# Jackrabbit (*Lepus californicus*) herbivory changes dominance in desertified Chihuahuan Desert ecosystems

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## Abstract

This study addressed the question: can herbivory by a medium size herbivore, black-tail jackrabbits (*Lepus californicus*), change dominance in desertified ecosystems dominated by two species of shrubs. Shrubs that were pruned by jackrabbits in plant communities dominated by creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*) were compared to shrubs not browsed by the rabbits. In the mixed shrub area, herbivory on *F. cernua* resulted in death of 46.6% of the shrubs, compared to only 4.8% of *L. tridentata* shrubs. There was no evidence of jackrabbit browsing of dead *F. cernua* in a tarbush monoculture area. The canopy volumes of *F. cernua* plants that survived repeated browsing were significantly smaller than predicted based on unbrowsed plants with the same basal stem areas. Jackrabbit browsing resulted in increased canopy volume of creosotebush shrubs. Creosotebush average canopy volume significantly exceeded predicted values because of compensatory growth of stems from nodes below the severed point. Close spatial association of lightly browsed creosotebushes with heavily browsed tarbush may be a factor contributing to low utilization of creosotebush stems by jackrabbits. Differential browsing by the rabbits is shifting these ecosystems toward an *L. tridentata* monoculture.
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## 1. Introduction

The most widespread result of desertification worldwide during the past two centuries has been the loss of grasslands and the establishment of shrubs and small trees in the former grasslands (Whitford, 2002). Changes in life form and species composition of the vegetation plus increased erosion by wind and water has been attributed to heavy grazing by livestock plus variation in rainfall resulting in drought (Archer, 1994; Buffington and Herbel, 1965; Grover and Musick, 1990). The Chihuahuan Desert in North America was primarily grassland in the 1850s and was rapidly converted to ecosystems dominated by creosotebush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*) and tarbush (*Flourensia cernua*) (Buffington and Herbel, 1965). When grasslands transition to shrublands, the resulting shrub dominated ecosystems are considered to be alternate stable states that resist attempts to re-establish grassland (Gibbens et al., 2005; Whitford, 2002). In some desertified ecosystems, the vegetation may still be changing albeit at a much slower rate. Such changes in plant community structure may result from activities of animals, which is an unappreciated role of animals in arid ecosystems.

In addition to livestock grazing, vegetation dynamics are directly and indirectly affected by animal activities (Chew, 1974; Chew and Whitford, 1992; Curtis et al., 2000; Steinberger and Whitford, 1983; Whitford and Kay, 1999). In the Chihuahuan Desert, the black-tailed jackrabbit (*Lepus californicus*) is the only mammalian herbivore that has been documented to feed on creosotebush (Dabo, 1980; Jaeger, 1948). Jackrabbits feed on shrubs primarily during the winter when there is little or no green vegetation available (Currie and Goodwin, 1966; Steinberger and Whitford, 1983; Westoby, 1980). Although availability of desirable forage largely determines jackrabbit diets, they do feed preferentially and utilize plants in different proportions from their relative abundance (Johnson and Anderson, 1984). Desertified landscapes in the Chihuahuan Desert include areas where creosotebush and tarbush are co-dominants and areas where these shrubs are essentially monotypic dominants. In areas where creosotebush and tarbush were co-dominant, we observed what we thought to be differential pruning of stems by jackrabbits on these species. Therefore, we designed a study to answer the following questions: (1) Does jackrabbit pruning affect the long-term growth characteristics of the shrubs? (2) Does differential pruning of one species potentially affect the species composition of the area? (3) Is there evidence that jackrabbit pruning of stems contributes to the mortality of either shrub species.

Following stem browsing by jackrabbits, shrubs often exhibit compensatory growth, producing multiple new shoots from nodes below the cut (Steinberger and Whitford, 1983). In many cases, heavy browsing changes the plant morphology, creating a shrub volume smaller than expected, with much denser foliage in comparison to unbrowsed shrubs. It has been suggested that heavy browsing enhances the plant's vigor and survivorship due to compensatory growth. We compared compensatory growth responses of *L. tridentata* and *F. cernua* in different topographic locations with different proportions of shrubs.

## 2. Methods

Two study sites were on the piedmont slopes of the Dona Ana Mountains in the northern Chihuahuan Desert of southern New Mexico. Elevation varies from 1200 to

1385 m. One study site was located at the lower piedmont slope approximately 500 m from the edge of the ephemeral lake at the terminus of the watershed. The second site was located on the upper piedmont slope where the surface was dissected by numerous small drainage channels.

The study was conducted on landscape units with creosotebush (*L. tridentata*) as the dominant shrub mixed with tarbush (*F. cernua*) as subdominant. These sites were compared with an area dominated by *F. cernua* in essentially a monoculture on a run-on area with clay-loam soils.

On the lower slope we established 20 plots of $6 \times 10$ m in which we measured the height and diameter of each shrub recording dead stems and stems that had been browsed by jackrabbits in the past. Canopy volume of *L. tridentata* was estimated from height and diameter using the equation for an inverted cone (Ludwig et al., 1975). Canopy volume of *F. cernua* was calculated as the volume of a cylinder using canopy height and diameter. In order to determine the effect of browsing on the shrub, we measured the diameters of all stems of each shrub at ground level or at the junction of the stem and root crown. The sum of the diameters of basal stems of a shrub provided the best predictor of canopy volume (Figs. 1 and 2). We used the stem diameter data with the canopy volume data of unbrowsed or lightly browsed shrubs to develop regressions to predict the canopy volume and biomass of the shrubs in the absence of jackrabbit browsing. On all shrubs that had been browsed by jackrabbits, we estimated the percent of stems that had been browsed. Stems that had been browsed by jackrabbits were characterized by an angular cut on stems greater than 2.0 mm diameter.

Regressions of plant volume of unbrowsed plants against the sum of basal stem diameters yielded $r^2$ of 0.90 for *F. cernua* and 0.86 for *L. tridentata*. Maximum values for predicted plant volume were set according to the largest individual measured in the field, $3.59 m^3$ for tarbush and $3.62 m^3$ for creosotebush (Figs. 1 and 2). The regression equation for calculating *F. cernua* volume in the absence of herbivory is: $y = 0.0131e^{18.298x}$;
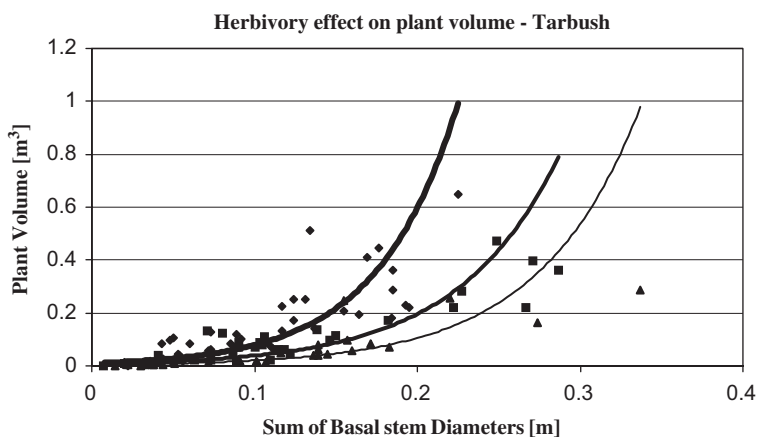


Fig. 1. The effect of different browsing levels on the actual canopy volume in comparison to the predicted canopy volume of tarbush (*Flourensia cernua*). ♦/—— Browsing level 0 < 10% of stems browsed; $r^2 = 0.67$ (Diamonds), ■/—— Browsing level 1; 10–50% of stems browsed; $r^2 = 0.70$ (Squares), ▲/—— Browsing level 2; > 50% of stems browsed; $r^2 = 0.73$ (Triangles).

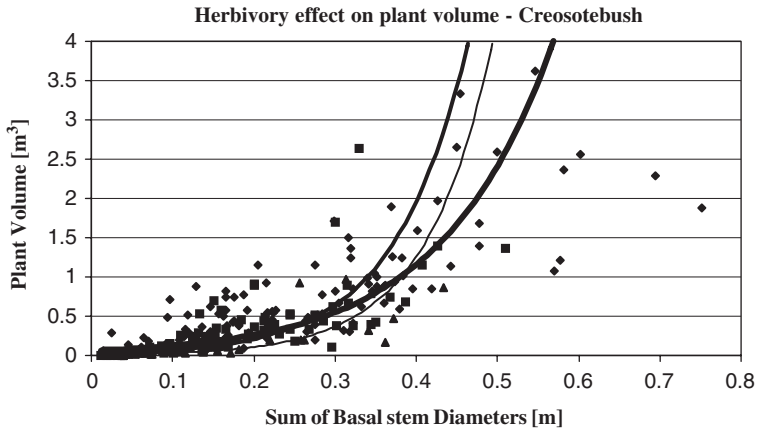**Herbivory effect on plant volume - Creosotebush**



Fig. 2. The effect of herbivory on creosotebush (*Larrea tridentata*) canopy volume in comparison to the predicted canopy volume based on plants with no evidence of prior browsing by jackrabbits. ♦/▬▬ Browsing level 0; <10% of stems browsed; $r^2 = 0.65$ (Diamonds), ■/▬▬ Browsing level 1; 10–50% of stems browsed; $r^2 = 0.61$ (Squares), ▲/▬▬ Browsing level 2; >50% of stems browsed; $r^2 = 0.64$ (Triangles).

$R^2 = 0.9004$ where $y$ is the plant volume and $x$ is the sum of the diameters of the basal stems. The regression equation for calculating plant volume of *L. tridentata* that exhibit no evidence of previous browsing is: $y = 0.0353e^{9.787x}$; $R^2 = 0.8638$ where $y$ is the volume and $x$ is the sum of diameters of basal stems. Browsed shrubs were assigned to one of three categories: (1) negligible signs of previous browsing to less than 10% clipped branches, (2) moderate signs of browsing, between 10% and 50% clipped branches, (3) heavy browsing, >50% clipped branches and/or a morphologic change in plant structure (morphologic change is a common outcome of heavy browsing in both species).

On the upper piedmont we examined the effect of water availability on shrub pruning by jackrabbits. We recorded canopy diameter and height of all shrubs on a total of 15 pairs (one plot on the ridge paired with a plot in the drainage channel) of $10 \times 4$ m plots. We recorded heavy browsing only. Relative abundance and frequency of heavy browsing was calculated for both shrub species, and a drainage channel/ridge comparison was made for both within and between species by ANOVA.

At the tarbush monoculture site we measured the canopy diameter and height of shrubs that exhibited signs of browsing and measured the diameters of the basal stems of the browsed plants in three $10$ m $\times 5$ m plots. Canopy area of all remaining shrubs was calculated from canopy diameter measurements.

Volume measurements were translated into biomass using regression equations found by Ludwig et al. (1975). Creosotebush (*L. tridentata*): $y = 5836 \times \pi/3r^2h$; $r^2 = 0.97$; Tarbush (*F. cernua*): $B = 1987 \times 4/3\pi rh^2$; $r^2 = 0.91$ where $B$ is mass in grams, $r$ is the canopy radius in m, and $h$ is the plant height in m.

All data were subjected to statistical analysis of variance using the SAS model (ANOVA, Duncan's multiple range test and Pearson correlation coefficient) and were used to evaluate the differences between separate means. Percent data were arc sine transformed for analysis. Differences obtained at level of $p < 0.05$ were considered significant.

## 3. Results

The present dominance of creosotebush in the lower piedmont area is obvious in both relative abundance ($2391 \pm 1285$ *L. tridentata* shrubs ha$^{-1}$) and biomass ($526.6 \pm 241 \, \text{kg ha}^{-1}$). Tarbush was less abundant ($1658 \pm 966$ shrubs ha$^{-1}$, $p < 0.05$) and was represented by lower biomass ($222.6 \pm 138 \, \text{kg ha}^{-1}$, $p < 0.05$). Nearly one-half of the *F. cernua* shrubs ($46.6 \pm 27.7\%$) were dead while only $4.8 \pm 11.4\%$ of the *L. tridentata* were dead. Sixty-three percent of the dead tarbush in this comparison exhibited evidence of moderate to heavy browsing before the shrubs died and a reduction of 50.6% of the predicted size. Significantly more tarbush shrubs were heavily browsed than creosotebush ($32.5 \pm 23.5\%$ vs. $10.9 \pm 10.1\%$, respectively, $p < 0.05$) (Fig. 1, Table 1).

The effect of jackrabbit browsing on plant size was evaluated by comparing the actual volume measurements of all plants in the lower piedmont study plots with the values predicted by the regression equations using the sum of basal stem diameters (Figs. 1 and 2). *F. cernua* plants were significantly smaller than predicted, only $62.7 \pm 39.41\%$ of the predicted volume. *L. tridentata* plants exceeded the predicted size and were $130.3 \pm 57.16\%$ of the predicted volume. The negative effect of heavy browsing on the actual volume is apparent in both shrub species. Heavily browsed *L. tridentata* shrubs were only $62.3 \pm 36.4\%$ of the predicted volume. Tarbush shrubs exhibited a significant decrease in plant volume even under the moderate browsing and were only $55.3 \pm 40.0\%$ of the predicted volume. The *F. cernua* shrubs that had been heavily browsed were only $36.6 \pm 30.0\%$ of the predicted volume.

Of a total of 287 *L. tridentata* shrubs on the lower piedmont plots, 48 plants exceeded the predicted volume by more than double ($> 200\%$). Thirty-three of these shrubs were growing within less 2 m from a dead *F. cernua* (measured as the distance between centers of the stem crowns). With the exception of three creosotebush shrubs, the remaining 12 shrubs were at the edge of the plot and no data on nearest neighbor tarbush was available. None of the 48 *L. tridentata* exhibited evidence of heavy browsing and 13 of the shrubs exhibited moderate browsing. The relationship between *L. tridentata* stems severed by rabbits and subsequent plant growth is complex. Creosotebush exhibiting evidence of moderate levels of browsing in years preceeding our study grew to larger volumes than their unbrowsed counterparts (Fig. 2). Heavy browsing also resulted in slightly larger plant volumes and the morphologies of these plants were markedly modified.

On the upper piedmont, creosotebush was dominant and tarbush density was higher in the drainage channels than on adjacent ridges. Tarbush was absent on six of the 15 ridge plots. There was no significant difference in abundance of creosotebush on ridges and along drainage channels. On the ridges $35.2 \pm 36.7\%$ of tarbush shrubs were heavily

Table 1

Proportion of shrubs on the lower piedmont plots with severed stems resulting from browsing by jackrabbits in the three categories expressed as percent of all stems

| Proportion stems browsed (%) | Larrea tridentate (%) | Flourensia cernua (%) |
|---|---|---|
| <10 | $57.5 \pm 19.7^{A}$ | $31.8 \pm 16.5^{a}$ |
| 10–50 | $31.6 \pm 14.9^{B}$ | $34.9 \pm 19.8^{b}$ |
| >50 | $10.9 \pm 10.1^{C}$ | $32.6 \pm 23.5^{c}$ |

Values with dissimilar letters are significantly different ($p < 0.05$).

Table 2
Comparison of shrub densities and the proportion of shrubs that exhibited evidence of heavy browsing on the upper piedmont sites

| Parameter | Location | *Larrea tridentata* (%) | N | *Flourensia cernua* (%) | N |
|---|---|---|---|---|---|
| Number shrubs ha$^{-1}$ | Ridge | $2450 \pm 1300^{Ac}$ | 15 | $300 \pm 275^{ad}$ | 15 |
| Number shrubs ha$^{-1}$ | Drainage channel | $1832 \pm 950^{Bc}$ | 15 | $1065 \pm 642^{bD}$ | 15 |
| Percent heavy browsing | Ridge | $4.5 \pm 9.7^{eg}$ | 15 | $35.2 \pm 36.7^{Eh}$ | 9 |
| Percent heavy browsing | Drainage channel | $0.66 \pm 2.6^{Fg}$ | 15 | $21.4 \pm 29.6^{fh}$ | |

N = number of plots with species present.
Values with dissimilar letters are significantly different ($p < 0.05$).

browsed compared to only $4.5 \pm 9.7\%$ creosotebush. Jackrabbits preferentially pruned tarbush shrubs in both locations but the differences in proportion of *F. cernua* shrubs pruned compared to *L. tridentata* shrubs was greatest in the drainage channels (Table 2).

The tarbush monoculture area supported an estimated 5870 *F. cernua* plants ha$^{-1}$. At the tarbush monoculture site, 9.1% of the *F. cernua* shrubs were dead. However, none of the dead shrubs exhibited signs of previous browsing by rabbits. The fraction of all tarbush that exhibited some sign of browsing by rabbits shrubs varied by nearly an order of magnitude among the plots (3.1%–28.1%). An average of 14.8% of the *F. cernua* shrubs had signs of previous browsing by rabbits. With one exception, all of the heavily browsed *F. cernua* shrubs were located in one small (4 m × 5 m) area in one plot. Heavily browsed tarbush shrubs were only 4.3% of the predicted volume of un-browsed shrubs whereas the moderately browsed tarbush averaged 31.0% of the predicted volume.

## 4. Discussion

Our measurements indicate that current creosotebush biomass is approximately five times higher than tarbush, in an area where *F. cernua* was documented as the dominant shrub species until less than a century ago (Gibbens et al., 2005). On both locations on the watershed, jackrabbits exhibited a clear preference for pruning stems of tarbush in areas where creosotebush was the dominant shrub. When stem pruning rates are combined with a density ratio of 2.13 creosotebush to 1 tarbush and a biomass ratio of 5.32 to 1, respectively, the differential selectivity of jackrabbits for the less abundant tarbush shrubs is re-emphasized. At the upper piedmont, on the ridges where the abundance ratio was 5.5 creosotebush to 1 tarbush, the chances of *F. cernua* experiencing heavy browsing were 8 times greater than *L. tridentata*. The most extreme jackrabbit preferential feeding behavior was found in the drainage channel plots where water stress is lessened, and an abundance ratio of 2.5–1 was documented. There, the chances of a tarbush shrub for suffering heavy browsing stress were over 32 times greater than those of a creosotebush.

*L. tridentata* shrubs exhibit compensatory growth in response to loss of stems by jackrabbit pruning (Steinberger and Whitford, 1983). The compensatory growth in response to jackrabbit cutting of stems accounted for previously browsed creosotebushes achieving a plant volume greater than that of unbrowsed shrubs with the same basal stem diameters. However, there was no evidence of compensatory stem growth in *F. cernua* shrubs that were moderately or heavily browsed by rabbits. In monotypic stands of

*F. cernua*, the plants that exhibited evidence of jackrabbit browsing no evidence of compensatory growth by new stems from lateral nodes below the severed end of the stem. However, the leaves on the severed stems were visibly larger than the leaves on unbrowsed plants and this is a type of compensatory growth. The inability of tarbush shrubs to compensate for the loss of stems to browsing by jackrabbits accounts for the high mortality rates of tarbush in the mixed shrub sites. The lack of evidence for jackrabbit browsing enchanced mortality of tarbush in the monoculture plots suggests that the soil differences and absence of competition by *L. tridentata*, may account for the survival of shrubs that experienced loss of all stems of suitable size to be severed by rabbits.

*L. tridentata* shrubs in close proximity to dead *F. cernua* shrubs on the lower piedmont exhibited greatly enhanced growth and low levels of stem loss to pruning by jackrabbits. This suggests that *L. tridentata* may benefit from the presence of *F. cernua* as a nearest neighbor because jackrabbits prefer to prune stems of the tarbush. This hypothesis is supported by data from a 50+ -year study of jackrabbit exclosures that showed significant reductions in tarbush canopy cover in jackrabbit access plots in comparison to plots with jackrabbits excluded (Gibbens et al., 1993). Lower rates of pruning on *L. tridentata* shrubs associated with drainage channels in comparison to the ridges on the upper piedmont may be related to the higher abundance of *F. cernua* plants along the channels and small ephemeral streams. The availability of *F. cernua* shrubs at the edges of drainage channels probably explains the low incidence of pruning of riparian *L. tridentata* by jackrabbits.The data of Gibbens et al. (1993) plus the data from our study support the conclusion that the influence of jackrabbits on ecosystem structure reflects feeding preferences of these animals.

Since there are individual shrubs of both species that exhibit no evidence of jackrabbit pruning there must be characteristics of those plants that are different from individuals that are heavily pruned by jackrabbits. Selectivity by herbivores may be influenced by chemical, physical, and physiological differences among plants (Lindroth, 1989). Ernest (1994) reported that jackrabbits pruned higher proportion of creosotebush shrubs exhibiting lower constitutive resistance to herbivory but provided no data on water status of pruned and un-pruned shrubs. Steinberger and Whitford (1983) suggested that the spatial variation in woody stem utilization of *Larrea* shrubs by jackrabbits was a function of soil depth and water storage because jackrabbits preferentially pruned stems of shrubs with higher stem tissue moisture content. They found that jackrabbits heavily pruned *L. tridentata* shrubs at the edges of irrigated plots. Jackrabbit use of shrubs during the cold dry season adds support to the water availability hypothesis (Westoby, 1980; Currie and Goodwin, 1966). Selection of some individual *F. cernua* plants for heavy browsing by jackrabbits is further evidenced by the distribution and proportions of tarbush browsed by rabbits in the tarbush monoculture plots. That all but one of the heavily browsed plants were in one small locale within one plot supports the idea that these plants had either higher water status or lower concentration of foliar feeding deterrent chemicals than the shrubs in the other plots.

Selectivity of individual tarbush plants may be related to the water content of the stems of the plants but may also be a function of the chemical constituents of the individual plants. The quality and quantity of anti-herbivore defensive mechanism may vary both among (Coley et al., 1985) and within species (Whitham, 1983). The preferential browsing exhibited by jackrabbits may represent an avoidance behavior motivated by the digestibility or toxicity of the food material, rather than its palatability or nutritional

quality. A greater concentration of epicuticular wax was detected on leaf surface of *F. cernua* plants less used by livestock (Estell et al., 1994). The concentration of total phenolics of creosotebush leaf litter was $2 \times$ greater than the concentration of total phenolics in tarbush leaf litter and the concentration of condensed tannins was $12 \times$ higher in *L. tridentata* than in *F. cernua* (Hyder et al., 2005). This suggests that feeding deterrent chemicals of the shrubs may account for the jackrabbit preference for tarbush over creosotebush.

Our study shows that the preference for tarbush by jackrabbits leads to reduced size and vigor and increased mortality of *F. cernua* in areas with mixed stands of tarbush and creosotebush. This differential use of one species may contribute to a shift in the dominant shrub species in mixed stand landscapes. A reduction in tarbush dominated areas and increased dominance by creosotebush has been documented by Gibbens et al. (2005). Their data show that tarbush has made some gains in areas formerly dominated by grasses but at the same time, tarbush declined in the majority of the areas where it is used to be the primary dominant. *F. cernua* has remained a sub-dominant over much of its former range. Creosotebush increased in abundance and is now dominant in most areas. That expansion occurred almost exclusively at the expense of tarbush. This study provides a possible mechanism for these changes in dominance and species composition.

The data in this study show how pruning of stems of one shrub species (*L. tridentata*) by jackrabbits results in increased vigor as a result of compensatory growth and in the other species (*F. cernua*) pruning of stems by jackrabbits results in reduced vigor and mortality. The long-term implications of these differences in responses to browsing by rabbits is change in community dominants in degraded grasslands that moved to tarbush and are now shifting to creosotebush dominance. We caution that the process of vegetation change in desertification may change drivers and direction before temporally stable plant communities are established as is evidenced by the mixed shrub communities on the lower piedmont in this study.

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