



Research Article

Effects of Grazing and Invasive Grasses on Desert Vertebrates in California

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ABSTRACT Much of California's San Joaquin Valley is a desert and, like portions of other North American deserts, is experiencing an ecological shift from being dominated by ephemeral native forbs, with widely spaced shrubs, to fire-prone non-native annual grasses. Small terrestrial vertebrates, many of which are adapted to open desert habitats, are declining. One hypothesis is that the invasive plants contribute to the decline by altering vegetative structure. Although cattle may have originally been a factor in the establishment of these non-native plants, their grazing may benefit the terrestrial vertebrates by maintaining an open structure, especially during average or wet winters when the exotic grasses grow especially dense. We experimentally tested the effect of cattle grazing on invasive plants and a community of small vertebrates at a site in the southwestern San Joaquin Desert. We established and monitored 4 treatment (grazed) and 4 control (ungrazed) plots from 1997 to 2006, and assessed the abundances of blunt-nosed leopard lizards (*Gambelia sila*), giant kangaroo rats (*Dipodomys ingens*), short-nosed kangaroo rats (*Dipodomys nitratoides nitratoides*), and San Joaquin antelope squirrels (*Ammospermophilus nelsoni*), all of which are listed as threatened or endangered by state or federal agencies. We also recorded abundances of the non-protected western whiptail lizards (*Aspidoscelis tigris*), side-blotched lizards (*Uta stansburiana*), San Joaquin pocket mice (*Perognathus inornatus inornatus*), and Heermann's kangaroo rats (*Dipodomys heermanni*). Based on repeated measures analysis of variance (ANOVA) and a 0.05 alpha level, only Heermann's kangaroo rats showed a treatment effect; they were more abundant on the control plots. However, this effect could be accounted for by the natural re-establishment of saltbush (*Atriplex* spp.) on part of the study site. Saltbush return also favored western whiptail lizards and San Joaquin antelope squirrels. A regression analysis indicated that populations of blunt-nosed leopard lizard and giant kangaroo rat increased significantly faster in grazed plots than the ungrazed controls, and abundances of 6 of 8 species were negatively correlated with increased residual dry matter. With relaxed alpha values to decrease Type II error, populations of blunt-nosed leopard lizards (500% greater), San Joaquin antelope squirrels (85% greater), and short-nosed kangaroo rats (73% greater) increased significantly on grazed plots over the course of the study compared to ungrazed plots. We did not find grazing to negatively affect abundance of any species we studied. When herbaceous cover is low during years of below average rainfall in deserts and other arid areas, grazing may not be necessary to maintain populations of small vertebrates. However, if cattle grazing is closely monitored in space and time to minimize adverse effects on the habitat, it could be an effective tool to control dense stands of non-native grasses and benefit native wildlife. © 2011 The Wildlife Society.

KEY WORDS antelope squirrels, cattle grazing, desert management, endangered species, invasive grasses, kangaroo rats, leopard lizards, San Joaquin Desert.

The deserts of North America are experiencing significant ecological changes with the invasion of exotic annual grasses (Brooks 1998, Lovich and Bainbridge 1999). We recently described and delineated the San Joaquin Desert in central California (Fig. 1; Germano et al. 2011), and this desert provides a good example of the conservation issues associated with the increasing density of exotic grasses in arid areas, not only in western North America (Young et al. 1972,

D'Antonio et al. 2007), but worldwide (D'Antonio and Vitousek 1992). The San Joaquin Desert supports a rich endemic flora and fauna (Germano et al. 2011). However, much of the arid habitats that once covered this region have been displaced by agricultural and urban development following the completion of the California Water Project and federal Central Valley Project in the early 1970s (U.S. Fish and Wildlife Service 1998). The largest remnant blocks of relatively undisturbed habitat in the southern San Joaquin Desert occur on the more arid western side, where habitat for several declining endemic plants and animals can be found.

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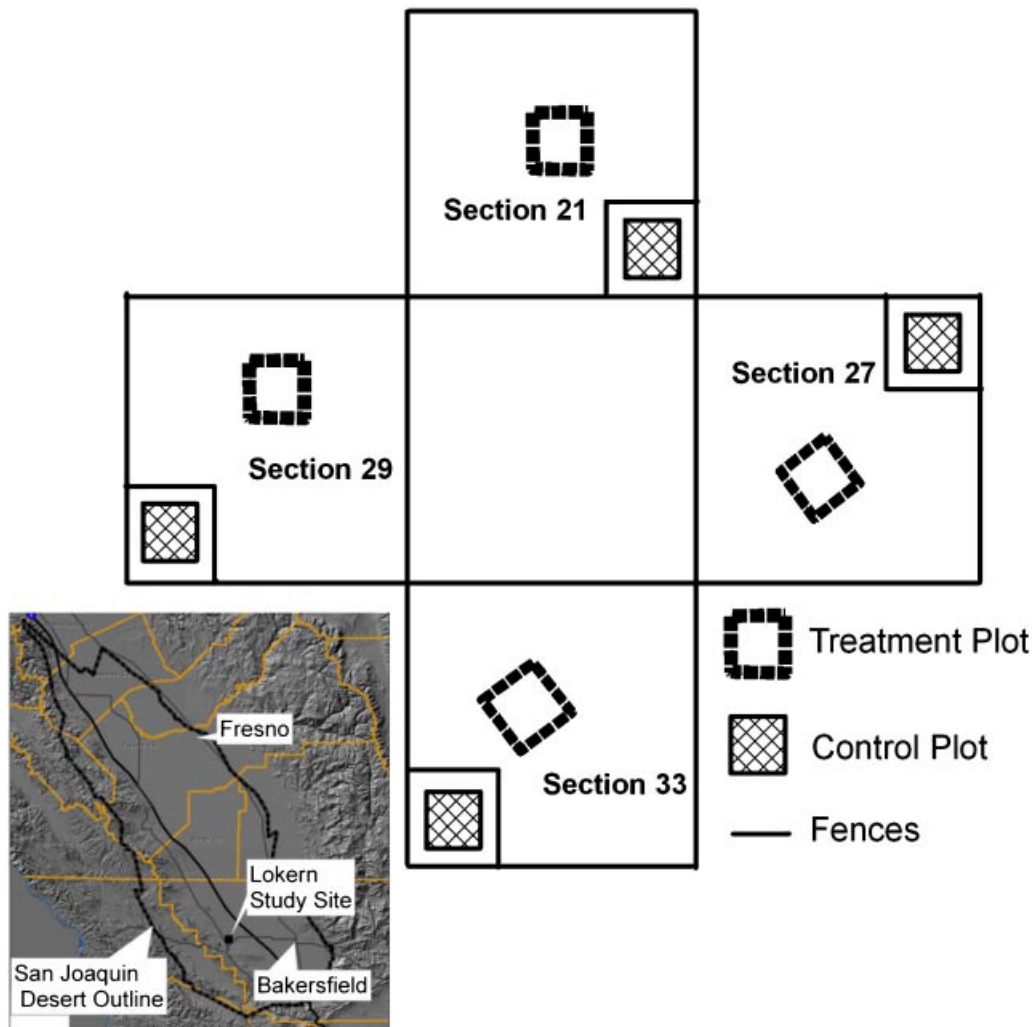


Figure 1. Location of the Lokern study site, west of Buttonwillow, Kern County, California located in the southwestern San Joaquin Desert (see Germano et al. 2011 for description of the desert) where we tested the effect of cattle grazing on desert vertebrates from 1997 to 2006. County boundaries are the light colored lines. The study area consisted of replicate experimental and control plots.

The composition of arid plant communities of the San Joaquin Desert has changed markedly since European settlement. Historically, the desert was probably relatively open saltbush (*Atriplex* spp.) habitat with much open ground between bushes through most of the year. Variable rainfall produced a patchy to extensive spring array of annual forbs (wildflowers), with some native annual grasses (Germano et al. 2001, Minnich 2008). Today, the remaining undisturbed vegetation types are either dense grassland dominated by non-native species or shrubland with a dense non-native grass understory. The shift in dominant plant cover to non-native annual grasses has resulted in a shift in vegetation structure, which is thought to contribute to the decline of native species (Germano et al. 2001, Minnich 2008). Annual non-native grasses now dominate the less abundant native grasses. Small terrestrial vertebrates that are adapted to open desert substrates, such as many lizards and kangaroo rats, probably can no longer travel effectively in the persistent non-native grass thatch. Another consequence of the persistent non-native grass cover is that fires are more frequent and larger in size than they were historically (Minnich 2008).

Because most of the native vegetation is not fire adapted, the fires tend to result in exotic grasses dominating many wildlands, resulting in livestock grazing being the principal use of most of the undeveloped lands in the southwestern San Joaquin Desert.

Negative effects on vegetation by intense livestock grazing have been identified as widespread worldwide (Milchunas and Lauenroth 1993, Perevolotsky and Seligman 1998, but see Thalen 1984). Livestock grazing on lands in western North America in the last few decades has become controversial, and sometimes even an emotional conservation issue (Fleischner 1994, Brown and McDonald 1995, Noss 1995). In some respects, this is because the conservation community has done an effective job of convincing the general public of the great damage that livestock has done to large areas of western North America, which is indeed often true. However, in California, grazing has been found to be beneficial to various herbaceous plant species in some grassland types (Jackson and Bartolome 2007), and at vernal pools, native plants and animals decrease if herbivore (livestock) grazing is eliminated (Marty 2005).

The plan to recover upland species from threatened and endangered status in the San Joaquin Valley (U.S. Fish and Wildlife Service 1998) identifies the importance of determining appropriate land management practices for the region. The objective of our research was to meet this recovery need by determining the effects of carefully managed cattle grazing (see Methods for prescriptions) on an assemblage of sensitive desert-adapted animals in the southwestern San Joaquin Desert. We hypothesized that well-managed livestock grazing in these arid lands that are now dominated by exotic annual grasses would benefit the small terrestrial vertebrates.

STUDY AREA

Our study site was located within the Lokern Natural Area of western Kern County, California, west of the agricultural community of Buttonwillow (Fig. 1). The Lokern Natural Area encompassed about 17,800 ha (44,000 acres) at an elevation of 122 m (400 feet) to 200 m (660 feet). Our study was located in the central portion of the natural area between state highways 33 and 58 and Lokern Road. Our study site was within the boundaries of the San Joaquin Desert (Germano et al. 2011), which unlike arid areas to the southeast that had monsoonal climate regimes, had an arid Mediterranean climate with hot, dry summers and cool, wet winters (Dallman 1998). At the agricultural community of Buttonwillow, 13.5 km east of the study area, average high temperatures in August were 35.7° C and lows were 17.3° C, and average January daytime highs were 12.9° C and night time lows were 1.0° C (World Climate 2010). Average yearly rainfall at Buttonwillow was 169 mm (6.65 in; 20-yr average; Buttonwillow Water Storage District, unpublished data), with virtually no rain falling from early April through October.

The study site is a gently sloping (2–5%) alluvial plain with soils classified as Kimberlina sandy loam and Kimberlina gravelly sandy loams, which are derived mostly from granitic and sedimentary rock (Soil Conservation Service 1988). The study area was dominated by Valley Saltbush scrub intermixed with large areas of largely non-native grassland. A wildfire occurred across about half of the study site (Sections 22 and 27; see Study Design below) in May 1997, just as we began collecting data and before any grazing was implemented. Because we did not want fire to confound our study design (see Methods), we conducted a prescribed burn on the remaining area (parts of Sections 29 and 33) on 22 July 1997 so that all plots had the same initial conditions. The fires created a study site dominated by exotic grasses because the shrubs, mostly the native desert saltbush (*Atriplex polycarpa*) and spiny saltbush (*A. spinifera*), are not fire-adapted and were killed. Saltbush became re-established in parts of the study area by 2000, and in the absence of fire, the shrubs became larger and more abundant over time. Herbaceous cover was dominated by non-native annuals (U.S. Fish and Wildlife Service 1998).

Vertebrates known or suspected to occur in the Lokern Natural Area included 2 amphibians, 8 reptiles, 21 birds, and 17 mammals (D. Germano, California State University,

personal observation). Five terrestrial vertebrates were special-status species or were listed as threatened or endangered: the blunt-nosed leopard lizard (*Gambelia sila*), giant kangaroo rat (*Dipodomys ingens*), short-nosed kangaroo rat (*Dipodomys nitratooides nitratooides*), San Joaquin antelope squirrel (*Ammodramus nelsoni*), and the San Joaquin kit fox (*Vulpes macrotis mutica*). These vertebrates are also endemic to the San Joaquin Desert (Germano et al. 2011). Except for the San Joaquin kit fox, we monitored all of these species and several abundant terrestrial vertebrates with no special conservation status: the western whiptail (*Aspidoscelis tigris*), side-blotched lizard (*Uta stansburiana*), San Joaquin pocket mouse (*Perognathus inornatus inornatus*), and Heermann's kangaroo rat (*Dipodomys heermanni*). Other terrestrial vertebrates on the study site were not included because either they range widely or are rare (e.g., coyote [*Canis latrans*], San Joaquin kit fox, Blaineville's horned lizard [*Phrynosoma blainvillii*], and burrowing owl [*Athene cunicularia*]).

METHODS

We compared abundance estimates of 8 focal species on grazed treatment plots and ungrazed control plots, with 4 replicates. We defined each treatment plot (2.6 km² or 1 mile²) by Section boundaries (Sections 21, 27, 29, and 33 of Township 29 South, Range 22 East). The treatments were adjacent to each other in a four-leaf clover pattern, with a fifth section enclosed in the middle (35.3762 N, 119.61614 W) that served as a pasture to temporarily place livestock while moving them into or out of the 4 surrounding treatment pastures. The 4 control pastures were 25 ha (62 acres) each, and each square enclosure was located within a corner of a treatment pasture (Fig. 1). The largest census plots (lizards and squirrels) were buffered by 100 m between the peripheral traps and the plot fencing, and the nocturnal rodent plots, being nested within the lizard plots, were buffered by 150 m. Although control plots were within a smaller surrounding area than treatment plots, the movements of our focal species (we purposefully did not include wide-ranging species), based on our mark-recapture data, indicated that our plot design was robust.

In cooperation with the land owner (Chevron Production Company) and a local cattle operator (Eureka Livestock Company), we used cattle grazing on the treatment plots. We determined the stocking rate and timing of grazing each year based on our objective of maintaining about 560 kg/ha (500 pounds/acre) of residual dry matter at the end of the winter growing season. We aimed to start grazing by 1 December each year, but would not release cattle into the treatment plots unless there was at least 784 kg/ha (700 pounds/acre) residual dry matter or 5 cm (2 in.) of new green growth. If grass growth did not attain the minimum standard in any year, then pastures were not grazed that year. Our objective was to attain the minimum dry mulch rate (or residual dry matter; RDM) by at least 1 Apr each year, when we removed the livestock. The duration of our study had to be long enough to

encompass variation from several environmental factors, including the wild fire in 1997, the El Niño winter of 1997–1998, initial low populations of terrestrial vertebrates, year-to-year variation in rainfall, and numerous other environmental factors that are typical of a desert. Our data extended over 10 continuous years, from 1997 through 2006.

Terrestrial Vertebrate Sampling

We estimated the relative abundance of diurnal lizards by walking 8 (4 treatment, 4 control) 9-ha grids and used total counts of each species as our estimate of abundance. Because the blunt-nosed leopard lizard is an endangered species, we followed the visual survey protocols accepted by the regulatory agencies (K. Tollestrup, U.S. Fish and Wildlife Service, unpublished report), which were based on the cruise survey method of Degenhardt (1966). Each grid consisted of 16 permanent transect lines that were 300-m long and spaced 20-m apart. Although decreased visibility of sighting lizards could be a bias when ground cover was dense, we found no differences in abundances of small lizard species between treatment and controls when vegetation cover differed, and few to no blunt-nosed leopard lizards were sighted on control grids when cover was low and similar to treatment grids in dry years (see Results). This indicated that visibility bias did not affect our study. We positioned the census grids near the middle of each control pasture and at least 100 m from any fences in the treatment areas. We surveyed each set of transects on 10 different days within 8 weeks, and used the cumulative number of lizards seen in the 10 days of surveying as the abundance estimate for that plot. We started surveys in May or early June and ended them in July, the optimal time of adult blunt-nosed leopard lizard activity (Germano and Williams 2005).

To estimate relative abundance of the diurnal antelope squirrels, we established permanent 8 × 8 live-trapping grids on each study plot consisting of 64 traps at 40-m intervals and used the total number of individuals caught per year on a plot as our estimate of abundance. We superimposed this grid on the transect grid set up for sampling lizards (see above). We baited the traps with rolled oats and opened and checked the traps during 6 consecutive mornings once a year, between the end of July and the first of September. We monitored 4 grids at once on treatment or controls, waited 1–2 weeks, and then trapped at the other 4 grids. Thus, the yearly trapping of treatment and control grids took 3–4 weeks. We used collapsible single-door live traps (Model 13, Tomahawk Trap Co., Tomahawk, WI), which we opened at dawn and closed at noon, or when ambient air temperature exceeded 35° C (95° F), whichever occurred first. Each trap was shaded from the sun with burlap. While open, we checked the traps every 2 hr. For each squirrel captured, we noted the trap location on the grid, recorded the sex and weight of the squirrel, and applied a unique mark on the squirrel's fur with a black felt tip pen (Sharpie® Permanent Marker, Sanford Corporation, Oak Brook, IL). We also tagged each squirrel with a passive integrated transponder (PIT) tag (Model TX1400 series,

Biomark, Boise, ID) inserted subcutaneously on the back with a hypodermic needle (Schooley et al. 1993).

We determined the relative abundance of the focal small, nocturnal mammals (mostly kangaroo rats) with a grid of live-traps (Model XLF, H.B. Sherman Traps, Tallahassee, FL) and used the total number of individuals caught per year on a plot as our estimate of abundance. Each grid consisted of 144 traps (12 × 12 lines) spaced at 10-m intervals. We centered this grid within the antelope squirrel trapping grid. We baited the traps with parakeet mix bird seed, which is a mix of several different small seeds. We opened and checked the traps during 6 consecutive nights between late July and 1 September each year during the same time the squirrel (Tomahawk) traps were open. We opened the Sherman traps in late afternoon and checked them at dawn the next morning. For each rodent captured, we followed the same marking procedures and collected the same data as with squirrels.

During the 2 6-day trapping sessions, we sampled 1 nocturnal rodent plot and 1 diurnal rodent plot on each section; 1 on the control and 1 on the treatment sites. We waited 1–2 weeks and then sampled nocturnal and diurnal plots again in the section, but reversed the plots sampled from the previous session. With this design, researchers checking nocturnal rodent traps starting at dawn did not interfere with diurnal rodent traps set at the same time. We used identical procedures on all small mammals concurrently on the treatment and control plots, which allowed us to make valid comparisons of relative abundance for each species between the control and experimental pastures.

Grasshopper and Invertebrate Assessments

We monitored the main prey items of lizards, and seasonally for antelope squirrels, by estimating the relative abundance of grasshoppers and ground-dwelling invertebrates on the control and treatment plots. We visually counted grasshoppers concurrently with the transect surveys for blunt-nosed leopard lizards. We used total grasshopper counts for each plot per year in our analyses. For ground-dwelling invertebrates, we installed 10 19-L (5-gallon) plastic buckets (pitfalls) into the ground on 2 adjacent sides of each lizard plot (5 buckets on a side), spaced every 40 m about 10 m outside of the lizard plot. We sank the lip of each bucket to the ground surface level, and when not being used, we closed all pitfalls with tight-fitting lids. We opened the pitfall traps for 6 consecutive days during the same days that we trapped for nocturnal rodents. We counted and displaced all invertebrates (thus eliminating recaptures) each morning after checking the rodent traps. Because numbers of ants were episodic and sometimes very abundant compared to all other invertebrates, we excluded ants from analyses.

Vegetation Assessments

We assessed the vegetation cover on the control and treatment plots during the same days we trapped nocturnal rodents. Each year we randomly selected 30 coordinates on each squirrel-lizard grid for sampling. We intended to use a synthetic variable to describe herbaceous biomass based

on the results of 3 vegetation sampling methods we used (cover class, height of vegetation, and amount of residual dry matter [RDM]), but the 3 methods were highly and significantly correlated (RDM—cover, $r = 0.793$, $P < 0.001$; RDM—height, $r = 0.894$, $P < 0.001$; cover—height, $r = 0.832$, $P < 0.001$). Because of its general use, we only used RDM as a measure of herbaceous biomass for our analyses. We used Bureau of Land Management (BLM) procedures to measure RDM by placing a wire hoop that defined a 0.089-m^2 (0.96-foot^2) area 2 m south and 1 m east of each randomly selected coordinate. With hand clippers, we removed all the annual or herbaceous vegetation to the soil surface and placed it in a paper bag, which we oven-dried and weighed. We then used the dry weight to calculate an estimate of the RDM per unit area (Daubenmire 1959, Bureau of Land Management 1996).

To determine whether livestock use was within the grazing prescription, we monitored the amount of green biomass or dry RDM during the grazing season each year using a modification of the comparative yield method (Haydock and Shaw 1975). Instead of 5 clip reference plots and 100 visual estimate plots, we used 3 0.089-m^2 (0.96-foot^2) clip reference plots to represent high, medium, and low levels of biomass and 25 visual estimate plots. We oven-dried and weighed herbaceous biomass from each of the reference plots and these data described a regression of plant biomass by reference class. The average class value determined from the 25 0.089-m^2 (0.96-foot^2) visual plots was used in the regression equation to estimate herbaceous biomass on a treatment section. Each year, we completed the evaluation immediately prior to livestock turnout (usually Feb) and at monthly intervals thereafter until the target RDM (560 kg/ha) was attained and cattle were removed.

Statistical Analyses

Because of year-to-year variability in conditions in the San Joaquin Desert, we knew that we would need a relatively long-term study to explain the expected variation. This variation also resulted in our using more than 1 analytical approach to the data; analysis of variance (ANOVA) to test fixed effects of grazing and regression to test for trends in abundances over the course of the study. We compared RDM across treatments, plots (nested in treatments), and years with a repeated measures ANOVA with a treatment by year interactive term. We also determined if average RDM on control plots was associated with rainfall amounts using Pearson's product-moment correlation analysis.

We tested the effect of cattle grazing on abundances of vertebrates, grasshoppers, and ground-dwelling invertebrates using repeated measures ANOVA with treatment (grazed, ungrazed), plot (nested within treatment), and year as main effects and treatment by year as an interaction. Because animal numbers were either not distributed normally or variances were not equal across plots, we log transformed abundance data before analysis. We used regression analysis and analysis of covariance (ANCOVA) to determine if significant differences existed between treatment and control plots in the trend of abundances over the course of the study.

Saltbush re-established on part of the study area 3 years after the burn, and by the end of the study, we found saltbush in high abundance throughout Section 29 and on the control plot in Section 21 (D. Germano, unpublished data). Because we suspected that saltbush cover could affect species abundances, apart from the effect of grazing, we used ANOVA to analyze abundances of animals from 2001 to 2006 on 3 plots (21C, 29T, and 29C) with re-established saltbush compared to 5 plots that had no or a low abundance of saltbush. We also compared abundances of species to RDM using Pearson's product-moment correlation by averaging abundances and RDM by treatment each year. We similarly compared animal abundances to rainfall. For all tests, $\alpha = 0.05$. We did not employ Bonferroni corrections to P values for multiple comparisons because we planned these comparisons and previous research has revealed validity concerns of using these corrections in ecological studies (Perneger 1998, Cabin and Mitchell 2000, Moran 2003).

RESULTS

Rainfall totals for the winter preceding and following the start of our study were close to the long-term average (164 mm) for the site (Fig. 2). However, rainfall from October to April after our first field season in 1997 was the highest recorded (412.5 mm) in the southern San Joaquin Valley, based on 110 years of data (D. Germano, unpublished data; <http://www.wrh.noaa.gov/hnx/bfl/normals/bflrnyr.htm>, accessed 10 Dec 2009) from Bakersfield, California, which is about 50 km east of the Lokern study site. Then, from 1999 to 2004, the site received below average rainfall with 2 particularly dry rainfall years in

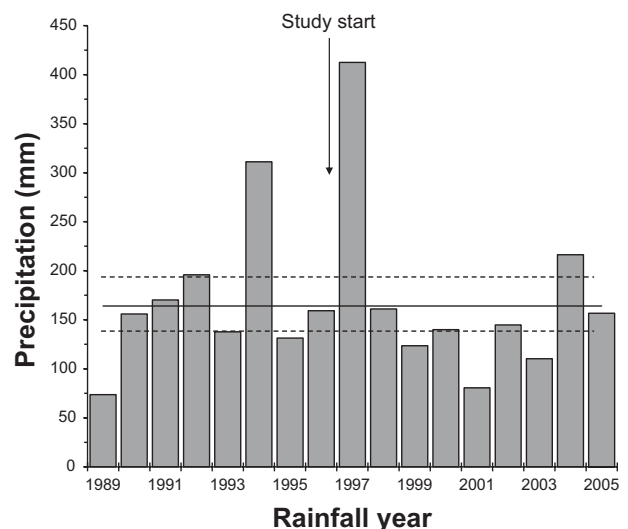


Figure 2. Yearly total rainfall (Jul–Jun) in the Lokern Natural Area from 1989 to the end of our study in 2006. The year shown is the first year (1989–1990 shown as 1989). Data are from the Buena Vista Water Storage District (BVWSD) in Buttonwillow, California, about 13.5 km east of our site. The solid line is the Buttonwillow 20-year mean of 164 mm, with the 95% confidence interval (dotted lines). We recorded precipitation at the study site from 2 rain gauges from 1999 to 2006 and amounts closely matched BVWSD values.

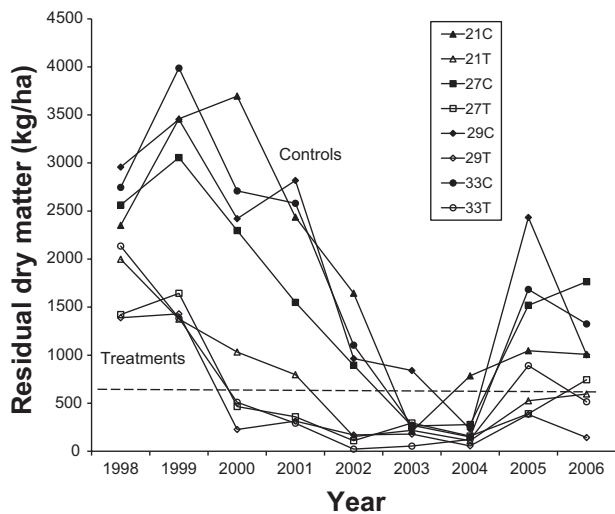


Figure 3. Amount of residual dry matter (RDM) in kg/ha measured each August from 1998 to 2006 on 4 control (solid shapes) and 4 treatment (open shapes) plots on the Lokern Study Area. We did not measure RDM at the study start in 1997 because of a wildfire over part of the study area and our subsequent prescribed burn over the rest of the study site. The dashed line is the estimated minimum level of forage (560 kg/ha) on pastures that triggered cattle grazing on the study site (see Methods).

2001–2002 and 2003–2004 (Fig. 2). Total rainfall returned to above average in the 2004–2005 winter, and was slightly below average the winter preceding the last year of our study. Rainfall totals in the 6 years preceding the start of the study were generally average to above average (Fig. 2), which set the stage for high amounts of plant biomass in the exceptionally wet El Niño year of 1997–1998.

We did not record herbaceous vegetation in 1997 because all vegetation was burned. Herbaceous vegetation based on RDM amounts on the ungrazed control plots was high in the first few years immediately following the fire, decreasing steadily, and increased again in the last 2 years of the study (Fig. 3). However, RDM amounts on control plots were not significantly correlated with rainfall totals each year ($r = 0.324$, $P = 0.395$) or with a 1-year lag of previous year's rainfall ($r = 0.574$, $P = 0.106$). The treatment plots were grazed relatively heavily from 1998 to 2000, fairly lightly in 2001 as the area dried, and not at all from 2002 to 2004 (Table 1). The treatment plots were grazed again in

2005 and 2006 when herbaceous ground cover increased (Table 1). As planned, grazing led to significantly less RDM in all years when grazing occurred (treatment by year interaction, $F_{8,48} = 9.16$, $P < 0.001$), and treatment plots differed from control plots in all years except 2003 ($F_{1,6} = 1.96$, $P = 0.211$) and 2004 ($F_{1,6} = 3.11$, $P = 0.128$) when both types of plots had the lowest RDM of the study (Fig. 3).

We applied equal trapping effort on the control and treatment plots, resulting in combined 10-year totals of 69,120 trap-nights for nocturnal rodents, 30,720 trap-days for antelope squirrels, and 800 census-days for lizards. Abundances of the 3 lizard and 5 rodent species we monitored were all below 10 individuals per plot at the beginning of the study, and for most species, increased through 2004 by at least 900%, decreased in abundance after the wet winter of 2004–2005 by 33–200% on treatment plots and 27–286% on control plots, and increased again in 2006 by 24–318% on treatment plots, but either continued to decline or increased up to 98% on control plots (Fig. 4). We did not see this trend for the number of Heermann's kangaroo rats, which peaked in 2002 and decreased by 364% at the end of the study, and the number of San Joaquin pocket mice, which oscillated up and down by 116–3,560% yearly starting in 1999 (Fig. 4). We found significant year differences in abundances for all species (Table 2). Although numbers of blunt-nosed leopard lizards were not found on control plots in most years and were up to 500% greater on treatment plots than on control plots in the few years we found leopard lizards on the controls (Fig. 4), we did not find a significant treatment main effect ($P = 0.10$) or a significant interaction of treatment and year (Table 2). Similarly, although numbers of San Joaquin antelope squirrels were greater by 27–350% on treatment than control plots in 6 of 9 years (Fig. 4), these differences were not significant (Table 2). We did not find a significant treatment or interaction for western whiptails, side-blotched lizards, short-nosed kangaroo rats, or giant kangaroo rats (Table 2). We did find significant interaction terms for both Heermann's kangaroo rats and San Joaquin pocket mice (Table 2) with up to 772% greater numbers of Heermann's kangaroo rats on control plots in some years, but the abundance trends of San Joaquin pocket mice were not consistent. During some years, we found up to 650%

Table 1. Intensity of cattle grazing by year in Animal Unit Months (1 AUM = 1 1,000-pound cow grazing for 1 month) on 4 treatment plots at the Lokern study site. Years with zero AUM are when no grazing occurred. In 1997, there was no forage for cattle to eat because of the wildfire and prescribed burns on the site (see Methods). From 2002 to 2004, the amount of forage did not exceed the threshold for turning out cattle on the plots.

Year	Treatment plots				Total
	21	27	29	33	
1997	0	0	0	0	0
1998	422	324	343	711	1,800
1999	643	648	730	1,156	3,177
2000	158	293	165	192	1,408
2001	59	68	97	91	315
2002	0	0	0	0	0
2003	0	0	0	0	0
2004	0	0	0	0	0
2005	502	212	392	261	1,367
2006	257	311	142	298	1,008

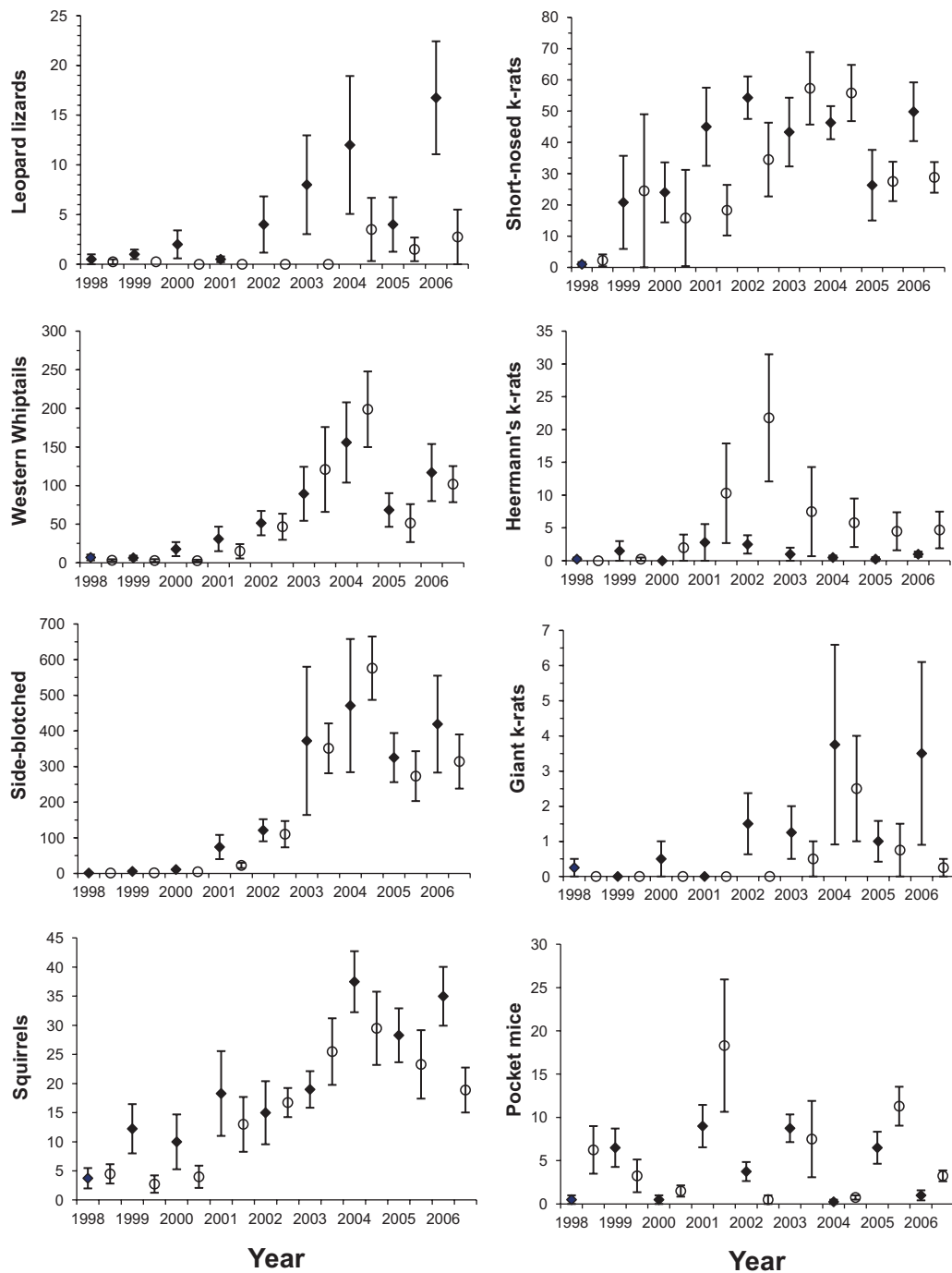


Figure 4. The mean abundances of 3 lizard (blunt-nosed leopard lizard, western whiptail, side-blotched lizard) and 5 rodent (San Joaquin antelope squirrel, short-nosed, Heermann's, and giant kangaroo rats [k-rat], and San Joaquin pocket mouse) species (± 1 SE) from 1998 to 2006 on treatment (solid diamond) and control (open circle) plots at the Lokern Study Area. The year is under the treatment symbol and the control abundance for that year is to the right.

greater abundance of pocket mice on treatment plots, but found up to 200% greater abundance on control plots in other years (Fig. 4).

We found no significant trends in abundances for short-nosed kangaroo rats, Heermann's kangaroo rats, or San Joaquin pocket mice for either control plots or treatment plots over the course of the study (Table 3), although the slope of the regression for short-nosed kangaroo rats on treatment plots was nearly significant ($P = 0.051$). Western whiptails, side-blotched lizards, and San Joaquin

antelope squirrels increased in abundance during the study on both control plots and treatment plots, but there were no differences in slopes or elevations between plot types. The number of blunt-nosed leopard lizards increased on treatment and control plots, but at a significantly greater rate (389%) on treatment plots than on control plots (Table 3; Fig. 5). Giant kangaroo rats increased significantly on treatment plots, but not on controls (Table 3; Fig. 5).

We also found that for all species except Heermann's kangaroo rats and San Joaquin pocket mice, there was a

Table 2. Results of repeated measures analysis of variance (ANOVA) of the effect of grazing on log abundance of 8 species of vertebrates, grasshoppers, and ground dwelling invertebrates censused 1998–2006 at the Lokern Natural Area. Results include main effects of treatment (grazing, no grazing), plot nested in treatment, and year, and the interaction of treatment and year.

Species	Df	MS ^a	F	P
Blunt-nosed leopard lizard				
Treatment	1	2.60	3.79	0.100
Plot(Treatment)	6	0.69	8.84	<0.001
Year	8	0.38	4.90	<0.001
Treatment × Year	8	0.13	1.73	0.116
Western Whiptail lizard				
Treatment	1	0.64	0.48	0.516
Plot(Treatment)	6	1.33	14.93	<0.001
Year	8	3.06	34.30	<0.001
Treatment × Year	8	0.09	1.01	0.439
Side-blotched lizard				
Treatment	1	0.51	0.71	0.433
Plot(Treatment)	6	0.73	9.21	<0.001
Year	8	7.13	90.33	<0.001
Treatment × Year	8	0.11	1.41	0.218
San Joaquin antelope squirrel				
Treatment	1	0.40	2.10	0.198
Plot(Treatment)	6	0.19	2.27	0.052
Year	8	1.12	13.53	<0.001
Treatment × Year	8	0.13	1.55	0.167
Short-nosed kangaroo rat				
Treatment	1	0.83	1.25	0.306
Plot(Treatment)	6	0.67	5.12	<0.001
Year	8	2.00	15.37	<0.001
Treatment × Year	8	0.16	1.25	0.289
Heermann's kangaroo rat				
Treatment	1	1.82	2.15	0.193
Plot(Treatment)	6	0.85	11.14	<0.001
Year	8	0.46	5.98	<0.001
Treatment × Year	8	0.19	2.44	0.027
Giant kangaroo rat				
Treatment	1	0.25	1.51	0.265
Plot(Treatment)	6	0.16	3.02	0.014
Year	8	0.16	3.00	0.008
Treatment × Year	8	0.03	0.63	0.751
San Joaquin pocket mouse				
Treatment	1	0.07	0.21	0.660
Plot(Treatment)	6	0.31	4.59	0.001
Year	8	0.80	11.71	<0.001
Treatment × Year	8	0.30	4.35	0.001
Grasshoppers				
Treatment	1	0.10	0.24	0.641
Plot(Treatment)	6	0.42	8.01	<0.001
Year	8	2.70	51.35	<0.001
Treatment × Year	8	0.09	1.80	0.100
Invertebrates				
Treatment	1	0.38	16.03	0.007
Plot(Treatment)	6	0.02	0.98	0.450
Year	8	0.34	13.87	<0.001
Treatment × Year	8	0.04	1.47	0.194

^a MS, mean square.

significant inverse relationship between abundance of individuals and the amount of RDM on the ground (r ranged from -0.557 to -0.743 , P ranged from <0.001 to 0.016). Abundances of Heermann's kangaroo rats ($r = -0.009$, $P = 0.970$) and San Joaquin pocket mice ($r = 0.172$, $P = 0.494$) were not related to changing RDM amounts. There also was no relationship between animal abundances and yearly rainfall amounts for any species (r ranged from -0.504 to 0.085 , P ranged from 0.167 to 0.828) except for

Table 3. Results of regression analysis of the trend in abundance of 8 species of vertebrates censused 1998–2006 at the Lokern Natural Area on control and treatment plots. Slope and R^2 values are only shown for significant regressions (*). Analysis of covariance (ANCOVA) of slopes is shown if there were significant regressions (*) for both treatment and control plots, and the results of intercepts are shown if slopes were not significantly different.

Species	Df	F	P	Slope	R ²
Blunt-nosed leopard lizard					
Treatment	1,7	13.31	0.008*	6.77	0.655
Control	1,7	6.74	0.036*	1.38	0.491
ANCOVA of slope	1,14	7.78	0.014*		
Western whiptail lizard					
Treatment ^a	1,7	40.11	<0.001*	0.330	0.861
Control ^a	1,7	23.73	0.002*	0.370	0.864
ANCOVA of slope	1,14	1.42	0.254		
ANCOVA of intercept	1,14	1.83	0.196		
Side-blotched lizard					
Treatment ^a	1,7	43.50	<0.001*	0.172	0.851
Control ^a	1,7	44.66	<0.001*	0.239	0.772
ANCOVA of slope	1,14	0.29	0.602		
ANCOVA of intercept	1,14	0.95	0.345		
San Joaquin antelope squirrel					
Treatment	1,7	33.86	0.001*	15.3	0.829
Control	1,7	16.24	0.005*	12.1	0.699
ANCOVA of slope	1,14	0.61	0.448		
ANCOVA of intercept	1,14	3.21	0.093		
Short-nosed kangaroo rat					
Treatment	1,7	5.54	0.051		
Control	1,7	2.42	0.164		
Heermann's kangaroo rat					
Treatment	1,7	0.03	0.860		
Control	1,7	0.47	0.517		
Giant kangaroo rat					
Treatment	1,7	9.83	0.016*	1.58	0.584
Control	1,7	2.19	0.182		
San Joaquin pocket mouse					
Treatment	1,7	<0.01	0.968		
Control	1,7	<0.01	0.996		

^a Semilog regression.

the short-nosed kangaroo rat, whose numbers were significantly negatively correlated to rainfall ($r = -0.748$, $P = 0.020$).

Neither blunt-nosed leopard lizard nor side-blotched lizard abundances were significantly affected by saltbush establishment, although we found a significant interaction of saltbush and year for western whiptails (Table 4). The number of whiptails sighted on saltbush plots did not differ from plots without dense saltbush in the first 2 years, but numbers were 108–139% greater thereafter on saltbush plots. Numbers of San Joaquin antelope squirrels were up to 166% greater on plots with few to no saltbush in the first 2 years, but were 20–80% greater on plots with denser shrubs from 2003 to 2006, although the interaction was only nearly significant (Table 4). Of the 4 nocturnal rodent species we followed, only the Heermann's kangaroo rat was affected by the re-establishment of saltbush (Table 4). Heermann's kangaroo rat numbers were high on plots with dense saltbush in 2001 and 2002, but their numbers decreased each year thereafter until eventually kangaroo rat abundances were similar between types of plots.

Average grasshopper numbers counted on plots were generally low throughout the study (8–357 grasshoppers counted per day), except in the last 2 years when average numbers of

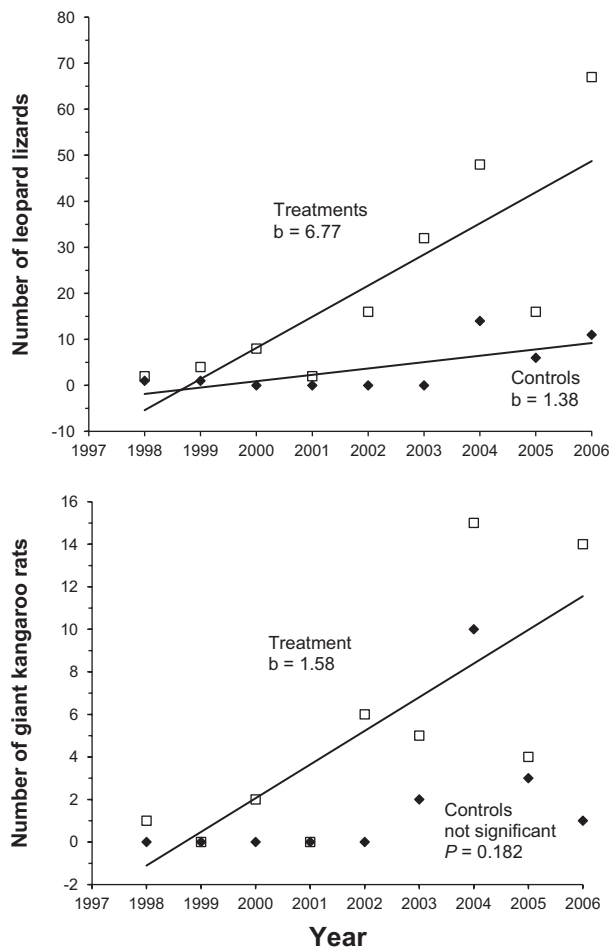


Figure 5. Relationship of abundance of blunt-nosed leopard lizards (top) and giant kangaroo rats (bottom) on treatment (open squares) and control (closed diamonds) plots from 1998 to 2006 on the Lokern Study Area. Slopes of both regression lines for blunt-nosed leopard lizards were significant, whereas only the line for the treatment plots of giant kangaroo rats was significant.

grasshoppers counted per day was about 600 in 2005 and exceeded an estimated 1,600 in 2006. Abundances of grasshopper did not differ significantly by treatment or the interaction of treatment with year (Table 2). In contrast, the average abundances of ground-dwelling invertebrates were very high in 1998 (controls = 4.68/pitfall/day, treatment = 6.68/pitfall/day), the year after the fire, and numbers dropped sharply in 1999 and stayed low (0.70–2.70/pitfall/day) throughout the rest of the study. We found a significant treatment effect (Table 2) with greater average numbers of invertebrates found on control plots in 6 of 9 years. Grasshopper numbers were not correlated to RDM ($r = -0.151$, $P = 0.550$) or rainfall ($r = 0.146$, $P = 0.708$), and invertebrate numbers were not correlated to RDM ($r = 0.302$, $P = 0.224$) but were correlated to rainfall ($r = 0.900$, $P = 0.001$).

DISCUSSION

Our data indicate that for most focal species, grazing either had no negative effect on abundances or focal species numbers increased on grazed sites, even though we found no fixed

Table 4. Results of repeated measures analysis of variance (ANOVA) of the effect of saltbush density on log abundance of 8 species of vertebrates censused 2001–2006 at the Lokern Natural Area. Results include main effects of treatment (dense saltbush, sparse or no saltbush), plot nested in treatment, and year, and the interaction of treatment and year.

Species	Df	MS ^a	F	P
Blunt-nosed leopard lizard				
Treatment	1	0.37	0.18	0.672
Plot(Treatment)	3	0.94	4.65	0.010
Year	5	0.39	1.94	0.121
Treatment × Year	5	0.15	0.72	0.614
Western Whiptail lizard				
Treatment	1	2.00	26.52	<0.001
Plot(Treatment)	3	1.40	18.59	<0.001
Year	5	1.19	15.71	<0.001
Treatment × Year	5	0.02	0.22	0.953
Side-blotched lizard				
Treatment	1	0.24	3.19	0.085
Plot(Treatment)	3	1.13	14.84	<0.001
Year	5	1.29	16.91	<0.001
Treatment × Year	5	0.04	0.52	0.758
San Joaquin antelope squirrel				
Treatment	1	<0.01	0.07	0.795
Plot(Treatment)	3	0.17	5.06	0.007
Year	5	0.18	5.41	0.001
Treatment × Year	5	0.08	2.31	0.072
Short-nosed kangaroo rat				
Treatment	1	0.05	1.09	0.305
Plot(Treatment)	3	1.19	4.37	0.012
Year	5	0.23	5.47	0.001
Treatment × Year	5	0.06	1.32	0.284
Heermann's kangaroo rat				
Treatment	1	0.50	4.48	0.044
Plot(Treatment)	3	1.12	10.08	<0.001
Year	5	0.37	3.29	0.019
Treatment × Year	5	0.19	1.67	0.176
Giant kangaroo rat				
Treatment	1	0.05	0.83	0.371
Plot(Treatment)	3	0.52	9.02	<0.001
Year	5	0.12	2.14	0.091
Treatment × Year	5	0.04	0.62	0.687
San Joaquin pocket mouse				
Treatment	1	0.02	0.15	0.704
Plot(Treatment)	3	0.21	1.81	0.169
Year	5	0.87	7.64	<0.001
Treatment × Year	5	0.07	0.61	0.695

^a MS, mean square.

effects. This was true for 2 endangered species: the blunt-nosed leopard lizard and the giant kangaroo rat. For both, their numbers increased significantly over the course of the study on the grazed sites, but either increased more slowly, or not at all, on the ungrazed control pastures. Only the abundance of Heermann's kangaroo rat (not a protected species) was greater on the ungrazed control plots, but this was coincident with the re-establishment of saltbushes on several plots, which may have influenced abundance of this rodent more than the lack of grazing. This species has been associated with saltbush in other areas of the Lokern (Nelson et al. 2007). In addition, we found that abundances of the 3 lizards and 3 of the 5 rodents that we studied (short-nosed kangaroo rat, giant kangaroo rat, and San Joaquin antelope squirrel) were negatively associated with increasing herbaceous biomass during the entire study period. This suggests that grazing may be beneficial to these species in years with a

persistent perennial accumulation of herbaceous plant material.

In applying an ANOVA test to our data, we adopted the common and largely traditional practice of using an alpha of 0.05. However, a growing body of literature, as reviewed by di Stefano (2003), suggests that such a conservative alpha level may not be justified in some circumstances, especially where the possibility of committing a Type II error (accepting a false null) would result in undesirable consequences to protected species (Scherer and Tracey 2011). We believe the threatened and endangered status of several of our focal species is such a case, where the habitat has shifted to dense grasses and few perennial shrubs, and will likely result in their continued decline without application of some form of active management. In addition, large variation in abundance from year to year increases sampling error, which makes it very difficult to obtain significant results in an ANOVA with the traditional alpha of 0.05. Examination of our analysis of grazing effects (Table 2) shows that if we relax the acceptable alpha level to 0.20 from 0.05, both the blunt-nosed leopard lizard and San Joaquin antelope squirrel benefited from the grazing treatment. In addition, the growth of populations of short-nosed kangaroo rats would be significantly faster on grazed plots than ungrazed controls, similar to blunt-nosed leopard lizards and giant kangaroo rats (Table 3). Thus, a more conservative approach to our data analysis shows that abundance of all the protected species (leopard lizards, squirrels, and short-nosed and giant kangaroo rats) are greater in grassy habitats when these areas are grazed.

Our data, which indicate carefully managed cattle grazing does not negatively affect the abundances of terrestrial desert vertebrates, is supported by a vast literature on closely related species in arid habitats. For example, many species of kangaroo rats are found most abundantly in open habitats, with much bare ground and sparse grass cover, which allows their unimpeded movement (Bartholomew and Caswell 1951, Rosenzweig and Winakur 1969, Price 1978, Goldingay et al. 1997, Jones et al. 2003). Studies of Merriam's kangaroo rats (*Dipodomys merriami*; Schroder 1987, Kerley and Whitford 2000), Texas kangaroo rats (*D. elator*; Stacey 2005), Stephens' kangaroo rats (*D. stephensi*; Brock and Kelt 2004), and chisel-toothed kangaroo rats (*D. microps*; Rowland and Turner 1964) have found these species most abundant in open areas. In most instances, numbers of these same species increased with grazing (Reynolds 1950, Bock et al. 1984, Jones and Longland 1999, Kelt et al. 2005, Stacey 2005). Also, Hoffmann (1974) found that Fresno kangaroo rats (*D. nitratoides exilis*), a sister subspecies to the short-nosed kangaroo rat, were more abundant on moderately to heavily grazed sites in alkali sink habitat west of Fresno, California. Grazing was removed from this site in the late 1970s and the subspecies disappeared (Williams and Germano 1992, U.S. Fish and Wildlife Service 1998). Several desert lizards also prefer open habitats. Abundances of the long-nosed leopard lizard (*Gambelia wislizenii*) in Oregon (Steffen and Anderson 2006); blunt-nosed leopard lizard in California (Montanucci 1965, Warrick et al. 1998); 2 species of whiptail lizards

(*Aspidoscelis* spp.), 2 horned lizards (*Phrynosoma* spp.), the collared lizard (*Crotaphytus collaris*), and the lesser earless lizard (*Holbrookia maculata*) in New Mexico (Davidson et al. 2008); and the long-nosed leopard lizard, the zebra-tailed lizard (*Callisaurus draconoides*), the greater earless lizard (*Cophosaurus texanus*), and the round-tailed horned lizard (*P. modestum*) in southwestern New Mexico (Baltosser and Best 1990) were found most abundantly in areas with sparse vegetation. In the few studies that have assessed the effects of grazing, lizards that prefer open habitats are either more abundant in grazed areas or abundances are not affected by grazing (Reynolds 1979, Jones 1981, Ballinger and Watts 1995, Newbold and MacMahon 2008).

One likely reason for the weak effect of grazing on our focal species was the remarkably low abundances at the start of our study, especially the nocturnal rodents. We caught only 2 rodents in 6,912 trap-nights across the 8 plots in 1997. It took several years until numbers of nocturnal rodents increased, irrespective of plot type. These low numbers probably occurred because of high rainfall and associated high herbaceous biomass. Rainfall totals in the 6 years preceding our study were generally average to above average, and had the effect of creating a dense growth of herbaceous cover throughout the San Joaquin Valley, and a general decrease in small vertebrate populations, particularly kangaroo rats (Single et al. 1996; Germano et al. 2001). At a different study site about 3.5 km north of our grazing site, the population of giant kangaroo rats crashed from a high of 112 individuals, caught in 6 nights in the fall of 1995, to 0 captures in 2 6-day trapping sessions in 1998 (D. J. Germano and L. R. Saslaw, unpublished data). Numbers of giant kangaroo rats slowly recovered over the next several years. The low numbers on our study site also may have been exacerbated by the wildfire and subsequent prescribed fire in May 1997. However, fires have not been found to greatly affect burrowing rodent populations (Wirtz 1982, Valone et al. 2002, Diffendorfer et al. 2011). The winter (1997–1998) following the fire was the wettest ever recorded in the southern San Joaquin Valley, and led to high levels of herbaceous biomass on our study site that took 3–4 years of grazing to decrease to our target level, which we believe dramatically suppressed animal populations at the start of the study.

Desert areas are characterized by highly variable climatic regimes, which are often not very predictable, and of course they are dry. We measured herbaceous biomass in August of each year, and the lack of correlation of RDM with rainfall likely was due to the persistence of grass stems for several years, even after rainfall decreased. This persistence probably was due to slow decomposition in low rainfall years, and the Mediterranean climate that concentrates rainfall during the cool winter months, when decomposers are less active. When average or above average rainfall years occur, then the accumulated RDM becomes very dense. If persistent high RDM levels need to be reduced, in the absence of natural mechanisms, then some form of active management must be implemented (Germano et al. 2001, DiTomaso et al. 2007).

Fire is not a natural disturbance in California desert environments (Lovich and Bainbridge 1999), but as deserts are

invaded by exotic grasses, it becomes more common. Fire also has been used as a management tool to remove the accumulated grass biomass (DiTomaso et al. 2007, Reiner 2007). Unfortunately, many desert plants are not fire-adapted. In the San Joaquin Desert, fire will kill perennial saltbushes (Germano et al. 2001), thus resulting in a perpetual cycle of burning that leads to a persistent grassland. If the severity of fires can be reduced (as by carefully managed grazing), the re-establishment of saltbush will likely occur naturally over several years. On our study site, the return of saltbush to parts of the area eventually favored several vertebrates, including the western whiptail lizard, San Joaquin antelope squirrel, and Heermann's kangaroo rat. Saltbush re-establishment did not negatively affect any of the vertebrates that we studied, and our grazing regime did not eliminate saltbush. Therefore, we believe herbaceous biomass should be reduced in years of high accumulation using livestock and not fire.

Both Tule elk (*Cervus elaphus nannodes*) and pronghorn (*Antilocapra americana*) once grazed in the San Joaquin Valley (Edwards 1992, Griggs 1992). Managers may be tempted to believe that these native grazers could now be used to manage the non-native grasses and herbs in the place of livestock. However, these large herbivores were probably highly migratory in the extremely seasonal Mediterranean climate regime of the area. Thus, we do not think that either elk or pronghorn could be concentrated and managed to perform the necessary control of herbaceous plant biomass nearly as well as livestock because native grazers will not be able to be confined to particular areas using normal fencing. In addition, infrastructure is in place for domestic livestock and it is a well established business; therefore, monetary incentives help managers and livestock owners to achieve their goals.

Because of the highly variable nature of desert weather patterns (and thus vegetative growth), we designed our study to avoid the often-repeated problems of being too short in length and lacking spatial replication; otherwise, we would have contributed to the many anecdotal studies on the topic (Legg and Nagy 2006), which by nature are inconclusive. Unfortunately, field conditions (which include finding suitable habitat, willing land owners and livestock operators, and adequate funding), often make it difficult or nearly impossible to implement ideal or even highly robust experimental designs that adequately address the variation in conditions across space and time, especially in a desert environment. Even our relatively robust data were not as conclusive as we had hoped. Nevertheless, our results will assist land managers to develop better strategies to protect, and even enhance, populations of declining terrestrial vertebrates.

MANAGEMENT IMPLICATIONS

Livestock operations have an advantage over other means of controlling exotic grasses (chemical, fire, and mechanical; DiTomaso et al. 2007) because their actions have the potential to be at least economically neutral. The difficulty of consistently achieving our target RDM on the treatment plots during wet winters raises an issue that will need to

be considered by land managers if livestock grazing is to be used as an effective tool to modify the structure of animal habitats in arid regions (Huntsinger et al. 2007). Because the year-to-year variation in desert rainfall is great, it results in an equally large variation in the yearly amount of forage available to livestock. Without considerable flexibility to add or remove grazers from pastures year-to-year, and often at relatively short notice, it will be difficult to consistently achieve target grazing prescriptions. The ability to add or remove cattle on demand is critical to achieving management goals without damaging habitats. However, this flexibility sometimes may not be the most economical for a cattle operator, whose objective is to bring cattle to market.

Given the temporal and spatial variation in vegetative structure in deserts, we believe resource managers should take into consideration the consequences of a series of average or even wet winters and the associated proliferation of exotic grasses. Recognizing these patterns of biomass production and anticipating appropriate management actions on an annual basis are critical to successful habitat management. Target species would benefit more from RDM below target levels than if an area was not grazed enough. We found that abundances of the species we studied were high even when RDM was significantly below target levels. Desert ecosystems are not static, especially in the face of future human perturbations, including climate change and new and aggressive invasive species. Although land use changes by people are usually rapid and dramatic, other less rapid anthropogenic changes, such as climate change and invasion by exotic biota, may be just as serious (Dukes and Shaw 2007) and probably will need to be considered in future conservation actions.

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