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Small mammal herbivory: Feedbacks that help maintain desertified ecosystems

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ABSTRACT

We tested the hypothesis that herbivores contribute to feedbacks maintaining arid ecosystems in a degraded state. We studied small mammal herbivory on a subshrub, broom snakeweed (*Gutierrezia sarothrae*), and perennial grasses at three sites: (1) ungrazed black grama (*Bouteloua eriopoda*) grassland; (2) grassland degraded by intense short-duration grazing; and (3) mesquite (*Prosopis glandulosa*) coppice dunes. Snakeweed was browsed by herbivores primarily during dry winter months.

The average percent of *G. sarothrae* standing crop biomass removed by browsing was 9.2 in ungrazed grassland, 7.4 in intensely grazed grassland, and 4.1 in the dunes. In ungrazed grassland, an average of 12% of grass cover was harvested by herbivores; in the intensely grazed plots – 80%. Herbivore exclusion plots showed that jackrabbits (*Lepus californicus*) were the primary browsers on snakeweed and rodents on grasses and *G. sarothrae* inflorescences. Rodent removal of *G. sarothrae* inflorescences allows wind dispersal of seeds in disturbed and desertified areas, thereby increasing abundance of this poisonous shrub. Grass-tiller cutting by rodents provides a strong feedback that may be responsible for keeping the grass cover low on the intensely grazed areas. Jackrabbit pruning has little effect on *G. sarothrae* abundance at any stage of desertification.

1. Introduction

According to the non-equilibrium conceptual model of Westoby et al. (1989), semi-arid and arid ecosystems may change from a state that appears to be in equilibrium to one or more states that are not in equilibrium, a process frequently identified as desertification. The driver of shifts from equilibrium to non-equilibrium states is often changes in land management. Desertified ecosystems exist in altered stable states, which appear to be largely resistant and/or resilient to restoration efforts.

Much of the pre-pastoral industry grassland in the Chihuahuan Desert has been degraded to shrub-dominated ecosystems (Buffington and Herbel, 1965; Gibbens et al., 2005). Desertification in the late 19th and 20th centuries occurred in the Americas, southern Africa, and Australia coincident with the development of the pastoral industries. In these regions, arid rangelands experienced rapid increase in abundance of unpalatable and poisonous woody shrubs concomitant with decreases in grass cover (Whitford, 2002). The conversion of desert grassland to shrubland has been ascribed to a combination of climatic factors, especially prolonged drought, and anthropogenic factors, especially overgrazing by domestic livestock. The stability, resistance, and resilience of desert scrub may be modified by the activities of native animals (Whitford, 2002; Roth et al., 2007). Small mammal herbivores are known to have an impact on desert grasses and shrubs. There are data from experimental studies that demonstrate that rodents and rabbits can reduce re-establishment of grasses and contribute to the stability of the vegetation in a desertified state (Curtin et al., 2000; Gibbens et al., 1993; Heske et al., 1993; Norris, 1950).

Broom snakeweed (*Gutierrezia sarothrae*) has been identified as an important rangeland weed problem in southwestern rangelands in the United States (Sterling and Hou, 1997). Broom snakeweed, a short-lived subshrub, is poisonous to livestock and increases in abundance in intensely grazed desert grasslands (Whitford et al., 1999). Despite its toxicity to livestock, snakeweed is utilized by rodents (*Dipodomys* sp.) and jackrabbits (*Lepus californicus*) in the winter months (Currie and Goodwin, 1966; Daniel et al., 1993; Hayden, 1966; Steinberger and Whitford, 1983; Westoby, 1980). Rodents harvest seed heads from the top of the plant by severing the inflorescent stems and jackrabbits cut the live stems close to the root crown. Only the seeds and a small portion of the stem are removed by the herbivores and the remainder is left on the ground near the plant from which it was removed. This is characteristic behavior of jackrabbit browsing on shrubs (Chew and Chew, 1970; Steinberger and Whitford, 1983) and rodents feeding on perennial grass tillers (Kerley et al., 1997).

It has been suggested that changes in abundance and species composition of some assemblages of animals in desertified ecosystems may contribute to feedbacks that maintain the

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system(s) in a degraded state (Whitford, 1993). In order to test this hypothesis, we designed studies of herbivory on *G. sarothrae* and native grasses in grassland in relatively good condition, overgrazed grassland, and mesquite coppice dunes, which constitute the end point in degradation of Chihuahuan Desert grassland ecosystems.

2. Methods

Study plots were established in an area in the Jornada Basin administered by the U. S. Department of Agriculture – Agricultural Research Service's Jornada Experimental Range (JER) located approximately 50 km NNE of Las Cruces, NM.

Herbivory studies were conducted at three locations within a 3 km radius. Two study sites were located in an ecotone between black grama grassland and mesquite coppice dunes. The third study site was located within a mature mesquite coppice dune area. The grassland was dominated by black grama (*Bouteloua eriopoda*), which accounted for more than 50% of the grass cover with dropseeds (*Sporobolus* sp.) and three awns (*Aristida* sp.) as subdominants. The grassland studies were conducted on three grazed (percent live grass cover of 0.8 ± 1.5) and three ungrazed (percent live grass cover of 17.4 ± 2.8), half-hectare plots from which all mesquite (*Prosopis glandulosa*) shrubs had been removed manually. Each plot was fenced with three-strand barbed wire to exclude other livestock from the experiment. The grazed plots were stocked with 20–40 yearling steers in each of three successive years: 1995–1997. Stocking rate was adjusted to remove 65–80% of the estimated available forage within a 36–48-h period (Nash et al., 2004).

The grassland plots were compared with a mesquite coppice dune site. We established 15, 4 m × 10 m plots at random within three sites of each treatment (grazed, ungrazed, and coppice dune). We measured species composition, cover, and volume, and evidence of previous browsing on all plants within each plot. We mapped the location of each snakeweed (*G. sarothrae*) and grass tussock in each plot in order to assess temporal patterns of herbivory. All plots were monitored each month between December 2002 and October 2003. All plants that exhibited signs of browsing were measured (height and two diameters) at each sampling period. All uneaten stems and leaves were collected, returned to the laboratory and dried at 60 °C for a minimum of 48 h. The biomass of *G. sarothrae* was calculated by an equation based on plant volume: $y = 460 \cdot 4/3\,\pi \cdot r \cdot h^2, r^2 = 0.91$ where y = biomass in grams, r = radius in cm, and h = height in cm (Ludwig et al., 1975).

A single assessment of grass herbivory was conducted in November 2002 on the black grama grassland in both the grazed and ungrazed plots. Grass herbivory was quantified by loss of cover measured by the area of the crown that was pruned. Grass species monitored were black grama (*Bouteloua eriopoda*), three awns (*Aristida* spp.), and dropseed (*Sporobolus* spp.).

We used the color and shape of fecal pellets deposited within 30 cm of browsed plants to identify the herbivore species. Black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) produce fecal pellets that are distinctively different in shape, size, and color, and both can be temporally classified by color. Fresh feces are characterized by a dark brown/black color.

In order to identify the pruning characteristics of the different herbivores utilizing snakeweed, we recorded browsing on snakeweed at three sites established by the Jornada Long-Term Ecological Research Program. We recorded data from four plots at each of the three sites: livestock exclosure (barbed wire fenced plot); livestock and rabbit exclosure (barbed wire fence and chicken wire 1 m high); livestock, rabbit, and rodent exclosure (barbed wire, chicken wire, and a metal sheet 50 cm above ground and 50 cm deep); control (no fence). All snakeweed plants were measured and severed plant material left on the ground by herbivores was collected from three 20 m × 1 m transects in each plot.

All the data were analyzed by analysis of variance (ANOVA) using the SAS model with Duncan's multiple range test used to evaluate the differences among means. Seasonal pattern of herbivory were examined by repeated measures analysis of variance.

3. Results

There were large differences in abundance (density) and biomass of snakeweed among the study sites with the intensively grazed sites having the highest number of plants and the highest biomass (Table 1). Snakeweed density, biomass, and plant volume were significantly lower in the mesquite coppice dune sites than in the grassland sites. There was three to four times as much snakeweed biomass removed by browsing in the grasslands than at the coppice dune sites (Table 1).

Spatial variability among those plants that were browsed by jackrabbits and plants that were untouched contributed to the lack of differences in biomass removed by browsing and the fraction of the total standing biomass of snakeweed at each location (Table 1). Some plants had all of the live stems removed and neighboring plants exhibited no sign of browsing.

There were large seasonal differences in the amounts of biomass removed by browsing herbivores. Total amounts of snakeweed biomass removed per month were greatest in the dry winter months (Fig. 1). Biomass removed during the winter months was related to the standing crop biomass of *G. sarothrae* at each site (Table 1, Fig. 1). Browsing on snakeweed from April to October was very low. During September and October virtually all of the biomass removed from snakeweed was the leafless inflorescence stems with multiple seed heads. Browsing of woody leaf-bearing stems ended in June.

Of 1683 snakeweed plants monitored at the grassland sites, (grazed and ungrazed plots combined), 619 plants were browsed and, of these, 173 (27.9%) were browsed twice and 43 (6.9%) were further browsed a third time or more. There were 835 incidents of rabbit browsing. There was insufficient repeat browsing on snakeweed in the mesquite coppice dune site to make a comparable analysis of browsing at this site.

Jackrabbit browsing accounted for 76.2 ± 20.7% of the browsed plants ($n = 15$) based on fecal pellets deposited near browsed plants on the ungrazed plots. On the grazed plots, jackrabbits accounted for 53.5 ± 16.8 ($n = 13$) of browsed plants based on fecal pellets near the browsed plants. There were no cottontail rabbit fecal pellets near browsed plants at any of the three study sites.

Since there was no evidence of browsing on snakeweed in the cattle/rabbit/rodent exclosure plots, these three groups of animals are potential herbivores on *G. sarothrae*. The data from exclosure

Table 1
Mean density, biomass, and biomass removed ± SE by browsing of broom snakeweed (*Gutierrezia sarothrae*) at three study sites on the Jornada Experimental Range.

Site	Density (no ha^{-1})	Biomass (kg ha^{-1})	Biomass removed (kg ha^{-1})
Ungrazed grassland	9217 ± 4220^{a}	173.7 ± 54.6^{a}	15.5 ± 8.2 (9.2 ± 4.3)
Grazed grassland	18,833 ± 10,030^{b}	257.7 ± 78.5^{b}	19.1 ± 11.6 (7.4 ± 4.1)
Mesquite dunes	3983 ± 2159^{c}	120.1 ± 65.6^{c}	4.8 ± 7.5 (4.1 ± 6.0)

Numbers in parentheses are percent of standing crop removed by browsing ± SE. Values in a column with different letters are significantly different ($p < 0.05$).