburiana*), were obtained using the program DISTANCE (Thomas et al. 2006).

Invertebrate surveys

Grasshoppers were counted during reptile surveys. Additionally, pitfall traps were placed on each plot between June 15–16, 2010 and collected 2 weeks later (n = 8 traps per plot, 240 total). Traps were made of standard plastic beer cups sunk into the ground such that the top of the cup was level with the ground (Figure 6A). Traps were covered with 10x10" pieces of aluminum flashing with an inch of space between the cover and ground (Figure 6B). Two cm of safe antifreeze (propylene glycol) was poured into each cup. A small piece of plastic aviary fencing (¾" mesh) was placed just inside each cup to keep lizards out of the traps (Figure 8A). This probably filtered out larger insects as well. Upon collection, the contents of each trap was rinsed and stored in 50-mL falcon tubes filled with ethanol. Samples were then sorted and all insects were counted and identified to order and morphotype. Each sample was weighed, and key insects (beetles, ants, and orthopterans) were also weighed separately.

A **B**

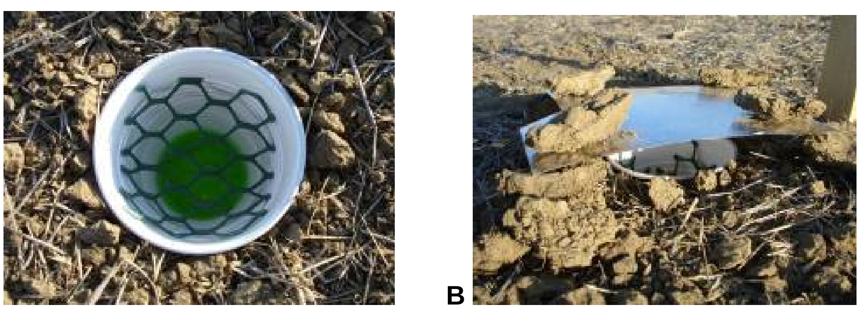

Figure 6. Pitfall trap viewed from above (A) and from the side with the aluminum cover (B).

Spotlight surveys

Ten spotlight routes along dirt roads in our study pastures ranging in length from 1.9-5.5 km (total distance = 35.4 km for all 10 routes) were surveyed in spring (May 18–21, n = 4 surveys) and summer (July 26–29, n = 4 surveys). We used 1-million candlepower spotlights aimed out either side of a slowly moving vehicle and animals were located by seeing eyeshine. Binoculars were used to aid identification.

All predators and lagomorphs were identified and recorded, along with their distance from the transect (using a rangefinder), angle from the vehicle, and location along the transect. Kit fox and lagomorph density estimates were obtained using the program DISTANCE.

Kit fox activity and diet

Kit fox dens found on plots or opportunistically while walking to plots were geo-referenced. Kit foxes often marked our rodent traps with urine and feces, and we collected scats deposited on our traps. We collected 118 kit fox scats. We also recorded all sightings of kit foxes.

Cattle grazing intensity

We counted the number of cows on our control plots in Center Well from April 13–June 29, 2010 (*n* = 29 surveys). Cows were counted during active foraging periods in the mornings and evenings. We also counted cow patties on our control plots shortly after the cows were removed.

Results and Discussion

Plants

General plant composition

Plant species richness in our study area was similar to richness in 2008 and 2009, but plant cover was much higher than in previous years (Table 1). The most common plants in Center Well were the native species *Vulpia microstachys* and *Lepidium nitidum*, followed closely by the exotic species *Erodium circutarium*. Clover (*Trifolium gracilentum*) was much more abundant in 2010 compared with previous years. *Erodium* and *Lasthenia californica* were the most common species in the Swain pasture.

Table1. Species richness and plant cover in the Center Well and Swain pastures, 2007–2009.

Metric	Type	Center Well				Swain			
		2007	2008	2009	2010	2007	2008	2009	2010
Species richness	native	18	29	29	31	15	43	40	45
	exotic	8	7	6	7	7	10	8	6
	total	26	36	35	38	22	53	48	51
Plant cover (%)	native	23	28	42	67	17	20	41	57
	exotic	17	37	28	25	32	33	32	34
	total	40	65	70	92	50	52	73	90

Table 2. Relative % cover of plant species in the Center Well and Swain pastures in 2010 (*n* = 400 plots), and without GKR ("No GKR", inside GKR exclosures, *n* = 160 plots) and with GKR ("GKR", outside GKR exclosures, *n* = 240 plots).

Species	Type	Center Well	Swain	No GKR	GKR
Vulpia microstachys	native	17.7	8.8	16.06	12.83
Lepidium nitidum	native	17.4	5.6	12.35	13.01
Erodium cicutarium	exotic	17.0	16.6	14.89	18.25
Trifolium gracilentum	native	15.0	3.0	7.76	11.97
Lasthenia minor	native	10.5	0.02	5.98	6.59
Schismus arabicus	exotic	5.7	8.1	3.82	8.62
Vulpia myuros	exotic	3.1	1.4	3.39	1.75
Amsinckia tessellata	native	2.4	4.3	2.81	3.35

Table 2 continued

Species	Type	Center Well	Swain	No GKR	GKR
Calandrinia ciliata	native	2.3	2.6	1.18	3.27
Tropidocarpum gracile	native	1.7	0.8	0.56	1.92
Lotus wrangelianus	native	1.6	3.6	3.17	1.82
Guillenia lasiophylla	native	1.3	0.4	0.59	1.21
Hordeum murinum	exotic	0.9	2.6	2.60	0.86
Microseris douglasii	native	0.8	0.1	0.63	0.45
Microseris elegans	native	0.4	0.8	0.68	0.50
Dichelostemma capitatum	native	0.4	0.4	0.49	0.37
Pectocarya penicillata	native	0.4	2.3	1.16	1.14
Bromus madritensis	exotic	0.3	8.4	5.48	2.13
Lasthenia californica	native	0.2	14.2	7.99	4.16
Trifolium albopurpureum	native	0.2	0.0	0.02	0.16
Astragalus oxyphysus	native	0.1	--	0.03	0.08
Lepidium dictyotum	native	0.09	0.2	0.18	0.11
Capsella bursa-pastoris	exotic	0.06	--	--	0.06
Eriogonum gracillimum	native	0.06	0.7	0.35	0.27
Astragalus didymocarpus	native	0.05	0.02	0.04	0.03
Lupinus microcarpus	native	0.04	0.7	0.47	0.15
Phlox gracilis	native	0.04	0.0	0.01	0.05
Poa secunda	native	0.03	6.6	2.18	2.99
Malacothrix coulteri	native	0.03	0.0	0.03	0.02
Amsinckia menziesii	native	0.02	--	--	0.02
Uropappus lindleyi	native	0.01	0.4	0.19	0.11
Trichostema lanceolatum	native	0.01	0.1	0.07	0.05
Lembertia congdonii	native	0.01	0.04	0.01	0.03
Monolopia lanceolata	native	0.01	--	--	0.01
Castilleja exserta	native	<0.01	0.05	0.03	0.01
Eremocarpus setigerus	native	<0.01	0.03	0.02	0.01
Stephanomeria pauciflora	native	--	0.03	--	<0.01
Allium sp.	native	<0.01	--	--	<0.01
Sisymbrium altissimum	exotic	<0.01	--	1.43	0.27
Chaenactis glabriuscula	native	--	1.9	1.26	0.21
Linanthus liniflorus	native	--	1.6	0.81	0.22
Chorizanthe uniaristata	native	--	1.2	0.22	0.30
Hollisteria lanata	native	--	0.7	0.49	0.05
Lastarriaea coriacea	native	--	0.6	0.02	0.33
Plagiobothrys canescens	native	--	0.5	0.19	0.12
Herniaria hirsuta	exotic	--	0.4	0.17	0.11
Astragalus lentiginosus	native	--	0.3	0.07	0.01
Camissonia campestris	native	--	0.08	0.07	--
Muilla maritima	native	--	0.07	0.02	0.01
Plantago erecta	native	--	0.03	0.02	--
Delphinium recurvatum	native	--	0.02	--	0.01
Lomatium sp.	native	--	0.02	--	0.01
Athysanus pusillus	native	--	0.01	0.01	--
Camissonia palmeri	native	--	0.01	--	0.01
Platystemon californicus	native	--	0.01	0.01	--
Castilleja leariloba	native	--	<0.01	--	<0.01
Crassula connata	native	--	<0.01	<0.01	--

Grazing intensity

Approximately 200 cows and calves were turned out in Center Well from March 23–June 30, 2010, for a total of 544 animal use months. Grazing intensity was higher and less variable among our plots in 2010 compared with previous years (Table 3). Cows grazed more intensively in areas with higher plant biomass (Figure 7, R^2 = 0.60, P < 0.001).

Table 3. Average counts of cows seen on control (grazed) plots in the Center Well pasture (n = 29 surveys), and the total number of cowpies found on each plot.

Plot	2008		2009		2010	
	N cows	N cowpies	N cows	N cowpies	N cows	N cowpies
C1	3.17	459	0	24	1.31	418
C2	0.83	216	0.25	25	0.38	402
C3	1.30	155	0.13	35	1.48	219
C4	2.09	166	0.13	32	1.86	273
C5	0	4	0	11	0	129
C6	1.70	162	0	12	4.21	439
C7	0	132	0	3	0.59	238
C8	0.13	143	0	40	0.28	213
C9	0.17	125	0	16	0.10	303
C10	0.26	86	0	2	0.38	289

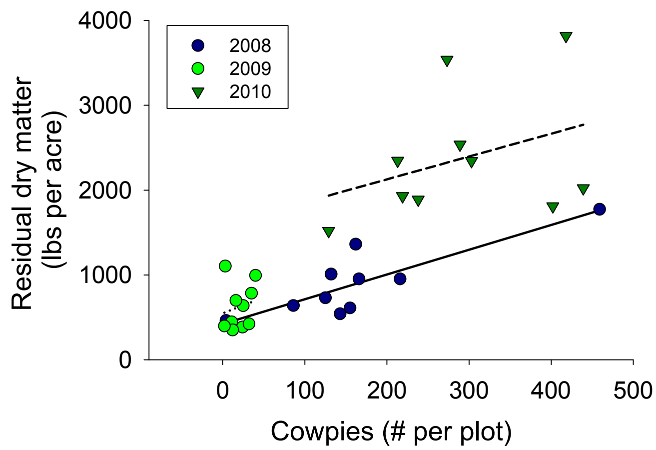

Figure 7. Relationship between grazing intensity (as measured by the number of cowpies) and plant biomass (residual dry matter) on plots in the Center Well pasture, 2008–2010. Plant biomass was measured in April each year.

Effect of cattle and kangaroo rat exclusion

Biomass removal by cattle and GKR. We calculated the biomass removed by cattle as follows: the biomass measured on plots exposed to grazing was subtracted from the biomass measured on paired plots within cattle exclosures (n = 10 replicate pairs in Center Well). Similarly, we calculated the biomass removed by GKR by subtracting the biomass measured within cattle exclosures (which were exposed to GKR but not cattle) from the biomass measured within GKR exclosures in Center Well. Biomass was measured in April (peak), June (post-grazing), and October (minimum).

The peak residual dry matter (RDM) prior to grazing by cattle was approximately 2,900 pounds per acre in 2010 (Table 4), which was far higher than levels in 2009, when peak RDM was 900 lbs/acre. Cattle grazing and GKR foraging each reduced plant biomass by approximately 500 lbs/acre (Figure 8). There was no difference in biomass inside and outside GKR exclosures in April, but by October removal by GKR was similar in magnitude to removal by cattle (Figure 8, Figure 9). Unlike in previous years, when differences in RDM measurements inside and outside cattle exclosures had disappeared by October, the cattle grazing effect was still apparent in October in 2010 (Table 4, Figure 8). Without grazing by GKR or cattle, RDM levels were reduced to a minimum of approximately 1100 lbs/acre by factors such as insect herbivory, wind, and foraging by squirrels (Table 4).

Table 4. Average (± standard error) plant biomass measured in pounds per acre on 10 replicate sites in the Center Well pasture, 2010. Each site consisted of a control plot grazed by cattle ("GKR and cattle" treatment), a cattle exclosure ("GKR only" treatment), and a GKR exclosure ("no GKR or cattle" treatment).

Treatment	April	June	October
GKR and cattle	2374 ± 237	1035 ± 196	305 ± 45
GKR only	2868 ± 244	1540 ± 146	679 ± 128
No GKR or cattle	2922 ± 247	1702 ± 221	1106 ± 113

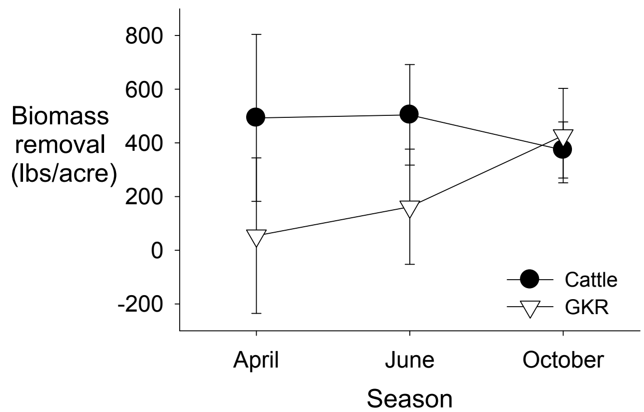

Figure 8. Biomass removal by cattle and GKR in 2010, measured as the difference in biomass among cattle and GKR exclosure treatments. Means and standard error bars are shown (*n* = 10 replicates).

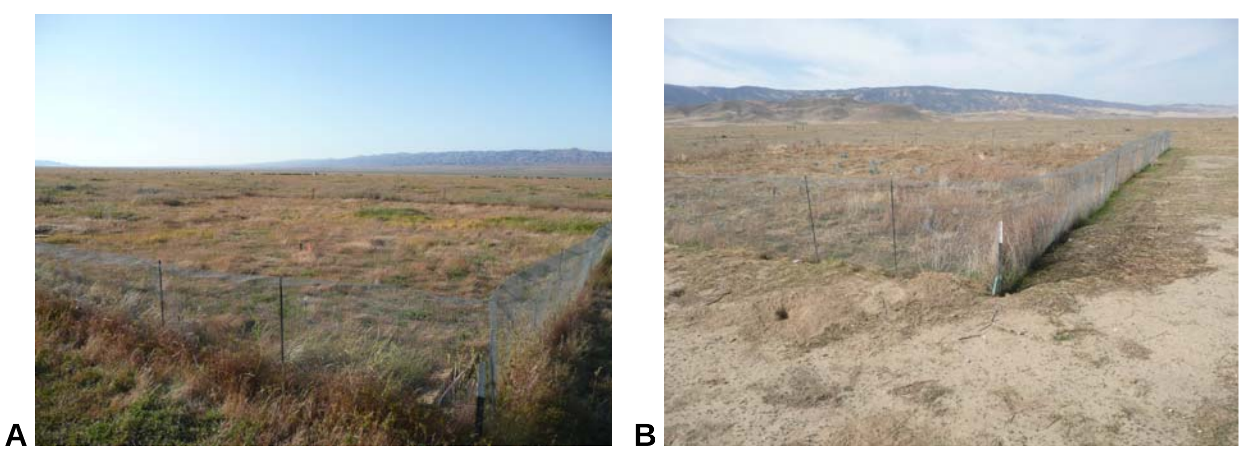

Figure 9. Photographs of the kangaroo rat exclosure at site Center Well 2 in (A) April 2010, when GKR had not started removing biomass, and (B) October 2010, when GKR had completed most of their clipping.

Native and exotic plant cover. Native plant cover has risen 3-fold throughout our study pastures since our study began in 2007, from 23% in Center Well in 2007 to 67% in 2010, and from 17% in Swain in 2007 to 57% in 2010. This general increase appears to be unrelated to our treatments (Figure 10), though some treatment effects did occur. Native plant cover in Center Well was higher where GKR were excluded (Figure 10; linear mixed effects model, $F_{1,116} = 9.5$, $P = 0.003$), but cattle grazing did not significantly affect native cover (Figure 10; $F_{1,115} = 1.81$, $P = 0.18$). In the Swain pasture, native cover was also higher where GKR were excluded ($F_{1,117} = 3.9$, $P = 0.05$).

The increased native cover in GKR exclosures was mainly due to higher cover of *Lasthenia sp.* and *Vulpia microstachys*, as well as higher cover of a variety of relatively rare species, such as *Lotus*, *Chaenactis*, *Linanthus*, *Lastarriaea*, and *Lupinus* (Table 2). However, some native species, such as *Poa*, *Trifolium*, and *Calandrinia* were more common where GKR were present (Table 2). Cattle grazing had a weak effect on the cover of most species, but *Trifolium* and *Schismus* were more common in grazed areas, and *Vulpia microstachys* was more common in cattle exclosures.

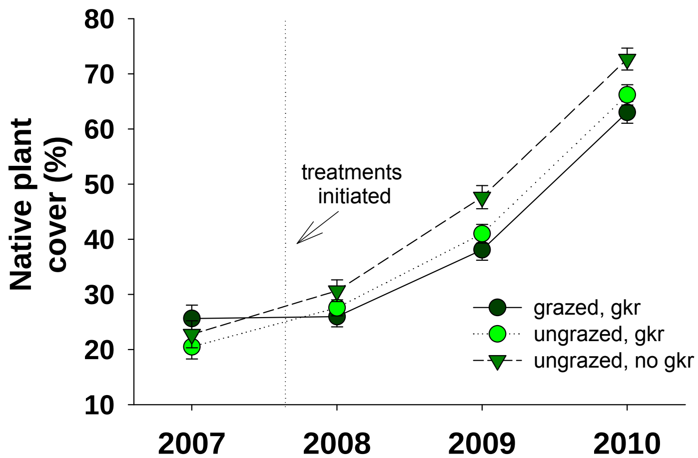

Figure 10. Native plant cover in experimental plots within the Center Well pasture. Three treatments were initiated prior to the spring of 2008: kangaroo rat exclosures (ungrazed, no gkr), cattle exclosures (ungrazed, gkr), and control plots (grazed, gkr). Means and standard error bars are shown ($n = 10$ replicates per treatment).

Soil disturbance by GKR promoted exotic grasses, especially in the Swain pasture (pasture x precinct interaction, $F_{1,272} = 27.1$, $P < 0.001$). However, results from the Swain pasture indicate that GKR foraging controls exotic grasses and promotes native bunchgrass, thus counteracting the effects of their soil disturbance (Figure 11). For example, *Poa secunda* was twice as abundant in areas where GKR were present despite the fact that they were less abundant on GKR precincts, where soil disturbance was high (Figure 11A). *Bromus m. rubens* showed the opposite pattern, in which it was nearly twice as abundant in areas without GKR but five times more abundant on GKR precincts (Figure 11B). Thus, red brome and other exotic grasses may outcompete *Poa* in the absence of GKR, whereas the presence of GKR likely reduces exotic grass dominance via preferential seed predation.

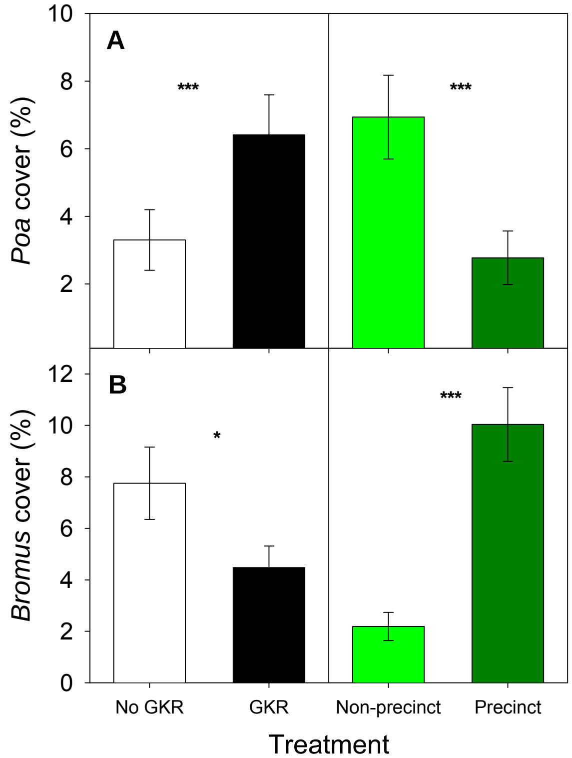

Figure 11. Cover of (A) *Poa secunda* and (B) *Bromus madritensis rubens* in the Swain pasture, 2010. Averages and standard errors are shown for plots in and out of GKR exclosures (No GKR/GKR), and on and off GKR precincts. A "*" indicates that treatment differences were significant at the $P < 0.05$ level, and "***" indicates differences were significant at the $P < 0.001$ level.

GKR abundance

A total of 1,637 individual kangaroo rats were captured in 2010; 977 (60%) of which had not been marked in previous years. Five of these kangaroo rats were *Dipodomys nitratoides*, and the other 1,632 individuals were *Dipodomys ingens*. Including recaptures, a total of 3,872 captures occurred in 2010. Mark-recapture estimates of GKR abundance varied widely among sites, from 5-64 GKR per plot (Table 5). Overall, the estimates indicate that populations are currently stable at moderate-high densities. GKR abundance in Swain has been steadily increasing and now exceeds Center Well, whereas densities in Center Well have been slowly declining (Figure 12). Apparent survival rates also varied widely among sites, ranging from 0.34-0.76 (Table 5).

2010 was a year with above average rainfall, and we started to see signs that cattle grazing under these conditions may benefit GKR. GKR densities tended to be higher in grazed plots in Center Well compared with ungrazed plots in cattle exclosures (paired t-test, t_9 = 2.12, P = 0.06). This increase in density may have been caused by adult immigration, because survival and reproduction did not differ among grazed and ungrazed plots in Center Well (reproduction paired t_9 = -1.73, P = 0.12, survival paired t_9 = 1.5, P = 0.16). Reproduction was low in 2010 compared with previous years (Table 6; 0.3 juveniles per adult, compared with 0.4 in 2008 and 2009). Both survival and reproduction were higher in the Swain pasture than in Center Well (survival t_{28} = 3.09, P = 0.005, reproduction t_{28} = 2.29, P = 0.03).

The seasonal genital lesions that appear in August trapping sessions, which are likely chiggers (trombiculid mites), greatly increased in prevalence in 2010. The overall affected rate was 66% (676/1026 individuals), compared to a rate of 16-17% in 2008 and 2009. An attempt was made to obtain a sample by scraping the affected area with an ethanol-soaked cotton swab. However, no material was transferred to the swab using this method. The higher precipitation levels in 2010 may have contributed to the rise in affected rates. It is unknown whether the lesions have any impacts on GKR demographics.

GKR estimates on each plot were correlated among surveys in 2009 and 2010 (r = 0.66-0.71, n = 30 plots), indicating that some plots consistently have higher densities than others.

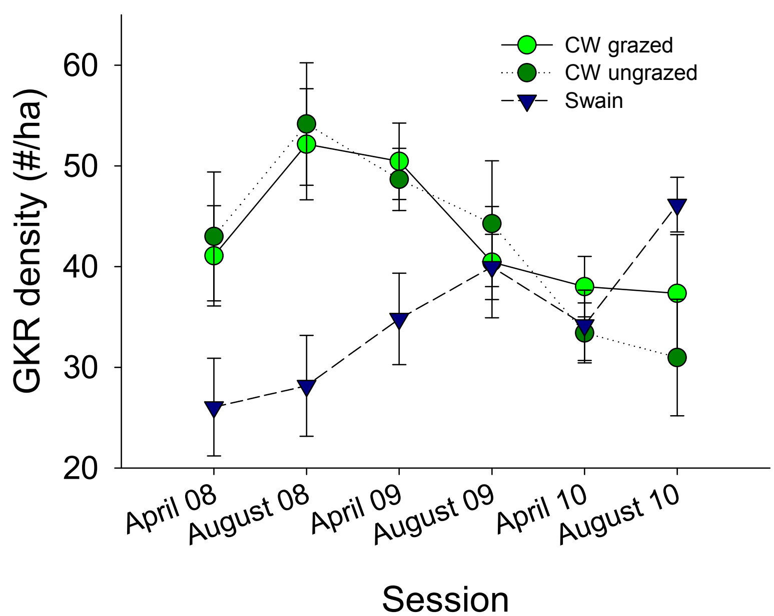

Figure 12. Average GKR population estimates in Center Well grazed plots, Center Well ungrazed plots, and Swain ungrazed plots, during each trapping session.

Table 5. GKR population size and apparent survival estimates in 2010. Apparent survival is the proportion of GKR remaining on each site between trapping periods. Population sizes are estimated numbers of GKR on each 1.96-ha plot (1-ha trapping grid plus 20-m buffer zone) during April and August trapping sessions. Standard errors (SE) are shown for each estimate.

Plot	# GKR April	April SE	# GKR August	August SE	Apparent survival	Survival SE
C1	35	0.91	27	2.43	0.74	0.06
C2	44	1.08	39	1.67	0.64	0.07
C3	30	0.58	27	1.68	0.75	0.06
C4	41	0.73	17	1.21	0.79	0.03
C5	48	0.54	42	0.95	0.75	0.03
C6	15	0.37	5	0.69	0.62	0.06
C7	43	0.94	42	1.88	0.72	0.07
C8	43	0.93	53	1.57	0.75	0.03
C9	42	0.70	58	1.23	0.76	0.03
C10	40	1.08	64	1.83	0.73	0.03
E1	31	0.70	14	1.83	0.69	0.07
E2	38	1.88	29	2.74	0.62	0.07
E3	28	0.56	15	1.52	0.74	0.06
E4	47	0.71	10	1.12	0.76	0.03
E5	51	0.50	56	0.90	0.73	0.03
E6	21	0.47	12	0.85	0.72	0.05
E7	27	1.28	27	2.38	0.65	0.08
E8	29	1.06	50	1.82	0.72	0.03
E9	36	0.50	46	0.90	0.74	0.03
E10	28	0.95	52	1.65	0.68	0.03
S1	47	0.73	54	1.27	0.78	0.03
S2	39	0.56	54	1.02	0.76	0.03
S3	53	0.84	51	1.41	0.78	0.03
S4	41	0.63	44	1.11	0.74	0.03
S5	33	0.72	34	1.28	0.73	0.05
S6	24	0.001	45	2.09	0.58	0.07
S7	30	0.001	60	2.57	0.74	0.06
S8	20	0.38	37	0.72	0.71	0.05
S9	20	0.30	37	0.58	0.74	0.05
S10	34	0.77	47	1.36	0.85	0.03

Table 6. Age and sex composition of GKR and San Joaquin antelope squirrels (SJAS) captured in 2010.

		Female	Male	Unknown	Total
GKR	Adult	625	626	3	1254
	Juvenile	203	158	2	363
	Unknown	2	0	18	20
	Total	830	784	23	1637
SJAS	Adult	42	72	3	117
	Juvenile	60	63	4	127
	Unknown	9	12	2	23
	Total	111	147	9	267

GKR diet

We examined the contents of 31 surface pit caches to estimate the diet of GKR. *Trifolium* seeds replaced *Lepidium* as the most common in 2010; *Lepidium* was nearly absent from caches in 2010, whereas *Trifolium* was absent from caches in 2008 and 2009 (Table 7). This change may reflect the >3-fold increase in *Trifolium* cover in 2010 and a dietary preference for *Trifolium*. *Trifolium* was not included in the diet trials conducted in previous years because of its rarity, so we do not have preference data for this species. The relative occurrences of *Vulpia*, *Bromus*, and *Erodium* in the diet were similar in 2009 and 2010 (Table 7).

Table 7. Relative occurrence of plant species in GKR surface seed caches collected in 2008 (*n* = 52 caches), 2009 (*n* = 61 caches), and 2010 (*n* = 31 caches).

Species	Relative occurrence 2008	Relative occurrence 2009	Relative occurrence 2010
Trifolium gracilentum	--	--	0.24
Vulpia microstachys	0.06	0.20	0.20
Bromus madritensis rubens	0.03	0.22	0.15
Erodium cicutarium	0.35	0.11	0.12
Vulpia myuros	0.004	0.004	0.10
Chaenactis glabriuscula	<0.01	--	0.03
Schismus arabicus	0.12	0.04	0.03
Guillenia lasiophylla	0.003	<0.01	0.02
Lepidium nitidum	0.20	0.33	0.02
Calandrinia ciliata	0.03	0.01	0.02
Tropidocarpum gracile	0.05	--	0.01
Lasthenia minor	0.04	0.01	0.01
Microseris elegans	0.01	0.002	0.01
Hordeum murinum	0.003	--	0.01
Poa secunda	--	0.01	0.01
Microseris douglasii	0.004	0.005	0.01
Amsinckia tessellata	0.05	0.03	0.01
Lotus wrangelianus	<0.01	<0.01	0.003
Lasthenia californica	0.03	0.02	--
Monolopia lanceolata	--	0.02	--
Isocoma acradenia	<0.01	<0.01	--
Eriogonum gracillimum	--	<0.01	--
Capsella bursa-pastoris	--	<0.01	--
Uropappus lindleyi	0.01	--	--
Plantago erecta	0.01	--	--
Lepidium dictyotum	<0.01	--	--
Vulpia sp.	<0.01	--	--
Lasthenia sp.	<0.01	--	--
Pectocarya penicillata	<0.01	--	--

SJAS abundance

Cattle grazing had a strong negative effect on San Joaquin antelope squirrels in 2010. SJAS densities continued to increase in Swain and on ungrazed plots in Center Well, but densities decreased on grazed plots in Center Well (Figure 13A). Densities were higher on ungrazed plots in each of the 10 replicate sites in Center Well (Figure 13B). This difference was highly significant (paired t_9 = -4.59, P = 0.001). A total of 267 individual antelope squirrels were captured, and a total of 687 captures (including recaptures) occurred. As in previous years, the sex ratio was male-biased (Table 6, 0.76 females per male). However, reproduction was higher than in previous years (Table 6, 1.1 juveniles per adult, compared with 0.26 in 2009 and 0.07 in 2008). The higher densities on ungrazed plots in Center Well were due to increased reproduction rather than differences in survival (Figure 14), whereas the higher densities in Swain were due to higher survival (Figure 14). SJAS estimates on each plot were correlated between 2009 and 2010 (r = 0.67, n = 30 plots, P < 0.001).

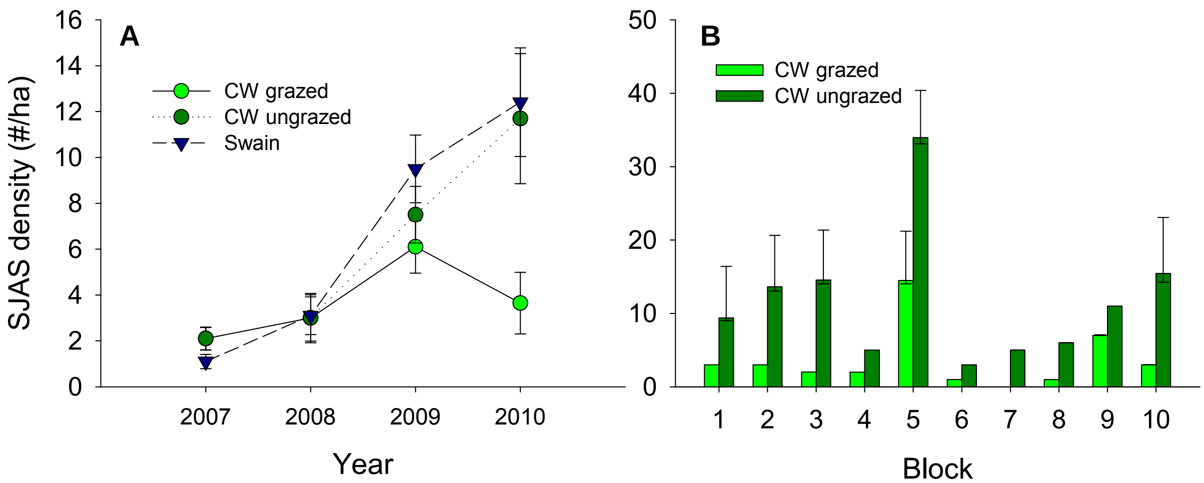

Figure 13. Estimates of San Joaquin antelope squirrel density. (A) Average annual density (± standard error) in Center Well grazed plots, Center Well ungrazed plots, and Swain ungrazed plots. (B) Density in 2010 on each replicate site (block) in Center Well, with 95% confidence intervals.

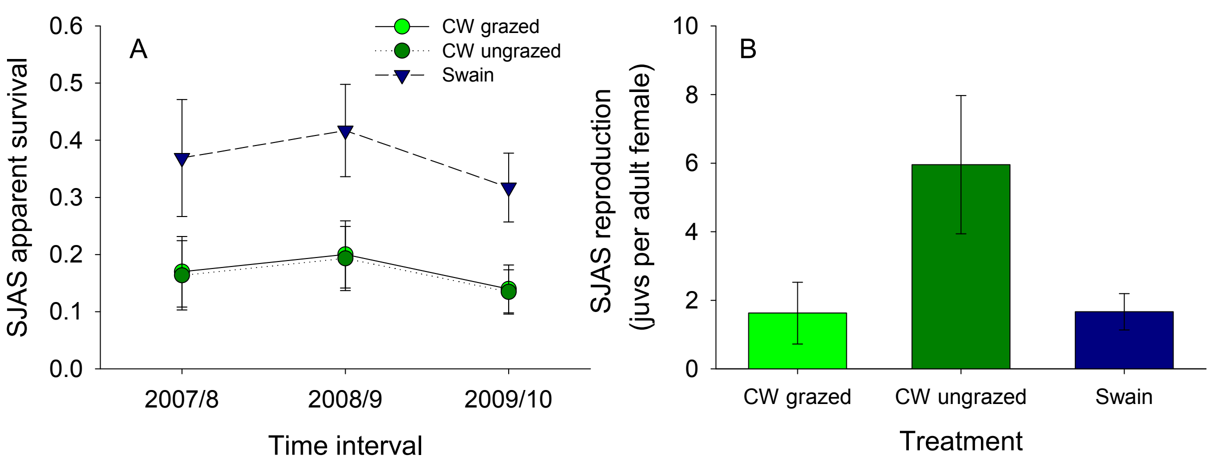

Figure 14. (A) Apparent survival of San Joaquin antelope squirrels on Center Well grazed plots, Center Well ungrazed plots, and Swain ungrazed plots, 2007-2010. (B) SJAS reproduction in 2010 in the three treatments. Standard error bars are shown.

Bird abundance

Bird abundance on our plots in 2010 was similar to 2009. A total of 1,869 individuals from 20 bird species were detected during point counts, 323 of which were either on or flying over our plots. As in previous years, the most common birds found on our plots were horned larks and ravens. There was a marked increase in savannah sparrow abundance in 2010, and American pipits and red-winged blackbirds were detected during our surveys for the first time (Table 8).

Table 8. Total counts of birds detected on or flying over plots, 2007–2010.

Common Name	Scientific Name	2007	2008	2009	2010
Horned Lark	*Eremophila alpestris*	545	61	203	158
Common Raven	*Corvus corax*	16	43	55	45
Savannah Sparrow	*Passerculus sandwichensis*	0	1	3	41
American Pipit	*Anthus rubescens*	0	0	0	39
Red-winged Blackbird	*Agelaius phoeniceus*	0	0	0	18
Western Meadowlark	*Sturnella neglecta*	11	3	33	8
Long-billed Curlew	*Numenius americanus*	0	0	0	5
Cliff Swallow	*Petrochelidon pyrrhonota*	0	0	0	3
Prairie Falcon	*Falco mexicanus*	0	0	0	2
Violet-green Swallow	*Tachycineta thalassina*	0	0	10	1
Red-tailed Hawk	*Buteo jamaicensis*	0	5	1	1
Northern Harrier	*Circus cyaneus*	0	0	0	1
White-crowned Sparrow	*Zonotrichia leucophrys*	0	0	0	1
Unidentified Flycatcher	*Empidonax sp.*	0	0	6	0
American Kestrel	*Falco sparverius*	0	0	2	0
Chipping Sparrow	*Spizella passerina*	0	0	1	0
Ferruginous Hawk	*Buteo regalis*	0	0	1	0
Mourning Dove	*Zenaida macroura*	0	0	1	0
Northern Mockingbird	Mimus polyglottos	0	0	1	0
Mountain Plover	Charadrius montanus	0	0	1	0
Sage Sparrow	Amphispiza belli	0	0	1	0
Lark Sparrow	Chondestes grammacus	0	2	0	0
Loggerhead Shrike	Lanius ludovicianus	0	2	0	0
Golden Eagle	Aquila chrysaetos	0	1	0	0
Vesper Sparrow	Pooecetes gramineus	0	1	0	0
Brewer's Blackbird	Euphagus cyanocephalus	3	0	0	0
Total		575	119	319	323

Reptile abundance

A total of 114 side-blotched lizards (*Uta stansburiana*) and 18 BNLL (*Gambelia sila*) were seen during reptile surveys. No other reptile species were seen during surveys. All BNLL sightings were geo-referenced. As in previous years, all BNLL sightings were in the Swain pasture. Sightings occurred on 7 of the 10 sites in Swain, indicating that BNLL are distributed throughout the pasture. Although BNLL abundance did not change, *Uta* abundance declined more than 5-fold in 2010 (Figure 15). *Uta* densities were higher on ungrazed plots in Center Well compared with grazed plots (0.6 *Uta* per ha on ungrazed plots vs 1.0 per ha on grazed plots, paired $t_{29} = -2.8$, $P = 0.008$). Despite differences in density levels among years, density estimates on each plot were correlated between 2009 and 2010 ($r = 0.64$, $n = 30$ plots, $p < 0.01$), indicating that certain areas are consistently high or low quality sites for *Uta*.

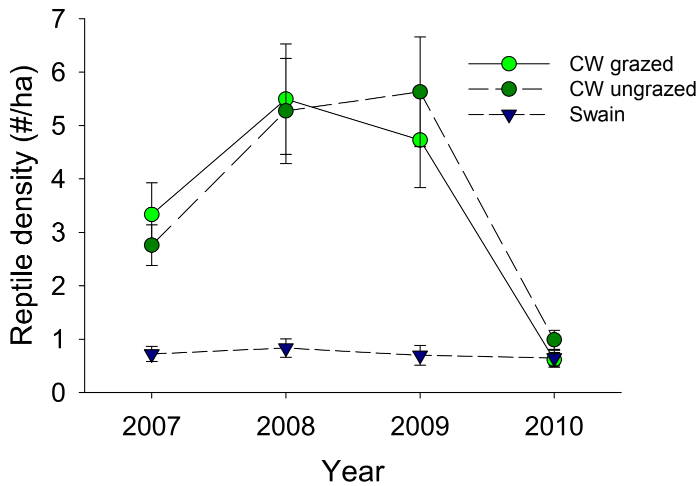

Figure 15. Estimates of reptile density each year from 3 replicate surveys on Center Well grazed plots, Center Well ungrazed plots, and Swain ungrazed plots. Standard error bars are shown.

Invertebrate abundance

GKR exclosures had strong effects on the invertebrate community in 2009 and 2010, and cattle exclosures had some minor effects. Invertebrate diversity was higher on grazed plots compared with ungrazed plots in Center Well, but only off of GKR precincts (Figure 16A, grazing x precinct interaction $F_{1,100} = 4.6$, $P = 0.03$). Beetle abundance was also higher on grazed plots, although the difference was not significant (Figure 16C, $F_{1,100} = 3.5$, $P = 0.06$). Invertebrate richness, beetle abundance, and orthopteran abundance (crickets and grasshoppers) were higher in the presence of GKR compared with GKR exclosures (Figure 16B&C, richness $F_{1,130} = 6.5$, $P = 0.01$, beetle $F_{1,130} = 9.0$, $P = 0.003$, orthopteran $F_{1,130} = 12.1$, $P < 0.001$). Arachnids and ants did not respond to GKR or cattle treatments in 2010 (all P > 0.05).

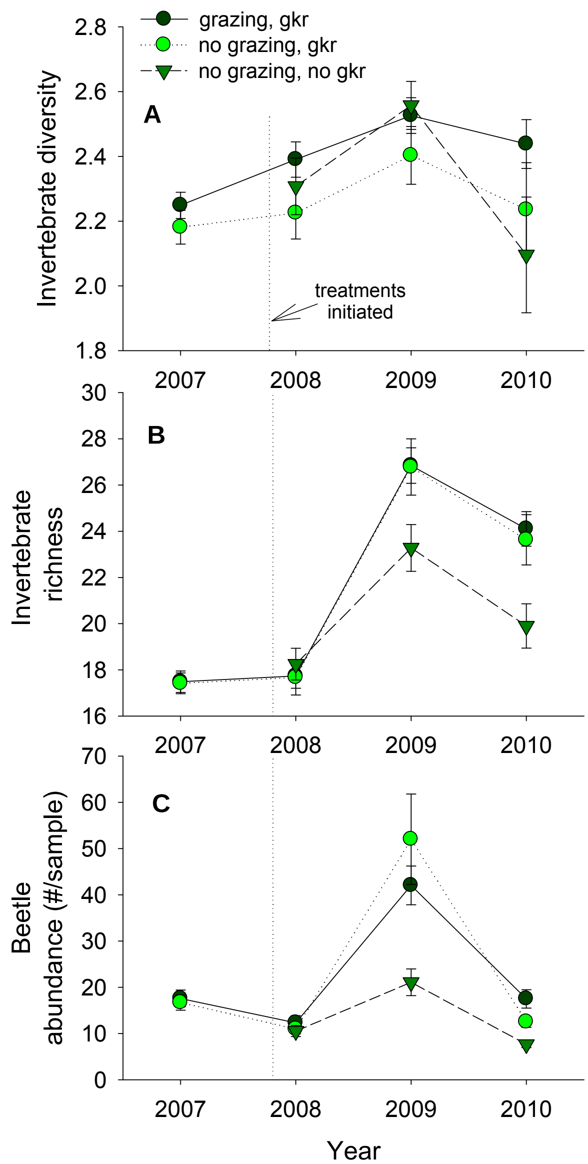

Figure 16. Response of (A) invertebrate diversity, (B) invertebrate richness, and (C) beetle abundance to GKR and cattle exclosures in the Center Well pasture, 2007-2010. Standard error bars are shown.

Species associations

Table 9 shows the associations among the flora and fauna on our plots. As in previous years, squirrel and lizard abundance was positively correlated with GKR abundance. Squirrel abundance, GKR abundance and survival, and bird abundance were all positively correlated with plant species richness. Plant richness and GKR survival were negatively correlated with plant biomass. Interestingly, despite a positive correlation between plant biomass and plant height, bird abundance was positively correlated with plant height but negatively correlated with plant biomass. Lizard abundance was positively correlated with invertebrate richness, and invertebrate richness was negatively correlated with plant height.

Table 9. Matrix of correlation coefficients (*r*) among species counts on each of the 30 plots. Significant correlations ($p < 0.05$) are highlighted in bold. Richness is the number of species.

2010	*N* squirrels	*N* GKR	GKR survival	*N* birds	Bird richness	*N* lizards	Plant biomass	Plant height	Plant richness
N GKR	0.35								
GKR survival	0.16	**0.57**							
N birds	0.19	0.26	0.32						
Bird richness	0.26	0.10	0.00	-0.03					
N lizards	0.28	**0.52**	0.18	0.05	-0.04				
Plant biomass	-0.14	-0.31	**-0.42**	-0.12	0.14	-0.07			
Plant height	-0.05	-0.15	0.01	**0.41**	0.32	-0.13	**0.49**		
Plant richness	**0.40**	**0.60**	**0.44**	**0.46**	0.35	0.14	**-0.36**	0.12	
Invert richness	0.18	0.28	-0.29	-0.21	-0.19	**0.45**	0.08	**-0.47**	0.00

Conclusions and Future Directions

Rainfall during the 2010 growing season (October 2009–April 2010) was above average (30 cm), representing the first “wet” year of our study (precipitation levels during 2007-2009 were 9-16 cm). Peak plant biomass was approximately three times higher than in previous years, and quantifiable impacts of cattle grazing on wildlife began to emerge. In fact, the effects of grazing on wildlife were generally stronger than effects on plant composition. Although not statistically significant (P = 0.06), GKR and beetles tended to be more abundant on plots that were grazed by cattle compared with paired plots in cattle exclosures. Invertebrate diversity was also higher on grazed plots. Beetles and other insects may have responded positively to the presence of cattle dung piles. In contrast to these positive effects of grazing, SJAS were far less abundant on plots grazed by cattle, primarily due to higher reproduction on plots within cattle exclosures. Likewise, lizards were more abundant in areas where cattle were excluded, despite a dramatic overall decline in lizard abundance. These results are surprising, because both lizards and squirrels are thought to prefer open habitats (Germano et al. 2001), and their invertebrate food supply was higher in grazed areas. We caution that these results represent only one year of wet conditions. Rainfall during the first three months of the 2011 growing season (26 cm) was already close to the total rainfall during the 2010 growing season, so results from next season will help to evaluate the robustness of these trends.

Peak vegetation biomass was 2,922 lbs/acre in April, and this was reduced to a minimum of 305 lbs/acre by October in areas exposed to grazing by all species (Table 4). Our exclosures allow us to determine what proportion of this 90% loss of vegetation was due to cattle, GKR, or other forces (wind, insects, etc.). Each of these three factors removed approximately 30% of the biomass that was lost. Both GKR (at an average density of 34/ha) and cattle (with 544 animal use months) removed approximately 500 lbs/acre. This removal rate by GKR (~ 5 lbs/GKR) was more than twice the rate in 2009 and may be close to the maximum possible removal rate for this species.

Our exclosures are revealing strong effects of GKR on plant composition and the invertebrate community. Despite the positive effect of soil disturbance on exotic grass cover, GKR foraging appears to reduce the dominance of these grasses, thus restricting exotic grass distribution primarily to their disturbed mounds. Although GKR precincts may function as foci of invasion, once exotic grasses are present in an area, GKR may actually benefit native bunchgrasses by removing exotic grass seeds and preventing their spread. However, native species that GKR prefer to eat, such as *Lotus*, are more abundant in the absence of GKR, and native cover overall was higher where GKR were excluded. Invertebrates as a group were positively affected by GKR, as invertebrate species richness and biomass (especially of beetles and orthopterans) was markedly higher in areas with GKR compared to GKR exclosures. This pattern may be due to provisioning of herbivorous insects by their clipping and seed caching behaviors.

In 2010, we made substantial progress towards addressing our key questions regarding the effects of cattle grazing and GKR in this system. We synthesized data collected from 2007-2009 to tease apart the many correlations we have documented among species on our experimental plots (Prugh and Brashares submitted, *Journal of Animal Ecology*). Using structural equation modeling, we compared the influence of soil properties, primary productivity, habitat engineering by GKR (i.e., creation of precincts), and density-mediated effects of GKR on the abundance and/or diversity of plants, insects, birds, squirrels, and lizards. We found that GKR had a stronger effect on other species than underlying site characteristics, and some species were affected more by engineering (plants and squirrels), while others were affected more by GKR density (lizards and invertebrates). We are currently in the process of using a similar model to examine the relative importance of GKR, cattle, and microsite characteristics on the plant community.

In the 2011 field season, we will continue to monitor flora and fauna on our experimental plots. Prior to the field season, manuscripts will be prepared for peer-reviewed publication. The three graduate student projects will also continue in 2011.

Products of the Carrizo Plain Ecosystem Project

18) Prugh, LR and JS Brashares. In review. Partitioning the keystone effects of an ecological engineer: kangaroo rats control community structure via multiple pathways. Journal of Animal Ecology.
17) Bean, W.T., R. Stafford, and J.S. Brashares. In review. The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. Ecography.
16) An insect collection was created for the Carrizo Plain visitor's center by Justin Cappadonna.
15) Bean, W.T., R. Stafford, S. Butterfield, L. Prugh, L. Saslaw, and J. Brashares. 2010. Towards an easy and inexpensive method for monitoring giant kangaroo rats in Carrizo Plain National Monument. San Joaquin Valley Natural Communities Conference, Bakersfield, CA (paper).
14) Prugh, L.R. and J.S. Brashares. 2010. Basking in the moonlight? Illumination increases the capture success of the endangered giant kangaroo rat. Journal of Mammalogy 91: 1205-1212.
13) Prugh, L.R. and J.S. Brashares. 2010. Cattle versus endangered kangaroo rats: Optimizing multi-use management in the Carrizo National Monument, CA. National Landscape Conservation System Science Symposium, Albuquerque, NM. (poster presented by K. Sharum)
12) Brashares, J.S., L.R. Prugh, J.W. Bartolome, B. Allen-Diaz, L. Saslaw, S. Butterfield, R. Stafford. 2010. Interactive effects of native rodents and cattle on the restoration of California rangelands. 63rd Annual Meeting of the Society for Range Management, Denver, CO. (paper)
11) Prugh, L.R. 2009. Carrizo Plain Ecosystem Project 2009 report. Prepared for agency partners. 22 pp.
10) Bean, T. 2009. Increasing accuracy and explanatory power of species distribution models with examples from the Carrizo Plain. Masters thesis, University of California Berkeley.
9) Prugh, L.R. and J.S. Brashares. 2009. Cattle versus endangered kangaroo rats: Optimizing multi-use management in the Carrizo National Monument, CA. 16th Annual Meeting of the Wildlife Society, Monterey, CA. (poster)
8) Prugh, L.R. 2009. Kangaroo rats: the great farmer-engineers of our deserts. Sierra Club *Desert Report* (Sept 2009): 15-17.
7) Prugh, L.R. 2008. Carrizo Exclosure Experiment 2008 report. Prepared for agency partners. 20 pp.
6) Prugh, L.R. and J.S. Brashares. 2008. Cattle versus endangered kangaroo rats. Human Dimensions of Wildlife Conference, Estes Park, CO. (paper)
5) Prugh, L. and J.S. Brashares. 2008. Teasing apart the effects of kangaroo rats and cattle. San Joaquin Valley Natural Communities Conference, CSU Bakersfield.
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3) Castillo, J. A. 2008. Endangered feces: An analysis of predator diet at Carrizo Plain National Monument, California. Senior honors thesis. University of California, Berkeley.
2) Olney, B. 2008. Seed preferences of the giant kangaroo rat (*Dipodomys ingens*) in grasslands of the Carrizo Plain, California. Senior honors thesis. University of California, Berkeley.

1) Prugh, L. R. 2007. Baseline surveys for the Carrizo exclosure experiment: final report. Prepared for The Nature Conservancy. 18 pp.

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