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Author(s): N. Thompson Hobbs, Dan L. Baker, George D. Bear, David C. Bowden

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UNGULATE GRAZING IN SAGEBRUSH GRASSLAND: EFFECTS OF RESOURCE COMPETITION ON SECONDARY PRODUCTION¹

N. THOMPSON HOBBS²

*Mammals Research Section, Colorado Division of Wildlife,
317 W. Prospect, Fort Collins, Colorado 80526 USA, and
Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA*

DAN L. BAKER AND GEORGE D. BEAR

*Mammals Research Section, Colorado Division of Wildlife,
317 W. Prospect, Fort Collins, Colorado 80526 USA*

DAVID C. BOWDEN

Statistics Department, Colorado State University, Fort Collins, Colorado 80523 USA

Abstract. In many areas of western North America, populations of elk are believed to harm production of cattle by competing with them for limited supplies of native forage. We examined effects of variation in the population density of elk (*Cervus elaphus canadensis*) during winter on growth and reproduction of cattle during spring, using 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/km²), replicated each level three times, and observed responses of cattle to these manipulations.

Mean birth dates of calves born to cows in the intermediate (9, 15 elk/km²) treatment levels were delayed by 5 d relative to birth dates of calves born to cows in controls (0 elk/km²), but these trends were not statistically significant (quadratic effect $F_{1,6} = 3.2$, $P = 0.13$). Calf body mass at birth was not significantly influenced by treatment, but calf body mass at the end of spring declined linearly ($F_{1,6} = 7.9$, $P = 0.03$) with increasing elk population density, from a mean of 80.2 kg in the control to 73.0 kg in the 31 elk/km² treatment. Calf body mass at weaning was weakly depressed by treatment, with the largest treatment effects occurring at the 9 elk/km² level ($F_{1,6} = 8.8$, $P = 0.02$).

Body mass of cows at the end of the spring grazing season tended to decline linearly with treatment, but these tendencies were not statistically significant (linear contrast $F_{1,6} = 1.9$, $P = 0.22$). We did not find significant effects of treatment on cow body mass at time of weaning (control vs. others contrast $F_{1,6} = 3.3$, $P = 0.12$) or on natality rates (control vs. other contrast $F_{1,6} = 1.2$, $P = 0.31$), although, in both cases, values for the control tended to exceed the treatments.

Body mass of cows ($t_1 = -3.9$, $P = 0.0003$) and calves ($t_1 = -3.9$, $P < 0.0001$) at the end of the spring grazing season were quadratically related to the biomass of available herbaceous forage during spring. We observed a threshold in effects of forage supply on cattle production at about 45 g/m² of live and dead herbaceous biomass. Cattle production declined with declining forage biomass when forage supply fell below this threshold.

Total cattle production (kilograms per cow per year), was quadratically related to elk population density ($F_{1,6} = 5.8$, $P = 0.05$). Average cattle production in the control ($\bar{X} = 248$ kg·cow⁻¹·yr⁻¹) exceeded the mean of the other treatment levels ($\bar{X} = 224$ kg·cow⁻¹·yr⁻¹, $F_{1,6} = 6.7$, $P = 0.04$). Quadratic responses in cattle performance were apparently caused by compensatory growth after the spring grazing season: growth rates of cows during spring were inversely related to their subsequent growth rates during summer and fall ($F_{1,46} = 33.5$, $P < 0.0001$, $r^2 = 0.50$).

We conclude that elk grazing caused reductions in cattle production, but the magnitude of the effects were not proportionate to elk population density. Our studies revealed that competition between cattle and elk operates in a threshold fashion. If sufficient forage is available to cattle following elk grazing, elk populations will not harm cattle performance. In the system we studied, this threshold occurred at ≈ 45 g/m² of live and dead herbaceous biomass.

Key words: body mass; cattle; competition; elk; grazing; growth facilitation; natality; secondary production; ungulates.

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² Address correspondence to: Mammals Research Section, Colorado Division of Wildlife, 317 W. Prospect, Fort Collins, Colorado 80526 USA.

INTRODUCTION

Shared use of resources by vertebrates has often been interpreted as *de facto* evidence of competition (e.g., Grant 1972, Hudson 1977, Dunbar 1978, Jarman and Sinclair 1979, Singer 1979, Seegmiller and Ohmart 1981, Hanley and Hanley 1982, Belovsky 1984, Sinclair 1985, Spowart and Hobbs 1985, Ambrose and Deniro 1986, Llewellyn and Jenkins 1987, Jenkins and Wright 1988, Bodmer 1991). However, many uncertainties result from inferring competition from patterns in resource use (Colwell and Futuyma 1971, Colwell and Fuentes 1975, Connell 1975, Wiens 1977, Thompson 1980, Connor and Simberloff 1986). Overcoming these ambiguities requires manipulative experiments that examine the direct effects of one species on the growth and reproduction of another when resources are limiting (Grant 1972, Connell 1975, Pianka 1976, Hastings 1987, Glasser and Price 1988, Tilman 1989). Such experiments are rare for vertebrates (Sinclair and Norton-Griffiths 1982, Brown and Batzli 1985, Brown et al. 1986, Dickman 1986).

Elk populations in western North America are believed to compete with cattle for limited supplies of forage in sagebrush grassland, and these competitive relationships are believed to harm cattle production (Smith 1961, Powell et al. 1986, Hogan 1990). We have shown that use of sagebrush grassland during winter and spring can cause reductions in daily intake of dry matter, energy, and nitrogen by cattle during the spring and summer (Hobbs et al. 1996). These reductions occur despite enhancing effects of elk on the nutritional quality of forage available to cattle, enhancements that facilitate their selection of high nitrogen diets (Hobbs et al. 1996). However, it remains uncertain whether or not changes in resource use by cattle cause changes in cattle growth or reproduction. Here, we report a manipulative experiment designed to examine the effects of increasing elk population density on production of cattle in sagebrush grassland.

METHODS

Study area and experimental design

We examined responses of vegetation and cattle to increasing population densities of elk (0, 9, 15, 31 animals/km²) in a randomized complete block experiment conducted during four consecutive years at the Colorado Division of Wildlife Little Snake Wildlife Management Area, near Maybell, Colorado. Three replications of each treatment level were established annually by stocking 12 fenced pastures (each 32 ha) with different numbers of elk during January through April. For details, see Hobbs et al. 1996.

Management of cattle

We stocked pastures with cattle during early May. Cattle were stocked at the same number (seven cow-

calf pairs and one heifer) in all pastures, including the control, during all four study years. Thus, cattle densities were held constant across pastures while elk densities varied. This allowed performance of cattle in the 0 elk/km² pastures to control for performance of cattle that shared rangeland with elk. Cattle remained in pastures during May through June, an interval we term the "spring grazing season." We varied the duration of cattle grazing to achieve $\approx 50\%$ utilization of the aboveground net primary production of perennial grasses in the control (0 elk/km²) pastures (details in Hobbs et al. 1996).

Cattle were obtained via contract with a local rancher, Mr. Bruce Seely of Craig, Colorado. We randomly allocated 84 cows and calves and 12 heifers among pastures. Randomization was accomplished by first stratifying the cow herd by age and then randomly choosing animals to accomplish similar age distributions among pastures. Cows were herefords. Calves were predominantly herefords and hereford \times angus crosses. To the extent possible, we maintained the same adults in each pasture from year to year and followed their growth and reproductive output throughout the study. This allowed effects of competition to accumulate with time. On average, cattle were kept in the study for 2.7 yr each; 34 of the original 96 cows remained in the study for all 4 yr. Some cows were replaced because of failure to breed, death losses, and other miscellaneous sources of attrition. Rates of replacement were similar across all treatments.

At the end of the spring grazing season, cattle were returned to Mr. Seely's ranch where they were maintained in a single group for the remainder of the year. They were maintained on native rangeland during the summer and fall, and were fed grass hay throughout the winter.

All cows were exposed to fertile bulls immediately after their removal from pastures. Each year's calf crop was sold each fall after weaning, except for some females retained as replacements. Any cows that failed to breed were sold after weaning, usually in mid-November.

After cattle were removed, pastures remained ungrazed by cattle or elk until they were restocked with elk during the following December.

Measurements of cattle production

Throughout this paper we use the term "growth" to mean a positive increment in body mass of mature or immature animals. Cattle growth and reproductive performance were measured as follows. During each study year, we weighed calves born to cows in the experiment within 2 d of their birth. Calves and cows were also weighed when they were introduced to pastures (≈ 15 May), when they were removed (≈ 1 July), and at weaning (≈ 10 November). Data on body mass of calves at weaning are limited to three study years (1987, 1989,

1990) because calves were sold prematurely during 1988.

To examine reproductive performance, we recorded birth dates of all calves and calculated natality rates for each pasture each year as the number of cows producing calves divided by the total number of cows in the pasture ($n = 8$). We estimated total annual production by cattle in each pasture as the product of the average natality rate times the average body mass of calves at weaning plus the average annual gain in mass of adults.

Statistical analysis

We analyzed effects of treatment on cattle body mass, birth dates, and natality rates using a split plot, factorial ANOVA. Factors were elk density, block, and year, all of which were assumed to be fixed. Pastures formed the whole plot and repeated measures (i.e., years) formed the split plot. We used responses of individual animals (sampling units) as observations, but we calculated all F ratios using the mean square error of the treatment \times block interaction in denominators. This allowed us to preserve responses of individual animals in the analysis (which was important when covariates were used), but simultaneously provided an estimate of experimental error appropriate to a randomized complete block design where pastures, rather than individuals, were the experimental units.

We used covariates to reduce experimental error. Pretreatment body mass data for cows and calves (measured when they were first introduced to pastures) were used as concomitant observations in analysis of covariance of body mass at the beginning of spring, at the end of spring, and at weaning. Pretreatment body mass measurements of calves at birth were used as concomitant observations for birth weights. We emphasize that concomitant observations were taken during an animal's initial study year, *before* animals had any opportunity to be influenced by treatment. When covariates were used, we report least-squared means adjusted to the average value of the pretreatment covariate. We did not use covariates to adjust birth dates because they did not increase precision in the analysis. Average rates of growth were calculated as the difference between least squared estimates of cow and calf body masses at the beginning and end of a time interval divided by the duration of the interval.

We tested *a priori* hypotheses using planned, orthogonal contrasts (Mize and Schultz 1985, Toothaker 1991). Contrasts included a comparison of each treatment level vs. the control and the control vs. the average of all treatment levels, as well as tests for linear and quadratic effects. We also report 90% confidence intervals on the size of treatment effects (see Hobbs et al. 1996 for details).

RESULTS

Effects of elk on cattle growth

Calf body mass.—Effects of elk grazing on body mass of calves varied with season of the year. We did

not observe significant effects of elk population density on calf body mass at birth (main effect $F_{3,6} = 0.44$, $P = 0.73$, Table 1). However, calves born to cows that were in control pastures the previous year tended to be slightly heavier (on average, ≈ 1 kg) than calves born to cows that were in the elk-grazed pastures. These trends were also seen at the beginning of the spring grazing season (≈ 10 May), when calves whose mothers were in the controls during the previous year were 0.9–8.7 kg heavier (90% effect confidence interval, ECI) than calves whose mothers were in the elk-grazed pastures (control vs. others $F_{1,6} = 5.8$, $P = 0.053$, Table 1). Quadratic effects on calf body mass at the beginning of the spring grazing season were significant ($F_{1,6} = 5.1$, $P = 0.06$); linear effects were not ($F_{1,6} = 1.3$, $P = 0.29$).

At the end of the spring grazing season (≈ 1 July), calf body mass declined in an approximately linear fashion with increasing elk density (linear contrast $F_{1,6} = 7.9$, $P = 0.03$, Table 1). On average, calves in the control were 1.3–8.2 kg heavier (90% ECI) than calves in the elk-grazed pastures (control vs. others $F_{1,6} = 7.2$, $P = 0.03$).

However, at weaning (≈ 10 November), we did not detect linear effects of elk density on calf growth (linear contrast $F_{1,6} = 0.05$, $P = 0.83$, Table 1); quadratic effects approached significance ($F_{1,6} = 3.6$, $P = 0.106$). The largest estimated effect of elk grazing on fall body mass of calves occurred at the 9 elk/km² level, where the 90% confidence interval on the effect size showed that mean body masses of calves were 4.9–23.3 kg lighter than those in the control (control vs. 9 $F_{1,6} = 8.8$, $P = 0.02$, Table 1). Calf body mass at weaning tended to be higher in the control pastures than in the treatments (Table 1), and the difference in fall body mass of calves in the control relative to the average of the three elk-grazed treatments was marginally significant (control vs. others contrast $F_{1,6} = 3.9$, $P = 0.097$). We can be 90% confident that, averaged across treatment levels, elk grazing reduced mean calf body mass in the fall by 0.08–15.4 kg. This is about 0–8% of the growth they would be expected to attain in the absence of competition with elk.

Year effects were significant for all calf responses (maximum year effect $P < 0.09$) except body mass at weaning (year effect $F_{2,12} = 1.9$, $P = 0.19$). Calf body mass at the end of spring grazing season tended to be lowest during year 3, when production of perennial grass and energy intake by cows were also at a low point (Hobbs et al. 1996). Although year effects were significant for all growth responses, the magnitude of the effect of elk density on calf body mass did not depend on year for any response (minimum year \times treatment interaction $P > 0.46$).

Cow body mass.—At the beginning of the spring grazing season, cows that were in control pastures during the previous spring weighed more than cows that were in the elk-grazed pastures (control vs. others con-

TABLE 1. Body mass (kg) of calves using sagebrush grassland during the spring, in relation to population density of elk using that rangeland during the winter and early spring. Table entries are least squared means across replicates ($n =$ three pastures), adjusted by covariance using pretreatment observations as a covariate. Significant differences between the control and treatments are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$) preceding values.

Timing of measurement	Year	Elk densities (animals/km ²)			
		0	9	15	31
Birth	2‡	34.5	33.9	34.0	32.5
	3	36.1	32.6	32.3	34.8
	4	32.3	32.2	33.9	32.7
	All	34.2	32.9	33.2	33.3
	CI§	32.4, 36.0	31.2, 34.5	31.5, 34.8	31.6, 34.9
	ECI	(0 vs. others)¶ -0.93, 3.2	(0 vs. 9) -1.0, 3.8	(0 vs. 15) -1.4, 3.6	(0 vs. 31) -1.6, 3.5
Beginning of spring	2‡	56.5	54.0	55.2	†50.1
	3	54.7	51.7	46.0	54.9
	4	61.2	52.6	52.9	56.9
	All	57.5	52.7	51.2	53.9
	CI	54.2, 60.8	49.3, 56.1	47.7, 51.2	50.4, 57.3
	ECI	(0 vs. others) 0.93, 8.7	(0 vs. 9) 0.03, 9.5	(0 vs. 15) 1.4, 11.0	(0 vs. 31) -1.4, 8.6
End of spring	1	79.1	78.6	79.9	75.1
	2	92.9	87.1	91.5	84.6
	3	72.4	**62.3	*65.7	**63.3
	4	76.2	70.0	77.6	68.7
	All	80.3	*74.6	78.9	*73.1
	CI	77.3, 83.3	71.7, 77.4	75.7, 82.0	70.1, 76.1
Fall	ECI	(0 vs. others) 1.3, 8.2	(0 vs. 9) 1.5, 9.8	(0 vs. 15) -2.9, 5.7	(0 vs. 31) 2.9, 11.5
	1	196	193	200	199
	2	NA#	NA	NA	NA
	3	190	†167	176	175
	4	192	176	187	190
	All	193	†178	188	188
	CI	186, 199	172, 185	181, 195	181, 195
	ECI	(0 vs. others) 0.08, 15.4	(0 vs. 9) 4.8, 23.2	(0 vs. 15) -4.8, 14.3	(0 vs. 31) -4.9, 13.7

‡ Measurement of body mass at birth and at the beginning of spring during year 1 were taken pre-treatment and were used as covariates to adjust post-treatment means.

§ 90% confidence intervals on the estimate of the all-year mean.

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

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

Data not available because calves were sold prematurely during year 2.

trast $F_{1,6} = 6.0$, $P = 0.05$, Table 2). However, we can be 90% confident that the average effect of elk was at most a reduction of 20.4 kg ($\approx 5\%$ of the body mass of animals that did not compete with elk), and could be as small as 2.3 kg.

We did not observe significant effects of elk grazing on cow body mass at the end of the spring grazing season, despite linear trends in the data (linear effect $F_{1,6} = 1.9$, $P = 0.22$, Table 2). However, effects of elk grazing on cow body mass in the fall approached significance (control vs. others $F_{1,6} = 3.3$, $P = 0.11$, Table 2). Year effects were significant for cow body mass for all sample dates (minimum $P < 0.002$), but the effect of treatment did not depend on year (maximum $P > 0.61$).

Calf growth rates.—Calves showed positive rates of growth throughout the spring and summer (Table 1). Growth rates of calves during the spring grazing season decreased in direct proportion to elk density (linear contrast $F_{1,6} = 8.5$, $P = 0.03$, Table 1) and the control differed significantly from the average of other elk lev-

els ($F_{1,6} = 4.4$, $P = 0.08$). However, these results should be interpreted with caution. When the general linear model for calf body mass at the end of spring was analyzed using body mass at the beginning of spring as a covariate, we found that early spring body mass accounted for 55% of the variance in mass at the end of spring, while treatment accounted for only 4% of that variance. Thus, although the level effect on growth rates was linearly related to treatment, much of the effect of treatment on growth rate was attributable to its effect on body mass at the beginning of spring.

We did not detect statistically significant effects of treatment on calf rates of growth after calves were removed from experimental pastures (i.e., during July through November), but rates of growth of animals in the moderate and high density treatments were slightly higher than those in the control (Table 1).

Year effects were significant for all measures of calf growth rate (maximum year effect $P < 0.10$), but the magnitude of the effect of elk density did not depend

TABLE 2. Body mass (kg) of cows using sagebrush grassland during the spring, in relation to population density of elk using that rangeland during the winter and early spring. Table entries are least squared means across replicates ($n =$ three pastures), adjusted by covariance using pretreatment observations as a covariate. Significant differences between the control and treatment means are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$) preceding values.

Timing of measurement	Year	Elk densities (animals/km ²)			
		0	9	15	31
Beginning of spring	2‡	416	405	412	403
	3	413	397	391	412
	4	416	408	406	399
	All	416	404	404	405
	CI§	407, 422	395, 413	395, 412	397, 412
	ECI	(0 vs. others) 2.3, 20.4	(0 vs. 9) 0.04, 23.2	(0 vs. 15) 0.4, 23.7	(0 vs. 31) -0.4, 21.5
End of spring	1	437	434	446	432
	2	447	421	426	†412
	3	398	389	377	371
	4	389	378	391	376
	All	417	405	410	398
	CI	398, 435	398, 418	390, 429	378, 418
Fall	ECI	(0 vs. others) -8.2, 35.0	(0 vs. 9) -14.5, 39.3	(0 vs. 15) -19.3, 34.7	(0 vs. 31) -6.3, 46.3
	1	478	460	462	479
	2	438	437	457	437
	3	481	464	467	467
	4	461	451	460	447
	All	468	453	457	458
	CI	457, 478	442, 463	446, 467	448, 468
	ECI	(0 vs. others) -0.7, 23.1	(0 vs. 9) -0.6, 29.1	(0 vs. 15) -4.6, 24.8	(0 vs. 31) -5.1, 23.7

‡ Measurements of body mass at the beginning of spring during year 1 were taken pre-treatment and were used as covariates to adjust post-treatment means.

§ 90% confidence intervals on the estimate of the all-year mean.

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

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

on year for any growth rate response (minimum year \times treatment interaction $P > 0.37$).

Cow growth rates.—Effects of elk grazing on growth rates of cows during the spring grazing season were not significant (main effect $F_{3,6} = 0.76$, $P = 0.55$). However, there was a negative linear trend in cow rates of gain relative to elk density during the spring grazing season (Table 3), and the magnitude of the linear effect depended on year (year \times linear effect $F_{3,4} = 7.7$, $P = 0.03$). The size of the effect of elk grazing on cattle growth rate was greatest during year 3, when forage supplies were at a low point.

During all years, we also observed a positive trend in cow growth rate with respect to elk density during summer and early fall (Table 3). Consequently, there was a highly significant *negative* relationship between rate of gain during the spring grazing season and rate of gain thereafter ($F_{1,46} = 46.0$, $P < 0.0001$, $r^2 = 0.50$, Fig. 1).

Effects on reproduction

Natality rates.—We measured natality rates of cattle as the number of calves born per 100 cows. The 4-yr average natality rate ranged from a high of 96% in the controls to a low of 85% in the low density (9 elk/km²) treatment (Fig. 2A). The average natality rate of cattle using the elk-grazed pastures did not differ signifi-

cantly from the control (control vs. others $F_{1,6} = 1.2$, $P = 0.31$). However, we were unable to rule out treatment effects that could be quite large (≈ 20 percentage points, Fig. 2A). Year effects were not significant (year effect $F_{3,4} = 1.2$, $P = 0.40$) and the effect of elk density on natality rate did not depend on year (year \times treatment interaction $F_{9,18} = 0.59$; $P = 0.78$).

Timing of reproduction.—Birth dates of calves born to cows in the moderate elk density treatments (9 and 15 elk/km²) averaged about 5 d later than birth dates of calves whose mothers were in the control or the high elk density treatments (Fig. 2B). Quadratic effects on birth date approached significance ($F_{1,6} = 3.2$, $P = 0.13$, Fig. 2B). The 90% confidence interval places the true effect of moderate grazing (15 elk/km²) as a delay of 0–12 d in mean birth date (Fig. 2B). We emphasize that these analyses include only calves whose mothers were in the experiment during the *previous* year, and thus had an opportunity to be influenced by treatment.

Effects on secondary production

Total production by cattle was reduced as a result of competition with elk, but the effects of competition on cattle production were not linearly related to elk density (linear contrast $F_{1,6} = 0.40$, $P = 0.55$, Fig. 3). We observed the greatest effects of competition at the 9 elk/

TABLE 3. Growth rates of cows and calves (kg/day) using sagebrush grassland during the spring, in relation to population density of elk using that rangeland during the winter and early spring. Table entries are means across replicates ($n =$ three pastures). Significant differences between the control and treatments are indicated by † ($P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$) preceding values.

Response	Year	Elk densities (animals/km ²)			
		0	9	15	31
Calf rate of growth during spring	1	0.75	0.73	0.77	†0.63
	2	0.90	0.81	0.80	0.80
	3	0.82	0.64	0.82	†0.61
	4	0.64	0.60	0.65	†0.46
	All	0.78	0.70	0.77	*0.63
	CI‡	0.72, 0.84	0.64, 0.76	0.71, 0.83	0.57, 0.69
	ECI§	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
Calf rate of growth during summer and fall	1	0.70	0.72	0.77	0.79
	2	NA¶	NA	NA	NA
	3	0.92	0.81	0.93	0.85
	4	0.74	0.74	0.73	0.79
	All	0.79	0.75	0.81	0.81
	CI	0.73, 0.82	0.69, 0.81	0.75, 0.87	0.75, 0.81
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
Cow rate of growth during spring	1	1.28	1.21	1.45	1.23
	2	1.49	1.10	1.15	†0.90
	3	1.08	0.85	0.72	0.19
	4	0.29	-0.14	0.14	-0.05
	All	1.03	0.76	0.86	0.56
	CI	0.67, 1.39	0.40, 1.12	0.50, 1.22	0.20, 0.92
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
Cow rate of growth during summer and fall	1	0.28	0.17	0.14	0.29
	2	0.05	0.15	0.12	†0.20
	3	0.57	0.61	0.64	0.69
	4	0.43	0.51	0.47	0.49
	All	0.33	0.36	0.34	0.42
	CI	0.23, 0.43	0.26, 0.45	0.24, 0.43	0.32, 0.42
	ECI	(0 vs. others)	(0 vs. 9)	(0 vs. 15)	(0 vs. 31)
		-0.18, 0.09	-0.19, 0.13	-0.17, 0.15	-0.25, 0.80

‡ 90% confidence intervals on the estimate of the all-year mean.

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

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

¶ Data not available because calves were sold prematurely during year 2.

km² level and the smallest effects at the 31 elk/km² level (quadratic contrast $F_{1,6} = 5.8$, $P = 0.05$, Fig. 3). Cattle production in the control differed from the average of the other three levels (control vs. others contrast $F_{1,6} = 6.8$, $P = 0.04$), with control values exceeding values for all treatments. We can be 90% certain that, on average, elk grazing reduced cattle production by 6–40 kg·cow⁻¹·yr⁻¹. However, we caution that these effects depended in large part on the strong response of secondary production to the 9 elk/km² level. Effects of elk grazing on cattle production at the moderate and heavy elk grazing levels were not significantly detectable (control vs. 15, 31, $F_{1,6} = 2.96$, $P = 0.14$).

Year effects on total cattle production were significant (year effect $F_{1,6} = 12.9$, $P = 0.01$), but the magnitude of treatment effects did not depend on year (year × treatment $F_{6,12} = 0.51$, $P = 0.79$).

Mechanisms causing changes in cattle growth and reproduction

Body mass of calves and cows at the end of the spring grazing season was curvilinearly related to the biomass

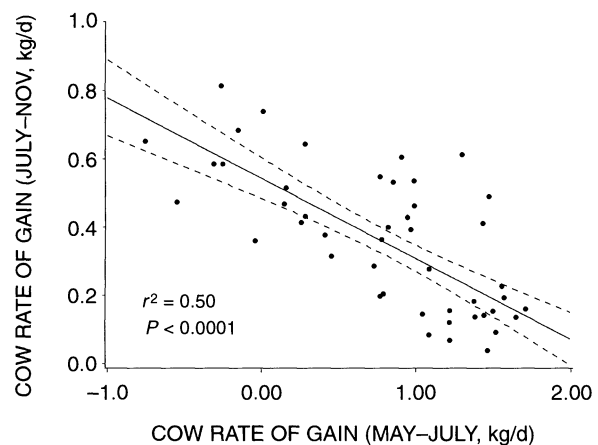


FIG. 1. Cow rate of gain during the summer and fall regressed on rate of gain during the spring and early summer. Data points are annual pasture means. Dashed lines show a 95% confidence interval on the prediction of the rate of gain during summer and fall for a given rate of gain during spring.

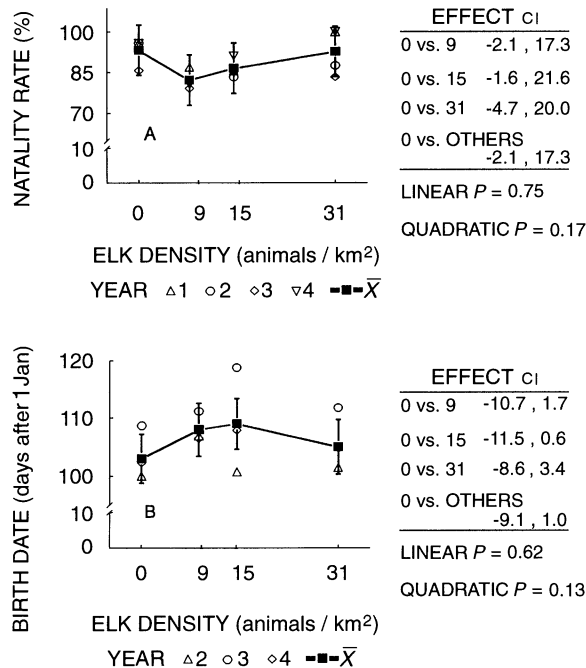


FIG. 2. Natalty rates of cows (A) and birth dates of calves (B) plotted against population density of elk sharing rangeland with cows. Open symbols are level means for each year. Solid squares show the 4-yr average with 90% confidence intervals (vertical bars) based on variation among blocks ($n = 3$). Effect confidence intervals (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 † ($P < 0.1$), * ($P < 0.05$) and ** ($P < 0.01$).

of total herbaceous forage available to cattle during the spring grazing season (Fig. 4). Quadratic effects were highly significant for both calves ($t_1 = -4.7$, $P < 0.0001$, $r^2 = 0.52$) and cows ($t_1 = -3.9$, $P = 0.0003$, $r^2 = 0.64$). These relationships illustrate that the effect of elk on cattle production is strongly affected by spatial and temporal variation in the availability of herbaceous forage, variation that could result from intrinsic differences among sites or from annual variation in rainfall.

The relationship between cattle body mass at the end of spring and forage biomass during spring appeared to be mediated by the effects of energy intake on growth rate. Rates of gain of cows during the spring grazing season were directly related to their daily intake of digestible energy ($F_{1,46} = 22.4$, $P < 0.0001$, $r^2 = 0.33$, Fig. 5). These effects, in turn, appeared to influence the performance of calves: calf rates of gain were linearly related to the rates of gain of their mothers ($F_{1,46} = 33.5$, $P < 0.0001$, $r^2 = 0.42$, Fig. 6).

DISCUSSION

Effects on secondary production

The use of resources during different seasons has been proposed as a mechanism allowing species of un-

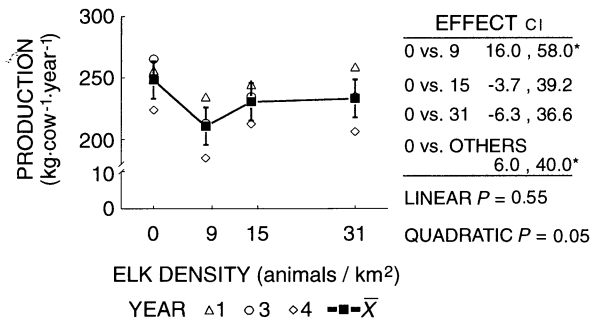


FIG. 3. Annual production of cattle using sagebrush during spring, plotted against population density of elk using that rangeland during winter and early spring. Open symbols are level means for each year. Solid squares show the 4-yr average with 90% confidence intervals (vertical bars) based on variation among blocks ($n = 3$). Effect confidence intervals (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 † ($P < 0.1$), * ($P < 0.05$).

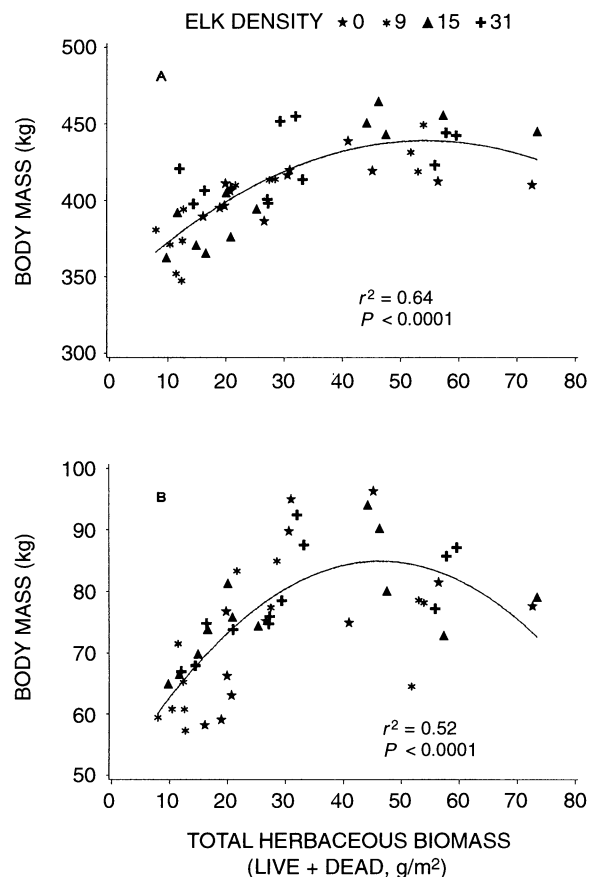


FIG. 4. Relationship between body mass of (A) cows and (B) calves at the end of the spring grazing season and total supply of live and dead herbaceous biomass during the spring grazing season.

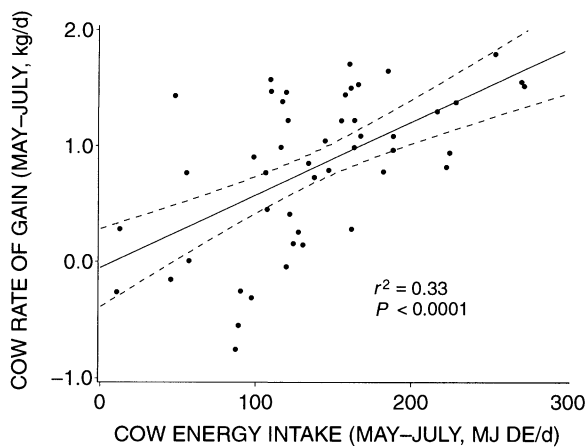


FIG. 5. Growth rates of cows during the spring grazing season declined in direct proportion to reductions in their rates of forage intake (DE = digestible energy). Data points are annual pasture means. Dashed lines show a 95% confidence interval on the prediction of the mean rate of gain.

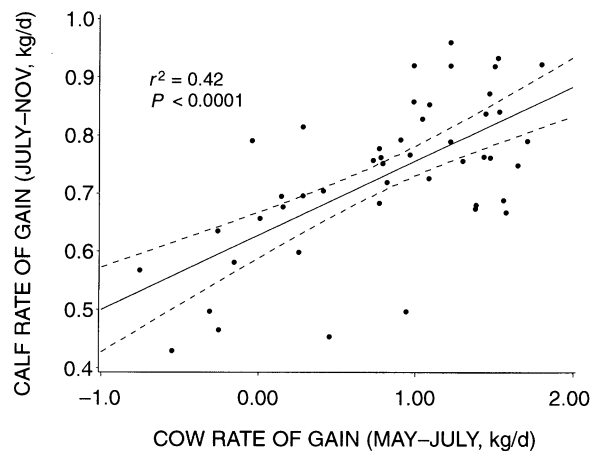


FIG. 6. Rates of gain of calves during the spring grazing season declined in direct proportion to rates of gain of their mothers. Data points are annual pasture means. Dashed lines show a 95% confidence interval on the prediction of the mean rate of gain.

gulates to avoid the deleterious effects of interspecific competition (Lamprey 1963, Leuthold 1978, Dinerstein 1979). Resource use by elk and cattle were completely distinct in time. On average, cattle grazed for only 5 wk/yr in pastures that had been used previously by elk. Nonetheless, this shared use of rangelands was sufficient to cause reductions in annual production by cattle averaging 10% of control values. Thus, we found that use of forage resources by elk during winter and early spring caused measurable effects on cattle production, even when cattle used those resources only briefly during the late spring and early summer.

Secondary production is a relatively high order response composed of several lower order responses, i.e., cow conception rate and fall body mass of cows and calves. These responses were not statistically significant when we examined them individually, but their collective expression in secondary production was significant. This suggests that competition can act as a composite of forces that may be difficult to detect when observed one at a time.

Although competition with elk reduced production by cattle, we suggest that it is unlikely that the presence of elk on sagebrush grassland caused a net decline in total secondary production by elk and cattle in the system we studied. To make this point, we estimated reasonable values for production by elk in a manner analogous to our calculations of cattle production (Fig. 7). We first assumed that the proportion of elk cows producing calves that survive to weaning declines linearly with increasing elk density. Based on data in Houston 1982 (Table 4.3, Fig. 5.2), we estimated this proportion as $0.68 + 0.02 \cdot \text{elk density (in animals/km}^2\text{)}$. Presuming growth of elk cows of 30 kg/cow during summer and fall and estimating calf body mass in fall as 125 kg, (Flook 1982), we calculated total production per elk cow as $(0.68 + 0.02(\text{elk/km}^2)(125 \text{ kg})) + 30 \text{ kg}$.

We estimated total production per square kilometre as the sum of per capita elk and cattle production multiplied by the stocking density (Fig. 7). These calculations suggest that production by elk populations could more than compensate for declines in cattle production resulting from competition with elk. However, such compensation can be realized on privately owned land only if the economic harm caused by elk grazing can be offset by economic benefits accruing from elk to landowners.

Population density and resource competition

We found that increasing population densities of elk caused linear reductions in calf body mass at the end of the spring grazing season, but that subsequent responses (i.e., cow growth rates during summer, cow

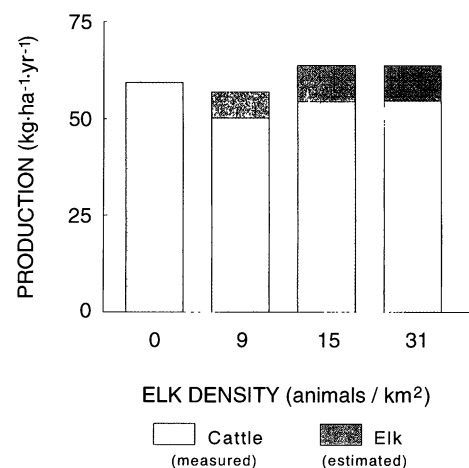


FIG. 7. Estimated production by elk and measured production by cattle in relation to elk population density on sagebrush grassland.

and calf fall body mass, conception rates, and early spring body mass of cows and calves the next year) were not linearly related to elk population density. In all of these cases, the values of the control tended to be higher than the treatments, but this tendency was often quadratic rather than linear.

We suggest that the absence of linear trends in these responses can be explained by considering the inverse relationship between rates of gain of cows during the spring grazing season and their subsequent rates of gain during summer (Fig. 1). We interpret this relationship as an illustration of compensatory growth. Increased rates of growth following nutritional deprivation are well documented for ruminants (Wilson and Osbourn 1959, Ailiden 1970, Butler-Hogg and Tulloh 1982, Suttie et al. 1983, Wright et al. 1986). Such compensation could explain the weakening of treatment effects that occurred after the spring grazing season. Compensatory growth is usually associated with increased rates of food intake (e.g., Wright et al. 1986). Thus, compensation may depend on relatively high levels of food availability following energy shortage (Milne et al. 1987, Wright et al. 1986).

Implications for population management

The absence of a linear relationship between elk population density and production by cattle (Fig. 3) makes it difficult to predict the effects of reducing elk populations on cattle production. This difficulty is compounded by questions of scale. Objectives for elk populations in the western United States are usually set at coarse spatial scales, often at 1000 km². In contrast, conflicts between livestock and elk are frequently more localized, occurring at scales closer to 10s of km². Our results suggest that large-scale population reductions may have no impact on local conflicts. For example, our data (Fig. 3) suggest that harvest regimes causing local densities of elk to decline by as much as threefold (i.e., from 31 to 9 elk/km²) would fail to produce a measurable change in the effects of elk grazing on cattle production. Thus, we suggest that management of the spatial distribution of elk populations, moving animals away from areas of conflict at small scales, may be more effective than reducing large-scale population densities in ameliorating competitive effects of elk on livestock.

Our results do not bear directly on the impact of elk grazing at densities <9 animals/km². Nonetheless, we can infer indirectly that sufficiently low densities of elk will not harm cattle production. This inference is based on the quadratic relationship between cattle body mass at the end of the spring and total forage supply available to cattle during the spring (Fig. 4). When total herbaceous biomass available to cattle (residual dead + live produced) fell below ≈ 45 g/m², cattle body mass at the end of spring declined as forage biomass declined. However, when forage biomass available to cattle exceeded ≈ 45 g/m², cattle body mass was largely

insensitive to changes in biomass (Fig 4). These results are consistent with our findings (Hobbs et al. 1996: Fig. 9) on effects of forage supply on cattle energy intake. Thus, we surmise that rates of grazing allowing >45 g/m² of herbaceous biomass to be available to cattle during the spring grazing season will not cause measurable competitive effects in systems that closely resemble the one we studied.

We emphasize, however, that the importance of this finding is not the precise numerical value of this threshold, which will vary in response to a variety of site-specific influences (cattle stocking rates, herbage composition, annual variation in primary production). Instead, the important conclusion is that such thresholds exist, and that, if properly estimated, they can facilitate managing elk populations to minimize competition with cattle.

The quadratic relationship between cattle body mass at the end of spring and total biomass available to cattle during spring can be explained by relationships between forage quantity and quality. High levels of biomass were negatively correlated with the digestible energy concentration of that biomass (Hobbs et al. 1996: Fig. 5) as a result of the diluting influence of standing dead crop (Hobbs et al. 1996: Fig 6).

CONCLUSIONS

The objective of our work was to determine if winter and early spring grazing by elk reduces cattle production in sagebrush grassland during spring. We conclude that elk grazing can harm production by cattle, despite temporal separation in their use of rangelands. However, we stress that the magnitude of the effects of elk on cattle production are not proportionate to elk population density. Our results show that elk populations can be managed to minimize competition with cattle by assuring that forage available to cattle during the spring grazing season exceeds threshold levels. In the system we studied, this threshold appears to occur at ≈ 45 g/m² of herbaceous forage.

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