Seed Preferences of the Giant Kangaroo Rat (*Dipodomys ingens*) in Grasslands of the Carrizo Plain, California

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Abstract Invasive grasses and endangered species are two major problems facing California's grasslands. This study examined seed foraging preferences of the giant kangaroo rat (*D. ingens)*, one endangered species whose diet includes both native and non-native species. Two foraging experiments were conducted in the summer of 2007 on the Carrizo Plain National Monument to a) determine if giant kangaroo rats prefer to harvest non-native seeds and b) how nutritional preferences change as they forage further from their burrows. Seed removal experiments were created using 10 local non-native and native grasses and forbs to understand how giant kangaroo rats select from different seed species. There was no significant difference between native and non-native seeds harvested ($X^2 = 0.89$, df = 1, p = 0.35), but strong preferences for non-native *E. cicutarium* and native *L. californica* and *L. nitidium* were found. However, other species did not show strong preferences and questions about how seeds are selected still remain. Oats and lentils were also used to determine how nutritional selectivity changes with foraging distance from burrow. A significant difference in nutritional preference for oats was found as kangaroo rats foraged further from their burrows (z = 73, p = 0.02, n = 24). In summary, giant kangaroo rats showed selective foraging of one non-native grass, but not greater foraging of native seeds overall. They also showed changing nutritional preferences as they harvested seeds further from their burrow. Understanding the effects giant kangaroo rats have on this ecosystem through granivory may have important implications concerning California's grassland ecosystems as well as future management of non-native grasses.

Introduction

A keystone species is defined as a one that has a strong effect on the composition of other species in the ecosystem compared to its own abundance (Paine 1966). In some ecosystems, rodents are considered keystone species (Brown and Heske 1990) because of their selective consumption of plant seeds. This preference in turn can have a strong effect on the composition and abundance of plant species in an ecosystem (Davidson 1993). Selective granivory, or the diet preferences of a seed-eating rodent, has been shown to promote (Longland *et al*. 2001) or suppress the plant species harvested by rodents (Samson *et al.* 1992, Howe 2000). For example, Samson (1992) showed that rodents' selection of annual grasses with larger seeds suppressed abundance of those grasses. In addition, several studies have found that larger rodents prefer larger seeds (Brown and Lieberman 1973, Mares and Williams 1977). Based on these studies, a rodent may very well a) prefer larger seeds that may be nutritionally beneficial and b) suppress that vegetation by harvesting its seeds. However, Longland (2001) determined that rodents aid in the dispersal of grass seeds by storing them in surface caches that are not retrieved later. Seeds can then germinate and result in increased abundance of that species. Despite thorough studies of plants and rodents in many types of ecosystems, these interactions are complex and depend on many other variables (Huntly 1991). Factors like seed dispersal and unharvested seed caches could have a positive effect the spread of prey grasses and forbs, but inhibition through seed predation and even disturbance of surrounding soils could have a negative effect on the spread of prey grasses and forbs (Schiffman 1994). It is not clearly known then the overall effect rodents have on the spread of the grasses and forbs they feed on.

Understanding this interaction is important in California's Carrizo Plain National Monument because it involves a keystone rodent as well as the spread of non-native vegetation, both of which are management foci for preserving this ecosystem. The giant kangaroo rat (*Dipodomys ingens*) (Merriam 1904) (Heteromyidae: Dipodomyidae) is the largest kangaroo rat species, with a mean weight of 150 grams in adults (Grinnell 1932). Giant kangaroo rats are granivores and obtain almost all of the calories and water in their diet from seeds (Williams and Kilburn 1991). They have an elaborate system of curing and storing harvested seeds as noted by Shaw (1934); individuals dig holes outside of their burrow about one inch in diameter and one inch deep and create small "pods" of harvested seeds. As many as 12 of such pods were measured in one square foot (Shaw 1934). These seeds are cured in the sun and later taken, one by one, into the kangaroo rat's extensive burrow system for storage (Shaw 1934). The giant kangaroo rat is endemic to California's San Joaquin Valley and was listed as a federally endangered species in 1980. It is still listed today; at least 82.4 % of its historic habitat has been lost due to expansion of agricultural lands and water projects (Williams 1992). The historic range detailed by Grinnell (1932) is much larger than known occurrences of kangaroo rats in 1985 (Braun 1985), and it is most likely even smaller today.

Many species of Mediterranean grasses and forbs have colonized California and the American west. Native grassland communities previously consisted primarily of native forbs and bunchgrasses (D'Antonio and Vitousek 1992), but such non-native invaders have fundamentally altered these native ecosystems. Invading grasses often weaken diversity of native species by out-competing a broad range of native plants; in many cases this leads to ecosystem instability, which has cascading effects on the health of native plants as well as native wildlife and ecosystem soils (DiTomasio 2000). Often these non-native seeds are larger than native seeds, partly because they were selected to be larger by farmers in their region of origin to maximize for human consumption (Baker 1972). On the Carrizo Plain, Schiffman (1994) found that non-native seeds were generally larger than native seeds, suggesting that this could result in the selection of larger non-native seeds by kangaroo rats because of increased nutritional or energetic gain.

Optimal foraging theory is a critical concept for understanding the foraging behavior and preferences of giant kangaroo rats. In simple terms, optimal foraging theory states that an activity of an organism will continue as long as the net gain is greater than the net loss (MacArthur and Pianka 1966). A one-dimensional example could designate gain as an energetic benefit and loss as energy lost from daily activity of the organism. More recently, optimal foraging theory has even been described as a connected neurological and evolutionary phenomenon; organisms physically choose diet components based on those choices selected over evolutionary time (Glimcher 2002). More advanced optimal foraging theory models include parameters for caloric value of food items, time of foraging, distance to food, calories spent in locomotion, frequency of discovering specific food source, as well as other additional factors (Emlen 1966). Considering optimal foraging theory makes it possible to understand the seed preferences of the giant kangaroo rat in an ecological context, it can connect granivory with the effects it has on plant communities.

How forage selectivity changes with predation risk is another important factor in the distribution of native and non-native grasses as well as the behavior of the giant kangaroo rat in the context of optimal foraging theory. Leaver and Daly (2003) found that other heteromyid rodents become more selective when risk of being preyed upon is greater; they chose seeds with a higher energy yield when moonlight and microhabitat were considered together. When an individual travels further away from its burrow it is visible for a longer time and takes longer to return to safety underground. One metric of predation risk could be distance between a burrow and a resource patch. This could make giant kangaroo rat more susceptible to potential predators including snakes, owls, and raptors (Williams and Kilburn 1991). How preference changes as distance is varied could show other optimal foraging trade offs in giant kangaroo rat seed selection.

Moonlight is an important consideration when studying seed preferences because it can shift foraging preferences by making giant kangaroo rats more visible and increasing predation risk. In situations of greater risk rodents have been found to choose seeds with greater net gain, and has been shown to significantly affect which seed species are removed (Bowers 1988).

This study will answer two questions using these ideas of local seed preference and preference changes under predation risk: First, does the giant kangaroo rat prefer to harvest native or non-native seeds species, and which species in particular does it harvest preferentially? Second, how do the diet preferences of the giant kangaroo rat change as they travel further from their burrows and predation risk becomes greater? Field trials measuring mass removed of locally present non-native and native seeds will determine which species the giant kangaroo rat preferentially harvests. Oat and lentil “bait” seeds presented at varying distances from burrows will determine how preference changes with distance traveled to resources. From previous studies, I predict that the giant kangaroo rats will prefer non-native seed species overall because of their larger size and greater nutrient content. I also hypothesize that the giant kangaroo rats will become more selective as distance from burrow and thus predation risk increases.

Methods

Local Non-Native and Native Seed Trials To determine foraging preferences, 10 different local seed species were made available to giant kangaroo rats to feed from and masses of removed seeds were measured. Study sites were chosen from 140 meter by 140 meter grids in two separate open grassland pastures within the Carrizo Plain National Monument. Inside those 140 meter grids, giant kangaroo rat burrow precincts were randomly chosen on either a pasture with recent grazing history (Center Well Pasture) or a pasture without recent grazing history (Swain Pasture). For the purposes of this study, precincts were defined as the burrow structure and holes that generally housed one giant kangaroo rat. Precinct maps and visual inspections were used to determine locations of randomly chosen precincts and whether they were viable. Precincts were excluded from use and alternates selected if they appeared inactive, if they were obviously disturbed from previous research efforts, or if there was no clear area to place seed piles. After selecting one suitable site inside a grid, an area approximately 0.5 meters long was cleared of other vegetation. Samples of ten different local species of seeds were then placed in separate piles within one meter of the selected burrow. These piles usually ranged in weight from 0.4 grams to 0.7 grams and were placed in a randomly determined order. The grass and forb species used for these local seed trials are listed in Table 1.

Table 1. Listing of seed species' names, author of origin and last revision, and species code used in this study.

Latin Name	Species Code	Species Author
Amsinckia tesselata	AMTE	(Gray)
Astragalus lenignosus	ASLE	(Douglas), Hook
Lasthenia californica	LACA	(Lindley)
Erodium cicutarium	ERCI	(Aiton)
Lepidium nitidium	LENI	(Torrey & A. Gray)
Hordeum murium	HOMU	(Linnaeus)
Poa secunda	POSE	(Presl)
Bromus madritensis ssp. madritensis	BRMA	(Linnaeus)
Vulpia myuros	VUMY	(Gmelin)
Vulpia microstachys	VUMI	(Nutt), Benth

Seeds used in the experiment were collected in spring of 2007 within one mile of the study area and were left on stems and unhusked. Seeds were put out within 30 minutes of sunset and collected within 30 minutes of sunrise. Moon phase was recorded every night. After overnight exposure, seeds were retrieved by hand and separated into marked plastic bags. Once collected, seeds were re-weighed and a difference in mass between pre- and post-foraging weight was calculated to determine the seed mass removed by the kangaroo rats. As much dirt as possible was removed upon weighing. This process was repeated for 28 grids, yielding a total of 280 different masses of seeds removed by kangaroo rats. Negative weight differences were assumed to be zero because small amounts of debris in seeds were difficult to remove. Fifteen out of the total 280 samples yielded a negative weight difference and were rounded to zero. To weigh the samples, an Acculab Vicon scale (Acculab Sartorius Group, Edgewood, NY, USA) accurate to hundredths of a gram was used.

From the seed mass differences, a selection ratio (SR) was calculated that put species removal weights in the context of all other seed species available to individual kangaroo rats (Manly *et al.* 1993). Seed use could change with seed availability, so seed mass removed should be compared with total seeds available and total unharvested seeds. This ratio was:

$$\hat{w}_i = \left(\frac{o_i}{\pi_i}\right) = \left(\frac{\text{Proportion of seeds of species}_\text{i}\ \text{taken}}{\text{Proportion of available seeds of species}_\text{i}\ \text{(out of total seeds available)}}\right)$$

A standardized selection ratio (SSR) was used for interpretation of seeds removed for individual species, and can be interpreted as the probability of that seeds species being chosen at that site when all species are equally available. This ratio was:

$$B_i = \frac{\hat{w}_i}{\sum_{i=1}^{I} \hat{w}_j}$$

Where $\hat{w}_j$ is equal to the nine selection ratios other than $\hat{w}_i$.

Selection ratios of each species were averaged by the attribute “non-native” or “native” and a Wilcoxon signed-rank test was used to determine if there was a significant difference between removal rates of these two groups. Additionally, to determine whether giant kangaroo rats differentially selected local seeds by species, mean SSRs of species were analyzed using a Kruskall-Wallis rank test. Tukey’s HSD test was used on the rank sums to detect significant differences between means of individual species. A separate Wilcoxon signed-rank test was used to determine if changing moonlight affected rate of seed removal.

A nutrient analysis of local seed species used was also conducted using 5 gram samples of the same seeds used in the removal experiment. Analyses were conducted at A&L Agricultural Laboratories (Modesto, CA) and samples were analyzed for 18 different nutritional metrics, as well as seed length. Samples were statistically analyzed with SSR of species for pair-wise correlation (R^2). All analyses were completed using JMP (version 5.1, SAS Institute, Cary, NC, USA).

Preference and Distance Trials To determine if giant kangaroo rats select higher quality seeds when foraging further from their burrows, seeds of differing nutritional quality were placed at two distances from burrow openings. Oats and lentils were used because of the assumed greater desirability of oats and an easily measured nutritional difference between the two; in Leaver in Daly (2003) oats were predicted to be of higher caloric value over lentils and thus energetically preferable for rodents. Seed trays were prepared using methods similar to Leaver and Daly (2003) that were originally established by Brown (1988). Twenty-five x 25 x 5 centimeter wooden seed trays were filled with a mixture of three grams of oats, three grams of lentils, and 400 milliliters of fine dirt sifted through a sieve. To minimize their appearance, trays were placed in shallow holes about five centimeters deep and tray walls were concealed under a layer of dirt. As described in Brown (1988), this yielded a seed measurement that replicated natural foraging by yielding diminishing marginal returns for each seed discovered. This is referred to as a giving up density (GUD), or the density of seeds in the dirt when an individual kangaroo rats decides to stop foraging. The GUD is a measure of the point at which gain from foraging becomes lower than loss, and they can give a good estimate of selective foraging effort for rodents because the diminishing marginal return of each additional seed found prevents individuals from taking all the seeds or none of the seeds (Leaver and Daly 2003).

At each suitable burrow, separate trays were placed at distances of zero meters from a precinct and five meters from that same precinct for a paired experimental design. Again, trays were put out for the same foraging period as the local seed studies and moon phase was recorded. Lentils and oats were separated by hand when samples were re-weighed and fine dirt particles were sifted from seeds. Again, negative weight differences were rounded to zero following the assumption that no seeds were removed. Twenty-two of 96 samples were rounded to zero. Three total sites were selected from larger 140 by 140 meter grids; one on Center Well Pasture and two on Swain Pasture. This procedure was replicated for eight burrows on each site, yielding a total of 24 paired-tray samples. Individual burrows were selected by random number generation and were not used if they were within roughly 10 meters of another precinct. Suitable burrows were selected based on distance from other burrow precincts; the further apart precincts were on a site, the lower the probability that more than one individual would harvest at a seed tray in one night and the better suited the site would be. Previous night vision observations showed that giant kangaroo rats generally foraged around their own precinct area.

To analyze the data from these preference and distance trials, differences between percent removed of oats – percent removed of lentils were compared using a paired Wilcoxon signed-rank test.

Results

Local Non-Native and Native Seed Trials Using the selection ratio as a measurement method, giant kangaroo rats did not remove significantly greater amounts of non-native seeds relative to native seeds (non-native SR = 1.1 ± 0.010, native SR = 0.92 ± 0.062, $X^2 = 0.89$, df = 1, $p = 0.35$) (Figure 1).

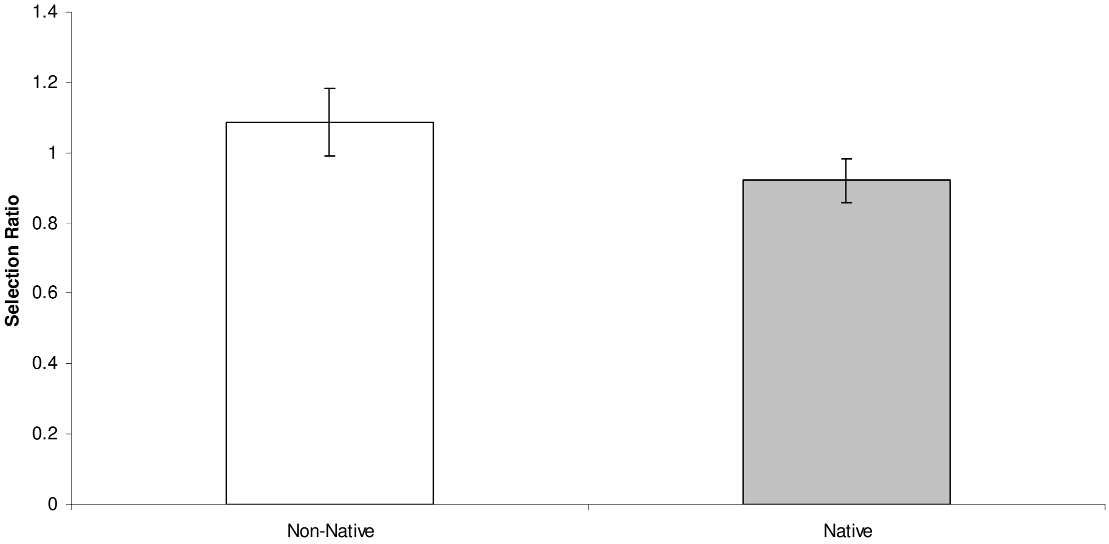

Figure 1. Average selection ratio of seeds removed for all sites with seed species grouped into native or non-native species. Bars represent mean ± 1 standard error. Native n = 168 seed piles; Non-Native n =112 seed piles.

The SSRs of seeds collected by the giant kangaroo rats were significantly different among plant species ($X^2 = 120$, df = 9, $p < 0.001$) (Figure 2, Table 2). Every species mean SSR showed no significant difference between at least three other seed species. Invasive ERCI had the highest average SSR (0.22 ± 0.015, n = 28) and was significantly different from every species except native LACA and native LENI. LACA (0.16 ± 0.015, n = 28) and LENI (0.15 ± 0.013, n = 28) had the highest SSRs for native species. Native ASLE had the smallest SSR on average (0.031 ± 0.0083, n = 28).

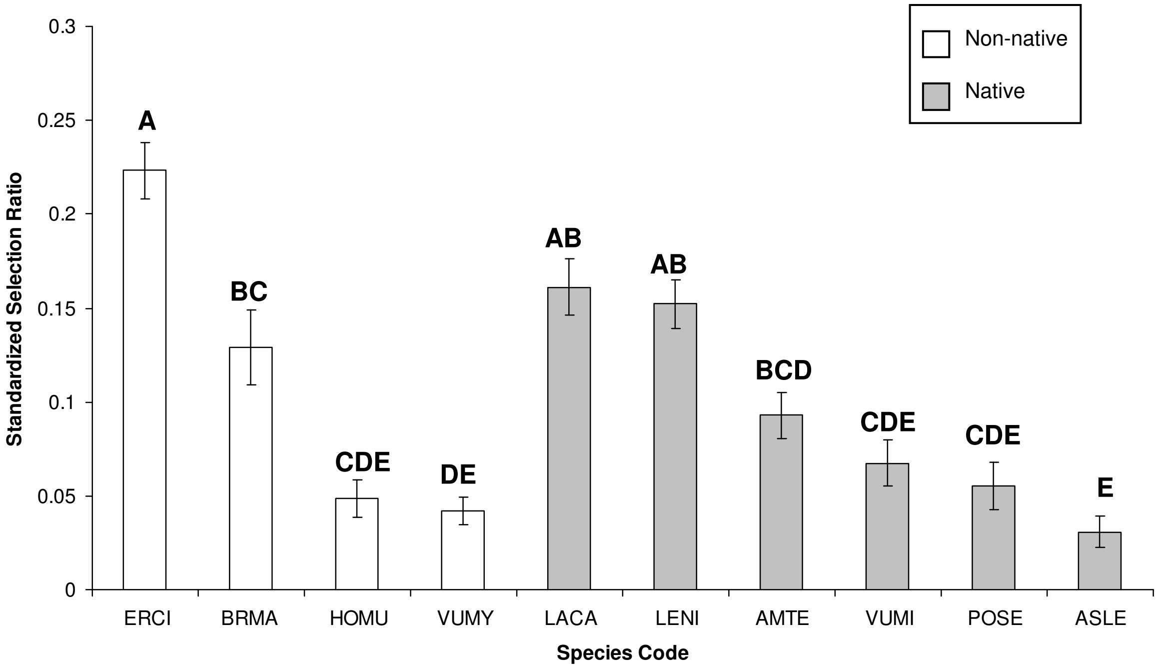

Figure 2. Species seed removal by giant kangaroo rats indexed by standardized selection ratios. Letters above bars are results of Tukey's HSD Test of rank sums of all species; seed species not connected by the same letter are significantly different. n_{total} = 280.

Table 2. Experimental removal data and general seed species information.

Species Code	Mean Standardized Selection Ratio	Seed Length (mm)	Non-Native/Native
ERCI	0.22 ± 0.015	5.5	Non-native
BRMA	0.13 ± 0.020	8.5	Non-native
HOMU	0.05 ± 0.020	6.0	Non-native
VUMY	0.04 ± 0.010	4.0	Non-native
LACA	0.16 ± 0.020	2.3	Native
LENI	0.15 ± 0.013	3.3	Native
AMTE	0.09 ± 0.013	3.3	Native
VUMI	0.07 ± 0.012	4.0	Native
POSE	0.06 ± 0.013	2.0	Native
ASLE	0.03 ± 0.010	3.0	Native

I did not find a significant difference between the amount of seed collected and the level of moonlight ($X^2 = 2.07$, df = 4, p = 0.72).

The nutritional metric with the strongest correlation to SSR was phosphorous with an R^2 value of 0.74 (Table 3). No other nutritional metrics had R^2 values greater than 0.5 or -0.5. Potassium (0.49) had the second-highest positive correlation and aluminum (-0.47) and total carbohydrate (-0.41) had the strongest negative correlations.

Table 3. Correlation between nutritional metrics and SSR.
n =1 for sample size of each nutritional metric.

Nutritional Metric	**Correlation with SSR (R^2)**
Fiber	-0.050
Sulfur	0.29
Phosphorus	0.74
Mg	0.61
Ca	0.28
Na	-0.21
Iron	-0.23
Aluminum	-0.47
Manganese	-0.05
Copper	0.26
Zinc	0.27
Moisture	0.13
Crude Protein	0.27
Crude Fat	0.12
Total Carbohydrate	-0.41
Nitrogen	0.27
Potassium	0.49
Seed length	0.20

Preference and Distance Trials A significant difference between percent removed of oats – lentils at 0 meter sites and 5 meter sites was found (0 meter: 0.002 ± 0.005, 5 meter: 0.02 ± 0.009, z = 73, p = 0.02, n = 24) (Figure 3).

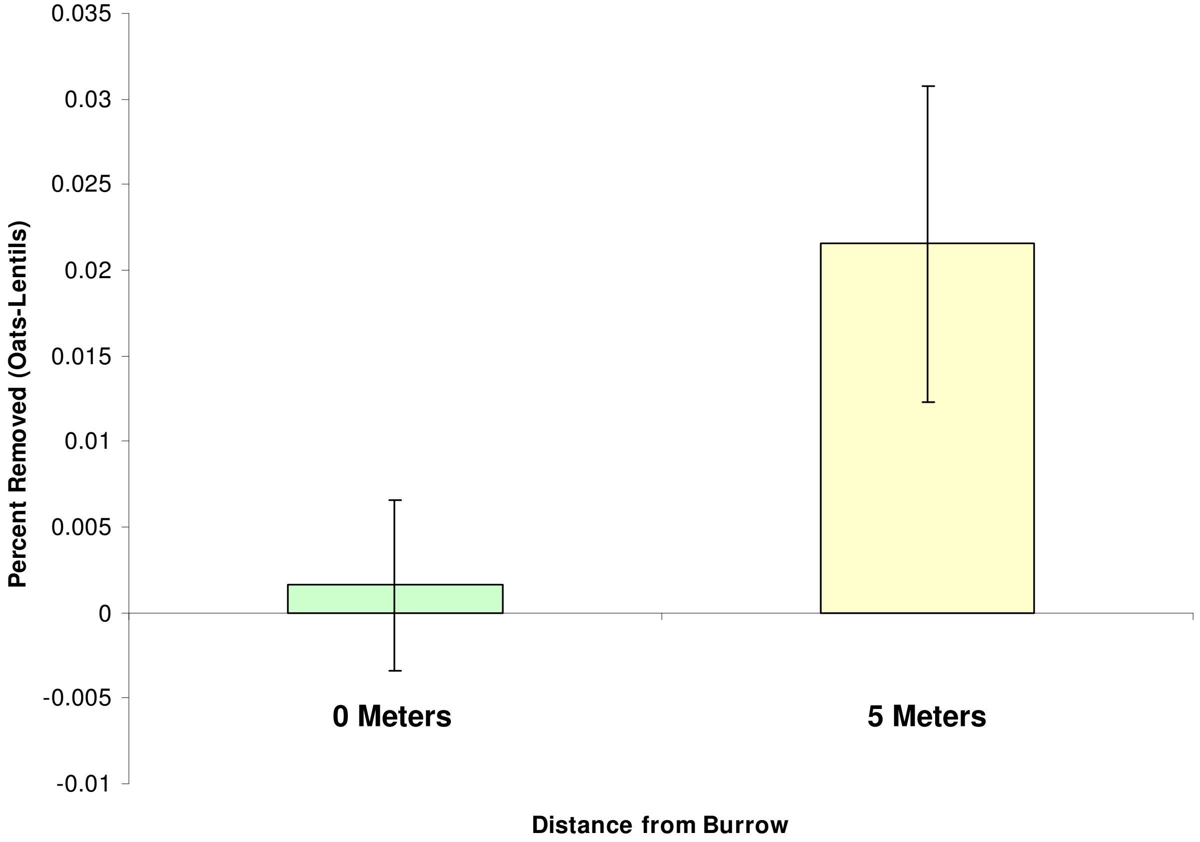

Figure 3. Mean difference in percentage of seeds removed (oats – lentils). Bars indicate ±1 standard error; n = 24 paired sets of trays.

Discussion

Local Non-Native and Native Seed Trials When presented with a selection of six native and four non-native local grasses and forbs, giant kangaroo rats did not remove non-native species in significantly greater amounts than they removed native species (Fig 1). Per site, kangaroo rats selected from non-native species 5 % more often than native species.

Among all species, invasive ERCI was removed the most (Fig. 2), but its SSR was not significantly different from two other seed species (LACA and LENI). Other than those three species, most species SSRs' were within 0.05 of one another and usually did not differ significantly. Preferences between averages of non-native and native seed removal seem to be driven by several species with especially high standardized selection ratios. Despite the lack of a general preference for non-native or native species, these results determined the several seed species that are preferred and could lead to species-focused management decisions. For example, Longland and Bateman (1998) discuss management strategies using seed dispersal in forgotten caches by desert granivores as an alternative to manual reseeding and replanting as an invasive vegetation management strategy; knowing which seed species the giant kangaroo rat prefers would be essential in structuring a similar management plan in this study site. Still, more research is needed in the multi-dimensional study of resource preferences of giant kangaroo rats to understand the overall effects a seed preference has on the distribution of a plant species. It is still not clear if preferences for ERCI, LACA, or LENI mean granivory is decreasing their abundance in the ecosystem or if seed dispersal and forgotten caches result in an increase in abundance of those preferred species.

It is important to note that the summer this study was conducted was one of the driest in the last several decades (J. Brashares, pers. comm.). The amount of rainfall during the spring and winter months is a strong determinant of vegetation abundance and preference could change as year-to-year availability changes. Future studies could consider vegetation abundance along with seed removal over several years to better understand how removal is explained by resource availability.

Distance and Preference Trials Foraging distance from burrow did significantly affect seed preference in this study, which supported the hypothesis that greater proportions of a higher quality food item would be removed as giant kangaroo rats foraged further away from their burrows (Fig. 3). While several other studies have also validated this hypothesis using factors like microhabitat (Leaver and Daly, 2003, O'Dowd and Hay) or moonlight (Bowers, 1988), distance traveled to forage is overlooked in predation risk studies in rodents. Spatially, giant kangaroo rat burrows cover extensive areas of the Carrizo Plain. Even though this study was conducted with seeds not available naturally, the results show that individuals will travel away from their own burrow for a seed species that is profitable enough. With this knowledge, future studies on hunting behavior of giant kangaroo rat predators and intraspecific behavior can be supported using behavioral characteristics of individuals. Knowing preferences shift with distance can also lead to future studies on grass species distribution on and between burrow areas. If this trend holds for naturally present species, it is possible that more vegetation with a lower nutritional preference could be found farther from multiple burrow areas. Thus, understanding how giant kangaroo rat behavior changes along a spatial gradient is important for protecting the species and could also lead to new insights about plant distribution.

Some limitations of this study could be built upon for future research on this effect. Finding an optimal distance from burrows is critical because many trays were over or under-foraged, potentially obscuring relative preferences. Also, seed choice was based on another study looking at different heteromyid rodents; because of their size and especially arid habitat, giant kangaroo rats may have clearer preferences among a different set of non-natural bait seeds.

Nutrient and Moonlight Analyses ERCI, BRMA, and HOMU have the three longest seeds, but none of these were significantly preferred over at least one smaller-seeded species. Additionally, no strong correlation was found between SSR and seed length (Table 3). I did not find support for my hypothesis suggesting that giant kangaroo rats would choose non-native seeds on the basis of seed size. However, Price (1983) found that while heteromyids don't seem to partition food only by selecting for one size or species of seeds, particle size has a greater effect on preference than any one nutritional component. More recent studies have cast doubt on the connection between seed size and preference, but Price (1983) acknowledges there still may be some correlation between the two factors. Other studies by Brown and Lieberman (1973) and Mares and Williams (1977) show that larger rodents would preferentially harvest relatively larger seeds available to them; the giant kangaroo rat is the largest species of kangaroo rats and may require larger seeds to compensate for energy consumption that is greater than other rodent species. Despite those past findings, seed size alone was not a strong indicator of kangaroo rat preference in this study.

Through a nutrient analysis, I found a relatively strong positive correlation between seed selection and phosphorous content, and a weaker positive correlation with potassium (Table 3). The strongest negative correlations were in aluminum and total carbohydrate, but these were not as strong as the correlation with phosphorous. Optimal foraging theory alone would predict that seeds with the greatest energy content would be preferred, but diet studies have shown that rodents will select other seeds to obtain specific nutrients (Frank 1988, Jenkins and Ascanio 1993). The strong positive correlation between SSR and phosphorus may be explained by this concept, as phosphorus is an important micronutrient for most animals (Wardlaw and Kessel 2002). Frank (1988) suggested that seed qualities like lipid, protein, carbohydrate, or moisture content would play a large role in rodent preferences, but this study showed weak trends with those nutrients. It is possible that giant kangaroo rats can acquire many of those nutrients in sufficient quantities from several seed species and showed no strong preference for one species in particular. Other factors that could affect selection may include volume of seeds presented, palatability of seeds, or even varying seasonal precipitation.

Moonlight was not found to significantly explain seed removal by itself or influence species selection. However, the p-value was close to 0.05. Other studies (Leaver and Daly, 2003, Bowers, 1988) have found that moonlight is an important part of seed selection. It is possible that in the giant kangaroo rat in this study system is not as susceptible to the increase in predation risk as other rodent species. More moonlight-centered studies on this system might yield a stronger answer to this question.

Giant kangaroo rats preferentially harvested non-native seed species on study sites on the Carrizo Plain, but did not become more selective as distance from their burrow increased when choosing between two bait seed species. Determining giant kangaroo rats' preference for non-native seed species is another effect contributing to a greater understanding of complex ecological behaviors. This is crucial because several studies have shown that kangaroo rats strongly effect species composition of vegetation in their environment. With increased funds and effort being put into the protection of endangered species and mitigation of negative effects of non-native vegetation, knowing seed preferences of the giant kangaroo rat could lead to more effective management of California's native ecosystems.

Acknowledgements

Thanks to Justin Brashares, Laura Prugh and Rebecca Wenk, Shelly Cole and the ES196 instructors, Susan Kishi and the SPUR program, and the Bureau of Land Management.

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