Effects of fire on kangaroo rats in the San Joaquin Desert of California

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ABSTRACT.—Fire can alter ecological communities, particularly those that are not fire-adapted, such as desert communities. We examined the effects of fire on rodent communities in the San Joaquin Desert of central California. Of particular interest were the effects on kangaroo rats (*Dipodomys* spp.) including 2 rare species, the giant kangaroo rat (*D. ingens*) and the short-nosed kangaroo rat (*D. nitratoides brevinasus*). Lightning caused multiple fires in arid scrub habitat in western Kern County in 1993. We trapped rodents at 7 sites along paired transects, with one transect in a burned area and one in a nearby unburned area. We conducted 5 trapping sessions from July 1993 to November 1995. Kangaroo rat abundance trends were similar between burn and control transects across the sessions. We also compared abundance of giant kangaroo rats between a trapping grid in an area subjected to controlled burning and a grid in a nearby unburned area on the Carrizo Plain in eastern San Luis Obispo County. Abundance trends were similar between the burned and unburned grids, although kangaroo rat numbers were maintained on the burn site over several sessions compared to the unburned grids, although kangaroo rat numbers were deffects of fire on kangaroo rats. Also, fire may actually benefit kangaroo rats by reducing groundcover density, thereby improving their mobility and predator detection. We do not recommend fire as a management strategy, however, because burning may adversely impact other species, kill shrubs, and erode air quality in a region where the air is chronically polluted.

RESUMEN.—Los incendios pueden alterar las comunidades ecológicas, especialmente aquellas comunidades desérticas que no están adaptadas al fuego. Examinamos el efecto de los incendios en las comunidades de roedores del desierto de San Joaquín en el centro de California, con particular interés en su efecto sobre las ratas canguro (Dipodomys spp.), incluidas dos especies raras, la rata canguro gigante (D. ingens) y la rata canguro de hocico corto (D. nitratoides brevinasus). Los relámpagos causaron múltiples incendios en hábitats de matorrales áridos en el oeste del condado de Kern en 1993. Atrapamos roedores en siete sitios a lo largo de transectos emparejados con un transecto en un área quemada y otro en un área cercana no quemada. Llevamos a cabo cinco sesiones de captura desde julio de 1993 hasta noviembre de 1995. Las tendencias de abundancia de ratas canguro fueron similares entre los transectos quemados y control en todas las sesiones. También comparamos la abundancia de ratas canguro gigantes entre un cuadrante de captura en un área sujeta a quema controlada y un cuadrante en un área cercana no quemada en Carrizo Plain en el este del condado de San Luis Obispo. Las tendencias de abundancia fueron similares entre los cuadrantes guemados y no guemados, aunque el número de ratas canguro se mantuvo en el sitio quemado durante varias sesiones de trampeo en comparación con el sitio no quemado. No detectamos ningún efecto adverso en la abundancia de ratas canguro debido al incendio en las dos áreas de estudio. El refugiarse en madrigueras y almacenar semillas bajo tierra, podría contribuir a mitigar los efectos del fuego en las ratas canguro. Además, el fuego podría beneficiar a las ratas canguro al reducir la densidad de la cubierta vegetal, mejorando su movilidad y detección de depredadores. Sin embargo, no recomendamos el incendio como estrategia de gestión, debido a que la quema podría afectar negativamente a otras especies, matar arbustos y erosionar la calidad del aire en una región donde el aire se encuentra crónicamente contaminado.

Fire can significantly alter natural communities, and the effects can be short-term, long-term, or both. Some communities are adapted to periodic burning, but desert communities typically are not (Kearney et al. 1914, Brown and Minnich 1986). Fires are occurring more frequently in desert ecosystems largely because invasive nonnative plants have been introduced and are providing a

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fuel source (Lovich and Bainbridge 1999, Brooks and Matchett 2006). The effects of fire on natural communities in other deserts have been investigated, but in the San Joaquin Desert of California, such studies have not been published, and we are not aware of any studies being conducted.

The San Joaquin Desert (Germano et al. 2011) is located in central California and supports a number of endemic species, many of which are considered rare. The cause of rarity for most of these species is profound habitat loss due to agriculture, oil extraction, and urbanization. As the amount of habitat declines, it is important to understand the effects of various factors on the remaining habitat. One of these factors is fire. Fires were likely uncommon in the San Joaquin Desert historically due to sparse groundcover (Minnich 2008, Sawyer et al. 2009). Wildfires now occur annually, and this is likely attributable to the profusion of nonnative grasses, particularly bromes (*Bromus* spp.), wild barleys (Hordeum spp.), and wild oats (Avena spp.). These annual grasses can form a dense and continuous groundcover that readily carries fires, especially when the grasses dry following the growing season.

A particular concern is the effects of fire on kangaroo rats (Dipodomys spp.). Kangaroo rats are important ecosystem modifiers (Williams and Germano 1992, Goldingay et al. 1997, Bean et al. 2021). Their burrows are used by numerous other species, and their seed harvesting and hoarding activities can significantly alter vegetation structure. Kangaroo rats also constitute prey for numerous predators. Three species occur in the San Joaquin Desert, and 2 of these are rare (Williams and Germano 1992, Goldingay et al. 1997, USFWS 1998). The giant kangaroo rat (D. ingens) is the largest of the species, and it is listed as Endangered at the federal and state level. Heermann's kangaroo rats (D. heer*manni*) are medium-sized and are ubiquitous. San Joaquin kangaroo rats (D. nitratoides) are the smallest, and 2 subspecies (the Fresno kangaroo rat, D. n. exilis, and the Tipton kangaroo rat, D. n. nitratoides) are listed as Endangered at the federal and state level while a third subspecies (the short-nosed kangaroo rat, D. n. brevinasus) is a California Species of Special Concern.

Wildfire caused by lightning strikes in western Kern County, California, served as a natural experiment to study the effects of fire on rodents, particularly kangaroo rats. The first 2 authors (DJG and LRS) also tracked giant kangaroo rats on a control and a treatment plot on the Carrizo Plain before and after prescribed fires. At both sites, we tracked numbers of rodents over several years to determine the short- and long-term effects of fire on these communities. Together, these experiments provide data on the immediate effect of fire on rodents in a grassland/shrubland matrix of San Joaquin Desert vegetation and on how increasing herbaceous groundcover leads to severe population reductions of rodent communities. We predicted that fire would have an immediate negative impact on rodents due to heat and smoke, and we expected significantly fewer rodent individuals on burned sites than on paired unburned sites. We also predicted that numbers of kangaroo rats on burned sites would be greater than on unburned sites within a year after a burn because of the decreased grass cover on burned sites.

METHODS

Study Areas

We studied the effects of fire on rodents by using 2 experiments: one based on a natural wildfire and the other based on a field manipulation. In the natural experiment, lightning strikes in May and June 1993 ignited multiple wildfires in the Lokern area in western Kern County, California (Fig. 1). The burned areas consisted of Atriplex shrubland interlaced with nonnative grasses and nonnative grasslands without shrubs. The wildfires removed the herbaceous groundcover completely and killed 98.1% of Atriplex shrubs in burned shrubland areas (Table 1). The other site in which we studied the effects of prescribed fires was on the Carrizo Plain in San Luis Obispo County, California (Fig. 1). The site did not have shrubs but was covered with nonnative grasses, particularly bromes (Bromus spp.) and wild barleys (Hordeum spp.). The site was burned by prescribed fire to attract Mountain Plovers (Charadrius montanus) for capture and study. Both sites are in the San Joaquin Desert (Germano et al. 2011), which has an arid Mediterranean climate with hot, dry summers and cool, wet winters. Where the wildfires occurred in the Lokern area and Buena Vista Valley, the elevation varies from 100 to 320 m. The Carrizo Plain study site is at an elevation of 608 m.

Field Methods: Lokern Wildfire

We established 10 paired transects (control, burned) 100 m in length within and adjacent to

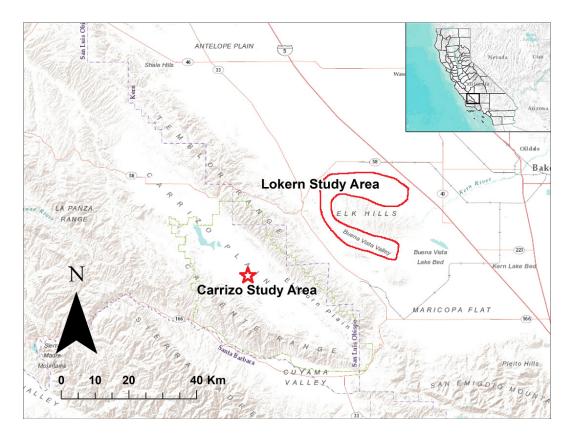


Fig. 1. The Lokern area in western Kern County: the red boundary encompasses the area where burns occurred and where we studied the effects of fire on communities of kangaroo rats (*Dipodomys* spp.). The red star marks the study site on the Carrizo Plain in San Luis Obispo County, California, where we studied the effects of fire on giant kangaroo rats (*D. ingens*).

TABLE 1. The number of *Atriplex* shrubs alive and dead on unburned (control) and burned transects around the Elk Hills in the southern San Joaquin Desert of California. Shrubs were counted within 5 m on either side (10-m width) of the 100-m rodent trapping transects. The wildfires occurred in mid-1993, and the counts of shrubs occurred on 6 December 1995.

Transect #		Atriplex shrub count		
	Treatment	Alive	Dead	% Alive
3	Burn	0	134	0
6	Burn	1	9	10.0
8	Burn	3	59	4.8
4	Control	280	20	93.3
5	Control	82	11	88.2
7	Control	71	5	93.4
Combined	Burn	4	202	1.9
Combined	Control	433	36	92.3

each burned area. Along each transect, we established 25 stations; 2 extra-large Sherman live traps (Model XLF15, H.B. Sherman Traps, Tallahassee, FL) were placed at each station, perpendicular to the line, for a total of 50 traps per line. We baited traps with birdseed in the late afternoon and checked traps either the following morning (07:00-08:00) in some sessions or between 23:00 and 01:00 in other sessions when nighttime temperatures were projected to be below 10 °C (50 °F). Trapping occurred for 3 nights per session. We placed 2 pairs of transects (2 burn, 2 control) in grassland habitat and 3 pairs of transects (3 burn, 3 control) in shrubland habitat.



Fig. 2. *Top panel*, Personnel of the U.S. Bureau of Land Management conducting a second controlled burn of the Carrizo Plain experimental burn site on 4 June 1995. *Bottom panel*, Ash on the ground after the second controlled burn of the site on 4 June 1995. Photographs by David J. Germano.

We trapped all 10 transects 5 times: 25–30 July 1993, 22 February–7 March 1994, 11–21 October 1994, 8–15 April 1995, and 17–22 November 1995. Because activity of kangaroo rats in the San Joaquin Desert is not affected by moonlight (Prugh and Brashares 2010; personal observation), we did not try to avoid trapping during moonlit nights. For each rodent we captured, we recorded the trap location on the transect, the sex and weight of the animal (using a spring scale), and its reproductive condition. Using a nontoxic marker, we marked rodents with a number on the ventral surface for identification within a session.

Field Methods: Carrizo Plain

In September 1993, we established two 144trap plots $(12 \times 12 \text{ lines})$ at the study site. We placed one plot about 50 m east of Soda Lake Road and the other plot about 100 m east of the eastern edge of the first plot. We placed wooden stakes at 10-m intervals and an extra-large Sherman live trap (Model XLF15) at each stake. The plot adjacent to Soda Lake Road was our burn plot. Before burning, we set traps on the burn plot for 6 consecutive nights and on the control plot for 7 consecutive nights from 29 September to 5 October. Personnel from the Bakersfield Field Office of the Bureau of Land Management (BLM) conducted a controlled burn of the site containing the burn plot on 19 October. We re-staked the burn plot and then trapped on both plots from 21 to 26 October.

For all trapping sessions, we baited traps with birdseed, and we included 1 or 2 sheets of tightly wadded brown paper towel as bedding material. We opened traps in late afternoon and checked them at dawn the next morning. After the initial pre- and postburn trapping sessions, we trapped on the plots from 30 April to 6 May 1994 and from 27 March to 1 April 1995. The burned plot was burned a second time by the fire crew of the BLM on 4 June 1995 (Fig. 2), and we trapped on both plots again from 12 to 18 June 1995. Subsequent to trapping directly after the second burn, we trapped on both plots from 6 to 13 October 1995 and again from 31 March to 5 April 1996. We conducted a final 4-night trapping session on the burn plot and a 5-night session on the control plot during 22 October to 9 November 1996. For each giant kangaroo rat we captured, we recorded the trap location on the grid, the sex and weight of the animal (using a spring scale), and its reproductive condition. We permanently marked kangaroo rats with monel ear tags (Style 1005-3, National Band and Tag Company, Newport, KY).

Analyses

For the Lokern wildfire data, because of marked differences in the number of individuals captured among the 3 species of kangaroo rats and across years, we used Kruskal-Wallis tests $(\alpha = 0.05)$ to compare the mean number of individuals caught between control and burn transects within a species. Also, because there were no or almost no captures of short-nosed kangaroo rats and Heermann's kangaroo rats in the 2 sessions in 1995, we statistically compared only the 3 sessions in 1993 and 1994 (6 groups per species). If there were group differences, we used Dunn's multiple range test with Bonferroni corrections to determine which groups differed significantly. For the Carrizo Plain data, we initially calculated population estimates per session using the Schnabel method (Schnabel 1938, Chapman and Overton 1966); however, calculated estimates were the same as the total number caught at the end of the session, and

the low values of the 95% confidence intervals were lower than the total caught. Therefore, we simply compared total number of individual giant kangaroo rats caught in each session between control and burn plots and across years.

RESULTS

Lokern Wildfire

With the exception of 3 captures of southern grasshopper mice (*Onychomys torridus*), all captures were of 3 species of kangaroo rats: short-nosed kangaroo rats (SNKR), Heermann's kangaroo rats (HKR), and giant kangaroo rats (GKR). For all 3 species, the average number of captures were similar between control and burn transects for the first trapping session (Fig. 3). For both SNKR and HKR, the number of captures on both control and burn transects decreased to almost no captures over the 5 trapping sessions (Fig. 3).

For SNKR, the average capture numbers on the control and burn transects were essentially even, but we caught 35% more individuals on the control transects than on the burn transects in February 1994, and 40% more on the controls in October 1994 (Fig. 3). In fact, the average number we caught on the controls in February 1994 was 28% higher than in July 1993, but 53% lower in October 1994 (Fig. 3). Over these first 3 trapping sessions, the number of SNKR we caught differed significantly between sessions (H = 19.58, df = 5, P = 0.002); however, the average number caught on burn and control transects only differed significantly (Dunn's test: P < 0.003) for the controls in February 1994 $(\overline{x} = 38.0)$ compared to the burn transects in October 1994 ($\bar{x} = 7.20$). In April 1995, we caught only 2 SNKR on the burn transects and none on the control transects, and in November 1995, we caught 6 on burn transects and 3 on control transects.

The number of HKR we caught on transects was 40% higher on the controls than on burn transects in July 1993 and 25% higher on controls in February 1994 (Fig. 3). Over the first 3 trapping sessions, average numbers of HKR we caught across sessions differed significantly (H= 14.90, df = 5, P = 0.011); however, the average number we caught differed significantly between burn and control transects (Dunn's test: P < 0.003) only on the control transects in July 1993 ($\bar{x} = 6.00$) and February 1994 ($\bar{x} =$ 4.80) compared to burn transects in October 1994 ($\bar{x} = 0.40$). We did not catch any HKR on either control or burn transects in 1995 or 1996 (Fig. 3). The number of GKR caught on transects was low throughout the 5 trapping sessions (Fig. 3), and there were no significant differences between control or burn transects or across years (H = 11.50, df = 9, P = 0.243).

Carrizo Plain

We caught 108 individual GKR on the burn plot before the site was burned the first time and 113 GKR a few days after burning (Fig. 4). On the control plot, we caught 96 GKR before the burn and 106 after the burn (Fig. 4). The number of GKR that we caught had increased on both plots when we trapped again in April 1994, with 141 GKR (31% increase) captured on the burn plot and 131 (24% increase) on the control. On the control plot, there was steady decline in the number of GKR from this high until only one individual was caught in October 1996 (Fig. 4). We walked over the plot on 10 October 1997 and did not see any activity of GKR. The number of GKR on the burn plot also decreased after April 1994, when we caught 94 GKR in March 1995 (33% decline). Both plots had a thick cover of grasses and annual dicots (Fig. 5). At that time, we had the burn plot burned again, and we caught 68 GKR in June 1995 directly after the burn. While the number of GKR continued to decrease on the control plot, the number of GKR that we caught on the burn plot held steady for the next 2 sessions: we caught 65 in October 1995 and 65 in March 1996 (Fig. 4). By October 1996, however, grass coverage was again thick on the burn plot (Fig. 5), and we only caught 2 GKR (97% decline). As with the control plot, we found no sign of GKR activity on the burn plot in March 1997.

DISCUSSION

We found that fire did not cause a significant effect on populations of kangaroo rats in the San Joaquin Desert. We reject our first prediction that the effects of fire would significantly decrease abundances of kangaroo rats immediately after the fire. None of the populations of the 3 species of kangaroo rats on the Lokern wildfire burn areas differed significantly from unburned control areas 1 month after the burn occurred. Similarly, the population of GKR on the plot that was burned by prescribed fire did not initially decrease in number, and in fact, we

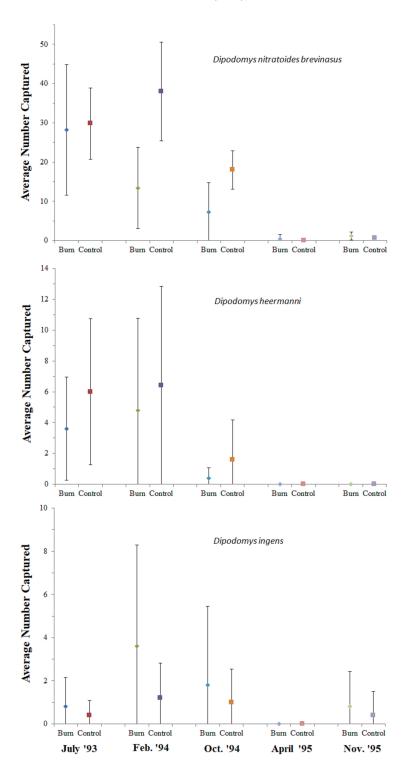


Fig. 3. Average number of short-nosed kangaroo rats (*Dipodomys nitratoides brevinasus*), Heermann's kangaroo rats (*D. heermanni*), and giant kangaroo rats (*D. ingens*) captured on control and burned transects in the San Joaquin Desert. Trapping occurred at 5 time periods starting within 1–2 months of the wildfires in western Kern County, California. The vertical lines are 95% confidence intervals. Note the difference in scales of the *y*-axes.

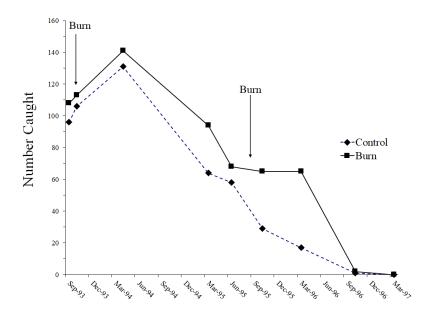


Fig. 4. The total number of individual giant kangaroo rats (*Dipodomys ingens*) captured during 5–7-day sessions on control and burn plots in the Carrizo Plain of the San Joaquin Desert. The arrows indicate the 2 prescribed burns on the burn plot carried out by personnel from the Bakersfield Field Office of the U.S. Bureau of Land Management.

found a larger population after the burn than before the burn. This was not due to animals coming in from near the plot because only 26 of the 113 GKR we captured were not marked before the burn. In a limited sense, our data on the number of GKR on the Carrizo experimental plot after a second burn support our second prediction that kangaroo rats on burned areas benefit from fire long-term, at least until herbaceous cover becomes dense again. The data from the natural fires in the Lokern area, however, did not support our second prediction.

Several factors may limit the effects of fire on kangaroo rats in the San Joaquin Desert. Kangaroo rats are fossorial, and they use burrows daily for cover, daytime resting, avoiding extreme temperatures, conserving moisture, and rearing young (Hawbecker 1953, Kinlaw 1999, Burda et al. 2007, White and Geluso 2012). Kangaroo rats likely avoid direct mortality from fire by retreating to their burrows. There, they are insulated from the heat of the fire by the overlying soil (Lawrence 1966), and smoke entering the burrows may not be of sufficient density or duration to cause suffocation. In addition, some kangaroo rats (i.e., GKR) plug their burrows at times (personal observation), which would provide additional protection from heat and smoke. We did find 1 GKR dead aboveground directly after the second burn at the Carrizo Plain site, but no other deceased rodents were found at any of the other sites after burns. Burning also can negatively impact some animals by removing vegetation that provides cover from predators; however, because kangaroo rats do not use cover to avoid predators, dense cover inhibits predator avoidance: the kangaroo rats are less likely to detect approaching predators and the vegetation can impede their movements thereby increasing their vulnerability (Williams and Germano 1992, Goldingay et al. 1997, Germano et al. 2001). Thus, burning may actually increase the ability of kangaroo rats to elude predators by reducing or removing groundcover.

Although vegetation reduction may facilitate predator avoidance, it could potentially also result in reduced food for granivorous and herbivorous species such as kangaroo rats. Kangaroo rats collect and store food under the soil surface; GKR are larder hoarders and may have liters of seed stored in middens within their burrow system (Williams and Kilburn 1991). Small kangaroo rats such as SNKR are typically scatter hoarders that store seeds in multiple shallow caches within their home range (Best 1991), and HKR may use a combination of these hoarding strategies (Kelt 1988). This stored food can sustain kangaroo rats when fires burn the surface vegetation.



Fig. 5. Herbaceous groundcover on control (*left panels*) and burn (*right panels*) sites at the Carrizo Plain experiment: 2 May 1994 (*top panels*), 4 June 1995 (*middle panels*), and 11 October 1996 (*bottom panels*). Photographs by David J. Germano.

In the arid San Joaquin Desert, vegetation can be patchy, particularly in dry years (personal observation). Not all of the patches may burn when a fire moves through an area, and unburned patches would provide a food source for kangaroo rats. Finally, as annual vegetation dries and breaks down after the growing season, dried stems and seed heads can accumulate as duff or thatch, particularly in small microtopographic depressions. If a burn is not particularly hot, then it is not uncommon for only the surface of this duff layer to burn, with the remaining unburned portion potentially providing a food source for kangaroo rats. A 1997 wildfire burn on the Lokern removed all the surface herbaceous cover, but a wet winter in 1997–1998 resulted in a thick cover of grasses and the dicot *Erodium* the next spring (Germano et al. 2012).

For all of the reasons above, kangaroo rat populations may suffer little or no effects from fires. As an example, HKR numbers increased following a fire at the Alkali Sink Ecological Reserve in the northern San Joaquin Valley (Potter et al. 2010). Similarly, San Joaquin kangaroo rat numbers were higher on burned plots compared to control plots at the Naval Air Station Lemoore, which is located approximately 100 km north of our study area (Kelly et al. unpublished report). Increased abundance following burns was also observed for Merriam's kangaroo rats (D. merriami; Bock and Bock 1978, Simons 1991, Fitzgerald et al. 2001, Monasmith et al. 2010, Vamstad and Rotenberry 2010, Horn et al. 2012), Pacific kangaroo rats (D. agilis; Price and Waser 1984), Stephens' kangaroo rats (D. stephensi; Eller 1994), and Dulzura kangaroo rats (Dipodomys simulans; Brehme et al. 2011). Abundance of both banner-tailed kangaroo rats (D. spectabilis; Valone et al. 2002) and Ord's kangaroo rats (D. ordii; Killgore et al. 2009, Dimitri and Longland 2022) was unaffected by fire. In all of the studies above, the increase in kangaroo rat abundance on burned areas was attributed to significant reductions in groundcover that likely enhanced the foraging efficiency of these bipedal rodents.

Shrubs in the San Joaquin Desert are typically not fire-adapted and can suffer high mortality from burns (Sawyer et al. 2009), as we also documented in this study. Indeed, as of 2022, shrubs were still absent from many of the areas that burned in 1993 (personal observation). Shrubs, however, do not appear to be a critical habitat component for kangaroo rats (Price et al. 1994, Cypher et al. 2021), although they do benefit other species, particularly birds.

In our study, kangaroo rat abundance did eventually decline, but this decline occurred on control transects as well as on burned transects. Indeed, by winter/spring 1995, kangaroo rats were declining throughout much of the San Joaquin Desert (Single et al. 1996). Aboveaverage precipitation during the winter of 1994– 1995 resulted in dense, wet groundcover throughout the region. Kangaroo rat populations rapidly decreased markedly, although the causal mechanism was not identified.

Based on our results, fires in wildlands in the San Joaquin Desert do not appear to adversely impact kangaroo rat populations. Fire may even produce a short-term positive effect by reducing groundcover density. We do not recommend fire as a habitat management strategy, however, because (1) the effects of fire on other species has not been assessed, (2) fire can eliminate shrubs from the community for several decades (as observed in the Lokern study sites), (3) the effects on herbaceous cover are short-lived, and (4) burning produces particulates that erode air quality in an already heavily polluted region.

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LITERATURE CITED

- BEAN, W.T., E.N. TENNANT, B.L. CYPHER, L.R. SASLAW, AND L. PRUGH. 2021. Animals: the final puzzle piece in a functioning natural community. Pages 45–56 in H.S. Butterfield, T.R. Kelsey, and A.K. Hart, editors, Rewilding agricultural landscapes: a California study in rebalancing the needs of people and nature. Island Press, Washington, DC.
- BEST, T.L. 1991. *Dipodomys nitratoides*. Mammalian Species 381:1–7.
- BOCK, C.E., AND J.H. BOCK. 1978. Response of birds, small mammals, and vegetation to burning sacaton grasslands in southeastern Arizona. Journal of Range Management 31:296–300.
- BREHME, C.S., D.R. CLARK, C.J. ROCHESTER, AND R.N. FISHER. 2011. Wildfires alter rodent community structure across four vegetation types in southern California, USA. Fire Ecology 7:81–98.
- BROOKS, M.L., AND J.R. MATCHETT. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980– 2004. Journal of Arid Environments 67:148–164.
- BROWN, D.E., AND R.A. MINNICH. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. American Midland Naturalist 116:411–422.
- BURDA, H., R. ŠUMBERA, AND S. BEGALL. 2007. Microclimates in burrows of subterranean rodents – revisited. Pages 21–33 in S. Begall, H. Burda, and C.E. Schleich, editors, Subterranean rodents. Springer, Berlin, Germany.
- CHAPMAN, D.G., AND W.S. OVERTON. 1966. Estimating and testing differences between population levels by the Schnabel estimation method. Journal of Wildlife Management 30:173–180.
- CYPHER, B.L., S.E. PHILIPS, T.L. WESTALL, E.N. TENNANT, L.R. SASLAW, E.C. KELLY, AND C.L. VAN HORN JOB. 2021. Conservation of endangered Tipton kangaroo rats (*Dipodomys nitratoides nitratoides*): status surveys, habitat suitability, and conservation recommendations. California Fish and Wildlife Journal, Special CESA Issue:382–397. https://doi.org/10.51492/cfwj.cesasi.23
- DIMITRI, L.A., AND W.S. LONGLAND. 2022. Long-term persistence of desert rodent species in a Great Basin sagebrush community: potential effects of fire, invasive annuals, and warming temperatures. Western North American Naturalist 82:603–610.
- ELLER, K.G. 1994. The potential value of fire for managing Stephens' kangaroo rat habitat at Lake Perris State

Recreation Area. Master's thesis, University of California, Riverside, CA.

- FITZGERALD, C.S., P.R. KRAUSMAN, AND M.L. MORRISON. 2001. Short-term impacts of prescribed fire on a rodent community in desert grasslands. Southwestern Naturalist 46:332–337.
- GERMANO, D.J., R.B. RATHBUN, AND L.R. SASLAW. 2001. Managing exotic grasses and conserving declining species. Wildlife Society Bulletin 29:551–559.
- GERMANO, D.J., G.B. RATHBUN, AND L.R. SASLAW. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. Journal of Wildlife Management 76:670–682.
- GERMANO, D.J., G.B. RATHBUN, L.R. SASLAW, B.L. CYPHER, E.A. CYPHER, AND L. VREDENBURGH. 2011. The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 31:138–147.
- GOLDINGAY, R.L., P.A. KELLY, AND D.F. WILLIAMS. 1997. The kangaroo rats of California: endemism and conservation of keystone species. Pacific Conservation Biology 3:47–60.
- HAWBECKER, A.C. 1953. Environment of the Nelson antelope ground squirrel. Journal of Mammalogy 34:324–334.
- HORN, K.J., B.R. MCMILLAN, AND S.B. ST. CLAIR. 2012. Expansive fire in Mojave Desert shrubland reduces abundance and species diversity of small mammals. Journal of Arid Environments 77:54–58.
- KEARNEY, T.H., L.J. BRIGGS, AND H.T. SHANTZ. 1914. Indicator significance of vegetation in Tooele Valley, Utah. Agriculture Research 1:365–417.
- KELT, D.A. 1988. Dipodomys heermanni. Mammalian Species 323:1–7.
- KILLGORE, A., E. JACKSON, AND W.G. WHITFORD. 2009. Fire in Chihuahuan Desert grassland: short-term effects on vegetation, small mammal populations, and faunal pedoturbation. Journal of Arid Environments 73:1029–1034.
- KINLAW, A. 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. Journal of Arid Environments 41:127–145.
- LAWRENCE, G.E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. Ecology 47:278–291.
- LOVICH, J.E., AND D. BAINBRIDGE. 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. Environmental Management 24:309–326.
- MINNICH, R.A. 2008. California's fading wildflowers: lost legacy and biological invasions. University of California Press, Berkeley, CA.
- MONASMITH, T.J., S. DEMARAIS, J.J. ROOT, AND C.M. BRIT-TON. 2010. Short-term fire effects on small mammal populations and vegetation of the Northern Chihuahuan Desert. International Journal of Ecology 2010: 189271. https://doi.org/10.1155/2010/189271

- POTTER, M.C., H.O. CLARK JR., P.A. KELLY, AND C.U. UPTAIN. 2010. Fire effects on a population of Heermann's kangaroo rats at the Alkali Sink Ecological Reserve, Fresno County, California. Transactions of the Western Section of The Wildlife Society 46:1–6.
- PRICE, M.V., R.L. GOLDINGAY, L.S. SZYCHOWSKI, AND N.M. WASER. 1994. Managing habitat for the endangered Stephens' kangaroo rat (*Dipodomys stephensi*): effects of shrub removal. American Midland Naturalist 131: 9–16.
- PRICE, M.V., AND N.M. WASER. 1984. On the relative abundance of species: postfire changes in a coastal sage scrub rodent community. Ecology 65:1161–1169.
- PRUGH, L., AND J. BRASHARES. 2010. Basking in the moonlight? Effect of illumination on capture success of the endangered giant kangaroo rat. Journal of Mammalogy 91:1205–1212.
- SAWYER, J.O., T. KEELER-WOLF, AND J.M. EVENS. 2009. A manual of California vegetation. California Native Plant Society, Sacramento, CA.
- SCHNABEL, Z.E. 1938. The estimation of the total fish population of a lake. American Mathematical Monthly 45:348–352.
- SIMONS, L.H. 1991. Rodent dynamics in relation to fire in the Sonoran Desert. Journal of Mammalogy 72:518–524.
- SINGLE, J.R., D.J. GERMANO, AND M.H. WOLFE. 1996. Decline of kangaroo rats during a wet winter in the southern San Joaquin Valley, California. Transactions of the Western Section of The Wildlife Society 32:34–41.
- [USFWS] UNITED STATES FISH AND WILDLIFE SERVICE. 1998. Recovery plan for upland species of the San Joaquin Valley, California. Region 1, U.S. Fish and Wildlife Service, Portland, OR.
- VALONE, T.J., S.E. NORDELL, AND S.K. MORGAN ERNEST. 2002. Effects of fire and grazing on an arid grassland ecosystem. Southwestern Naturalist 47:557–565.
- VAMSTAD, M.S., AND J.T. ROTENBERRY. 2010. Effects of fire on vegetation and small mammal communities in a Mojave Desert Joshua tree woodland. Journal of Arid Environments 74:1309–1318.
- WHITE, J.A., AND K. GELUSO. 2012. Seasonal link between food hoarding and burrow use in a nonhibernating rodent. Journal of Mammalogy 93:149–160.
- WILLIAMS, D.F., AND D.J. GERMANO. 1992. Recovery of endangered kangaroo rats in the San Joaquin Valley, California. Transactions of the Western Section of The Wildlife Society 28:93–106.
- WILLIAMS, D.F., AND K.S. KILBURN. 1991. *Dipodomys ingens*. Mammalian Species 377:1–7.

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