Impacts of Black-tailed Jackrabbits at Peak Population Densities on Sagebrush-Steppe Vegetation

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Abstract

In the northern Great Basin, populations of black-tailed jackrabbits *(Lepus californicus)* are cyclic, reaching high densities at approximately 10-year intervals. This project examined impacts of jackrabbits during a peak in their cycle on sagebrush-steppe vegetation in southeastern Idaho. Total vascular plant cover was significantly lower on plots open to jackrabbit herbivory than on exclosure plots, but in no case was cover of a specific species significantly reduced on open plots. The most severe impacts were on shrubs during winter; most aboveground tissues of both winterfat *(Ceratoides lanata)* and green rabbitbrush *(Chrysothamnus viscidiflorus)* plants were completely eaten by spring. However, these impacts were largely ameliorated by compensatory growth during the following growing season, and there was no difference in total biomass for either species between the open and protected plots by July. New growth of winterfat plants that had been browsed the previous winter was significantly greater than that of protected plants. Thus, although the cumulative effects of herbivory reduced total plant cover, no single species was irreparably impacted. Over a year, jackrabbits exert feeding pressure on nearly all of the important species in these communities; therefore, these hares do not appear to apply differential grazing pressure that would alter the course of vegetation development on northern Great Basin rangelands.

The black-tailed jackrabbit *(Lepus californicus)* is an important native herbivore on rangelands in the western United States (Vorhies and Taylor 1933, Dunn et al. 1982). In northern portions of the species' range, populations are cyclic, reaching high densities at approximately 10-year intervals (Gross et al. 1974, Johnson and Peak 1984). Numerous studies of food preferences and seasonal dietary trends for black-tailed jackrabbits provide a reasonably complete picture of feeding behavior (see Johnson and Anderson 1984), but the effects that black-tailed jackrabbits have on native plant populations are not completely understood.

It is generally assumed that peak population densities will have severe impacts on range ecosystems (Vallentine 1971, MacCracken and Hansen 1984), but speculation about such impacts has been based largely upon casual observation. Vorhies and Taylor (1933) argued, "Under all but the most conservative stocking with cattle the tendency of grazing by jackrabbits will be to accentuate overgrazing, to eliminate the more palatable grasses and favor their replacement by somewhat less desirable species and by weeds." In contrast, Bond (1945) speculated that jackrabbits would "exert a force in favor of succession toward the climax" on range that was only moderately deteriorated, whereas on range "deteriorated to the point of having more weeds than grasses, their effect would be towards further deterioration." More recently, Rice and Westoby (1978) found that protection from jackrabbits for periods of 5 to 15 years had no consistent effects on vegetation. The impacts of jackrabbit herbivory on long-term vegetation trends are complicated because jackrabbits may suppress or eliminate certain species (Westoby 1974, McKeever and Hubbard 1960) or enhance propagule dispersal of others (Riegel 1941, 1942; Timmons 1942).

This project was initiated to assess the impacts of a high population density of black-tailed jackrabbits on sagebrush-steppe vegetation and to examine those impacts in relation to long-term trends in vegetation development. In this paper, we describe the short-term impacts of a peak in a jackrabbit population on cover, biomass, and leaf length of several important plant species and discuss the implications of these measurements in relation to vegetation dynamics.

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Study Area

The study was conducted on the Idaho National Engineering Laboratory (INEL), which occupies over 2,300 km² of cold-desert rangeland on the upper Snake River Plain in southeastern Idaho. The area, at an elevation of about 1,500 m, lies in the rain shadow of the Lost River Mountains. Mean annual precipitation is 21 cm, and about 40% of that typically falls during April, May, and June. July is predictably hot and dry (Anderson and Holte 1981). Average annual temperature is about 5.5° C, and the frost-free period averages 91 days. Soils are mostly shallow, calcic *Aridisols* of eolian origin that have accumulated on top of basalt.

The vegetation of the INEL is generally dominated by 2 subspecies of big sagebrush *(Artemisia tridentata)* (authorities for nomenclature are in Table 1). Other conspicuous shrubs include winterfat *(Ceratoides lanata)*, green rabbitbrush *(Chrysothamnus viscidiflorus)*, prickly phlox *(Leptodacylon pungens)*, and various species of *Atriplex*. The most important grasses are bottlebrush squirreltail *(Elymus elymoides)*, Indian ricegrass *(Oryzopsis hymenoides)*, needle-and-thread grass *(Stipa comata)*, and thickspike wheatgrass *(Elymus lanceolatus)*.

Table 1. Plant species composition as measured in 1979 on all 12 permanent plots at study areas C1 and C2, Idaho National Engineering Laboratory.

Species[1]	Relative Cover	
	Study Area	
Shrubs:	C1	C2
Ceratoides lanata (Pursh)J.T. Howell	29.12	
Artemisia tridentata Nutt. ssp. *wyomingensis*	25.60	
Artemisia tridentata Nutt. ssp. *tridentata*		10.68
Chrysothamnus viscidiflorus (Hook.) Nutt.	6.03	26.12
Leptodactylon pungens (Torr.)Nutt.	0.34	1.38
Atriplex spinosa (Hook.) Collotzi	5.86	
Other shrubs	0.32	
Grasses:		
Elymus lanceolatus (Scribner & J.G. Smith) Gould	22.80	3.97
Elymus elymoides (Raf.) Sweezy	3.58	3.28
Oryzopsis hymenoides (R. & S.) Ricker	2.02	35.72
Stipa comata Trin. & Rupr.		16.93
Poa nevadensis Vasey		0.25
Forbs:		
Phlox hoodii Rich.	3.47	0.79
Other Forbs	0.86	0.88

[1]Nomenclature follows Hitchcock and Cronquist (1973) except for grasses of the Triticeae, where we have used the taxonomic revision proposed by Dewey (1983).

Methods

In 1979, 2 clusters of study plots were chosen to assess effects of feeding by jackrabbits on important shrub and grass species. One cluster, C1, is in an area where winterfat is abundant (Table 1). The C1 study area has not been grazed by domestic livestock since 1950, but the area supports considerable numbers of pronghorn *(Antilocarpa americana).* The second cluster, C2, is in an old burn site that is dominated by Indian ricegrass and green rabbitbrush (Table 1). This second area is open to spring/fall grazing by sheep. Specific locations of the clusters and descriptions of the plot layouts are found in Anderson and Johnson (1983).

Each cluster of study plots consisted of 6 pairs of 5 m × 5-m plots. To establish each pair of plots, we subjectively chose two 5 m × 5-m areas of vegetation that were as similar as possible. All 12 plots were permanently staked, and then 1 member of each pair was selected by a coin toss to be fenced with a 15 m × 15-m rabbit-proof exclosure. Because cluster C2 is in area that is open to spring/fall grazing by domestic sheep, the open plots were also fenced, but with the fence suspended about 30 cm above the ground to preclude access by livestock but not by jackrabbits. Pellet counts inside and outside the livestock exclosures confirmed that these fences were not a significant barrier to jackrabbits ($P>0.1$, paired t test).

In July of 1979, perennial vascular plants were mapped in 15 1-m^2 quadrats on each plot. Maps were drawn freehand; a sighting frame consisting of superimposed dm^2 string grids was used to facilitate vertical projection of the plants. Cover of each species was estimated from the completed maps. In 1982, plant cover on the same 1-m^2 quadrats was estimated by point interception (Floyd and Anderson 1982). The methods changed between 1979 and 1982 because Floyd (1982) showed that point interception was a reliable and objective method that was also less tedious. Because of this change, we will not compare 1979 cover data with that for 1982.

For statistical comparisons, the 5 m × 5-m plot was the sample unit, and the cover estimate for each species was the mean value from the 15 quadrats. Paired t tests were used to compare cover of open vs. fenced plots for a given year. The *a priori* alternative hypothesis was that cover would be significantly reduced on the open plots; thus, a one-tailed test (alpha = 0.05) was used.

On 26 May 1982, crown volume of randomly selected winterfat plants from both inside and outside the permanent exclosures at the C1 study area were measured. In order to measure the growth of the plants outside the exclosures without complications from further browsing, half of the plants outside the exclosures were protected by a temporary exclosure aprroximately 1 m in diameter. All plants were tagged and then remeasured 1 month later. Crown volume was calculated by assuming the crown to be a cylinder. The average radius of the cylinder was equal to the sum of perpendicular crown diameters divided by 4. The height of the cylinder was measured from the ground to the top of the crown. Growth of winterfat plants was expressed as the ratio of average crown volume on 29 June 1982 to that on 26 May 1982. A ratio of 1.0 would indicate that no growth occurred in that 1-month interval. Ratios among the permanent exclosures, the temporary exclosures, and the open plots were compared using an one-way analysis of variance (ANOVA) and a Student-Newman-Keuls (SNK) multiple range test.

Aboveground biomass of winterfat plants at C1 and green rabbitbrush plants at C2 was measured on randomly selected plants from both inside and outside the permanent exclosures. Plants were clipped at ground level, separated into current year vs. older tissues, dried at 80° C for 24 h, and weighed. Leaf length of spiny hopsage *(Atriplex spinosa)* plants was measured on the longest leaf on 10 arbitrarily chosen twigs on each of 10 randomly selected plants from both inside and outside the C1 exclosures. All biomass and leaf length measurements were made in mid July 1982.

The densities of the jackrabbit population at C1 and C2 were estimated from pellet counts on 12 5-m^2 quadrats (two 1 m × 5-m quadrats per permanent 5 m × 5-m open plot). Density was calculated assuming that 1 jackrabbit deposits 530 pellets per day (Arnold and Reynolds 1943). Overall population trends from 1980–1984 were monitored by counting jackrabbits at night, using a vehicle equipped with spotlights, along a 45-km backroads route on the INEL (Johnson and Anderson 1983). All jackrabbits within a 50-m strip on both sides of the vehicle were tallied. Counts were made in early June each year. Population densities were estimated by the method in Flinders and Hansen (1973).

Results

Population Trends and General Observations

The black-tailed jackrabbit population on the INEL peaked during 1981 (Fig. 1). Jackrabbit density increased by 3.4 fold in the year from June 1980 to June 1981. The population density then dropped precipitously during the next 3 years. The average density along the backroads route in June 1984 was 0.02 jackrabbits/ha, which is less than one-hundredth of the average peak density of 2.7 jackrabbits/ha. Population densities at the 2 exclosure sites, estimated from pellet counts, were 6 to 8 jackrabbits/ha during the summer of 1981 and about 2 jackrabbits/ha during the following fall, winter, and spring. The density estimates from the 2 techniques should not be compared because the backroads spotlight counts provided an average for a large area whereas pellet counts were used to assess numbers at local study areas. Local densities along the backroads route varied widely (Anderson and Johnson 1983).

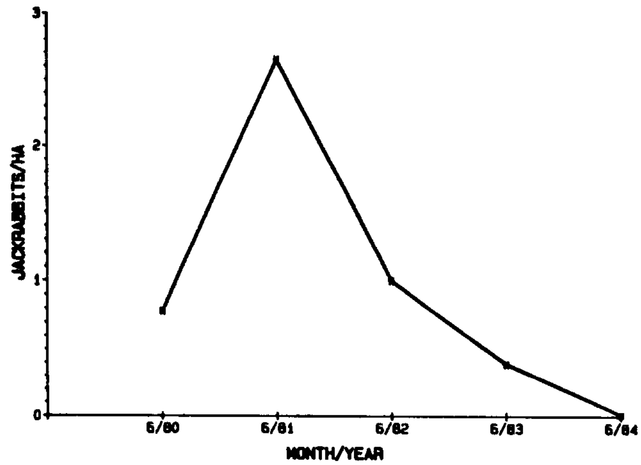

Fig. 1. *Mean densities of black-tailed jackrabbits along a 45-km backroads route on the Idaho National Engineering Laboratory, based on spotlight counts made each June, 1980 – 1984.*

During the summer of 1981, distinct rabbit trails became ubiquitous, and, in some areas, heavy use of perennial grasses was observed. July and August of 1981 were exceptionally dry, which may have forced the hares to make greater than normal use of shrubs. By fall, evidence of browsing on shrubs was common. Snow cover blanketed the INEL from mid-December through February, and it was obvious that food supplies were very limited. Hundreds of jackrabbits could be observed at night feeding on lawns around INEL facilities, and heavy damage was inflicted on ornamental shrubs growing there. Thousands of jackrabbits were killed by farmers in rabbit drives near Mud Lake and Howe, Idaho, which lie to the north and northwest of the INEL. By April, 1982, evidence of browsing could be found on most plants of any shrub species on the INEL. On sagebrush, the rabbits would clip and discard the youngest shoots and then eat the older shoots just beneath. Similar observations were reported by Vorhies and Taylor (1933), Currie and Goodwin (1966), and Westoby (1973). Piles of clipped sagebrush shoots were common beneath sagebrush plants.

Table 2. Percent cover of key species groups in July 1982 at area C1, Idaho National Engineering Laboratory. Each value is the mean for six plots; 15 m² were sampled on each plot. Results of pairing-design *t* tests are shown under 'statistics' heading.

	Cover (%)		Statistics[1]		
	Open Plots	Exclosure Plots	D	s_D	*t*
All vascular plants	14.9	18.3	–3.38	1.59	2.13*
Total grasses	2.91	3.07	–0.16	0.45	0.37
Ceratoides lanata	3.00	4.33	–1.33	0.75	1.78
Artemisia tridentata	5.53	5.60	–0.30	1.32	0.07
Chrysothamnus viscidiflorus	1.40	1.86	–0.43	0.70	0.61
Atriplex spinosa	1.15	1.96	–0.81	0.59	1.38
Oryzopsis hymenoides	0.53	0.40	0.14	0.20	0.67
Elymus lanceolatus	1.81	2.03	–0.22	0.30	0.74

*$P<0.05$; one-tailed test, 5 d.f.
[1]D and s_D are the mean difference and standard deviation of the difference respectively.

Vegetal Cover

In 1979, no significant difference was found in total cover or cover of any common species between the exclosure and open plots at either C1 or C2 ($P>0.05$; pairing design *t* test). In July of 1982, total vascular plant cover was significantly greater on the exclosure plots than on the open plots at both C1 and C2 (Tables 2 and 3). However, there was no case of a significant difference between open and exclosure plots in the cover of specific species at either site (Tables 2 and 3).

Table 3. Percent cover of key species or species groups in July 1982 at area C2, Idaho National Engineering Laboratory. Each value is the mean for six plots; 15 m² were sampled on each Plot. Results of pairing-design *t* tests are shown under 'statistics' heading.

	Cover (%)		Statistics[1]		
	Open Plots	Exclosure Plots	$\bar{D}$	s_D	*t*
All vascular plants	15.3	18.5	–3.06	1.25	2.44*
Total grasses	9.5	10.1	–0.59	1.22	0.48
Artemisia tridentata	3.73	5.67	–1.92	1.11	1.75
Chrysothamnus viscidiflorus	1.87	2.13	–0.25	0.84	0.29
Stipa comata	2.53	2.53	–1.02	0.98	1.04
Oryzopsis hymenoides	5.87	5.53	0.36	0.82	0.43
Elymus elymoides	0.73	0.67	0.06	0.18	0.33

*$P<0.05$; one-tailed test, 5 d.f.
[1]$\bar{D}$ and s_D are the mean difference and standard deviation of the difference respectively.

Crown Volume, Biomass, and Leaf Length

During the winter of 1981–82, all of the winterfat plants outside the exclosures were completely eaten to their woody bases. In the month following 26 May 1982, growth of winterfat plants that had been browsed the previous winter (temporary exclosures and open) was significantly greater than that of protected plants (permanent exclosures) (Table 4). There was no difference in growth of plants protected by temporary exclosures compared to those in the open (Table 4), suggesting minimal browsing on this species during the month. There was no significant difference in mean aboveground biomass for winterfat plants protected from jackrabbits (6.2 ± 3.2 g; mean ± 95% C.I.) vs. those exposed (3.6 ± 1.6 g), although there was a significant difference in the amount of old biomass between protected plants (1.6 ± 1.1 g) and those subject to browsing (0.3 ± 0.1 g). Thus, current-year growth constituted a much larger proportion of total aboveground biomass of winterfat plants outside the exclosures compared to that of protected plants.

At both clusters of plots, aboveground portions of most green rabbitbrush plants were completely eaten during the 1981–82 winter. Regrowth on these plants was typically vigorous. Because of the large differences in morphology between protected plants and those subjected to browsing, we could not compare growth of crown. Growth of protected plants was restricted to the ends of old branches. The average length of the longest new shoots on a sample of 35 protected plants was 11 ± 1.2 cm, whereas on plants exposed to browsing, new shoots averaged 21 ± 2.4 cm in length. There was no significant difference in total aboveground biomass of green rabbitbrush plants inside (15.2 ± 6.4 g) vs. those outside (18.8 ± 8.7 g) the exclosures, but most of the aboveground biomass of plants outside the exclosures was new growth (old biomass for exclosure plants = 2.9 ± 1.4 g compared to 0.5 ± 0.3 g for unprotected plants).

Table 4. Growth of winterfat *(Ceratoides lanata)* plants expressed as the ratio of average crown volume on 29 June 1982 to that on 26 May 1982, Idaho National Engineering Laboratory. A ratio of 1.0 would indicate that no growth occurred.

	Crown Volume Ratio		
Location	Mean	Range	*n*
Permanent Exclosure	1.08*	0.85 – 1.63	11
Temporary Exclosure	1.66	1.04 – 3.30	18
Open	1.72	0.79 – 4.02	18

*Significantly different from the other two means at $P<0.05$ by ANOVA and SNK multiple range test.

Productivity of spiny hopsage plants may have been significantly reduced, because unprotected plants typically had more dead stems and branches and far fewer live stems than protected plants. However, mortality of plants that had been heavily browsed seemed rare, and growth of new shoots of unprotected plants was vigorous. Leaf morphology was very different on new shoots of browsed plants compared to that on protected plants. Average leaf length of spiny hopsage plants outside the exclosure was 2.7 ± 0.5 cm, compared to 1.5 ± 0.3 cm on protected plants.

Discussion

Gross et al. (1974) reported a 10-fold difference in population densities between highs and lows over 3 population cycles in the Curlew Valley of northern Utah. Our data show a 7-fold decrease in population density between 1981 and 1983 and another order of magnitude decrease by the summer of 1984, indicating a fluctuation of about 100-fold over a cycle in the jack rabbit population on the INEL.

Following the peak in the cycle, total plant cover was reduced at both exclosure study areas (Table 2 and 3), but we were unable to document any case in which the cover of a particular species was significantly reduced. This suggests that the overall difference in cover may reflect the cumulative impacts of herbivory on numerous species, rather than heavy use of one or a few species. The variance is much higher for cover comparisons involving individual species than for total plant cover; thus the failure to reject the null hypothesis in the case of individual species despite differences in overall cover may be a result of the small sample size. Certainly, however, there was no case where the cover of a dominant shrub or perennial grass species was drastically reduced, despite the facts that shrubs were heavily used during the previous winter and grasses are the preferred foods during the spring and summer (Johnson and Anderson 1984).

Many of the native perennial bunchgrasses of this region are very susceptible to damage by heavy grazing, especially spring grazing (Caldwell et al. 1981, Mack and Thompson 1982). Indian ricegrass and needle-and-thread grass are important forage species throughout the Great Basin and elsewhere, and they are among the preferred foods of black-tailed jackrabbits (Currie and Goodwin 1966, Hayden 1966, Uresk 1978, Johnson 1979). The C2 site was selected specifically to assess impacts on those species.

Data from our exclosures provide no evidence for a significant impact of jackrabbits on any perennial grass populations. Jackrabbits and their impacts are patchily distributed, however, and it is quite possible that in other localized areas the effects could be significant. Such impacts would be extremely difficult to quantify. We have observed heavy cropping on individual Indian ricegrass and needle-and-thread plants while neighboring plants were left untouched. In one area, there was an obvious reduction in standing crop of the rhizomatous grass *Leymus triticoides*. Nearby stands of Indian ricegrass and needle-and-thread grass showed evidence of rabbit grazing, but the cropping was not severe. Diet studies (Johnson 1982) and our field observations indicate that *L. triticoides* and thick-spiked wheatgrass *(E. lanceolatus)*, another rhizomatous species, are both important in the jackrabbit diets. These species appear to be well adapted to heavy grazing.

During the spring and early summer of 1981 and 1982, periods when the native cool-season grasses were most susceptible to herbivore damage, the supply of grass forage was generally abundant on the INEL. Although evidence of jackrabbit grazing was common, severe cropping or damage was seldom observed. When dormant, later in the summer or during fall and winter, the grasses are much less susceptible to damage, and the shrubs become the staple foods of the jackrabbits.

The 3 species of shrubs included in our studies showed a remarkable ability to recover following severe cropping of above-ground tissues. Whether comparable responses could be effected under repeated winter browsing over several years is questionable, but the cyclic nature of the jackrabbit population would probably preclude that necessity. Indeed, the theoretical analysis of Hilbert et al. (1981) suggested that compensatory growth would be more likely under infrequent cropping events than under repeated browsing at short intervals. Stevens et al. (1977) noted that winterfat was remarkably tolerant to winter grazing. Cook and Child (1971) reported that winterfat plants made a full recovery of crown cover in 7 years after 90% herbage removal in winter and spring for 3 years.

Cook and Child (1971) found that nonsuffrutescent shrubs were more susceptible to damage by their clipping treatments. The compensatory response of the nonsuffrutescent green rabbitbrush in our study was certainly comparable to that of winterfat; both were generally cropped to the ground and both showed vigorous regrowth. Spiny hopsage plants appeared to be more susceptible to damage from heavy browsing, possibly because of girdling of larger stems (McKeever and Hubbard 1960), but this species too showed vigorous compensatory growth.

McNaughton (1979b) reviewed numerous studies indicating that "...compensatory growth upon tissue damage by herbivory is a major component of plant adaptation to herbivores." He pointed out that grasses are particularly well adapted to grazing pressures because growth is primarily from intercalary meristems that are less accessible to large herbivores than the terminal meristems of dicots (McNaughton 1979a, 1979b). Compensatory growth or stimulation of productivity in response to browsing or clipping has also been reported for shrubs (Garrison 1953, Lay 1965, Ferguson and Basile 1966), and many shrubs sprout vigorously following top removal by fire (Wright et al. 1979). McNaughton's (1979a, 1979b) studies also suggest that productivity may be maximized at some moderate level of herbivory.

What are the implications of these results and observations in terms of long-term vegetation development? Although they are selective feeders at a given time, jackrabbits may not apply differential grazing pressure that would influence the course of vegetation development in this ecosystem. Over the course of a year jackrabbits feed on most if not all of the important plant species in these communities. The most severe impacts appear to be on shrubs when the rabbit's winter food supply becomes limiting, but compensatory growth ameliorates these impacts. The cyclic nature of the jackrabbit population would provide ample time for recovery of species or individuals. Thus, it appears that a peak in the jackrabbit cycle has little impact on the overall structure or development of these plant communities. It should be emphasized, however, that this conclusion may apply only to rangelands that are in good to excellent condition where there is not heavy competition with livestock for forage.

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