



## Mesquite establishment in arid grasslands: an experimental investigation of the role of kangaroo rats

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Kangaroo rats are thought to play a role in promoting the establishment of woody shrubs in arid grasslands by caching mesquite seeds. We examined this hypothesis experimentally by comparing mesquite establishment on plots from which kangaroo rats have been continuously removed for either 10 or 21 years to control plots with kangaroo rats present. Contrary to the above hypothesis, mesquite establishment was lowest on plots that contained kangaroo rats and highest on plots from which kangaroo rats have been absent for 21 years. We suggest that herbivory, either by kangaroo rats or lagomorphs, who were found to be more active on plots with kangaroo rats, more negatively affects mesquite seedling establishment than the potential positive effects of kangaroo rat seed-caching behavior in arid grasslands.

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### Introduction

Over time, the vegetation structure of arid grassland habitats around the world has changed dramatically; grass cover has declined and the density of woody shrubs has increased (e.g. Van Vegten, 1983; Scofield & Bucher, 1986; Archer, 1988; Friedel *et al.*, 1993). In south-western North America, these changes, symptomatic of desertification, have occurred on millions of hectares of desert grassland which now contain high densities of mesquite (*Prosopis*) and other woody shrubs (e.g. Buffington & Herbel, 1965; Hennessy *et al.*, 1983; Bahre, 1991; Archer, 1995).

The numerous hypotheses developed to explain this change in vegetation can be divided into those that primarily involve either abiotic or biotic mechanisms. Changes in regional climate, fire regimes or atmospheric CO<sub>2</sub> have been hypothesized to have played a major role in the conversion of grasslands to shrublands (e.g. Humphrey, 1949; Hastings & Turner, 1965; Wright & Bailey, 1982; Neilson, 1986; Idso, 1992; Brown *et al.*, 1997). Others have emphasized the importance of biotic factors, such as the introduction of large numbers of domestic livestock or changes in the abundance of

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native rodents such as prairie dogs (*Cynomys*) and kangaroo rats (*Dipodomys*) (e.g. Reynolds & Glendening, 1949; Brown & Archer, 1989; Bahre, 1991; Cox *et al.*, 1993; Weltzin *et al.*, 1997). While most researchers agree that several factors acting in combination contributed to historic increases in woody shrubs in the American Southwest, it has been difficult to determine the relative importance of each factor because historic data are generally lacking.

It is possible, however, to examine the role of these factors for recent shrub establishment. Here, we evaluate the role of kangaroo rats (*Dipodomys*) in affecting mesquite establishment. Several lines of evidence suggest that kangaroo rats may promote the establishment of mesquite and facilitate shrub invasion in arid grassland ecosystems. Kangaroo rats collect seeds of many species, including mesquite, and bury them in surface seed caches (e.g. Reynolds, 1958). Kangaroo rats often remove the seed coat from collected mesquite seeds prior to caching which promotes rapid germination of seeds (Reynolds & Glendening, 1949; Cox *et al.*, 1993). In addition, some studies report a positive correlation between the density of mesquite seedlings and the abundance of Merriam's kangaroo rat, *Dipodomys merriami* (Paulsen, 1950; Reynolds, 1950).

Kangaroo rats may also facilitate mesquite establishment indirectly by affecting grass cover. Mesquite seeds which germinate on sites with high perennial grass cover suffer significantly higher seedling mortality than seeds which germinate on sites with low grass cover because perennial grasses are superior competitors (Glendening & Paulsen, 1955; Bush & Van Auken, 1991, 1995). Kangaroo rats clip perennial grasses which may enhance grass mortality (Kerley *et al.*, 1997) and perennial grass cover is known to increase following the long-term removal of kangaroo rats (Brown & Heske, 1990; Heske *et al.*, 1993; Smith *et al.*, 1997). As such, kangaroo rat activity appears to suppress perennial grass cover which can facilitate mesquite establishment.

Alternatively, kangaroo rat behavior may negatively affect mesquite establishment. While *D. merriami* is primarily a granivore, as much as 5% of its diet can include other vegetative parts (Reynolds, 1958). Kangaroo rats are known to clip vegetation (Kerley *et al.* 1997) and so one possibility is that kangaroo rats kill young mesquite seedlings by clipping (Glendening & Paulsen, 1955), but data regarding kangaroo rat herbivory on mesquite seedlings are sparse.

Here, we examined relationships between kangaroo rat abundance and mesquite establishment on a long-term study site in south-eastern Arizona. The site contains plots on which kangaroo rats have been excluded continuously for 10 and 21 years and plots on which kangaroo rats have been continuously present. We examined the density of small-stemmed mesquite plants to determine how the long-term presence or absence of kangaroo rats has affected mesquite establishment rates.

## Methods

In 1977, a 20-ha grazing exclosure was established on the Cave Creek bajada, near Portal in southeastern Arizona (Brown & Munger, 1985). Vegetation consists of upper elevation Chihuahuan Desert shrubs including *Acacia constricta*, *Ephedra trifurca*, *Flourensia cernua*, *Gutierrezia sarothrae*, *Prosopis glandulosa*, and scattered perennial grasses (Heske *et al.*, 1993; Valone & Kelt, 1999). Historic records indicate that the site occurred in a transition zone between open grassland and shrubland in the 19th century and that woody shrubs increased greatly in abundance by the early 20th century (Valone & Kelt, 1999).

Within the exclosure, 24 0.25-ha plots were established. The experimental plots are surrounded by wire mesh and contain gates of different size that regulate access by rodents (see Brown & Munger, 1985 for details). Plots with large gates (3.7 × 5.7 cm) allow access to all rodents. Plots with small gates (1.9 × 1.9 cm) prevent access by kangaroo rats but allow all other smaller rodents to freely use the plots. Plots with no

gates prevent access by all rodents. Thus, with respect to rodents and for present purposes, we distinguish two types of plots. The large-gated plots are control plots. The small-gated plots and plots with no gates are lumped together as kangaroo rat removal plots.

From 1977 to 1987, there were 16 control plots and eight kangaroo rat removal plots. In 1988, six of the control plots were converted into new kangaroo rat removal plots (Heske *et al.*, 1994). We examined eight old kangaroo rat removal plots (established in 1977), six new kangaroo rat removal plots (established in 1988) and 10 control plots (Valone & Brown, 1996).

For one night each month beginning in July 1977, rodents on all plots were counted (see Brown & Munger, 1985 for details). Three species of kangaroo rats occur at the site. *Dipodomys merriami* has consistently been the most abundant species over the 21-year period (5–15 individuals  $\text{ha}^{-1}$ ). *Dipodomys ordii* has been consistently rare (< four individuals  $\text{ha}^{-1}$ ). *Dipodomys spectabilis* was fairly common from 1977 to 1983 (5–10 individuals  $\text{ha}^{-1}$ ), but has been rare since (< four individuals  $\text{ha}^{-1}$ ) (Valone & Brown, 1996). Thus with respect to kangaroo rats, control and kangaroo rat removal plots differed mainly in the abundance of *D. merriami*.

The density of kangaroo rats on the treatment plots has differed significantly over time. Approximately 1–4 kangaroo rats have been captured on each control plot each month while kangaroo rats have been virtually absent on removal plots (Zeng & Brown, 1987; Brown & Zeng, 1989; Heske *et al.*, 1994; Valone & Brown, 1996).

In July 1998, we censused the mesquite shrubs on all plots. Each individual was mapped and its maximum basal stem diameter was measured. Many shrubs were multi-stemmed (e.g. Haas *et al.*, 1973). We treated a single continuous canopy emanating from the multiple stems as a single individual and measured the largest basal stem for that individual (Scifres *et al.*, 1971).

In this paper, we are interested in mesquite shrub recruits that became established since 1977 at the start of the treatments. Mesquite growth rate depends on soil moisture and ranges from 1 to 4 mm in basal stem diameter per year in Arizona and Texas (Glendening & Paulsen, 1955; Scifres *et al.*, 1971; Haas *et al.*, 1973; Archer, 1988). We have no data to estimate the basal stem diameter growth rates for mesquite shrubs at our site. In lieu of such data, we assume both that the published range is a good approximation and that stem diameter growth rates do not differ with shrub size at our site. Then we examined our data several ways by establishing maximum basal stem diameter cutoff values of different size. We first examined only those shrubs that had a basal stem diameter less than 10.0 mm because we are confident that all such individuals established after 1977. We then increased this cut off to 12.5 mm, then to 15.0 mm and finally to 20.0 mm. These larger cutoff values increase the sample size of individuals in our study and should include, but with decreasing certainty, very few, if any, individuals that established prior to 1977. If basal stem diameter growth rates of mesquite shrubs at our site are less than 1 mm per year, only the highest cutoff may include individuals established prior to 1977. If basal stem diameter growth rate of mesquite on our site is greater than 1 mm per year, then all of our cutoff values will conservatively ensure that we are examining only individuals that recruited after 1977. We also assumed that all mesquites with stem diameter > 20.0 mm were present on the plots in 1977; these are referred to as large-stemmed individuals. For each maximum stem diameter cutoff value, we examined differences in the number of individuals per treatment plot using a nonparametric Kruskal–Wallace ANOVA.

One factor that may affect the number of mesquite recruits per plot is the number of seeds produced per plot by large-stemmed individuals. While we do not have seed set data for shrubs at our site, we assume that large-stemmed (older) trees produce more seed than smaller-stemmed young trees. To determine if the number of recruits per plot was affected by the number of large-stemmed shrubs, we

**Table 1.** Mean (S.E.) number of shrubs per treatment plot for different maximum stem diameter cut-off values and results of Kruskal-Wallis ANOVA tests. Each cutoff value includes all shrubs of stem size less than the cut-off size

Treatment	Basal stem diameter category (mm)				
	Small-stemmed recruits				Large-stemmed recruits
	< 10.0	< 12.5	< 15.0	< 20.0	> 20.0
Control	0.6(0.4)	1.5(0.5)	2.3(0.7)	2.9(0.7)	1.4(0.4)
New kangaroo rat removal	3.5(1.3)	5.7(1.9)	7.0(2.0)	9.2(2.9)	2.7(1.7)
Old kangaroo rat removal	6.4(4.3)	9.1(5.5)	10.1(5.8)	12.1(6.4)	3.3(1.0)
<i>p</i> value	0.03	0.06	0.05	0.06	0.54

calculated the Spearman rank correlation coefficient of the number of large-stemmed shrubs versus the number of recruits per plot using each of our diameter cutoff values for the recruits.

## Results

We recorded 239 mesquite individuals on the 24 study plots. The number of mesquite plants per plot varied from 1 to 66 (mean = 10.2, S.E. = 2.8). Maximum basal stem diameters ranged from 3.2 to 79.6 mm (mean = 17.8, S.E. = 1.0).

Treatment plots did not differ significantly in the number of large-stemmed mesquite shrubs (> 20.0 mm; Table 1). However, treatment plots differed conspicuously in the number of small-stemmed mesquite recruits (Table 1). Old kangaroo removal plots contained an approximately 4–10-fold greater number of recruits than control plots while new kangaroo removal plots contained approximately 3–6 times more recruits than control plots across all stem diameter cutoffs examined (< 20.0 mm, Table 1).

We found no evidence that the number of mesquite recruits per plot was correlated with the number of large-stemmed individuals. For each cutoff examined, the number of recruits was not significantly correlated with the number of large-stemmed individuals: all correlations were clustered around zero (Table 2).

## Discussion

In direct contrast to the prediction of the kangaroo rat hypothesis, we found significantly greater numbers of mesquite shrub recruits on plots from which kangaroo rats have long been absent compared to plots on which kangaroo rats have continuously been present. The effect of kangaroo rat removal on mesquite establishment is clear from three patterns present in Table 1. First, the number of large-stemmed individuals was similar across all treatment plots thus greatly reducing the possibility that observed recruitment differences were due to differences in seed set across treatment plots. Second, the number of mesquite recruits per plot was similar to the number of large-stemmed individuals on the control plots, an indication that recruitment on such plots has been fairly constant over time. In contrast, the number of mesquite recruits on removal plots was two to four times higher than the number of large stemmed individuals, indicating higher levels of recent recruitment on these plots. And third, the number of mesquite

**Table 2.** Spearman rank correlation coefficients ( $R_s$ ) between the number of large-stemmed mesquite ( $> 20$ -mm stem diameter) and the number of small-stemmed mesquite recruits for each cutoff value

Basal stem cutoff value	$R_s$	$p$
10.0 mm	-0.15	0.50
12.5 mm	-0.08	0.70
15.0 mm	0.10	0.96
20.0 mm	0.18	0.40
$n = 24$ plots		

recruits on plots from which kangaroo rats have been absent for 10 years (new kangaroo rat removal plots) was intermediate between the number on control plots and the number on plots from which kangaroo rats have been absent for 21 years (old kangaroo rat removal plots). These patterns, taken together, strongly suggest that in the absence of kangaroo rats, mesquite establishment rates over the duration of the study have been significantly higher than on plots where kangaroo rats have been present.

These data are inconsistent with the hypothesis that kangaroo rat caching behavior promotes high levels of mesquite establishment. Our results do not necessarily imply, however, that kangaroo rat caching behavior does not affect mesquite seedling establishment. Kangaroo rats cache mesquite seeds and uncollected cached seeds germinate (Reynolds & Glendening, 1949). It is even possible that mesquite plants became established on control plots as a result of kangaroo rat caches. But, our data demonstrate that in the absence of kangaroo rats, mesquite seedlings establish at higher rates than in their presence.

One factor that affects mesquite seedling establishment is competition from perennial grasses (Glendening & Paulsen, 1955; Bush & Van Auken, 1991, 1995). At our site, however, perennial grasses were more abundant on kangaroo rat removal than on control plots, at least during summers of high rainfall in the late 1980s (Brown & Heske, 1990; Heske *et al.*, 1993; Smith *et al.*, 1997). Thus, the removal plots should have been less favorable sites for establishment and differences in grass cover (competition) cannot explain the higher recruitment of mesquite shrubs following kangaroo rat removal.

It seems most likely that differential establishment of mesquite shrubs on treatment plots involves different levels of herbivory. Mesquite seedling mortality can be quite high if young seedlings are subject to herbivory (Paulsen, 1950). Thus, differential kangaroo rat herbivory on mesquite seedlings could explain the observed patterns. Mesquite seedling mortality via kangaroo rat herbivory has been proposed (Glendening & Paulsen, 1955) and kangaroo rats do include some green foliage in their diets (Flake, 1973; Kerley & Whitford, 1994).

Kangaroo rats, however, are not the only potential herbivore. Lagomorphs are known to feed on mesquite seedlings (e.g. Turkowski, 1975; Glendening & Paulsen, 1955; Daniel *et al.*, 1993) and one study has shown that mesquite shrub cover is higher on long-term lagomorph exclusion plots (Havstead *et al.*, 1999). Both desert cottontail (*Sylvilagus auduboni*) and black-tailed jackrabbits (*Lepus californicus*) have been seen on the study plots and low-statured mesquite shrubs at the site show evidence of herbivory (personal observation).

Jackrabbits are too large to pass through the gates and instead must enter plots by jumping the fences. Small cottontails can pass through the control plot gates (personal observation) and can jump the fences. We suspect the fences limit lagomorph activity on the plots if individuals are reluctant to jump the fences. However, overall lagomorph

activity may be higher on control plots than on kangaroo rat removal plots since small cottontails can move through the larger gates on control plots.

To evaluate this hypothesis, we estimated lagomorph activity on plots by conducting a standardized lagomorph pellet census 21–26 July 1999 (*sensu* Westoby & Wagner, 1973; McAdoo *et al.*, 1987). On each experimental plot, we established 49 2-m radius circle quadrats in an equally spaced  $7 \times 7$  array. We recorded the presence or absence of lagomorph pellets in each quadrat. For each plot, we tallied the total number of quadrats that contained pellets (0–49). Lagomorph activity varied greatly on the plots with the number of quadrats containing pellets ranging from 0 to 24 (mean = 9.3, S.E. = 1.3). Lagomorph activity was significantly higher on control than removal plots: an average of 12.1 (S.E. = 1.3) quadrats contained pellets on control plots compared to an average of 7.2 (S.E. = 2.3) quadrats on removal plots (one-tailed *t*-test,  $p = 0.03$ ). Thus, differential lagomorph herbivory remains an alternative hypothesis for the observed patterns.

Unfortunately, the current experimental design does not allow us to distinguish the relative roles of kangaroo rat from lagomorph herbivory on mesquite seedling establishment. Re-examination of previous data, however, demonstrates that herbivory strongly influences mesquite seedling establishment. Paulsen (1950) found that mesquite seedlings open to rodents suffered much higher mortality than seedlings protected from rodents: data he used to support the kangaroo rat hypothesis. In Paulsen's study, however, mesquite seedlings were protected by a 0.6-cm wire mesh cone that would also have prevented herbivory by lagomorphs. Thus, protection from rodents and lagomorphs resulted in the high survivorship of mesquite seedlings observed: a pattern similar to that of our study. Such data are consistent with the idea that herbivory by kangaroo rats or lagomorphs, strongly affects mesquite establishment via high mortality of seedlings.

In sum, our findings do not support the hypothesis that kangaroo rat caching behavior promotes widespread mesquite establishment. On the contrary, we observed significantly higher mesquite establishment on long-term kangaroo rat removal plots. We suggest that herbivory by lagomorphs or kangaroo rats may inhibit mesquite shrub establishment more strongly than kangaroo rat caching behavior promotes it. Additional work will be required to elucidate the relative importance of kangaroo rat and lagomorph behavior on vegetation structure in arid grassland ecosystems.

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