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UNGULATE GRAZING IN SAGEBRUSH GRASSLAND: MECHANISMS OF RESOURCE COMPETITION[1]

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Abstract. In many areas of western North America, populations of Rocky Mountain elk (*Cervus elaphus canadensis*) avoid snow at high elevations during winter by migrating to sagebrush grassland communities in mountain valleys, communities that are used by cattle in the spring and early summer. As a result of these patterns of habitat use, the impact of elk on forage supplies for cattle has emerged as an important issue in range and wildlife management throughout the West.

We examined effects of variation in population density of elk on the availability and use of forage resources by cattle in a randomized complete block experiment conducted in sagebrush grassland during four years. We manipulated elk numbers to achieve four levels of population density (0, 9, 15, and 31 elk/km^2), replicated each level three times, and observed responses of vegetation and cattle to these manipulations.

At high densities (31 animals/km^2), elk annually removed 57% of the standing crop of dead perennial grass and 12% of the total annual production of live perennial grass. Standing crops of dead perennial grass in early spring declined in direct proportion to increasing elk density (linear effect $F_{1,6} = 10.0$, $P = 0.02$) from a mean of 8.7 g/m^2 in the controls (0 elk/km^2) to 3.3 g/m^2 in the high density (31 elk/km^2) treatment. Early spring standing crops of live perennial grass also declined as elk population density increased, but these trends only approached significance (linear effect $F_{1,6} = 3.4$, $P = 0.12$). Effects of elk grazing on herbaceous aboveground net primary production were not significant (minimum $P > 0.38$), but the total supply of herbaceous dry matter available to cattle (standing dead + primary production) declined in linear relation to elk density (linear effect $F_{1,6} = 7.7$, $P = 0.03$). Canopy cover of shrubs was least and canopy cover of grass was greatest at intermediate levels of elk density (quadratic effect $F_{1,6} = 9.4$, $P = 0.03$).

We found weak enhancing effects of elk populations on nutritional quality of spring forage. Elk grazing caused linear increases in the digestibility ($F_{1,6} = 5.0$, $P = 0.07$) and nitrogen content ($F_{1,6} = 15.1$, $P = 0.008$) of perennial grass available to cattle. Nitrogen content of cattle diets increased in the moderately grazed treatments (control vs. 15 elk/km^2, $F_{1,6} = 4.3$, $P = 0.06$), but dietary digestibility and fiber content did not change significantly with treatment.

Daily forage intake by cattle (kilograms of dry matter per cow per day) declined in direct relation to elk density ($F_{1,6} = 5.2$, $P = 0.06$), primarily as a result of reductions in intake of standing dead grass. Consequently, cattle daily intake of digestible energy (linear effect $F_{1,6} = 5.1$, $P = 0.06$) and nitrogen (control vs. others $F_{1,6} = 5.4$, $P = 0.06$) declined as elk population density increased. The mechanism responsible for this decline was a Type II functional response of cattle to forage biomass.

We conclude that effects of elk on cattle represent a composite of facilitative and competitive effects. When forage production is low and cattle density is high, competition is a much stronger force than facilitation.

Key words: cattle; competition; diet quality; diet selection; elk; facilitation; forage quality; functional response; grazing; net primary production; ungulates.

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Introduction

Competition between populations of elk (*Cervus elaphus canadensis*) and cattle in the western United States is widely believed to harm the production of cattle (Smith 1961, Wagner 1978, Powell et al. 1986, Hogan 1990, Cool 1992, Williamson 1992). A particularly important interaction between elk and cattle occurs in sagebrush grassland communities of the Rocky Mountains. During winter, elk populations avoid snow at high elevations by migrating to mountain valleys (Sweeney and Sweeney 1984), areas where sagebrush is the predominant cover type. During early spring, elk usually return to montane and alpine communities at higher elevation as snow recedes and green forage becomes available (Frank and McNaughton 1992). In contrast, cattle are usually absent from sagebrush rangelands during winter, but depend on them for spring pasture (Blaisdell et al. 1982, Powell et al. 1986). Pasture is scarce for cattle during spring because rangelands at high elevation fail to provide forage in a phenological condition appropriate for grazing cattle (Powell et al. 1986), while valley bottoms are committed to hay production. As a result, sagebrush grassland at mid-elevations offers spring cattle forage that is substantially limited elsewhere.

Use of sagebrush grassland by elk populations is believed to reduce the quantity of forage available to cattle (Smith 1961, Powell et al. 1986, Hogan 1990). Such reductions could occur as a direct result of consumption by elk of senescent forage during winter and live forage in early spring. In addition, excessive defoliation of young plants could reduce forage availability indirectly by retarding rates of plant growth during the remainder of the growing season. If standing crops of forage and forage production available to cattle decline as a result of winter grazing by elk, it is plausible that elk populations could compete with cattle, even though cattle and elk use sagebrush grassland at different times.

Opposing these potential competitive effects is the potential for a facilitative relationship between elk and cattle. Consumption of standing dead grass by elk during winter could enhance the nutritional quality of spring forage for cattle by shifting the live/dead ratio in bunch grasses to favor live tissue (Willms et al. 1980*a*, 1981), and could increase grass production by removing litter (Allaye-Chan 1984, Willms 1986; but also see Sauer 1978). Such shifts could facilitate selection of high-quality diets by cattle (Willms et al. 1980*b*). Moreover, shrubs can contribute a substantial portion of the winter diets of elk (reviewed by Kufeld 1972), and defoliation of shrubs during winter can increase production of grasses during spring by reducing competition for water and nutrients (Robertson 1947, Rittenhouse and Sneva 1976; but also see Wright 1970). Thus, elk browsing during winter might enhance conditions for cattle grazing during summer (Laycock 1967, 1970, 1979).

TABLE 1. Data on precipitation for Maybell, Colorado during the four study years. Total precipitation averages 27.5 cm/yr.

Year	Growing season (May–July) precipitation (cm)	Total annual precipitation (cm)
1987 (year1)	6.9	37.0*
1988 (year 2)	4.8	28.0
1989 (year 3)	3.8	13.0
1990 (year 4)	5.7	15.9

* Data from Craig, Colorado, ≈30 km east.

Resource competition can be partitioned into three general processes: effects of consumption on resource supply, effects of changes in resource supply on resource acquisition, and effects of changes in resource acquisition on growth and reproduction. We conducted a manipulative experiment to examine how changes in elk population density affect these processes in sagebrush grassland. In this paper, we report tests of the hypothesis that winter grazing by elk does not affect forage supplies available to cattle and, hence, does not influence cattle energy and nutrient intake. In a companion paper (Hobbs et al. 1996), we examine effects of elk on cattle growth and reproduction.

Methods and Materials

Study area

We conducted experiments at the Colorado Division of Wildlife Little Snake Wildlife Management Area in northwestern Colorado (40°N, 108°W). Topography and climate are typical of the high, cold deserts of the Intermountain Sagebrush Steppe (West 1983). The area includes slopes, gullies, and flats ranging in elevation from 1800 to 2000 m. Aspects are predominantly southern and southwestern, with an average slope of 15°. Soils are mostly sand and sandy loam with a rooting depth of ≈100–120 cm and moderate to high permeability. Brown's Park sandstone forms the underlying substrate.

Climate of the area is cold and dry; annual mean temperature is 6.06°C and mean annual precipitation is 27.5 cm, about two-thirds of which usually falls as snow. The growing season averages only 81 d. Winter snow depths are highly variable, but accumulations of 10–30 cm are common on level ground from December through March. Wind scours snow from ridge tops, depositing it on lee slopes. Growing season (May to July) precipitation during our study was slightly below the annual average of 5.9 cm and varied substantially among study years (Table 1).

Vegetation is representative of the Wyoming Basin Province (McKell and Garcia-Moya 1989). Big sagebrush (*Artemisia tridentata*) dominates the overstory; other important shrubs include rabbit brush (*Chryso-*

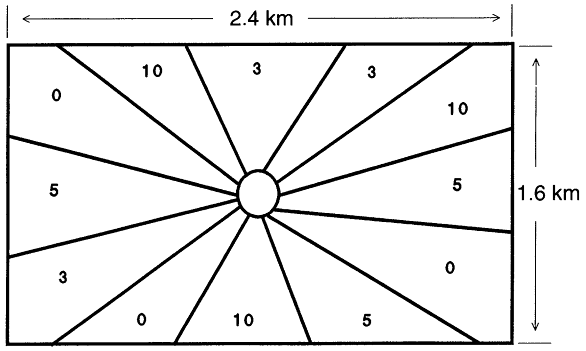

FIG. 1. Layout of 32-ha pastures used in studies of effects of winter and spring grazing by elk on cattle performance during the spring. Numerals within each pasture show the number of adult elk females stocked each year from 27 December to 15 April. The 0-elk pastures served as controls; the pastures with three animals achieved a density of 9.3 animals/km^2 (5.1 ha/animal-unit-month); the pastures containing five elk achieved a density equivalent to density of 15.4 animals/km^2 (3.04 ha/animal-unit-month), and the 10-elk pastures achieved a density of 30.9 animals/km^2 (1.5 ha/animal-unit-month). All pastures were stocked with cattle (seven cow/calf pairs and one heifer) during May–June of each study year. See text for explanation of cattle stocking rates. Pastures were constructed of high-tensile electric fence. Water was provided near the center hub in each pasture.

thamnus vicidiflorus, C. nauseous), horse brush (*Tetradymia spinosa*), and snake weed (*Gutierzia glomerella*). Predominant grasses are needle and thread (*Stipa comata*), western wheatgrass (*Agropyron smithii*), Indian Junegrass (*Koleria cristata*), bluegrass (*Poa* spp.), Indian ricegrass (*Oryzopsis hymenoides*) and cheatgrass (*Bromus tectorum*). Important forbs include wallflower (*Erysimum asperum*), peppergrass (*Lepidium perfoliatum*), silver lupine (*Lupinus argenteus*), and scarlet globe mallow (*Sphaeralcea coccinea*). Our study area was protected from livestock grazing during 5 yr previous to the start of our work. Condition of the range at the beginning of our studies was good-excellent.

Experimental design

We examined responses of forage and cattle to four levels of elk population density (0, 9, 15, 31 animals/km^2) in a randomized complete block experiment with three replications. We repeated the experiment annually during four consecutive years (1987 through 1990). Experimental units consisted of 12 fenced pastures constructed specifically to implement our research design. Each pasture was 32 ha in area and triangular in shape (Fig. 1).

Treatments were allocated to experimental units as follows. Four pastures were assigned to each of three blocks on the basis of pre-treatment biomass of live + dead perennial grasses estimated by harvesting and weighing 30 0.25-m^2 plots in each pasture on 20 May of the year previous to initiating the experiment. Thus, there was one block with low biomass of perennial grass, one with medium biomass, and one with high biomass. Treatment levels (0, 9, 15, 31 elk/km^2) were randomly assigned within each of the three blocks.

Stocking rates of elk and cattle

We varied elk population density by stocking pastures with different numbers of elk during winter and early spring. Controls were pastures that contained no elk (Fig. 1). Treatment pastures were stocked with three elk to achieve a density equivalent to 9.3 animals/km^2 (5.1 ha/animal-unit-month), five elk to achieve 15.4 animals/km^2 (3.04 ha/animal-unit-month), and 10 elk to achieve 31.4 animals/km^2 (1.5 ha/animal-unit-month) (Fig. 1).

Treatment levels were chosen to reflect a wide range of elk population densities. Elk populations in northwest Colorado typically average about 5–12 animals/km^2 of winter range. We chose one level (9 elk/km^2) to represent this large scale average. However, elk densities can be much higher at finer scales. Thus, we choose the highest treatment level (31 elk/km^2) to mimic local concentrations of animals and to examine forage and cattle responses to extraordinary levels of elk grazing. We acknowledge that the 31 elk/km^2 treatment is an unusually high concentration of animals. However, non-hunted elk populations have been observed to attain such densities on sagebrush grassland winter ranges (e.g., Houston 1982: Fig. 4.1, Table 4.3).

All elk introduced into pastures were females $\geq$2 yr old. Each year, animals were trapped from the surrounding area in portable corral traps. Average date of release of elk into the experimental pastures was 27 December. Elk were held in pastures until $\approx$15 April, when they were released to the surrounding rangeland.

Because our objective was to examine effects of elk on vegetation in sagebrush grassland that was also grazed by cattle, pastures were stocked with cattle immediately after elk were removed. Stocking rates of cattle were chosen to achieve about 50% removal of the net annual aboveground production of perennial grasses in the control pastures. Although this stocking rate is typical for sagebrush grassland on public and private land in the region, it should probably be considered heavy rather than moderate grazing by cattle (Laycock and Conrad 1981).

Cattle stocking rates were adjusted by changing the duration of cattle grazing each year to achieve annually similar levels of forage utilization in the control pastures in spite of annual fluctuations in rainfall and forage production. Pastures were stocked with cattle for 6 wk during years 1 and 2 (8 May–18 June 1987 and 12 May–21 June 1988: 2.8 ha/animal-unit-month), for 3 wk during year 3 (10 May–31 May 1989: 6.9 ha/animal-unit-month); and for 5 wk during year 4 (9 May–13 June 1990: 3.3 ha/animal-unit-month). Hereafter, we will refer to the time interval that cattle were stocked in the pastures as the "spring grazing season."

Details on management of cattle are reported in Hobbs et al. (1996).

We acknowledge that interactions between cattle and elk in nature are not controlled by fences as they were in our studies. However, we were willing to sacrifice the realism offered by free-ranging animals to achieve the experimental control provided by constraining their movements. Our experiment was specifically designed to examine the case where elk and cattle use the same habitats and, hence, our findings will not apply to cases where habitat segregation is strong.

Primary production, forage intake, and utilization

We estimated primary production, rate of forage intake by cattle, and utilization of herbaceous forage by elk and cattle using 480 pairs of movable 0.55-m^2 plots (Klingman et al. 1943). Forty pairs of plots were randomly placed in each of the 12 pastures. Grazing was excluded from one member of each pair by enclosing it with a movable, cone-shaped cage (diameter = 0.83 m, height = 1.2 m) constructed of heavy-gauge, concrete-reinforcing wire (mesh size = 10 cm). Cages were staked to the ground with 64 cm lengths of steel rebar.

Although cages like the ones we used are known to influence primary production (Daubenmire 1940, Cowlishaw 1951, Williams 1951, Owensby 1969, Sharrows and Motazedian 1983, Parsons et al. 1984), we assumed that such influences were constant across all treatment levels. Thus, by using the same methods to estimate production in the control as well as the treatment pastures, we obtained reliable estimates of the relative effects of elk grazing on production, even if cage effects biased our absolute estimates of production.

Plot pairs were randomly located within each pasture during September before the first study year. After positioning one plot randomly, we subjectively chose a second plot within a 30-m radius to mimic the standing crop and vegetative composition of the initial plot. Both plots were marked with a 25-cm surveyor's stake. One member of the pair was chosen by coin flip to receive the cage. This process was repeated for each of the 40 pairs in each pasture.

Aboveground herbaceous biomass was harvested from each plot on 1 May, 1 June, and 1 July of each study year. On each sample date, plots were clipped and harvested, and were subsequently moved to a new location. New plot pairs were subjectively chosen to mimic the grazed condition in the previous open (uncaged) plot. After the last sample date, plot locations for the next study year were chosen randomly within a 30-m radius of the last established plot.

Plots were harvested as follows. All herbaceous vegetation contained within a steel hoop (0.75 m diameter) centered on the plot stake was clipped to stubble height ($\approx$1 cm) and sorted into three categories (perennial grass, annual grass, forbs) in the field. Clipped samples were taken to our facilities in Fort Collins, Colorado, were dried at 55°C for 48 h, and were subsequently separated by hand (many hands) into live and dead components. We then weighed the live and dead components of each of the three categories to the nearest 0.01 g.

To increase precision in analysis of rare categories, we pooled data into three classes: live perennial grass, dead perennial grass, and other live herbs. The "other live herbs" category included pooled data for annual and perennial forbs and annual grasses. Standing dead annual grass and forbs were too rare to measure at a reasonable level of precision.

Aboveground net primary production of each forage class was estimated as the sum of positive increments in live standing crop biomass within caged plots observed on the three sample dates (May–July). Total biomass of herbaceous forage available to cattle during the spring grazing season was estimated as the sum of the annual production of live tissue and the residual biomass of dead standing crop that remained after elk grazing. Energy supply in herbaceous forage was the total digestible energy contained in the residual dead forage plus the live forage produced after elk were removed from pastures; nitrogen supply was estimated similarly.

Forage intake rate of cattle was estimated as the sum of the differences between grazed and ungrazed plots on each sample date divided by the number of cows in a pasture (Van Der Kley 1955). Using differences in biomass between caged and uncaged plots tends to overestimate forage consumption by large herbivores because such differences include effects of trampling and wastage (Van Der Kley 1955). Moreover, we must assume that such effects are constant across treatments, which may not be the case (Allison et al. 1983). Nonetheless, all techniques for estimating intake rate of herbivores involve difficult assumptions (e.g., review of Van Dyne et al. 1980), and we believe (as do others, e.g., Meijs 1986, Mitchell et al. 1986, Frank and McNaughton 1992) that paired plots provide reasonable estimates of average daily intake given large sample sizes like those in our study.

We estimated digestible energy intake rate as the product of daily dry matter intake and digestible dry matter coefficients, using a constant of 18.4 kJ/g to convert dry matter to energy. Nitrogen intake was calculated similarly. Utilization was calculated as the ratio of dry matter removal to production for live forage categories, and as the ratio of removal to ungrazed standing crop for standing dead categories.

Forage nutritional quality

Samples of material in each forage class were composited to form a 20-g sample for each pasture. We ground composites to pass a 0.5-mm screen and analyzed them for total dry matter, ash, nitrogen content, and in vitro dry matter digestibility. Dry matter and ash were determined gravimetrically. Total nitrogen was determined using Kjeldahl procedures (A.O.A.C. 1980). Dry matter digestibility was estimated using two-stage in vitro procedures of Tilley and Terry (1963) as modified by Pearson (1970). We obtained rumen inocula for these procedures from a fistulated Holstein cow fed native grass hay.

Canopy cover

Pretreatment measurements indicated that the sampling effort required to estimate biomass of shrubs was prohibitive. However, we were interested in the effects of elk on the balance between shrubs and grasses in sagebrush communities and on the availability of palatable shrubs to cattle. To address these questions, we estimated percent cover of herbs and shrubs based on intercepts of canopies (Canfield 1941) along 25 12-m line transects in each pasture during 6–11 July of each study year. Locations of transects were established during year 1 and were maintained throughout the study. Transect locations were chosen by dividing a map of each pasture into 10 × 10-m cells, numbering all grid intersections, and randomly choosing (without replacement) among numbered locations. Transect endpoints were marked with steel pins (1 × 30 cm). In addition, a 1-m wooden surveyor's stake (painted high-visibility orange) was placed 10 m south of a transect endpoint to facilitate locating pins. After locating pins, we stretched a surveyor's tape between transect endpoints and read intersections of plant canopies with the tape to the nearest 1 cm.

Cattle diet composition and quality

During the last two years of the study (1989, 1990), we examined effects of elk grazing on nutritional quality and botanical composition of diets of nine cows fistulated at the esophagus. Grazing trials were separated into two periods, early and late spring. Early spring trials were conducted 5 d before introducing resident cows into experimental pastures (2 May in 1989; 5 May in 1990) and late spring trials were conducted 5 d after resident cows were removed from pastures (23 June in 1989; 19 June in 1990). Fistulated cows were randomly assigned to treatments within each block. One block of treatments was sampled each day so that, by the end of the grazing trial, all groups of cows experienced all treatments. Between grazing periods, fistulated cows were held in an adjacent pasture resembling experimental pastures. Supplemental feed was provided between sampling periods in order to maintain condition of fistulated animals.

Pasture forage was sampled 1 d after cows were introduced to treatment pastures and every day thereafter for 3 d. Between 0600 and 1100, each group of cows was gathered and fitted with screen-bottomed collection bags attached to fistulas. They were then lead to a random starting location and allowed to graze freely for 30–40 min. Following these collections, an aliquot of each extrusa sample was frozen in a plastic bag and stored for later analysis. At the end of each morning of grazing, cows were gathered and moved to the block of pastures to be sampled the next day. This protocol was repeated each day until all pastures were sampled. Cows were not fasted before extrusa collections.

Esophageal samples were freeze-dried and ground in a Wiley mill through a 1-mm screen. Samples were subdivided: one portion was used to determine botanical composition and the other portion was retained for forage quality analysis. Botanical composition of diets was estimated by microhistological examination of esophageal masticate samples (Composition Analysis Laboratory, Department of Range Science, Colorado State University, Fort Collins, Colorado). Ten systematically located fields per slide and five slides per sample (individual cow samples) were examined at 100× magnification. Extrusa samples were analyzed for dry matter, ash, and nitrogen by standard procedures (A.O.A.C. 1980). Neutral detergent fiber, acid detergent fiber, and acid detergent lignin were determined using sequential analysis according to procedures of Goering and Van Soest (1970). Digestibility of organic matter was estimated following Van Soest et al. (1987). Rumen inoculum was taken from a rumen-fistulated Holstein cow fed high-quality grass hay.

Statistical analysis

Responses to elk grazing were examined using a randomized complete block ANOVA with a repeated measures structure. The experimental unit in all analyses was the pasture. Thus, there were three, independent spatial replications for each treatment level within each year. Repeated measurements within pastures were treated as subsamples, were averaged before analysis, and did not contribute degrees of freedom in tests of hypotheses. Repeated measures over years were treated as within-subject effects using a multivariate approach (Cole and Grizzle 1966, Gill and Hafs 1971).

Covariance using pretreatment observations of forage biomass failed to significantly reduce experimental error in post-treatment responses, largely because the range in pretreatment values was substantially less than the range in values post-treatment and because our blocking presumably reduced the effect of pretreatment variation. Consequently we did not use pretreatment biomass as a covariate in the ANOVA.

Annual rainfall could be used as a covariate to reduce variation among years, but it would not be useful in reducing experimental error among blocks because rainfall was presumably quite similar among pastures within years. We wished to portray the magnitude of the year effect relative to the magnitude of the effect of treatment, so we did not adjust data using rainfall as a covariate. However, we did separate the effects of rainfall from the effect of year using regression, and we report that analysis separately from the ANOVA.

We tested a priori hypotheses using planned single

TABLE 2. Forage utilization by cattle and elk during the four-year Colorado study. Utilization of live forage is the percentage of the aboveground net primary production removed by herbivores. Utilization of dead forage is the percentage of the standing crop of the previous year's production that is removed. Table entries are means across replicates (n = three pastures). Significant differences between the control and treatment means are indicated by † ($P < 0.1$), * ($P < 0.05$), or ** ($P < 0.01$) preceding values.

Response	Year	Elk densities (animals/km²) 0	9	15	31
Utilization of dead perennial grass by elk‡	1	0.5	*13.4	**28.4	**44.0
	2	−13.5	13.2	6.4	**53.9
	3	9.9	**28.8	**36.4	**62.5
	4	*15.2	**40.5	**57.5	**65.8
	All	3.02	*23.9	**32.2	**57.0
	CI§	−5.16, 11.2	15.7, 32.0	24.0, 40.4	48.4, 65.2
	ECI‖	(0 vs. others)¶	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−43.9, −25.1	−32.5, −9.4	−40.6, −17.6	−65.0, −42.0
Utilization of live perennial grass by elk‡	1	1.2	4.2	9.8	7.7
	2	−2.1	0.5	4.3	3.9
	3	5.1	14.5	17.7	*24.9
	4	5.4	8.3	12.4	12.8
	All	2.4	6.9	†11.1	†12.3
	CI	−3.1, 7.9	1.4, 12.4	5.6, 16.5	6.81, 17.7
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−14.0, −1.4	−11.1, 2.1	−16.4, −0.9	−17.6, −2.2
Utilization of other live herbs by elk‡	1	−1.0	4.0	−2.7	3.1
	2	3.0	8.8	12.4	7.1
	3	2.7	2.9	9.2	7.5
	4	3.5	3.5	−0.2	5.1
	All	0.3	†4.8	4.6	†5.7
	CI	−3.5, 4.1	1.02, 8.5	0.8, 8.38	1.9, 9.4
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−9.1, −0.4	−9.1, −0.04	−9.4, 0.8	−10.8, −0.1
Utilization of dead perennial grass by cattle	1	18.1	14.1	*3.5	*7.7
	2	44.1	34.6	33.1	*9.1
	3	20.3	20.4	7.8	11.7
	4	41.9	33.2	25.5	†16.3
	All	31.3	25.6	**17.4	**11.2
	CI	26.9, 35.6	21.3, 29.9	13.1, 21.7	6.9, 15.5
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		6.3, 19.8	−2.7, 13.9	5.4, 21.9	11.6, 28.2
Utilization of live perennial grass by cattle	1	52.9	51.2	44.3	50.4
	2	62.3	73.2	61.3	67.2
	3	44.4	35.6	24.0	27.9
	4	48.6	42.6	39.5	†35.1
	All	51.8	50.6	*42.3	*45.2
	CI	47.7, 55.8	46.5, 54.6	38.2, 46.3	41.2, 49.2
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		2.3, 9.2	−3.1, 5.3	5.2, 13.7	2.4, 10.8
Utilization of other live herbs by cattle	1	23.1	22.8	40.7	35.8
	2	32.7	24.8	42.3	24.0
	3	33.8	10.1	9.4	12.3
	4	35.5	40.9	61.8	50.7
	All	31.3	24.6	38.6	30.7
	CI	15.9, 46.6	9.2, 40.0	23.2, 53.9	15.3, 46.0
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−17.7, 17.6	−15.0, 28.3	−28.9, 14.4	−21.1, 22.2

‡ Non-zero values for utilization by elk in the control reflect sampling error. Averaged across years, estimates of utilization by elk in the control pastures did not differ from 0.

§ 90% confidence intervals on the estimate of the 4-yr mean.

‖ Effect confidence interval: 90% confidence intervals on the difference between 4-yr means for treatment and control ($\bar{X}_{control} - \bar{X}_{treatment}$).

¶ Difference between the control and the mean of the treatment levels.

degree of freedom contrasts (Mize and Schultz 1985, Toothaker 1991). We examined each of four contrasts identified as a control (0 elk/km²) mean minus a treatment mean. We also used contrasts to test for linear and quadratic changes in response means with increasing elk density. To achieve a reasonable compromise between the probability of a Type I error and the power of our tests (Bransby 1989), we chose critical values of F at $\alpha = 0.10$ for all contrasts. However, we report the calculated significance of individual test statistics

TABLE 3. Aboveground net primary production (g/m^2) of grasses and forbs during spring and summer in Colorado sagebrush grassland, in relation to elk population during the previous winter. Table entries are means across replicates (n = three pastures). Significant differences between the control and treatment means are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$).

Category	Year	Elk densities (animals/km^2) 0	9	15	31
Perennial grass	1	24.8	24.5	28.0	20.6
	2	15.0	14.9	15.5	14.6
	3	6.6	5.5	6.1	6.1
	4	8.8	7.8	8.1	6.2
	All	14.1	13.2	14.4	11.9
	CI‡	11.5, 14.8	12.7, 16.0	10.02, 13.0	12.5, 15.75
	ECI§	(0 vs. others)‖	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−1.4, 3.2	−1.9, 3.7	−3.2, 2.4	−0.6, 3.2
Other herbs	1	19.2	22.3	17.9	18.7
	2	8.7	9.3	11.4	9.1
	3	7.1	6.7	6.2	6.5
	4	12.2	12.7	13.8	10.7
	All	11.8	12.7	12.3	11.2
	CI	8.7, 14.9	9.6, 15.8	9.2, 15.4	8.1, 14.3
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−3.8, 3.3	−5.9, 4.1	−4.8, 3.9	−3.8, 5.0

‡ 90% confidence intervals on the estimate of the 4-yr mean.
§ Effect confidence interval: 90% confidence intervals on the difference between 4-yr means for treatment and control ($\bar{X}_{control} - \bar{X}_{treatment}$).
‖ Difference between the control and the mean of the treatment levels.

to allow the reader to use an alternative significance level if desired.

We also report 90% confidence intervals on the size of treatment effects (Toothaker 1991), which should be interpreted as follows. The effect size is the value of the contrast of interest, i.e., the true treatment mean subtracted from the true control mean ($\mu_0 - \mu_t$). The estimated effect size is the value of the contrast when the estimated means are used to replace the true means (i.e., $\bar{X}_0 - \bar{X}_t$). A confidence interval on the estimated effect size is the true difference with 90% confidence. An effect size whose value is positive ($\bar{X}_0 - \bar{X}_t > 0$) indicates that that the control mean exceeds the treatment mean; similarly, a negative effect size ($\bar{X}_0 - \bar{X}_t < 0$) indicates that the treatment mean exceeds the control mean.

We performed all statistical analyses using the SAS System for General Linear Models (Freund et al. 1986) and the SAS Interactive Matrix Language.

RESULTS

Effects of elk grazing on forage supplies

Grazing intensity.—On average, elk stocked at 31 elk/km^2 annually removed 57% of the standing crop of dead perennial grass and removed 12% of the annual production of live perennial grass. Utilization of standing dead perennial grass increased linearly at a rate of 1.7% per unit (elk/km^2) increase in elk density (linear effect $F_{1,6}$ = 82, $P < 0.0001$, Table 2). Utilization of live grass increased at 0.3% per unit increase in elk density (linear effect $F_{1,6}$ = 6.5, P = 0.04, Table 2). Although average utilization of other live herbs by elk differed from the control, where there was no elk grazing (control vs. others $F_{1,6}$ = 4.5, P = 0.08, Table 2), linear effects were weak (linear effect $F_{1,6}$ = 3.2, P = 0.13). Elk utilization of live and dead perennial grass increased significantly with year (minimum P = 0.006), but the magnitude of the effect of elk density on utilization rates did not depend on year (maximum P = 0.39).

Utilization of standing dead perennial grass by cattle declined in direct proportion to elk density (linear effect $F_{1,6}$ = 24.2, P = 0.003, Table 1) and, thus, opposed the trends in utilization of standing dead grass by elk (Table 2). Similarly, utilization of live perennial grass by cattle was virtually a mirror image of utilization by elk (Table 2). As a result of these opposing trends, the proportion of the annual production of perennial grass removed by cattle and elk remained relatively constant, across all levels of elk density, at ≈60%.

Herbaceous primary production.—Effects of elk grazing on aboveground net primary production (ANPP) of perennial grasses were not significant (main effect $F_{3,6}$ = 1.2, P = 0.38, Table 3). Effects of elk grazing on ANPP of other live herbs were substantially more variable than effects on perennial grass, but we can be 90% certain that elk grazing, averaged across treatment levels, did not reduce ANPP of live herbs by >3.2 g/m^2 (Table 3).

Total herbaceous ANPP did not change with treatment (main effect $F_{3,6}$ = 0.40, P = 0.76). Effects of year on total herbaceous ANPP were strong ($F_{3,4}$ = 196, $P < 0.0001$) but year effects did not interact with the effects of treatment ($F_{9,18}$ = 1.1, P = 0.42). Annual variation in rainfall accounted for 70% of the variation in ANPP (Fig. 2). The effect of rainfall on ANPP was

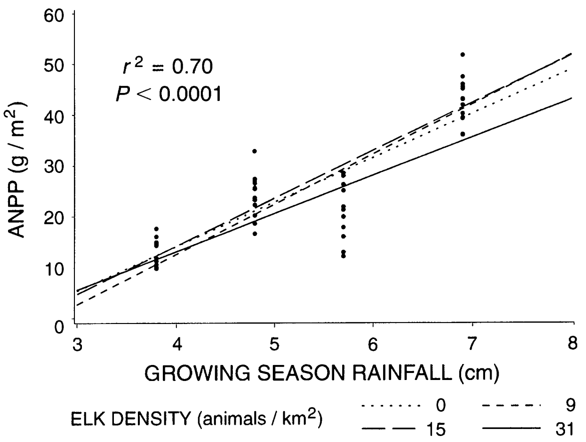

FIG. 2. Relationship between aboveground net primary production (ANPP) and rainfall in Colorado sagebrush grassland during four years, under four experimental elk densities. Equation for the best fit line including all treatment levels is $y = -22 + 8.8x$.

not modified by the elk grazing treatment (difference among slopes, minimum $P = 0.28$, Fig. 2).

To examine the year effect after the effects of rainfall were removed, we regressed the residuals of the ANPP vs. rainfall regression on year (Fig. 3). This regression showed a consistent downward trend and residuals were predominantly negative during the fourth study year, indicating that rainfall progressively overestimated ANPP as the study proceeded. Treatment did not affect this trend (difference among slopes, minimum $P = 0.58$, Fig. 3). These results suggest that depressing effects of grazing on ANPP accumulated over time in all pastures, including the controls.

Herbaceous standing crop biomass.—Grazing by elk reduced standing crops of forage available to cattle at the beginning of the spring grazing season. Averaged across years, the standing crop of dead perennial grass declined in direct proportion to elk density (linear effect $F_{1,6} = 10.0$, $P = 0.02$, Table 4) from a mean of 8.7 g/m^2 in the controls to 3.2 g/m^2 in the high density (31 elk/km^2) treatment. We also observed linear trends in effects of elk on the early spring standing crop of live perennial grass, but these trends only approached significance (linear effect $F_{1,6} = 3.2$, $P = 0.12$, Table 4). Effects of elk population density on the early spring standing crop of other live herbs (annual grasses + forbs) were not significant (main effect $F_{3,6} = 0.91$, $P = 0.49$, Table 4).

Year effects on standing crops were strong for all forage categories (maximum year $P < 0.05$, Table 4). The strength of the effect of elk on standing crops of dead perennial grass diminished as the study progressed (year $\times$ linear effect $F_{3,4} = 8.0$ $P = 0.04$). Year $\times$ linear effect interactions were not significant for live forage (minimum $P = 0.14$). The strong year $\times$ linear effect interaction for dead grass resulted in large part because the spring standing crop of dead grass approached 0 in all pastures during the final study year.

Canopy cover of shrubs and herbs.—Canopy coverage of the dominant shrub, *Artemisia tridentata,* was greatest in the control and in the highest density elk treatment (Table 5). As a result, quadratic effects approached significance ($F_{1,6} = 2.3$, $P = 0.13$, Table 5). We failed to observe significant effects of elk population density on canopy coverage of palatable shrubs (Table 5). However, differences among levels were obscured by high levels of variation among blocks. Canopy cover of *Artemesia tridentata* increased with year ($P = 0.03$), while canopy cover of other shrubs declined with year ($P < 0.02$). Year effects did not interact with treatment (year $\times$ treatment $P > 0.51$) for either shrub class.

Canopy cover of perennial grasses tended to be greatest in the moderately grazed (9, 15 elk/km^2) treatments, but this tendency was not significant (quadratic effect $F_{1,6} = 2.3$ $P = 0.18$, Table 5). Because the canopy coverage of grass was greatest at the moderate grazing levels and the cover of shrubs was least, grass contributed the greatest proportion of the total plant canopy at intermediate levels of elk grazing (quadratic effect $F_{1,6} = 4.5$, $P = 0.08$, Table 5).

Herbaceous canopy cover declined steeply with year ($F_{3,4} = 63$, $P = 0.0008$) as did the total cover of shrubs ($F_{3,4} = 9.4$, $P = 0.03$). The magnitude of the effect of treatment on herbaceous cover and shrub cover did not change as the study proceeded (year $\times$ treatment minimum $P = 0.25$).

Forage nutritional quality.—We did not detect effects of elk grazing on digestibility of live perennial grass (main effect $F_{3,6} = 1.23$, $P = 0.37$, Table 6). Digestibility of standing dead perennial grass (averaged across years and sample dates) increased in direct relation to elk density (linear effect $F_{1,6} = 4.6$, $P = 0.08$, Table 6), but these effects were small. We can be

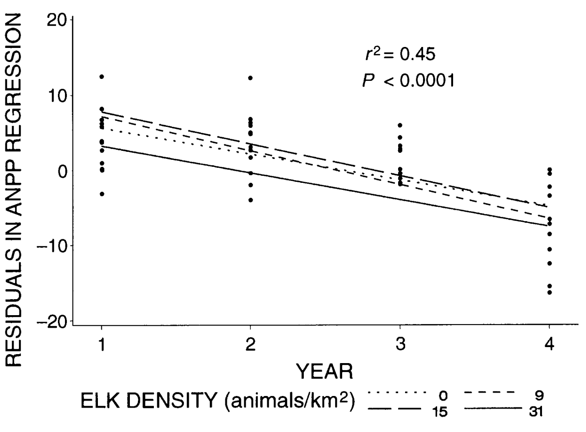

FIG. 3. Relationship between year and the residuals from ANPP vs. rainfall regression. A substantial year effect on ANPP remained after the effects of rainfall were removed. Equation for the best fit line including all treatment levels is $y = 2.63 - 3.5x$.

TABLE 4. Herbaceous standing crops (g/m^2) in Colorado sagebrush grassland during early May in relation to elk population density during the previous winter. Table entries are means across replicates (n = three pastures). Significant differences between the control and treatment means are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$) preceding values.

Category	Year	Elk densities (animals/km^2) 0	9	15	31
Dead perennial grass	1	18.2	17.0	12.5	*8.6
	2	11.2	8.4	9.4	†3.4
	3	4.3	**2.1	*2.5	**0.76
	4	1.2	†0.71	*0.47	**0.31
	All	8.7	7.0	6.2	*3.2
	CI‡	13.6, 19.0	12.1, 17.4	8.9, 14.2	13.1, 18.4
	ECI§	(0 vs. others)‖	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		0.4, 6.0	−1.7, −5.1	−0.9, 5.9	2.0, 8.8
Live perennial grass	1	7.8	6.1	6.1	†4.5
	2	4.2	3.6	3.7	2.9
	3	3.5	2.9	3.2	2.6
	4	2.5	2.1	2.4	1.8
	All	4.5	3.7	3.8	3.0
	CI	3.7, 5.3	2.8, 4.5	3.0, 4.6	2.18, 3.8
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−0.3, 2.3	−0.7, 2.4	−0.9, 2.2	0, 3.1
Other live herbs	1	5.8	3.7	4.9	3.5
	2	1.8	1.4	2.5	1.6
	3	3.6	5.0	3.9	3.2
	4	3.9	3.1	†2.7	*2.0
	All	3.8	3.3	3.5	2.6
	CI	3.2, 4.6	2.5, 4.1	2.7, 4.2	1.8, 3.4
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−0.9, 1.9	−0.5, 1.9	−1.2, 1.8	−0.3, 2.7

‡ 90% confidence intervals on the estimate of the 4-yr mean.

§ Effect confidence interval: 90% confidence intervals on the difference between 4-yr means for treatment and the control ($\bar{X}_{\text{control}} - \bar{X}_{\text{treatment}}$).

‖ Difference between the control and the mean of the treatment levels.

90% confident that, on average, digestibility of dead grass in high-density (31 elk/km^2) grazed pastures did not exceed control values by more than two percentage points. However, effects of elk grazing on digestibility of total grass biomass (live + dead) were more substantial. Linear effects were significant ($F_{1,6} = 7.7$, $P = 0.03$, Table 6) and digestibility values of grass biomass in the 31 elk/km^2 treatments were as much as 3.0 percentage points higher than control values (90% CI). Digestibility of other live herbs also increased linearly with elk grazing level ($F_{1,6} = 4.2$, $P = 0.08$, Table 6). Year effects on dry matter digestibility were strong for all forage categories (maximum $P < 0.001$, Table 6). However, year × treatment interactions only approached significance (minimum $P = 0.11$). The effect of year on forage digestibility can be attributed to annual differences in phenology and in dead/live ratios.

Effects of elk grazing on nitrogen content of live perennial grass were not significant (main effect $F_{3,6} = 0.25$, $P = 0.86$, Table 7). Nitrogen content of standing dead perennial grass (averaged across years and sample dates) increased in direct proportion to treatment (linear effect $F_{1,6} = 8.6$, $P = 0.03$, Table 7), as did the nitrogen concentration of the total grass biomass (linear effect $F_{1,6} = 15.1$, $P = 0.007$, Table 7). We did not detect effects of treatment on nitrogen content of other live herbs (main effect $F = 0.89$, $P = 0.54$). Year effects on forage nitrogen content were strong for all forage categories (maximum $P < 0.001$, Table 7), but effects of year and treatment did not interact (year × treatment, minimum $P = 0.50$).

Total forage and nutrient supply.—Total supply (biomass) of herbaceous dry matter available to cattle declined in direct proportion to elk population density (linear effect $F_{1,6} = 5.0$, $P = 0.08$, Fig. 4A), as did the supply of digestible energy (linear effect $F_{1,6} = 4.2$, $P = 0.09$, Fig. 4B) and nitrogen (linear effect $F_{1,6} = 4.5$, $P = 0.08$, Fig. 4C). Year effects were significant for all measures of forage supply (maximum $P < 0.0003$), and the size of the effect of elk grazing on forage supply was consistent across all years (year × treatment interaction, minimum $P > 0.37$).

Forage quantity/quality interactions.—The average concentration of digestible energy in the total biomass available to cattle declined 1.7% per 10-kg increase in that biomass ($r^2 = 0.59$, $P < 0.0001$, Fig. 5). This decline occurred primarily as a result of changes in the dead to live ratio of the total available biomass, which increased asymptotically as biomass increased (Fig. 6). Thus, when biomass available to cattle was high, a large component of the biomass was contributed by residual standing dead; consequently, the average nutritional quality of the available biomass was low.

Effects on cattle foraging

Cattle diet composition and quality.—Herbaceous plants dominated cattle diets (Table 8); shrubs uni-

TABLE 5. Canopy coverage of shrubs and grasses in Colorado sagebrush grassland in early July in relation to elk population density. Table entries are means across replicates (n = three pastures). Significant differences between the control and treatment means are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$) preceding values.

		Elk densities (animals/km^2)			
Response	Year	0	9	15	31
Canopy coverage of *Artemisia tridentata*	1	15.4	14.8	11.2	14.6
	2	13.0	14.0	10.2	14.5
	3	16.6	14.1	11.3	17.0
	4	20.2	16.1	13.8	17.3
	All	16.3	14.8	†11.6	15.8
	CI‡	13.6, 19.0	12.1, 17.4	8.9, 14.2	13.1, 18.4
	ECI§	(0 vs. others)‖	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−1.9, 6.4	−3.5, 6.7	−0.4, 9.8	−4.6, 5.6
Canopy coverage of other shrubs	1	0.4	0.1	0.7	0.4
	2	0.2	0.4	†0.7	†0.7
	3	1.4	0.7	1.3	0.3
	4	0.1	0.1	0.2	0.1
	All	0.5	0.2	0.5	0.3
	CI	0.3, 0.7	0, 0.4	0.3, 0.7)	0.1, 0.5
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−0.1, 0.5	−0.1, 0.7	−0.4, 0.4	−0.2, 0.7
Canopy coverage of perennial grass	1	9.8	12.3	10.5	7.5
	2	4.01	4.2	5.6	2.8
	3	2.8	2.1	2.9	1.7
	4	2.3	2.5	2.0	2.4
	All	4.7	5.3	5.3	3.6
	CI	3.7, 5.6	4.4, 6.2	4.4, 6.2	2.7, 4.5
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−1.4, 1.5	−2.3, 1.2	−[illegible].3, 1.3	−0.7, 2.9
Perennial grass canopy as % of total cover	1	22.1	32.4	32.1	23.6
	2	19.2	20.2	†26.7	13.6
	3	11.8	11.4	15.3	8.3
	4	8.6	10.5	9.4	10.2
	All	15.4	18.6	20.9	14.2
	CI	12.0, 18.7	15.2, 21.9	17.5, 24.2	10.8, 17.5
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−7.8, 2.8	−9.6, 3.2	−19.0, 1.0	−5.4, 7.4

‡ 90% confidence intervals on the estimate of the 4-yr mean.
§ Effect confidence interval: 90% confidence intervals on the difference between 4-yr means for treatment and the control ($\bar{X}_{control} - \bar{X}_{treatment}$).
‖ Difference between the control and the mean of the treatment levels.

formly contributed <12% of dry matter consumed. Although the contribution of shrubs to cattle diets more than doubled in response to elk grazing (Table 8), these effects were not significant (main effect $F_{2,8} = 1.1$, $P = 0.37$). We found no year effect on the botanical composition of cattle diets (minimum $P > 0.12$), and the effect of treatment did not depend on year (year × treatment, minimum $P > 0.18$).

Nitrogen content of cattle diets increased significantly in response to elk grazing in the moderately grazed treatment (control vs. 15 elk/km^2 $F_{1,6} = 4.3$, $P = 0.06$, Table 8) and approached significance over all treatments (control vs. others $F_{1,6} = 3.1$, $P = 0.10$). We did not detect effects of elk on the digestibility or fiber constituents of cattle diets (Table 8). Nutritional quality of cattle diets did not change with year (minimum $P > 0.48$), and we found no interactions between treatment and year (minimum $P > 0.33$).

Daily forage intake by cattle.—Daily dry matter intake of live forage by cattle tended to decline as elk density increased, but this tendency was not significant (level main effect $F_{3,6 = 0.62,}$ $P = 0.62$, Fig. 7A). In contrast, cattle intake of standing dead forage declined in direct proportion to elk density (linear effect $F_{1,6} = 16.2$, $P = 0.007$ Fig. 7A). Consequently, total (live + dead) dry matter intake of cattle also declined in response to increasing elk density (linear effect $F_{1,6} = 5.3$, $P = 0.06$, Fig. 7A).

Reductions in dry matter intake rates caused declines in daily intake of energy (linear effect $F_{1,6} = 5.1$, $P = 0.06$, Fig. 7B) and nitrogen (control vs. others $F_{1,6} = 5.4$, $P = 0.06$, Fig. 7C), despite enhancements in concentrations of energy and nitrogen in forage and in cattle diets that were attributable to treatment (Tables 6–8). Year effects on digestible energy and nitrogen intake of cattle approached significance (energy: $F_{3,4} = 3.9$, $P = 0.11$; nitrogen: $F_{3,4} = 3.5$, $P = 0.13$). The magnitude of treatment effects on digestible energy intake changed significantly with year (year × quadratic effect $F_{3,4} = 5.5$, $P = 0.07$; year × control vs. others $F_{3,4} = 5.6$, $P = 0.06$; year × control vs. 15 $F_{3,4} = 6.9$, $P = 0.05$).

TABLE 6. In vitro dry matter digestibility (% of dry matter) of herbaceous forage in sagebrush grassland in relation to elk population density. Table entries are means across replicates (n = three pastures) of composites collected during 15 May–30 June. Significant differences between the control and treatment means are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$) preceding values.

Forage categories	Year	Elk densities (animals/km²) 0	9	15	31
Live perennial grass	1	55.6	†58.9	55.6	56.4
	2	62.6	62.9	64.5	64.1
	3	60.1	60.1	60.2	59.1
	4	62.4	63.1	63.0	62.0
	All	60.2	61.2	60.1	60.4
	CI‡	59.6, 60.8	60.6, 61.8	59.5, 60.7	59.8, 61.0
	ECI§	(0 vs. others)‖	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−1.5, −0.33	−2.2, 0.3	−1.7, 0.5	−1.2, 1.4
Dead perennial grass	1	48.1	*46.0	**45.5	48.3
	2	48.9	48.5	48.9	50.3
	3	52.7	52.5	†54.8	†54.9
	4	50.7	50.9	*52.7	50.1
	All	50.1	49.4	50.5	*51.1
	CI	59.5, 50.7	48.8, 50.0	49.9, 51.1	50.5, 51.6
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−1.2, 0.7	−0.5, 1.7	−1.5, 0.7	−2.0, 0.2
Total perennial grass	1	50.8	51.2	49.8	51.2
	2	54.1	54.7	55.2	58.0
	3	56.3	57.0	58.0	58.0
	4	59.1	†60.4	**61.4	*60.5
	All	55.1	55.8	56.1	*56.9
	CI	54.4, 55.8	55.1, 56.4	55.4, 56.7	56.2, 57.5
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−1.3, −1.0	−2.0, 0.5	−2.2, 0.3	−3.0, −0.53
Other live herbs	1	60.3	63.1	60.4	62.6
	2	62.0	63.3	60.9	65.8
	3	62.9	†66.8	61.9	66.0
	4	63.8	63.8	62.7	66.2
	All	62.3	64.3	61.4	†65.1
	CI	61.1, 63.4	63.1, 65.4	60.2, 62.5	63.9, 66.3
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−3.2, 0.5	−4.2, 0.3	−1.4, 3.1	−5.1, −0.6

‡ 90% confidence intervals on the estimate of the mean.
§ Effect confidence interval: 90% confidence intervals on the difference between treatment and the control means ($\bar{X}_{control} - \bar{X}_{treatment}$).
‖ Difference between the control and the mean of the treatment levels.

Utilization of the total forage supply by elk accounted for 18% of the variation in daily digestible energy intake by cattle (Fig. 8). On average, each percentage point increase in utilization of the herbaceous forage supply by elk was associated with a 2.9 ± 0.9 MJ (mean and 90% confidence interval) reduction in cattle daily energy intake. However, scatter about the regression was large. For example, utilization rates in the range of 10–15% were associated with a 50-fold range in digestible energy intake by cattle.

Daily intake of forage dry matter and digestible energy by cattle were asymptotically related to the total herbaceous forage supply available to cattle during the spring grazing season (Fig. 9). Increases in total forage supply above ≈45 gm/m² exerted negligible effects on cattle intake rates of dry matter or energy (Fig. 9). However, when forage supplies dropped below this level, daily intake rates of dry matter and energy declined steeply as forage supplies declined. This result reveals that effects of elk grazing on cattle forage intake depend on spatial and temporal differences in pasture productivity. Given the same cattle stocking rates, effects of elk grazing on cattle intake are likely to be undetectable when pastures are sufficiently productive.

DISCUSSION

Effects of elk on forage resources for cattle

A necessary condition for the expression of interspecific resource competition is a reduction in availability of resources for one species resulting from use of those resources by another species (Tilman 1982). Elk grazing during winter and spring reduced the total supply of forage dry matter, digestible energy, and nitrogen available for consumption by cattle in spring. These reductions occurred as a direct result of removal of live and dead biomass by elk; we found no effects of elk grazing on primary production.

The magnitude of the effect of year on net primary production was far greater than the effect of elk population density. The major portion of the year effect

TABLE 7. Nitrogen content (% of dry matter) of herbaceous forage in sagebrush grassland in relation to elk population density. Table entries are means across replicates (n = three pastures) of composites collected during 15 May–30 June. Significant differences between the control and treatment means are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$) preceding values.

Forage category	Year	Elk densities (animals/km²) 0	9	15	31
Live perennial grass	1	2.11	2.34	2.20	2.31
	2	2.11	2.16	2.17	2.14
	3	1.96	2.00	1.98	1.94
	4	2.21	2.04	2.05	2.17
	All	2.10	2.14	2.10	2.14
	CI‡	2.03, 2.16	2.07, 2.20	2.03, 2.16	2.07, 2.20
	ECI§	(0 vs. others)‖	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−0.13, −0.07	−0.16, 0.07	−0.13, 0.11	−0.16, 0.06
Dead perennial grass	1	0.84	0.84	0.86	0.86
	2	0.77	0.80	0.81	0.84
	3	0.92	0.95	0.98	*1.2
	4	0.98	0.98	1.1	1.03
	All	0.88	0.89	0.93	*0.98
	CI	0.84, 0.92	0.85, 0.93	0.89, 0.93	0.94, 1.01
	ECI	(0 vs. others)	(0 vs. 8)	(0 vs. 15)	(0 vs. 31)
		−0.12, 0.0	−0.09, 0.06	−0.12, 0.02	−0.18, −0.03
Total perennial grass	1	1.36	1.41	1.42	1.55
	2	1.31	1.38	1.37	**1.56
	3	1.45	1.59	1.60	**1.75
	4	1.90	1.82	1.91	2.01
	All	1.51	1.55	1.58	**1.72
	CI	1.45, 1.56	1.49, 1.60	1.52, 1.63	1.66, 1.77
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−0.2, 0.02	−0.2, 0.1	−0.2, 0.04	−0.3, −0.1
Other live herbs	1	2.42	2.42	2.44	2.10
	2	2.49	2.14	*1.81	2.90
	3	1.96	2.08	1.94	*2.47
	4	2.23	2.31	2.69	2.60
	All	2.27	2.24	2.22	2.36
	CI	2.65, 2.90	2.58, 2.83	2.10, 2.34	2.24, 2.48
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		−0.19, 0.20	−0.23, 0.24	−0.19, 0.30	−0.32, 0.15

‡ 90% confidence intervals on the estimate of the 4-yr mean.
§ Effect confidence interval: 90% confidence intervals on the difference between control and control ($\bar{X}_{control} - \bar{X}_{treatment}$).
‖ Difference between the control and the mean of the treatment levels.

was attributable to annual variation in rainfall, but effects of year on primary production remained even after the influence of rainfall was removed. We emphasize that this remaining annual effect was evident in the control as well as the treatment pastures. We suggest that these effects can be explained as follows. Because our study area was not grazed by livestock for 5 yr before the study began, the introduction of grazing represented a significant perturbation of the system we studied. We suggest that part of the effect of year on ANPP was a response to this perturbation, and that downward trends in ANPP were, in part, a response to the introduction of grazing after a history of rest. Because effects of year (independent of rainfall effects) were evident in the control pastures, it appears that cattle grazing may have contributed to a downward trend in ANPP on this site.

However, with few exceptions, year × treatment interactions were not significant, and we can conclude in these cases that effect of elk grazing on forage supplies did not depend on annual effects of rainfall or the cumulative effects of elk and cattle grazing. When these interactions were significant, however (e.g., for standing crops of dead perennial grass), it remains unclear whether the interaction was caused by annual variation in rainfall or resulted from cumulative effects of grazing.

Effects on resource acquisition

A sufficient condition for the expression of interspecific competition for resources is a reduction in acquisition of limiting resources by one species that results from use of those resources by another species (Tilman 1982). Elk consumed forage that otherwise would have been available to cattle and, as a result, the amount of dry matter, energy, and nitrogen consumed by cattle declined as elk population density increased. The mechanism linking elk population density to cattle resource use was a Type II functional response (Holling 1965) of cattle to the total supply of forage available during spring (i.e., Fig. 9). When forage supplies were sufficently low, cattle forage intake declined

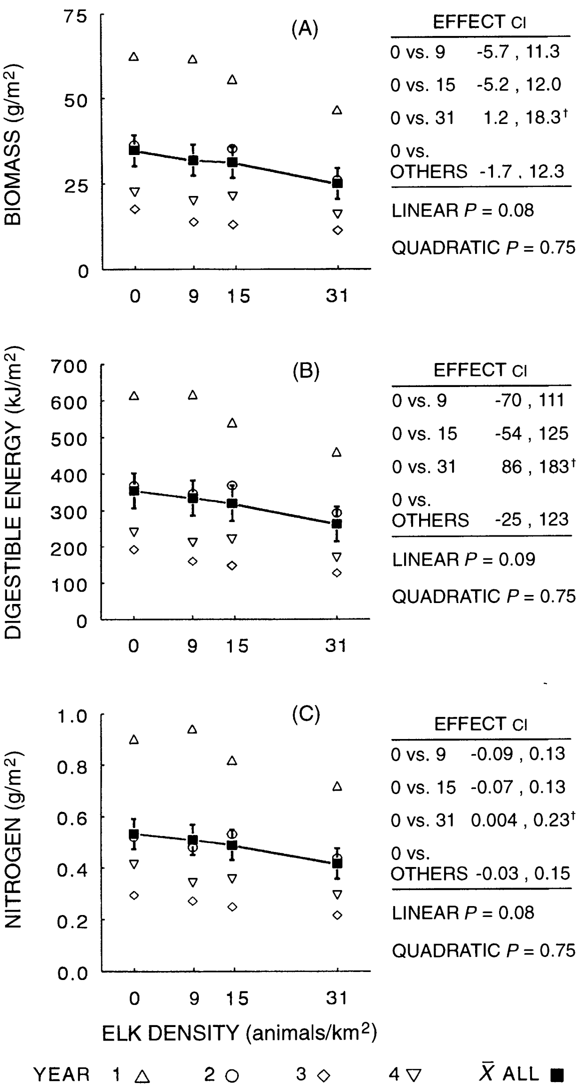

FIG. 4. Amounts of dry matter (A), digestible energy (B), and nitrogen (C) available to cattle during May–July on sagebrush grassland range, plotted against population density of elk using that range during winter and early spring. Open symbols are level means for each year and solid squares show the 4-yr average, with 90% confidence intervals (vertical bars) based on variation among replicates (n = three pastures). Effect confidence intervals (Effect CI) enclose the true difference between level means (control μ − treatment μ) with 90% confidence. Significant differences between treatment means and the control are indicated by † ($P < 0.10$), * ($P < 0.05$), and ** ($P < 0.01$).

steeply. Thus, elk grazing that caused forage supplies to drop below this threshold caused reductions in cattle intake.

Similar responses of large herbivores to changes in forage availability have been observed in other grazing systems (Allden 1962, Trudell and White 1981, Allison 1985, Forbes and Hodgson 1985, Short 1985, Birrell 1991). A Type II response of daily intake to total forage biomass occurs for large herbivores because they are able to compensate for the effects of reduced availability on instantaneous intake by increasing daily grazing time (Allden and Whittaker 1970, Arnold 1970, Chacon and Stobbs 1976, Allison 1985, Bunnell and Gillingham 1985, Short 1986, Penning et al. 1991). This compensation allows daily intake to remain relatively constant over a broad range of forage availabilities. However, animals cannot increase grazing time without limit: the need to ruminate and rest constrains maximum grazing time of cattle to no more than ≈12 h/d (Stobbs 1975). When this constraint is reached, daily intake must decline as availability declines because animals can no longer offset reduced instantaneous intake by expanding grazing time. Such compensatory mechanisms are not without cost. Pro-

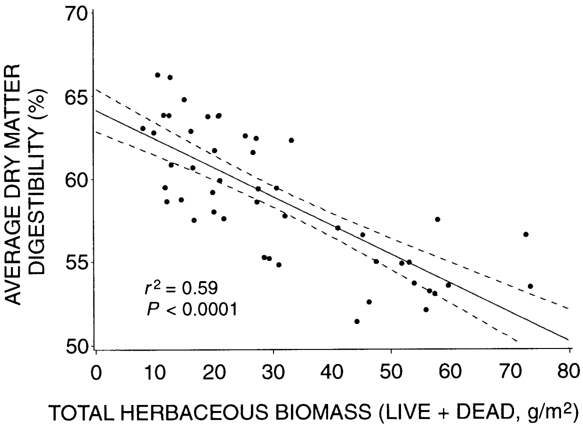

FIG. 5. Relationship between average forage digestibility and total herbaceous biomass available to cattle during the spring and early summer in sagebrush grassland. Each data point shows a pasture mean during one year. The solid line is $y = 64 - 0.17x$. Dashed lines are 90% confidence intervals on the prediction of the average y at a given x.

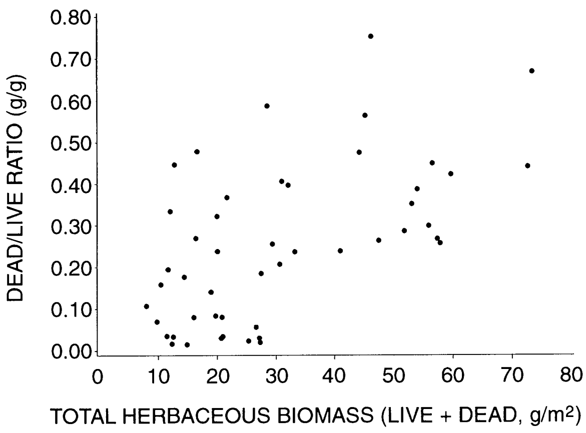

FIG. 6. The live/dead ratio in total herbaceous biomass available to cattle increased asymptotically with increasing total herbaceous biomass. Each data point is a value for one pasture for one year.

TABLE 8. Effects of winter and spring grazing by elk on composition (% of dry matter) of cattle diets during the spring and summer.

	Elk density (animals/km^2)				Contrast					
					(0 vs. 15		(0 vs. 31		(0 vs. others	
	0 $\bar{X}$	15 $\bar{X}$	31 $\bar{X}$	SE*	P	Effect CI†	P	Effect CI	P	Effect CI
IVDDM‡	70.2	70.4	69.4	0.7	0.88	−2.7, 2.1	0.45	−1.3, 2.3	0.72	−1.4, 2.1
Nitrogen	1.32	1.47	1.40	0.06	0.08	−0.25, 0.03	0.40	−0.31, −0.01	0.14	−0.23, −0.09
NDF§	55.1	52.7	54.9	2.3	0.48	−4.1, 8.7	0.94	−6.2, 6.6	0.66	−4.3, 6.8
ADF‖	26.9	24.7	25.5	1.2	0.18	−0.92, 5.4	0.38	−1.7, 4.6	0.20	−0.90, 0.46
Lignin	4.92	4.81	5.13	0.28	0.80	−0.67, 0.61	0.61	−0.98, 0.57	0.88	−0.71, 0.61
Grass	65.4	56.1	61.3	6.7	0.35	−9.5, −28.1	0.67	−14.7, 22.9	0.43	−9.6, 23.0
Forbs	29.9	33.4	27.4	7.1	0.72	−23.0, 15.9	0.81	−17.0, 21.9	0.95	−17.4, 16.3
Shrubs	4.8	11.7	11.8	3.1	0.13	−15.3, 1.7	0.12	−15.5, 1.6	0.08	−14.2, −0.49

* Pooled estimate of standard error of mean.
† Effect confidence interval: 90% confidence interval on the difference between the control and treatment means.
‡ In vitro dry matter digestibility.
§ Neutral detergent fiber.
‖ Acid detergent fiber.

longed grazing elevates energy expenditures (Young and Corbett 1972, Havstad and Malecheck 1982), which may reduce animal growth and reproduction by harming energy balance even if energy intake remains constant.

Based on the relationship between forage supply and cattle intake rate (Fig. 8), we conclude that, under conditions similar to those we studied, a threshold in forage supply of ≈45 gm/m^2 of live and dead herbaceous biomass appears to determine the nature of the interaction between elk and cattle in sagebrush grassland. When biomass remaining after elk grazing exceeds this threshold (as a result of spatial or temporal variation in forage productivity or differences in cattle stocking rate), then we would expect that effects of elk grazing on forage supplies for cattle would be relatively minor. However, when elk numbers and spatial distribution cause forage availability to cattle to decline below this threshold, then resource competition between elk and cattle will be strong and will increase in intensity as forage availability declines. Thus, we suggest that under conditions closely resembling those we studied, elk populations in sagebrush grassland can be managed to reduce competition with cattle by controlling their spatial distribution and population density to assure that forage available to cattle during spring exceeds ≈45 g/m^2 of herbaceous live and dead biomass.

The balance between competition and facilitation

Much effort has been invested in understanding facilitative relationships among herbivores that share forage resources (Bennett et al. 1970, Bell 1971, McNaughton 1976, Jarman and Sinclair 1979, Sinclair and Norton-Griffiths 1982, Coppock et al. 1983, McNaughton 1984, Gordon 1988, Gordon and Lindsay 1990). There is ample evidence that grazing can enhance the nutritional quality of forage supplies by maintaining vegetation in an immature, rapidly growing state, and by removing standing dead forage (review in Gordon and Lindsay 1990). In so doing, grazers retard the accumulation of structural tissue in plant communities, tissue that would otherwise dilute nutrients and reduce digestibility of forage plants (McNaughton 1984).

However, Hobbs and Swift (1988) urged caution in interpreting facilitative effects. They showed that nutritionally beneficial effects of grazing on forage quality may be compromised by nutritionally detrimental effects of grazing on the amount of forage available. Such compromises are important in understanding effects of elk grazing on forage supplies for cattle. We found that grazing by elk enhanced the average digestibility and nitrogen content of forage available to cattle and increased the nitrogen content of cattle diets. These enhancements apparently resulted from shifts in the dead to live ratio of the forage available to cattle. However, we also found that elk grazing caused substantial reductions in cattle daily intake of dry matter, digestible energy, and nitrogen. Reduced forage intake rates by cattle appeared to be caused by reductions in forage biomass resulting from elk grazing. Thus, although facilitation and competition operated simultaneously in the same grazing system, the effects of competition prevailed.

Competitive effects of elk on cattle in sagebrush grassland resulted in large part because elk grazing reduced the residual standing crop of dead perennial grass that was carried forward from year to year. Although dead plant tissue can be viewed as diluting nutrients in the standing crop, it also represents an important buffer against annual variation in forage supply. Standing dead plant biomass mitigates the effect of low rainfall on the availability of total herbaceous forage. Large residuals of standing dead biomass resulting from high levels of primary production during high rainfall years can buffer the effect of reduced production during low rainfall years. Elk grazing weakened this buffering effect by removing residual biomass that would otherwise be available to cattle.

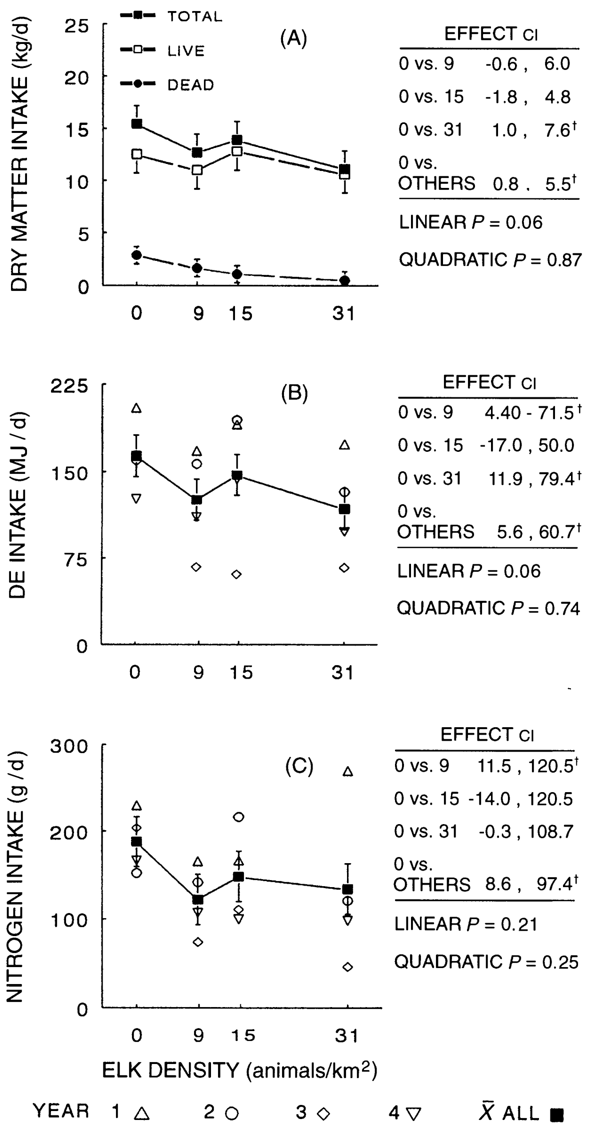

FIG. 7. Rates of intake of (A) dry matter, (B) digestible energy (DE), and (C) nitrogen by cattle using sagebrush grassland range during the spring grazing season (≈10 May–20 June), plotted against population density of elk using that range during winter and early spring. Open symbols are level means for each year and solid squares show the 4-yr average, with 90% confidence intervals (vertical bars) based on variation among replicates (n = three pastures). Effect confidence intervals (Effect CI) enclose the true difference between level means (control μ − treatment μ) with 90% confidence. Significant differences between treatment means and the control are indicated by † ($P < 0.10$).

However, residual standing dead biomass declined precipitously with year in the *control* as well as in the treatment pastures. We surmise from this result that stocking rates of cattle were probably excessive. Grazing sagebrush grassland ranges to achieve 50% removal of the production of live perennial grass will not provide a forage residual adequate to sustain cattle grazing during low rainfall years.

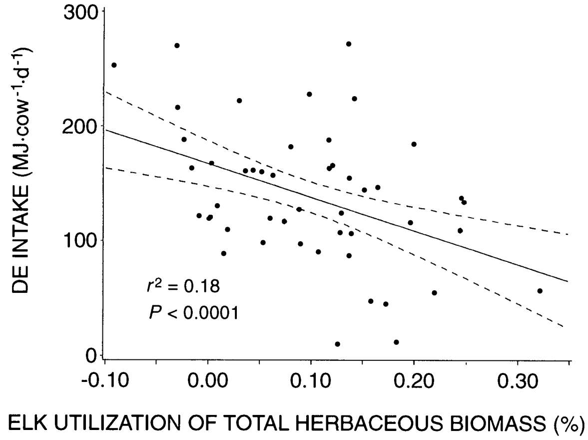

FIG. 8. Relationship between digestible energy (DE) intake of cattle and forage utilization rates by elk in sagebrush grassland. Solid line is $y = 167 - 291x$. Dashed lines are 90% confidence intervals on the mean of y for a given x.

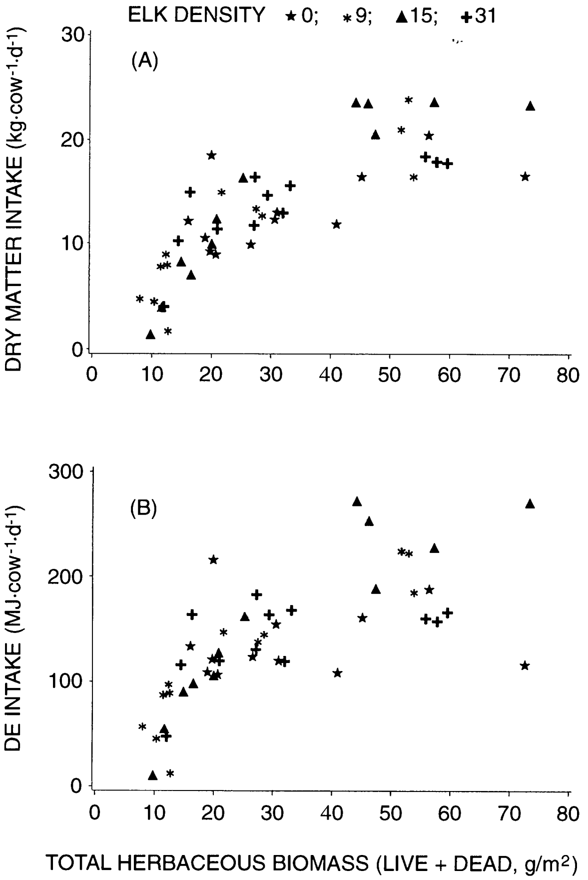

FIG. 9. Functional response of cattle to changes in forage supply during spring and summer in sagebrush grassland. Forage supply is the sum of the live and dead biomass available to cattle during the spring grazing season. Data points are pasture means for cattle daily intake of (A) dry matter and (B) digestible energy (DE) paired with pasture means for forage supply for each of the four study years.

Conclusions

The objective of the work reported here was to test the hypothesis that winter grazing by elk does not influence forage resources for cattle during the spring. We reject that hypothesis: elk grazing exerted enhancing as well as harmful effects on forage available to cattle. In particular, elk grazing enhanced the nutritional quality of forage available to cattle by increasing live to dead ratios of standing crops. However, these improvements were not sufficient to overcome the harmful effects of elk grazing on forage availability. Reductions in supplies of forage available to cattle appeared to cause declines in their daily intake of dry matter and digestible energy. In the system we studied, harmful impacts of elk grazing on cattle dry matter and energy intake began to occur when herbaceous forage available to cattle after elk grazing fell below $\approx$45 g/m^2 of dry matter.

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