The Influence of Fall Supplemental Feeding on Giant Kangaroo Rats (*Dipodomys ingens*) and Associated Small Mammal Community

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Final Draft: June 30, 2016

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Executive Summary

The giant kangaroo rat (*Dipodomys ingens*) is a species of burrowing, granivorous rodent in the heteromyid family. The species is listed as endangered under the Federal and California Endangered Species Acts. Due to the ongoing, historic drought in California, giant kangaroo rat populations have declined across their range. This decline is associated with an almost complete lack of vegetation and therefore food resources for the species.

We tested the effectiveness of supplemental feeding to sustain or increase giant kangaroo rat populations on nine paired plots across their remaining range. In fall 2015, we provided wild birdseed mix *ad libitum* on 9 paired experimental and control plots, three each in the Carrizo Plain National Monument, Lokern Ecological Reserve, and Ciervo-Panoche Natural Area. Population size was estimated in the summer of 2015 and spring 2016 using live trapping for three to five consecutive nights. Population sizes were estimated using mark-recapture models, and overall effect size was calculated using Hedge's *d*.

Supplemental feeding increased giant kangaroo rat population size by a mean of 19 individuals (95% Confidence Intervals = 6 to 32). Eight of the nine plots had increases greater on the experimental plots than on the controls. Supplemental feeding had no observed effect on body weight or reproductive status. Most small mammal species declined on plots where giant kangaroo rats increased, however on three plots in the Carrizo Plain, short-nosed kangaroo rat (*Dipodomys nitratoides brevinasus*) populations also appeared to increase in response to supplemental feeding.

Supplemental feeding appears to be an effective tool for sustaining or increasing giant kangaroo rat populations in times of drought. In comparison to captive breeding, supplemental feeding may be a more effective, efficient, and less invasive measure for sustaining small and decreasing populations of small mammals in arid systems. The precise mechanisms by which supplemental feeding increased giant kangaroo rat populations ought to be further investigated. Supplemental feeding may also be used to re-establish extirpated populations within their existing range to ensure site fidelity and increase abundance. Reliable, consistent measurements of seed bank availability would be an important tool for understanding the role that food resources play in causing kangaroo rat population declines.

Introduction

The San Joaquin Valley is a unique biome whose main community and population dynamics are driven by annual precipitation (Germano et al. 2011). A century of land use conversion for agriculture, urban, and energy extraction has led to the loss of over 95% of natural habitat in the area (Williams et al. 1998). This loss has caused 11 species native or endemic to the area to be listed as federally threatened or endangered (Williams et al. 1998). Habitat management in the area generally focuses on managing non-native grasses to recreate more open habitats through grazing, burning, or mechanical treatments. Intact habitat in the area is characterized by open bunch grasses, shrubs, and perennial herbs and forbs (Germano et al. 2011). Habitat management has historically been developed under the assumption that this biome functions as a bunchgrass prairie. However, due to the low levels of annual precipitation, and plant and animal community that more resembles the Mojave Desert, Germano et al. (2011) suggested this area would be more appropriately managed as a desert. The 2012-2014 drought, an event without precedent in California (Robeson 2015) has presented a number of challenges and opportunities for wildlife management. While the faunal community appears to have evolved within the context of low and highly variable annual rainfall, the unprecedented nature of this drought has caused concern over the potential harm to listed and endangered species.

There is a suite of non-volant small mammal species and subspecies endemic to the San Joaquin Valley desert, including the federally- and state-endangered giant kangaroo rat (*Dipodomys ingens*). Giant kangaroo rats (GKR) are a granivorous, burrowing rodent (Williams and Kilburn 1991). Individuals select open habitats to facilitate movement and detect predators (Williams and Kilburn 1991). The species therefore is only found in areas within a narrow range of mean annual precipitation: too dry, and individuals cannot acquire enough food to survive and reproduce; too wet, and cover from non-native grasses becomes too thick. GKR are therefore restricted to areas between approximately 20-30 cm of mean annual precipitation (Williams and Kilburn 1991, Bean et al. 2014).

Precipitation, however, is also highly variable in these areas, and thus populations, particularly at the edge of their range, may be volatile. In high quality habitat, giant kangaroo rats are competitively dominant. From 2007-2012, trapping in core areas of the Carrizo Plain National Monument resulted in over 99% of captures being giant kangaroo rats (Prugh and Brashares 2014). However, in years of abnormally high or abnormally low rainfall, giant kangaroo rat populations decline (Germano 1992, Cypher 2001). In core areas, this decline can coincide with an increase in small mammal species including Heermann's kangaroo rat (*Dipodomys heermanni*), San Joaquin kangaroo rat (*Dipodomys nitratoides*), California pocket mouse (*Chaetodipus californicus*), southern grasshopper mouse (*Onychomys torridus*), deer mouse (*Peromyscus maniculatus*) and, most strikingly, a dramatic increase in San Joaquin pocket mouse (Bean et al. 2016). Similar patterns have been found elsewhere. This pattern and consistent microhabitat spatial partitioning among the species suggests that giant kangaroo rats may competitively exclude smaller species (Cypher 2001, Germano and Rathbun 2012). During the recent drought, trapping efforts throughout giant kangaroo rat range have documented significant declines. This decline is believed to be caused by the near or total absence of suitable food resources over a multi-year period.

The role that food plays in limiting populations has been of great interest to and debate among ecologists for many decades (Power 1992). A long series of supplemental feeding experiments have suggested that additional food increases a number of key individual and population characteristics, including body mass, survival, litter size, abundance, and density, reviewed in (Boutin 1990). Supplemental feeding has been a key tool for wildlife managers, particularly for game species (Leopold 1986, Silvy 2012). Supplemental feeding has also been used in a number of cases for recovery of endangered species, including Mauritius kestrel(Jones et al. 1995), Mauritius parakeet (Tollington et al. 2015), Hihi (Castro et al. 2003), Florida Scrub-jay (Schoech et al. 2008), and California condor (Cortés Avizanda et al. 2016).

In this study, we tested the use of supplemental feeding as a tool to support giant kangaroo rat populations in the face of a historic drought. We provided a millet-based bird seed *ad libitum* at 9 plots, three each at three different sites throughout the species' range. These plots were paired with control plots. Plots were trapped in the late summer of 2015 before supplemental feeding began and in the spring of 2016. We documented changes in the overall small mammal community at each site. We then compared changes in giant kangaroo rat abundance, weight, and reproductive status.

Methods

We selected three sites on public land in known giant kangaroo rat habitat: the Carrizo Plain National Monument, Lokern Ecological Reserve, and Ciervo-Panoche Natural Area (**Figure 1**). The Carrizo Plain National Monument is located in San Luis Obispo and Kern Counties, Lokern in Kern County, and Ciervo-Panoche Natural Area in San Benito and Fresno Counties. All three sites have been trapped for consecutive years: the Carrizo sites as part of the ongoing Carrizo Plain Ecosystem Project led by U.C. Berkeley, the Lokern sites as part of ongoing trapping by California Department of Fish & Wildlife and the Endangered Species Recovery Program, and Ciervo-Panoche as part of ongoing monitoring by the Spatial Wildlife Ecology Lab at Humboldt State University.

All three sites are typical of the San Joaquin Valley desert grassland biome. Vegetation is characterized as valley sink scrub, valley saltbush scrub, and annual and perennial grassland. These sites are all necessarily similar given that the specialist giant kangaroo rat is present. However, subtle differences in annual precipitation, soil type, and historical land use have caused relatively large differences in the small mammal community at each site. Lokern is generally characterized as having the highest diversity of small mammals, with the lowest density of giant kangaroo rats (Germano and Rathbun 2012). The plots in Carrizo are located within "core areas" for giant kangaroo rats on the Monument, and the species has generally made up the near complete capture record on the trapped plots. This dominance, however, has diminished during the drought (Prugh and Brashares 2014). The Ciervo-Panoche represents a place somewhere in the middle between Lokern and Carrizo. While giant kangaroo rats are not as dominant in the Carrizo, they historically have made up the majority of capture records on the plots we trapped.

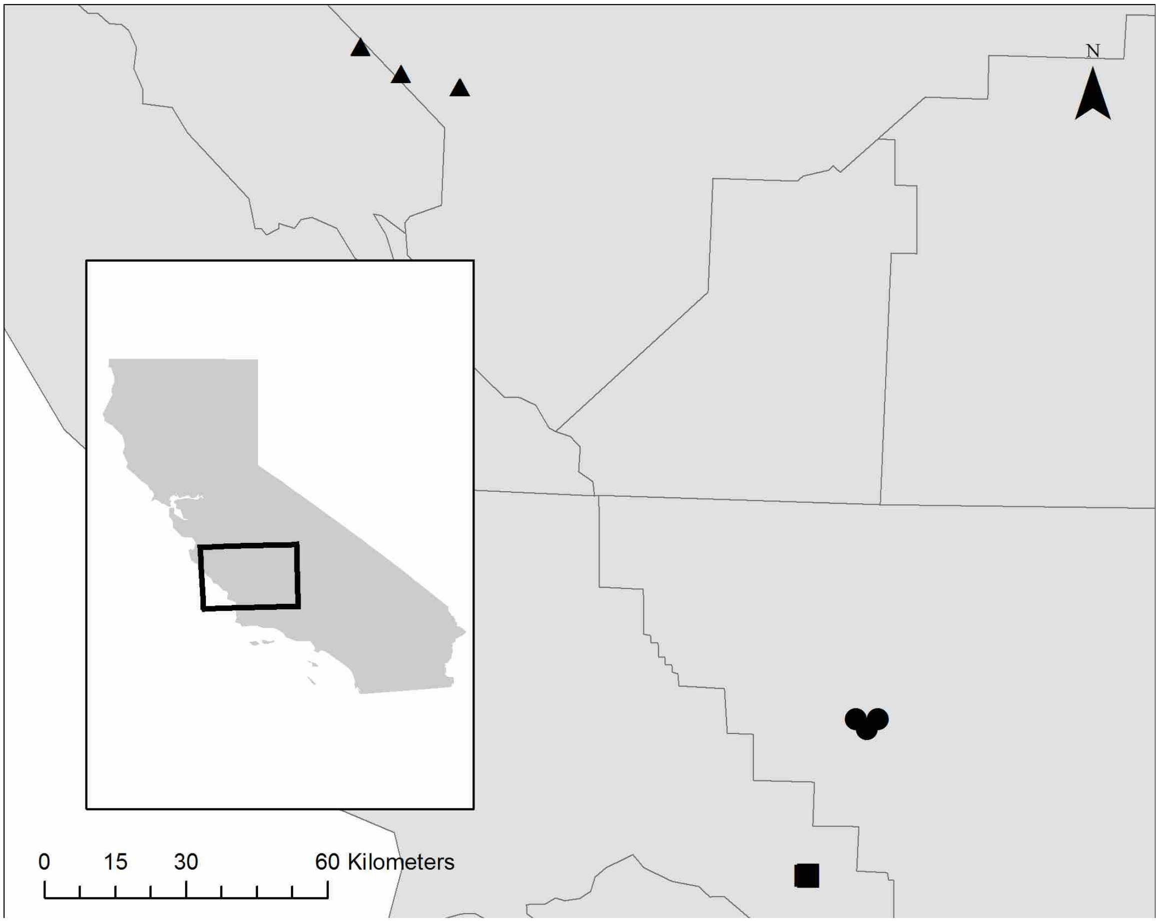

Figure 1. Locations where supplemental feeding experiments were conducted. Triangles=Ciervo-Panoche Natural Area; Squares=Carrizo Plain National Monument; Circles=Lokern Ecological Reserve.

Plots that received the experimental supplemental birdseed were paired with plots that had been previously trapped. The experimental plots were placed 60-80 m apart and placed in a random direction from the existing trapping plots. This distance was used based on experience with a similar paired design in the Carrizo. No giant kangaroo rats have been observed moving between plots at that distance; therefore, they offered similar environmental conditions without the possibility of individual rats moving between plots.

We purchased 1,000 lbs. of wild birdseed mix, consisting mostly of millet but no sunflower seeds. This seed was provided *ad libitum* on the experimental plots for approximately six weeks in fall 2015. Feeding stations were constructed with two, one-foot sections of PVC pipe connected by a 2” conduit box (Figure 2). Feeding stations were placed 20m apart, following the trapping scheme described below. Approximately 1 cup of birdseed was placed in each feeding station to deter theft by birds. In total, we provided approximately 100 lbs. of seed on each plot.

Figure 2. Feeding station example taken at Carrizo Plain National Monument and set in front of an active giant kangaroo rat burrow.

Each plot was trapped in late summer 2015 and again in late spring 2016. Trapping grids consisted of 60, extra-long Sherman live traps set in a checkerboard fashion at 20m intervals. Traps were baited with a small handful of millet and a paper towel was provided for insulation. In Carrizo and Panoche, traps were opened at dusk and checked starting at midnight. In Lokern, traps were opened at dusk and checked at dawn. In Panoche, we trapped each plot for five consecutive nights. In Lokern and Carrizo, we trapped for three consecutive nights. Trapping in Panoche was conducted following protocols established in Federal Fish & Wildlife Permit TE37418A-2 and Humboldt State Institutional Animal Care & Use protocol 13/14.W.109-A; trapping in Carrizo was conducted under Federal Fish & Wildlife Permit TE157221-1 and U.C. Berkeley Animal Care and Use Committee protocol R304. Trapping in Lokern was conducted by employees of California Department of Fish & Wildlife under cooperative agreement with U.S. Fish & Wildlife Service provided for in Section 6(c) of the Federal Endangered Species Act.

Captured giant kangaroo rats were tagged with Monel #1 aluminum ear tags, on one ear in Carrizo and on both ears in Panoche and Lokern. In Carrizo, rats were also given a unique passive integrated responder (PIT) tag. Other species were either ear tagged or marked with a sharpie to identify recaptured individuals within a single trapping session. We recorded the following measurements for all captured small mammals: weight, sex, age, and reproductive status. Due to inconsistencies between seasons and among sites, reproductive status was coded for analysis as simply "reproductive" or "non-reproductive." Reproductive individuals included lactating or pregnant females and scrotal males, as well as any rat with some evidence of transitioning from or to those reproductive stages. During the spring session, giant kangaroo rats were not individually ear tagged on the experimental grids in Lokern. Instead, they were marked with a Sharpie.

We attempted to individually identify recaptures based on rats trapped previously on the nearest trap on the grid; however, the specific analysis we used to estimate population size does not require precise individual capture histories (see below). Finally, the control grids in Carrizo were trapped twice in spring 2016, once in April and again in June. The experimental grids were only trapped in June. We therefore used only the trapping results from June to compare the differences between the plots.

We estimated total population size at each plot during each session (before and after supplemental feeding) using the Huggins closed capture model without heterogeneity in Program Mark (White and Burnham 2009). While populations were not closed between sessions (i.e., from summer to spring), populations were assumed closed during the three- to five-night trapping session. This model, relies on the original Lincoln-Petersen estimator, based on probability of capture ($\hat{p}$), to estimate population size ($\hat{N}$):

$$\hat{N} = \frac{n}{\hat{p}} \qquad \text{Equation 1}$$

The Huggins model extends the Lincoln-Petersen model for additional nights of trapping, and can include estimates of initial probability of capture ($\hat{p}$) as well as probability of re-capture ($\hat{c}$) (Huggins 1989). If there is no behavioral response to initial capture (i.e., rats are neither “trap-happy” nor “trap shy”), each individual capture can be used to estimate $\hat{p}$. If rats are more or less likely to be trapped after they have initially been trapped, $\hat{p}$ is estimated only from the initial capture. For a three night trapping session, population size is estimated as

$$\hat{N} = \frac{M_{t+1}}{[1-(1-\hat{p})(1-\hat{p})(1-\hat{p})]} \qquad \text{Equation 2}$$

We tested seven models of giant kangaroo rat behavioral response based on our collective trapping history across the eighteen plots. Three models - a model based on unique probability of detection and probability of re-capture at each plot; a model where probability of detection and re-capture were different at each site; and a model where probability of initial capture changed from the first night to subsequent nights - were removed from the analysis because they did not produce reliable estimates of detection probability. The final four models were compared using Akaike’s Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). Any model with <7 ΔAIC was considered supported by the data and used to produce a model-averaged estimate of $\hat{p}$, $\hat{c}$, and $\hat{N}$. Specifically, we created models where:

1. Rats were neither trap happy or trap shy (i.e. $p=c$)
2. Rats were more or less likely to be re-captured than initially captured (i.e. $p!=c$)
3. Rats were neither trap happy or trap shy, but probability of capture differed at the Carrizo control sites in June 2016
4. Rats were more or less likely to be re-captured than initially captured, and probability of capture differed at the Carrizo control sites in June 2016

The final two models were included due to the change in trapping protocol in Carrizo in spring 2016. Because of the consecutive trapping periods in April and again in June on the control plots, we believed that initial capture probability would be higher at the control plots in June. Previous studies have demonstrated that giant kangaroo rats have a higher probability of re-capture than initial capture. The trapping session in June therefore was likely to have higher initial capture probabilities because rats had recently been captured in April. Huggins closed-capture models and model comparison were conducted in Program Mark (White and Burnham 2009).

Population size was estimated separately at each plot in each time period. To calculate an overall effect size of experimental supplemental feeding, we calculated an un-standardized form of Hedge's *d* (Koricheva et al. 2013) using package *metafor* (Viechtbauer 2010) in Program R. Hedge's *d* is a metric created for meta-analysis to compare results across multiple studies and can incorporate random effects (i.e. heterogeneity across studies). Because our results were in consistent units (number of rats), we did not standardize effect sizes. Results are therefore presented as the difference in change in giant kangaroo rat population size between paired treatment and control grids. A positive number represents a greater increase in population size on the experimental grid. We also tested for heterogeneity among sites, however there were no significant differences (Cochran's $Q = 3.89$, d.f. = 8, $p = 0.87$). We therefore used a fixed effects model to estimate the overall effect of supplemental feeding on giant kangaroo rat abundance.

Supplemental feeding can increase population size in a number of different ways: supplemental feeding may increase recruitment or simply cause a numerical response (Fryxell et al. 2014). We therefore attempted to examine the mechanisms by which supplemental feeding may have acted. We tested changes in body weight and reproductive status across individuals. We compared body weight using an Analysis of Variance with treatment crossed with time and sex as a covariate. We examined only adult giant kangaroo rats that were not pregnant. Adults were identified in the hand based on overall coat quality and color, whether the ears were fully intact, and body size. Adults were further restricted in the final analysis to individuals greater than 100g. We tested for changes in reproductive status using logistic regression, with treatment and time crossed.

Finally, we calculated the minimum number of individuals alive for all other small mammal species.

Results

We captured 411 giant kangaroo rats during the course of the study. No rats were observed moving between the grids – all recaptured rats were caught on the same grid they were initially captured on. The top model in the mark-recapture analysis included different probability of initial capture and probability of re-capture. In addition, this top model also included a separate estimate of probability of initial capture on the Carrizo control grids in the spring (Table 1). These differential recapture rates were observed in the raw capture data. Rats tagged in the previous session comprised 17% of all rats caught across all grids in the spring. However, on the control grids in Carrizo in the spring, rats tagged in previous sessions represented 65% of those captured.

Table 1. Model selection results for four models based on the Huggins closed-capture design. A model including behavior response to initial capture and a different initial capture probability on the Carrizo control plots was the only model with support.

Model	AICc	ΔAICc	AICc weight	Parameters
p!=c, Carrizo controls different	2154.44	0.00	1.0	3
p!=c	2169.11	14.67	0.0	2
p=c	2302.13	147.69	0.0	1
p=c, Carrizo controls difference	2304.13	149.69	0.0	2

Probability of initial capture was low ($\hat{p}$=0.09, S.E.=0.042), while recapture probability was high ($\hat{c}$=0.58, S.E.=0.018). Probability of initial capture was more similar to recapture probability on the Carrizo control grids than to initial capture on other grids ($\hat{p}$ =0.46, S.E.=0.065).

Population size estimates ranged from 0 to 141 (Figure 3). Four plots before supplemental feeding began had zero giant kangaroo rats. Eight of the nine plots showed expected results, with change in estimated population size higher on the experimental plots than the controls. Individual plots were not significantly different, but the overall effect was significantly positive. Across the nine plots, supplemental feeding resulted in an increase of approximately 19 giant kangaroo rats (Figure 4). Changes in abundance of other small mammals were idiosyncratic (Figure **6**). Most plots showed declines in other small mammals on experimental plots in comparison to controls. However, short-nosed kangaroo rats (*Dipodomys nitratoides brevinasus*) increased on the experimental feeding plots in the Carrizo compared to the controls.

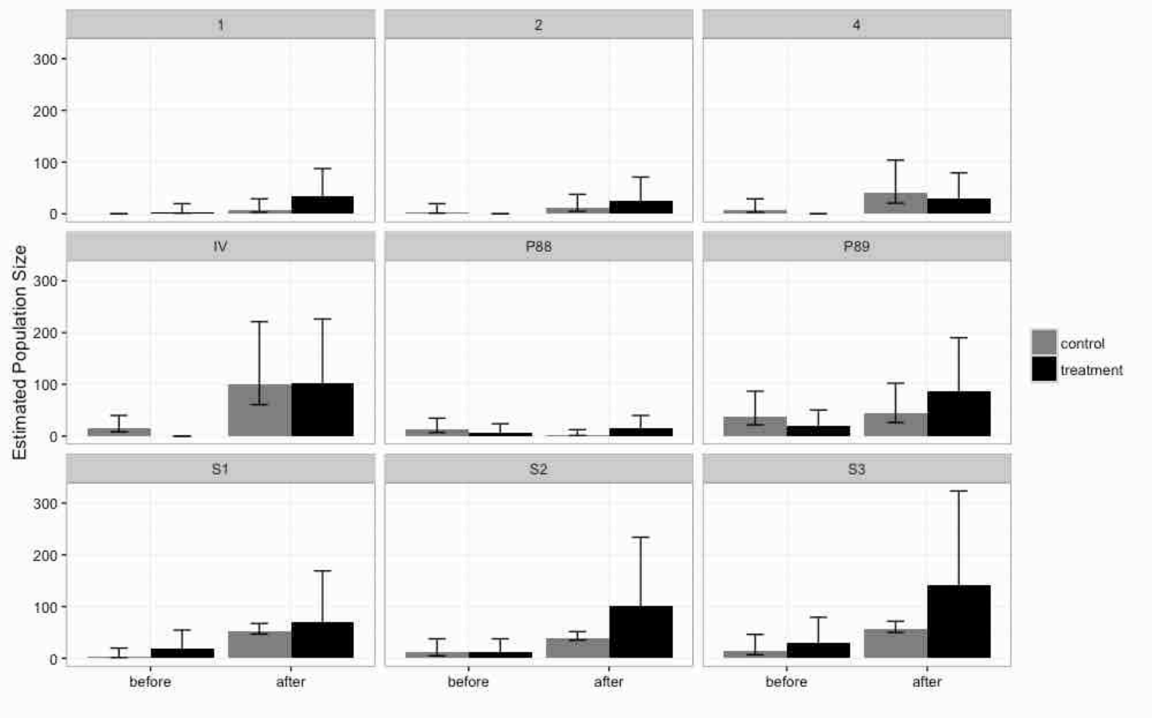

Figure 3. Estimated giant kangaroo rat population size (+/- 1 S.E.) on paired control and treatment plots before (late summer 2015) and after (late spring 2016) supplemental feeding in fall 2015. Top row are three paired plots in the Lokern Ecological Reserve, three middle plots are in the Ciervo-Panoche Natural Area, and three plots on the bottom are in the Carrizo Plain National Monument.

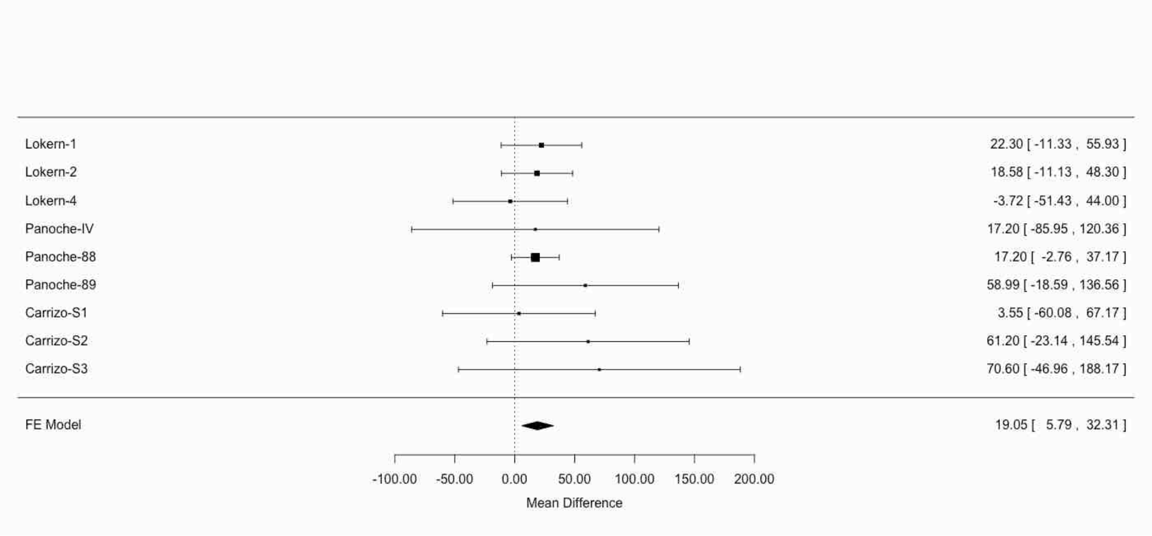

Figure 4. Forest plot of effect size of supplemental feeding on change in giant kangaroo rat population size. Black dots represent estimated difference in change in giant kangaroo rat populations between treatment and control plots with 95% confidence intervals. Black diamond at the bottom shows overall effect size across nine plots.

There were no significant differences in weight (

Table 2, Figure 5) or reproductive status (Table 3) between experimental and control plots.

Table 2. Analysis of variance results for changes in weight on treatment and control grids before and after supplemental feeding.

Coefficient	Estimate	S.E.	t-value	p
(Intercept)	124.61	2.00	62.161	<0.001
treatment	3.05	3.47	0.88	0.38
after	-1.63	2.09	-0.78	0.44
M	1.50	1.13	1.33	0.18
treatment:after	-0.34	3.67	-0.09	0.93

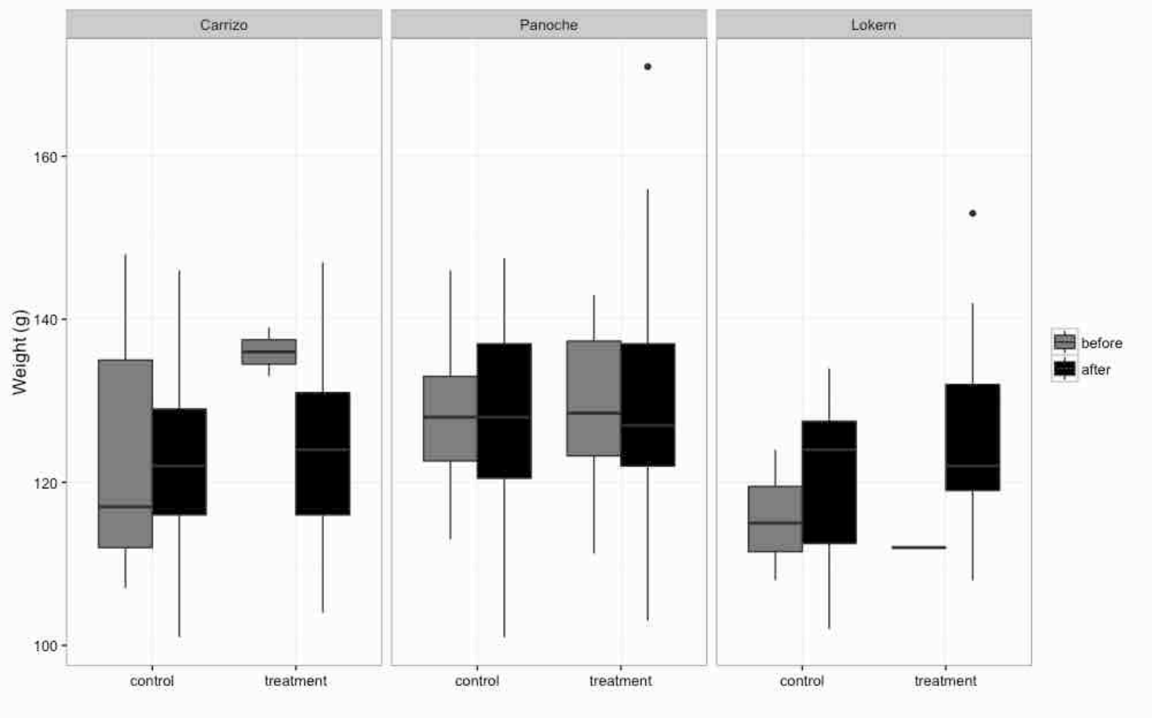

Figure 5. Differences in weight in adult, non-pregnant giant kangaroo rats on treatment and control plots, before and after supplemental feeding.

Table 3. Analysis of variance results for changes in reproductive status on treatment and control grids before and after supplemental feeding.

Coefficient	Estimate	S.E.	t-value	p
(Intercept)	4.437	0.71	6.238	<0.001
treatment	-0.06	1.01	-0.06	0.95
before	-1.03	1.24	-0.84	0.40
treatment:before	16.23	2346.72	0.007	0.99

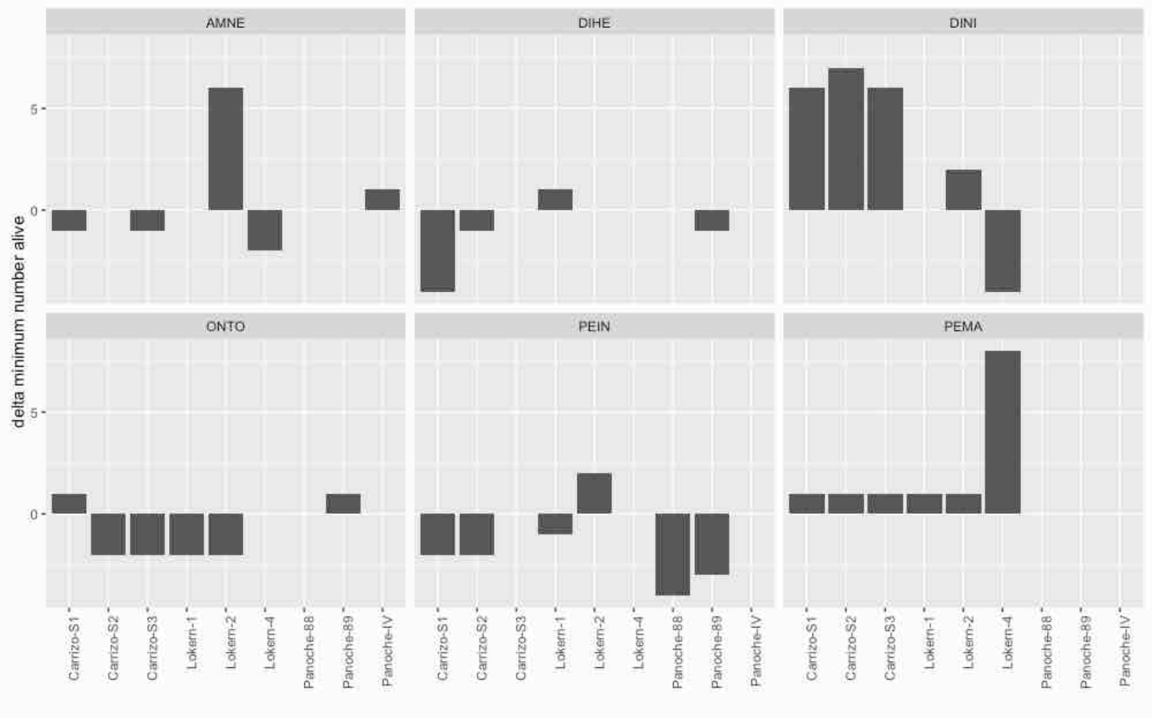

Figure 6. Change in differences of minimum number of alive individuals across species on nine paired experimental feeding and control plots. Minimum number alive was estimated as total marked individuals of each species. Total reported here calculated as the difference between the experimental and control plots after supplemental feeding minus the difference between the plots before. AMNE=*Ammospermophilus nelsoni* (San Joaquin antelope squirrel); DIHE=*Dipodomys heermanni* (Heermann's kangaroo rat); DINI=*Dipodomys nitratoides* (San Joaquin kangaroo rat); ONTO=*Onychomys torridus*); PEIN=*Perognathus inornatus* (San Joaquin pocket mouse); PEMA=*Peromyscus maniculatus* (deer mouse).

Discussion

Supplemental feeding in fall 2015 had a strong, positive effect on giant kangaroo rat population size. We estimated that supplemental feeding added a mean of 19 individual giant kangaroo rats compared to control plots. In general, the small mammal community also responded as expected: with an increase of giant kangaroo rats, populations of other small mammals declined. This pattern was not observed on the Carrizo grids with short-nosed kangaroo rats. In fact, it appears that supplemental feeding also increased their populations as well.

In a review of supplemental feeding studies in songbirds, Harrison et al. (2010) highlighted the importance of understanding the mechanisms by which supplemental feeding might act. They found that while feeding increased certain vital rates (i.e., earlier clutch initiation date, shorter incubation period), it also lowered others, including clutch size and hatching success. We were unable to identify the mechanisms by which supplemental feeding increased giant kangaroo rat population size on the experimental grids. Individuals were not heavier on average, and there was no difference in reproductive status. One possibility is that survival was higher on the experimental grids than on the control grids. Estimating survival, however, requires a more complicated, data-intense analysis (i.e. a “robust design”) and would require additional years of trapping and more nights per trapping session. We initially attempted to model survival with a robust design model. However, we did not have enough captures in the first trapping session, and the models failed to converge. Given our estimates of capture probability, and the very small population sizes in the fall, it is not possible that higher adult survival was the only cause for increased abundance from supplemental feeding.

Supplemental feeding may have simply attracted individuals from outside of the grid. That is, there could have been higher immigration in response to increased food availability. However, giant kangaroo rats are highly territorial and faithful to their existing burrow mounds. There is little evidence for adult dispersal in this species. Higher immigration would have been due to over-winter juvenile dispersal. However, we showed no movement of marked individuals between grids (a distance of 60-100m), suggesting the effect of immigration from off the plot was likely limited to areas directly adjacent to the study area, and would have had a minimal effect on total abundance.

The only remaining explanation for increased abundance on the experimental plots is higher juvenile recruitment. We cannot identify the precise mechanisms –whether increased numbers of litters, higher number of offspring per litter, or higher apparent survival of juveniles (i.e., juveniles that survived and remained on the site).

Supplemental feeding has been infrequently used as a tool for conservation. For the most part, supplemental feeding has been used in condor recovery programs, with a few notable examples elsewhere. To our knowledge, supplemental feeding has not been used for recovery of a small mammal species. As anthropogenic climate change increases drought risk in California (Diffenbaugh and Swain 2015)and across the world (Dai 2013), small mammal species may increasingly face limited access to resources, particularly in arid environments. Peterson et al. (2005) raised the specter of “domestication” as a potential negative consequence of supplemental feeding, and similar questions have been raised for vulture recovery (e.g. Piper and Houston 2005). Nevertheless, while supplemental feeding may not be a feasible or appealing long-term solution, we demonstrated that it can be an effective approach for maintaining or increasing population sizes over shorter time periods. This approach also offers a less expensive and less invasive solution than captive breeding. Further, supplemental feeding may be an effective tool for re-establishing extirpated populations or increasing densities within marginal sites.

Of course, it ought to go without saying that supplemental feeding can stabilize declining populations only if the cause of the decline is a lack of resources in the first place. In this study, we tested the use of supplemental feeding on nine different declining giant kangaroo rat populations. We believed that this decline was due proximately to the lack of food caused by the ongoing, historical drought in California. Supplemental feeding appeared to increase giant kangaroo rat population sizes locally.

Future work ought to dig further into the mechanisms by which giant kangaroo rats responded to the additional food. Increased population sizes may be due to greater reproductive success or activity, immigration, or higher survival. Giant kangaroo rats have evolved to cache large amounts of seed in preparation for seasonal and long-term droughts. A consistent and standardized measure of the existing seed bank and seed caches are a critical component to understanding habitat quality for this species and would add insight to the role that food plays in supporting giant kangaroo rat populations. More detailed calculations based on the energetics of the species could provide a rule of thumb for the amount of supplemental food necessary to maintain or increase populations.

Acknowledgments

The authors thank the many field assistants - N. Alexander, M. Cokeley, I. Widick, H. Smith, A. Semerdjian, I. Axsom, E. Tennant, C. Fiehler, S. Carey, M. Roberts, A. Gwinn, T. Anderson - who contributed time and energy to conducting the trapping and the biologists at CDFW responsible for distributing the seed. We thank California Department of Fish & Wildlife, especially R. Stafford, for providing logistical support and funding for the experiment, data collection, and analysis.

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