



# An ecosystem approach to population management of ungulates

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Harvest objectives for wild ungulates have traditionally been based on population models that do not consider ecosystem effects of ungulate herbivory, nor interactions between native and domestic ungulate species. There is a need for ecosystem models to allow wildlife managers to evaluate potential ecosystem effects of management scenarios. The utility of the SAVANNA simulation model for estimating elk population objectives within an ecosystem context was demonstrated for North Park, Colorado, USA. Effects of different elk population levels were evaluated for range condition, elk and cattle forage, elk and cattle condition, forage and condition of mule deer and moose, plant production, and plant community composition. Analyses were based on 30-year simulation runs using variable, historical weather. Another set of analyses utilized stochastic weather patterns.

For management scenarios using the historical climate pattern, increasing elk populations caused biomass reductions of palatable plant species, particularly on areas of high winter density, where mean leaf biomass of palatable shrubs declined from 26.97 g/m<sup>2</sup> at 0 elk to 20.82 g/m<sup>2</sup> at 4000 elk (3.73 elk/km<sup>2</sup>), a 23% decline. At population levels of 5000 elk (4.68 elk/km<sup>2</sup>) or greater, elk body condition declined sharply following a severe winter. The availability of palatable browse on critical winter range was likely the limiting factor. However, when random climate patterns were simulated for the same scenarios, the threshold level for density-dependent effects varied with climate, ranging from 2000 to 10 000 elk.

We suggest that elk population levels from 4000 to 5000 animals represent a conservative population objective for the North Park elk herd. Also, increasing elk population levels appears to intensify intraspecific competition among elk, far more than interspecific competition with cattle. Resolution of elk-cattle conflicts is likely to be facilitated by managing elk distribution, rather than overall elk population levels.

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## Introduction

Setting goals for harvest of ungulate populations represents one of the traditional functions of wildlife management agencies around the world. These decisions have broad consequences for the functioning of ecosystems and the vitality of human economies. Traditionally, harvest objectives have been based on population models, designed to assess how

harvest regimes will influence future population sizes (White, 2000; Caswell, 2001; Trenkel, 2001). These population-based approaches have some advantages: they are widely used, easy to understand, and require relatively little input data or model parameterization. However, population models provide little or no information on feedbacks between ungulate herbivory and vegetation, or the ways that different densities of wild ungulates may influence ecosystems.

The emergence of ecosystem management as a central focus of land managers (Christensen *et al.*, 1996) has increased the importance of efforts to manage ungulates in reasonable balance with the

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vegetation that supports them. However, until recently managers have lacked the tools necessary to represent how different objectives for population management practices might influence other ecosystem components. The coexistence of wild ungulates with large populations of domestic livestock further complicates the issue, forcing wildlife and range managers to consider the effects of all herbivores on the ecosystem, rather than those of just one species at a time.

In the western United States, strong interactions have been documented between elk (*Cervus elaphus canadensis*) and cattle (Hogan, 1990; Cool, 1992; Hobbs *et al.*, 1996a; Werner and Urness, 1998). These interactions may be competitive, where elk consumption of standing dead biomass in winter and green biomass in early spring directly reduces the amount of forage available to cattle. Elk may also cause economic loss for cattle ranchers by consuming stored cattle feed (e.g. hay) in winter. However, facilitative interactions are possible, where elk consumption of standing dead grass in winter increases the live/dead ratio of perennial grasses in spring, enhancing forage quality for cattle (Hobbs *et al.*, 1996a). Elk browsing of shrubs in winter can reduce competition with grasses for water and nutrients, thus increasing spring cattle forage. Such interactions may be particularly complex in sagebrush grassland communities of the Rocky Mountains, where, although cattle and elk rarely occupy the same habitat during the same seasons of the year, cattle often rely upon areas of elk winter range for spring forage. For a sagebrush grassland in northwestern Colorado, Hobbs *et al.* (1996a) concluded that elk effects on cattle are an integration of facilitative and competitive effects, but that competitive effects dominate when forage production is low and cattle density is high.

Ecosystem simulation models can trace interactions between herbivores and vegetation under varying weather conditions. Such approaches allow us to test the validity, and explore the implications, of commonly held assumptions about herbivory. Since herbivores continually modify their movement patterns and foraging behavior in the effort to maintain a positive energy balance, it is also important to model herbivore-vegetation feedbacks over spatially heterogeneous landscapes. The significance of the spatial dimension for interpreting herbivore-vegetation relationships has been apparent from spatially explicit models of large herbivores within patchy landscapes (Roese *et al.*, 1991; Coughenour, 1992; Loza *et al.*, 1992; Turner *et al.*, 1994; Moen *et al.*, 1997; Risenhoover *et al.*, 1997). Some previous efforts to model spatially

explicit dynamics of large herbivore populations, foraging or energetics did not consider feedback effects of herbivory upon vegetation (Moen *et al.*, 1997; Risenhoover *et al.*, 1997), variable weather between years (Roese *et al.*, 1991; Moen *et al.*, 1997), or effects of variable weather upon primary production (Roese *et al.*, 1991; Turner *et al.*, 1994; Moen *et al.*, 1997; Risenhoover *et al.*, 1997). Spatially explicit, temporally dynamic models of herbivore-vegetation systems, that incorporate weather variability and long-term feedback effects of herbivory on forage, may help provide wildlife managers with a rational basis for making decisions.

Here, we describe initial efforts to apply an existing spatially-explicit, ecosystem simulation model (SAVANNA) to management scenarios reflecting elk population objectives for North Park, Colorado, USA. This is an area with significant potential for conflict between cattle ranching and elk hunting interests, both important to the local economy. Using SAVANNA, we analyzed the potential effects of different elk population levels on range condition, elk and cattle forage, elk and cattle condition, plant production, and plant community composition. Our primary objective was to demonstrate the utility of the ecosystem simulation approach in general, and the SAVANNA model in particular, as a novel means for providing information useful to wildlife and range management.

## Study area

The North Park study area (40.5°N, 106.3°W) comprises all of Jackson County, Colorado, USA, and consists mainly of intermontane dry parkland surrounded on three sides by steep mountain ranges. The area occupies approximately 4216 km<sup>2</sup>, and varies in elevation from 2377 to 3952 meters. The floor of North Park has pronounced local relief, including numerous ridges, small hills, and mesas. North Park is underlain by sedimentary rocks, primarily sandstone and shales of the Coalmont Formation. The climate is characterized by long, cold winters and short, cool summers, with an extremely short and variable growing season of 15–45 frost free days. On the floor of North Park, annual precipitation averages 29 cm, with an average annual temperature of 3.2°C (range: –46 to 32°C). The surrounding mountains experience greater precipitation and lower temperatures.

North Park vegetation ranges from the sagebrush grassland zone on the floor of the basin, to the alpine zone in the mountains. Approximately 41% of

the area is covered by sagebrush grassland, 44% by forests of aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), and spruce-fir (*Picea engelmannii-Abies lasiocarpa*), and 8% by irrigated hayfields. The primary land use practices in the study area are the raising of beef cattle and hay production.

Elk populations in North Park have fluctuated greatly over the past 150 years. An 1842 visitor described an, 'entire country . . . crowded with game, in countless numbers, both [sic] of buffalo, elk and deer' (Sage, 1857). Uncontrolled hunting during the late 1800s nearly eliminated elk from North Park, but conservation legislation and a transplanting program allowed elk populations to recover to approximately 2000 during the late 1950s (Porter, S.H., Snyder, K.F., Duvall, A.C., and Steinert S.F. unpublished report on file at the Colorado Division of Wildlife (CDOW), 'Elk Management Plan for Data Analysis Unit E-3'). Over the 41-year period from 1948 to 1988, the average estimated elk population was 2680 elk. The 1999 elk population objective for North Park was 4000 elk (about 4 elk/km<sup>2</sup> of winter range) (J. Wenum, CDOW, personal communication).

## Methods

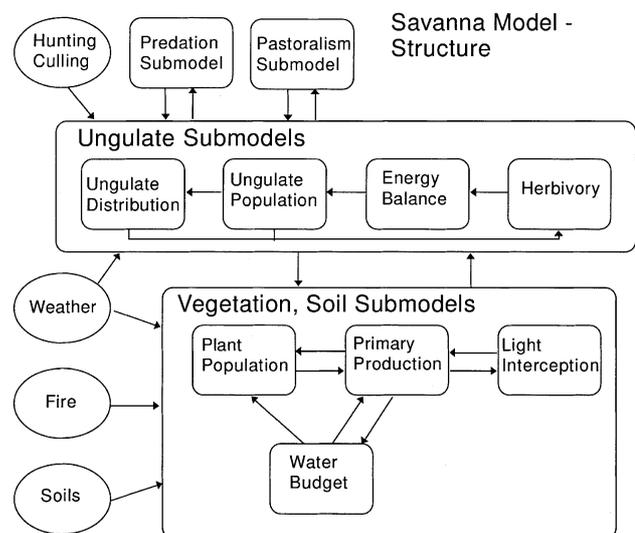
### The SAVANNA model

The SAVANNA model represents the long-term dynamics of grazing systems in a spatially explicit manner, and has been applied to grassland, shrubland, savanna, and forested ecosystems on three continents (Coughenour, 1992; Ellis *et al.*, 1993, Coughenour and Singer, 1996; Ellis and Coughenour, 1998; Boone *et al.*, 2001). The model is composed of interacting submodels for weather, soils, carbon, nitrogen, water, light, fire, predators, vegetation production and population dynamics, and ungulate production and population dynamics (Figure 1). The model simulates: (1) vegetation dynamics in terms of changes in plant functional group composition, (2) plant production in response to climatic variables, including seasonal patterns, (3) plant responses to herbivory and fire, and (4) animal distributional, production, and population responses to climatic variables and changing patterns of plant production and vegetation composition. SAVANNA simulates plant functional groups such as deciduous and evergreen trees, perennial and annual herbaceous species, warm-season and cool-season grasses, and generic crops.

Over weekly time steps, SAVANNA simulates landscapes at three nested spatial scales. The coarsest scale is the region or landscape partitioned into square grid cells. At this scale, the model may be loosely coupled to a Geographic Information System (GIS) for input maps and analysis of output. Grid cells represent the finest spatial unit modeled explicitly, although two spatially inexplicit patch types are modeled in a distributional sense. Landscape positions, or subareas represent physical features invariant over time, such as areas of runoff and runoff, or slope aspects. At a finer spatial scale, patches dominated by herbaceous, shrubby, or wooded vegetation are modeled within subareas as dynamic outcomes of competition between plant functional groups.

Plant water use and soil water availability are central to the plant production submodel. Photosynthesis is simulated as an optimal rate, scaled by effects of light, soil moisture, potential evapotranspiration, photosynthetically active radiation, and temperature, each of which is modeled using detailed representations of microclimate. Stomatal conductance is subsequently calculated from photosynthesis according to specific parameters for each plant functional group (Ball *et al.*, 1987), upon which soil moisture is recalculated.

Ungulate submodels simulate foraging, energetics, population dynamics, and habitat selection. Forage intake is reduced by low forage biomass according to functional response relationships (Swift, 1983; Spalinger and Hobbs, 1992), or by low forage quality. Herbivory is distributed among plant types and tissues (i.e. green leaves, dead leaves,



**Figure 1.** Structure of the SAVANNA ecosystem model (source: Coughenour 1993).

current annual growth, woody stems) according to the diet selection submodel (Ellis *et al.*, 1976). Outputs from the energy balance submodel are used to drive ungulate population dynamics. Ungulates are redistributed among habitat patches each time step according to environmental conditions such as green forage biomass, topography, woody cover, and distance to water (Coughenour, 1992).

SAVANNA includes a simple decomposition and nitrogen mineralization submodel, and tracks soils carbon and nitrogen through plants, structural litter, metabolic litter, and active forms. Although SAVANNA has been linked to the CENTURY Soil Organic Matter (CSOM) submodel to obtain more detailed representation of belowground biogeochemical processes (Parton *et al.*, 1987; Coughenour and Parton, 1996), this was not considered necessary for this application to elk population and habitat relationships in North Park. For a more detailed description of SAVANNA, see Coughenour (1993).

### **Application of SAVANNA to north park**

This application of SAVANNA required developing a GIS database for spatially distributed input variables; extensive review of the literature for detailed model parameterization; obtaining historical data on animal numbers and climate variables; obtaining vegetation data for species composition and plant production; calibration and model verification for simulated plant production, plant phenology, and snow depth, using available field data; and, model validation using an independently derived data set. We adapted the model for four ungulate species: cattle, elk, mule deer (*Odocoileus hemionus*), and moose (*Alces alces*). Eight plant functional groups were modeled: palatable grasses (parameterized as perennial bunchgrasses), palatable forbs, unpalatable forbs, willow, palatable upland shrubs, unpalatable upland shrubs (including big sagebrush, *Artemisia tridentata*), aspen, and conifers.

Model implementation required spatial data inputs for elevation, slope, aspect, vegetation, soils, distance to water, animal ranges, normalized difference vegetation index (NDVI), and historical climate. Arc/Info and ArcView softwares (Environmental Systems Research Institute) were used to develop the spatial database and manipulate spatial data layers. All maps were aggregated to a resolution of 2 km × 2 km grid-cells, which was the resolution used in the modeling experiment, giving 1059 simulated cells. Elevation, slope steepness, and slope aspect were derived from a 100 m digital

elevation model (dem). We used the Colorado GAP analysis vegetation layer (Colorado Gap Analysis Land Cover Map 1998) for vegetation patches, after incorporating additional information on clear-cuts through 1998, obtained from the US Forest Service (Steamboat Springs Ranger District) and Colorado State Forest (Walden office), and reclassifying to 18 vegetation classes. Colorado GAP analysis habitat types are photointerpreted from LANDSAT imagery with a 100 hectare (ha) minimum mapping unit for uplands, and a 40 ha minimum mapping unit for riparian areas. We derived a soils layer using the State Soil Geographic Database (STATSGO) (NRCS, 1992), which consists of digital soil survey maps compiled to a 1 : 250 000 scale. Distance to water was calculated for perennial and intermittent streams and rivers from hydrography layers obtained from the US Geological Survey (USGS), using routines in ArcView's Spatial Analyst extension.

Maps of animal ranges and habitat suitability indices (HSIs) derived within the model for each time step were used to distribute animal populations. For cattle, we incorporated three seasonal movements based roughly on the distribution of animal unit months (AUMs) among land ownership categories. From November through May, cattle were removed from the simulated rangeland ecosystem and fed sufficient hay to maintain average weight. In June, cattle were concentrated at lower elevations, on Arapaho National Wildlife Refuge (ANWR), Bureau of Land Management (BLM), State Land Board, and private lands. From July through September, cattle were permitted to occupy areas within USFS and Colorado State Forest ownerships. In October, cattle HSI was weighted strongly toward irrigated hayfields that had been harvested the previous month, to emulate cattle feeding on haymeadow stubble. Hayfield harvest was simulated by removing 90% of aboveground herbaceous biomass from hayfield grid-cells.

Elk HSIs were weighted seasonally according to four distribution maps. The Colorado Division of Wildlife (CDOW) Wildlife Resource Information System (WRIS) map for elk winter range was used from November through April. A map of elk calving areas from the same source was used for May. From June through August, elk HSIs were reduced slightly in areas with a high density of roads. For September and October (hunting season), elk HSIs were greatly reduced in areas that had high road density, particularly on public lands. Throughout western North America, elk have been shown to avoid roads, particularly during hunting season (Lyon, 1979; Morgantini and Hudson, 1979; Lyon, 1983; Cole *et al.*, 1997). Deer HSIs were similarly

weighted according to three distribution maps, constructed similarly as for elk except that a map of calving areas was not used. Moose in the study area occupy forested lands at higher elevations except in the most severe of winters, and so moose HSI's were weighted only by maps showing the effects of road density and hunting season.

Weather data (temperature, precipitation, relative humidity, windspeed, snow depth) from 11 stations within 75 km of the study area were used to derive climate for the model simulations. The model was calibrated for the 1966–1995 period using historical and recent data for weather, animal numbers, plant community composition, shrub cover and primary production. Historical livestock numbers were obtained from the USDA National Agricultural Statistics Service. Historical population levels for elk, deer and moose were obtained from the Colorado Division of Wildlife. Using these historical time series as inputs, plant production for 1994 and 1995 was calibrated by comparison with observed production data from Owl Mountain Partnership (OMP) field studies conducted within the study area.

### Model validation

The model was validated for Jackson County by comparing simulated herbaceous biomass in hayfields, calculated for the end of August, with Colorado Agricultural Statistics hay sales data for Jackson County over the 1984–1995 period. The model was further validated using data for plant species composition, primary and secondary production, and ungulate utilization from a sagebrush grassland study near Maybell, in northwestern Colorado (Hobbs *et al.*, 1996a, b). The Maybell experiment of Hobbs *et al.* (1996 a, b) utilized a randomized complete block experiment with four experimental pastures assigned to each of three blocks, representing different levels of biomass for perennial grass. Treatments were four levels of elk population density: 0 elk km<sup>-2</sup>, 9 elk km<sup>-2</sup>, 15 elk km<sup>-2</sup>, and 31 elk km<sup>-2</sup>. For the intermediate biomass block at a density of 9 elk km<sup>-2</sup>, we calibrated SAVANNA to observed values for live and dead aboveground biomass of forbs and grasses at the beginning of May, June, and July. Simulated outputs were then compared with observed data from the low and high biomass blocks, for live biomass, dead biomass, and elk utilization of dead perennial grass. We evaluated the validation graphically by using time series plots, and by plotting observed ( $y$ ) *vs.* predicted ( $\hat{y}$ ) data directly, with the line  $y = \hat{y}$  marked, as recommended by Mayer and

Butler (1993). A good fit would be indicated by intermediate biomass blocks falling along the  $y = \hat{y}$  line, low biomass blocks below the line, and high biomass blocks above. Simulation results were also evaluated statistically against observed intermediate block data, at different elk densities, using paired t-tests, linear regression analysis, and the modeling efficiency (EF) statistic (Mayer and Butler, 1993). This statistic is identical to the commonly used  $R^2$  statistic, except that the EF represents the proportion of variation explained by the line  $y = \hat{y}$ , and not a fitted, regression line.

### Model experiments

We conducted two model experiments, each with multiple scenarios for different elk population levels: a historical climate experiment, and a stochastic climate experiment. The historical climate experiment used the historical record of temperature and precipitation for all scenarios. Results from this experiment are indicative of what might be expected given climate patterns similar to those of the recent past. The stochastic climate experiment allows quantification of the degree to which results from the historical climate experiment may be extrapolated to future climate patterns, that do not mirror those of the recent past.

The model was initialized for the 1966–1998 period, using historical time series for climate and animal numbers. Values for state variables at the end of the 33-year run were used to initialize a series of 30-year experimental runs from 1999 to 2028. For the historical climate experiment, all variables were held constant between runs except for elk population numbers, which varied over the following levels: 0 elk, 2000 elk (1.87 elk km<sup>-2</sup> of winter range), 4000 elk (3.73 elk km<sup>-2</sup> of winter range), 5000 elk (4.68 elk km<sup>-2</sup> of winter range), 6000 elk (5.61 elk km<sup>-2</sup> of winter range), 8000 elk (7.46 elk km<sup>-2</sup> of winter range), 10 000 elk (9.36 elk km<sup>-2</sup> of winter range), and 12 000 elk (11.22 elk km<sup>-2</sup> of winter range). Within a run, elk population was held constant with an age/sex distribution of 23% calves, 8% female yearlings, 8% male yearlings, 58% cows, and 3% bulls. Cattle population was held constant at 45 005 head (15 752 calves, 9001 yearlings, 19 352 cows, 900 bulls). This cattle population level represents the 1998 count for Jackson County. Age/sex structures of cattle were based on a survey of 17 ranchers within the study area, while those of wild ungulates were derived from aerial surveys conducted by the Department of Wildlife (DOW). Deer and moose populations were held constant at 600 each.

Time series of climate variables from 1966 to 1995 were repeated as model inputs for the 1999 to 2028 period.

The stochastic climate experiment consisted of replicate random weather runs, where climate parameters were randomly drawn from a normal distribution with mean and variance taken from the 1966 to 1995 observations for temperature and rainfall. Each of ten stochastic weather runs was simulated over the eight elk population levels described above.

## Data analysis

Model outputs for the 1966–1995 historical climate experiment were analyzed graphically by averaging results for each elk population level over years, or using time series plots of results for selected elk population levels. The SAVANNA model allows the user to input a GIS layer representing a spatial mask over which results are aggregated for output and data analysis. Most results were aggregated over the area of elk winter range. Some results are reported for areas of especially high winter elk density, represented by a 36 km<sup>2</sup> area of sagebrush grassland, derived from model outputs for elk density at the end of March.

Outputs for the last year of the 30-year stochastic climate runs were averaged over the ten random simulations; the resulting means were then compared among the eight elk population levels using ANOVA and the Bonferroni Multiple Comparisons Test to determine significant differences ( $\alpha = 0.05$ ) between means. Statistical analyses were conducted using S-Plus for Windows software. No statistical analyses were conducted for the historical climate experiment. Since model runs for this experiment were deterministic, there was no replication within treatment levels, and additional statistical tests would not have been appropriate.

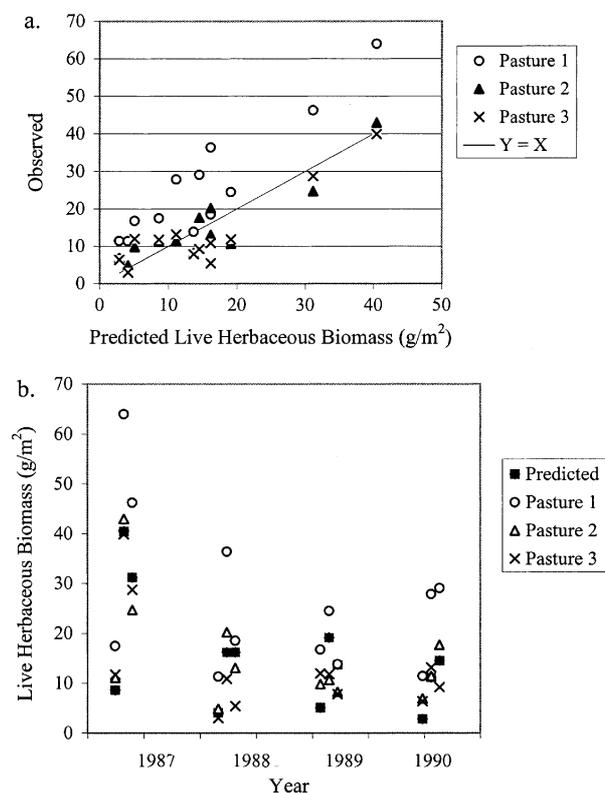
## Results

### Model validation

Simulated herbaceous biomass in hayfields for the 1984–1995 period was well within the range of observed hay sales data. Mean simulated biomass for the period was 285.7 g/m<sup>2</sup> yr<sup>-1</sup>, compared to a mean observed biomass of 277.4 g/m<sup>2</sup> yr<sup>-1</sup>. Differences between observed and simulated values were not significantly different from 0 (paired  $t = 1.01$ ,  $df = 11$ ,  $P = 0.34$ ). However, the model predicted

inter-annual variability of hay production poorly ( $EF = -0.1453$ ), and simulated variability was much less than for the observed hay sales data. In model runs, vegetation in irrigated hayfields is never water-limited, and so weather effects are limited to temperature and insolation effects on photosynthetic rate.

Application of SAVANNA to the Maybell study area (Hobbs *et al.*, 1996a, b) demonstrated a reasonable model with some minor biases. At the 9 elk km<sup>-2</sup> level, which was the level calibrated for, live herbaceous biomass was predicted reasonably well in terms of both overall fit and equality of means between simulated and observed data (Table 1, Figure 2). High biomass pastures are plotted above, and low biomass pastures below, the  $Y = X$  line, indicating a good relationship (Figure 2a). However, live biomass was under-predicted slightly for May 1 over all elk population levels, as indicated by regression slopes of less than one, and was under-predicted for the last simulation

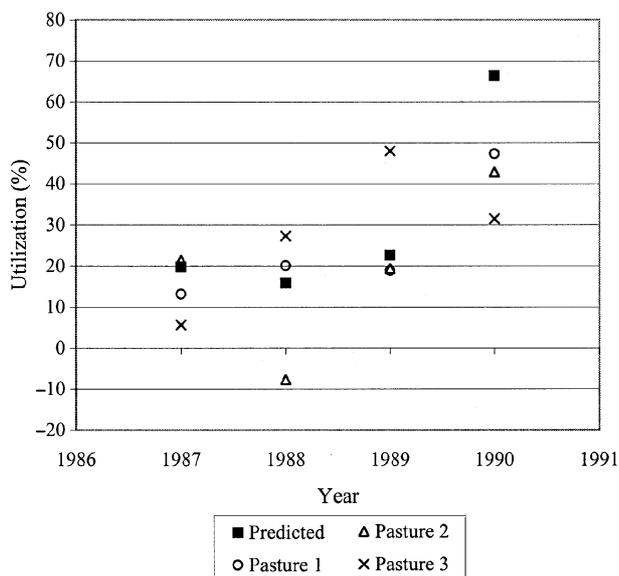


**Figure 2.** Comparison of observed live vs. simulated live herbaceous biomass, for the 9 elk km<sup>-2</sup> treatment of the Maybell, Colorado study of Hobbs *et al.* (1996a, b). Pasture 1 represents a high biomass block, pasture 2 a moderate biomass block, and pasture 3 a low biomass block. (a) plot of observed vs. simulated data, where the  $Y = X$  line indicates a perfect fit. (b) Time series plot, showing live herbaceous biomass for 3 sampling dates (May 1, June 1, July 1) for each of 4 years.

**Table 1.** Validation measures for live herbaceous biomass, for different elk population densities. We have pooled three measurements (May 1, June 1, July 1) for each of four years to obtain 12 values for each level. The significance of mean differences was tested using paired *t*-tests, with  $\alpha = 0.05$ . The intermediate biomass block of Hobbs *et al.* (1996a) was used to calculate these measures

Elk Population Level	0 elk/km <sup>2</sup>	9 elk/km <sup>2</sup>	15 elk/km <sup>2</sup>	31 elk/km <sup>2</sup>
Number of observations	12	12	12	12
Mean (simulated)	17.36	15.26	14.48	12.09
Mean (observed)	19.90	15.14	15.14	12.89
Mean Difference	-2.54 <sup>ns</sup>	0.12 <sup>ns</sup>	-0.66 <sup>ns</sup>	-0.80 <sup>ns</sup>
(95% CI)	-8.32-3.25	-2.79-3.02	-6.44-5.12	-5.54-3.93
Regression R <sup>2</sup>	0.45	0.83	0.49	0.59
Regression slope	0.58	0.86	0.58	0.60
(95% CI)	0.18-0.98	0.62-1.10	0.22-0.95	0.29-0.91
Regression Bias F <sub>(2, 20)</sub>	2.08	0.66	2.49	3.13
( <i>P</i> -value)	0.15	0.53	0.11	0.07
Modelling Efficiency	0.15	0.81	0.24	0.32

<sup>ns</sup> not significant; \* *P* < 0.05; \*\* *P* < 0.01.



**Figure 3.** Comparison of observed vs. simulated elk utilization of dead perennial grass, for the 9 elk km<sup>-2</sup> treatment of the Maybell, Colorado study of Hobbs *et al.* (1996a, b). Pasture 1 represents a high biomass block, pasture 2 a moderate biomass block, and pasture 3 a low biomass block. The graph shows elk utilization for 3 sampling dates (May 1, June 1, July 1) for each of 4 years.

year at the 15 and 31 elk km<sup>-2</sup> levels (Table 1, Figure 2b). The mean differences between simulated and observed live biomass were not significantly different over any of the levels, when pooled over all 12 sample dates (Table 1).

Dead herbaceous biomass was generally predicted with a greater modeling efficiency than live herbaceous biomass, indicating a better fit (Table 2). Modeling efficiencies for the 15 and 31 elk km<sup>-2</sup> levels were comparable to that for the 9 elk km<sup>-2</sup>

level, indicating that the model was correctly representing the seasonal effects of elk population level on dead herbaceous biomass, composed mainly of standing dead perennial grasses. At the 9 elk km<sup>-2</sup> level, dead herbaceous biomass was consistently, but slightly, over-predicted relative to the intermediate biomass block. This resulted in a significant difference of means between simulated and observed dead biomass for this elk population level (Table 2).

Elk utilization of standing dead perennial grass was within, or very near, observed values for the three experimental pastures in every case except the last year of the 9 elk km<sup>-2</sup> scenario (Figure 3). In this instance, elk utilization was over-predicted when dead herbaceous biomass was quite low, suggesting that simulated elk were able to maintain overly high rates of forage intake when forage biomass was low, even though Type II functional response curves were used in the model to regulate elk intake rates.

## Historical climate experiment

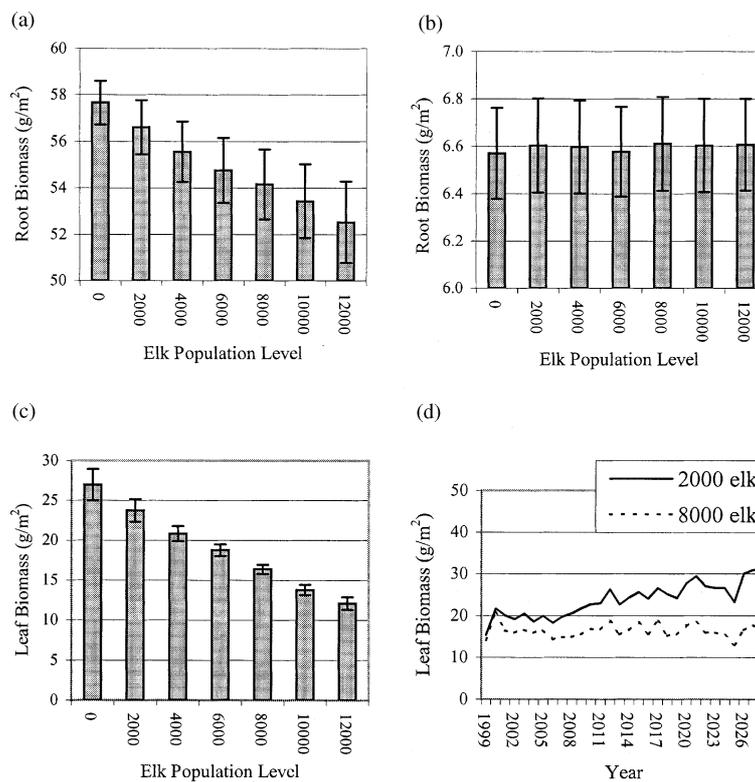
### Elk ecosystem effects

Plant productivity was relatively unaffected by changes in grazing intensity associated with different elk population levels. Simulated aboveground net primary productivity (ANPP) of herbaceous species decreased linearly but very gradually with increasing elk density (from 57.78 g/m<sup>2</sup> at 0 elk to 56.68 g/m<sup>2</sup> at 4000 elk, a 1.6% decrease), but this trend was minor relative to differences between years from interannual weather variability. Simulated ANPP for shrub species was not much

**Table 2.** Validation measures for dead herbaceous biomass, for different elk population densities. We have pooled three measurements (May 1, June 1, July 1) for each of four years to obtain 12 values for each level. The significance of mean differences was tested using paired *t*-tests, with  $\alpha = 0.05$ . The intermediate biomass block of Hobbs *et al.* (1996a) was used to calculate these measures

Elk population level	0 elk/km <sup>2</sup>	9 elk/km <sup>2</sup>	15 elk/km <sup>2</sup>	31 elk/km <sup>2</sup>
Number of observations	12	12	12	12
Mean (simulated)	8.63	6.83	5.53	3.31
Mean (observed)	7.98	4.84	5.23	3.58
Mean Difference (95% CI)	0.65 <sup>ns</sup> -3.58-4.88	1.99* 0.94-3.04	0.30 <sup>ns</sup> -1.64-2.24	-0.27 <sup>ns</sup> -1.53-0.99
Regression R <sup>2</sup>	0.49	0.92	0.64	0.72
Regression slope (95% CI)	1.05 0.38-1.72	1.21 0.99-1.43	1.01 0.54-1.48	1.06 0.65-1.48
Regression Bias F <sub>(2,20)</sub> ( <i>P</i> -value)	0.01 0.99	1.83 0.19	0.01 0.99	0.05 0.96
Modelling Efficiency	0.48	0.72	0.63	0.71

<sup>ns</sup> not significant; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .



**Figure 4.** Elk population effects on plant species composition, as measured by (a) root biomass of palatable herbaceous species; (b) root biomass of unpalatable herbaceous species; (c) leaf biomass of palatable shrub species; and, (d) time series of palatable shrub leaf biomass at population levels of 2000 and 8000 elk. Results for herbaceous species are averaged over elk winter range, while results for shrub species are averaged over areas of high density elk winter range. For (a), (b), and (c), columns represent means of 30-year simulation runs for each elk population level, while error bars represent 95% confidence intervals. These are results from the Historical Climate experiment.

influenced by elk population level, despite a consistent linear increase (e.g. from 43.52 g/m<sup>2</sup> at 0 elk to 44.07 g/m<sup>2</sup> at 4000 elk, a 1.3% increase).

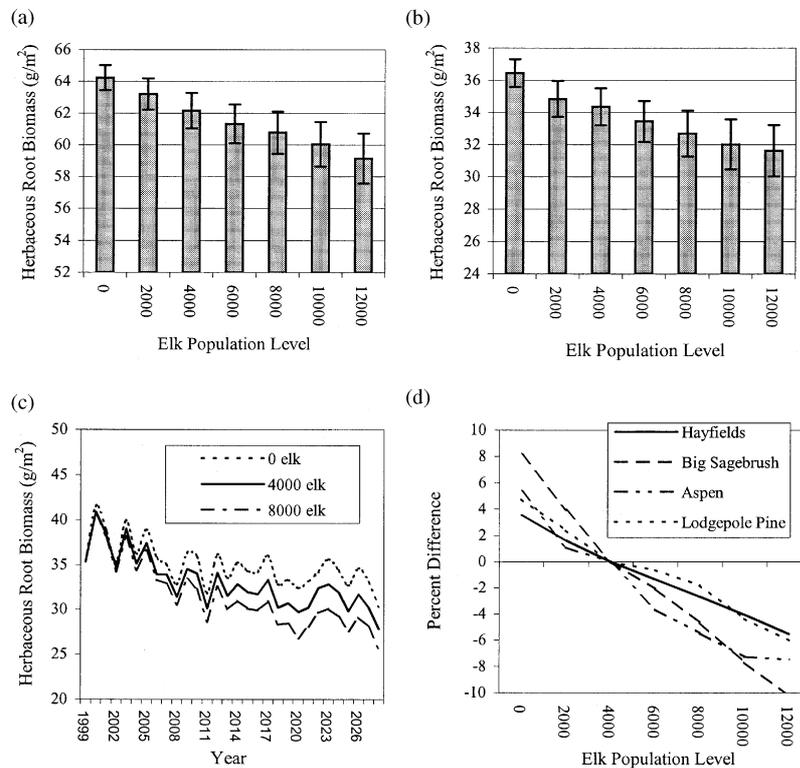
Unpalatable plant types were favored over palatable ones at higher elk population levels. Root biomass of palatable herbaceous species

(e.g. graminoids) declined an average of 0.43 g/m<sup>2</sup> with every 1000 elk population increase (Figure 4a), although root biomass of unpalatable herbaceous species (e.g. *Astragalus* spp.) did not change with elk population level on winter range (Figure 4b). This decline was greatest from the 0 elk through

4000 elk levels. The effects of higher elk densities on shrub species composition were more dramatic, particularly on areas of high winter elk density, where the mean leaf biomass of palatable shrubs (e.g. *Amelanchier* spp.) declined from 26.97 g/m<sup>2</sup> at 0 elk to 20.82 g/m<sup>2</sup> at 4000 elk, a 23% decline (Figure 4c). The concurrent increase in mean leaf biomass for unpalatable shrubs (e.g. *Artemisia tridentata*) was from 82.50 to 87.02 g/m<sup>2</sup> (a 5% increase). Averaged over the entire elk winter range, these effects were a 9% decline in palatable shrub leaf biomass from 24.31 g/m<sup>2</sup> to 22.03 g/m<sup>2</sup>, and a 5% increase in unpalatable shrub leaf biomass from 36.80 g/m<sup>2</sup> to 38.56 g/m<sup>2</sup>. Willow (*Salix* spp.) leaf biomass, averaged over elk winter range, declined from 3.92 g/m<sup>2</sup> at 0 elk to 3.74 g/m<sup>2</sup> at 4000 elk, a 5% decrease.

The effects of elk population level on plant species composition were cumulative, in that differences increased over the course of the 30-year simulations (Figure 4d). Therefore, the 30-year means shown in Figures 4 and 5 overestimate the effects of elk population level early in the simulation, but underestimate the effects later in the simulation.

Herbaceous root biomass was considered an indicator of range condition, and is closely related to herbaceous cover in the SAVANNA modeling context. Mean herbaceous root biomass (averaged over the 30-year period) declined from 64.23 g/m<sup>2</sup> at 0 elk to 62.15 g/m<sup>2</sup> at 4000 elk (a 3% decrease) on elk winter range (Figure 5a), and from 36.44 g/m<sup>2</sup> at 0 elk to 34.35 g/m<sup>2</sup> at 4000 elk (a 6% decrease) on areas of high winter elk concentrations (Figure 5b). Over a broad range of population levels, the effects of elk density on herbaceous root biomass were not as great as the influence of inter-annual variation in climate, shown as the error bars in Figures 5a and 5b. When the current grazing pressure of 4000 elk and 45 005 cattle was simulated, herbaceous root biomass declined consistently a small amount each year. On areas of high winter elk concentrations, mean September herbaceous root biomass decreased from 41.6 g/m<sup>2</sup> in 1999 to 30.3 g/m<sup>2</sup> in 2028, a 27% decrease (Figure 5c). Increasing elk populations exacerbated this trend only slightly. However, the effects of elk on root biomass were cumulative, and amplified over time (Figure 5c).



**Figure 5.** Elk population effects on herbaceous root biomass, for (a) all species averaged over elk winter range; (b) and (c) all species averaged over high density elk winter range; and, (d) all species averaged over four vegetation types. For (a) and (b), columns represent means of 30-year simulation runs for each elk population level, while error bars represent 95% confidence intervals. The plot in (c) shows a time series of herbaceous root biomass at the 0, 4000, and 8000, elk population levels. For (d), the y-axis refers to the percent difference in herbaceous root biomass for each population level on the x-axis, relative to the 4000 elk population level. These are results from the Historical Climate experiment.

The simulated decline in herbaceous root biomass with increasing elk population levels was greatest for sagebrush grassland and aspen vegetation types, and least for coniferous forests and irrigated hay-fields (Figure 5d). In fact, some forest patches experienced increased herbaceous root biomass at higher elk population levels, due to decreased woody cover from elk browsing.

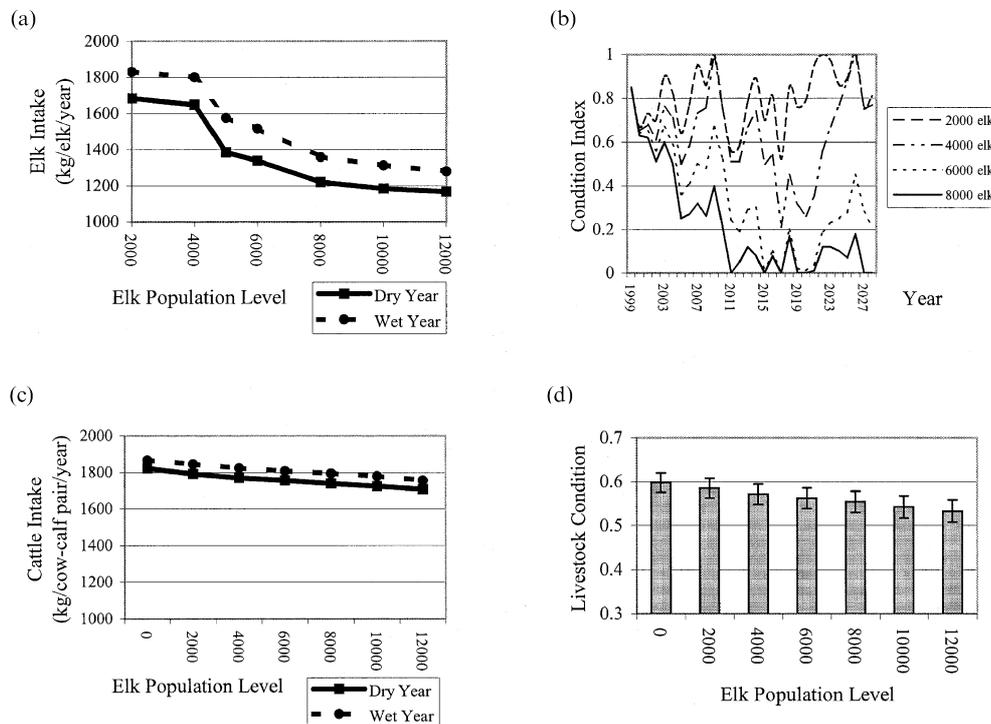
### Effects of elk population level on elk, moose, deer

At a threshold population level between 4000 and 5000 elk, per-capita forage intake by elk declined markedly (16% in a dry year *vs.* 12% in a wet year) (Figure 6a) and weight recovery following a snowy winter was slow (Figure 6b). At populations of 8000 and above, elk did not recover from a severe weight loss in year 8 of the simulations (Figure 6b). Effects of elk population level on forage for other wild ungulates (deer and moose) were insignificant ( $P \geq 0.9999$  for deer and moose forage biomass and digestibility), probably due to their low numbers. As

a result, condition indices for deer and moose were not altered by changing elk population levels.

### Elk effects on forage, and elk-cattle interactions

One effect of the 4000 elk population level (relative to the 0 elk level) was to decrease live herbaceous biomass throughout the spring and summer. This decrease was modest: 0.41 g/m<sup>2</sup> (or 2.7%) at the end of May, 0.73 g/m<sup>2</sup> (or 2.9%) at the end of June, and 0.62 g/m<sup>2</sup> (or 4.6%) at the end of September. By consuming standing dead herbaceous biomass in the winter, elk grazing diminished dead herbaceous standing crop more than live herbaceous standing crop in the spring, and so increased the live/dead ratio for spring cattle forage. However, this effect was slight and short-lived. At the end of May, the effect of the 4000 elk level was to increase the live/dead ratio, averaged over elk winter range, from 3.17 to 3.40. By the end of June, this effect was insignificant compared to variation due to weather.



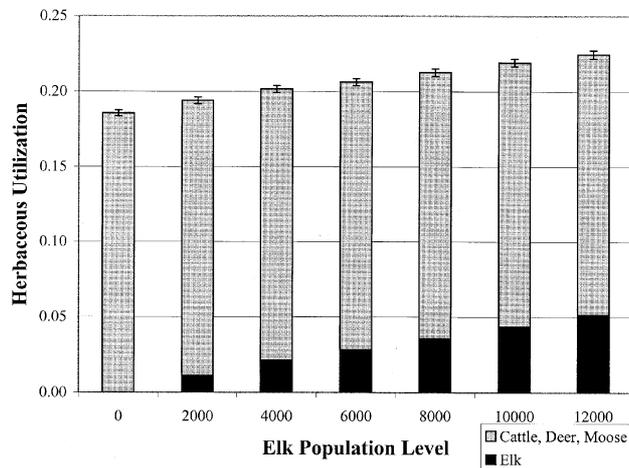
**Figure 6.** Results for animal intake rates and body condition, from the Historical Climate experiment: (a) Elk population effects on mean elk annual intake, for a dry year and a wet year; (b) Elk population effects on elk condition index over time, for four levels of elk population; (c) Elk population effects on mean annual intake for a cow-calf pair, for a dry year and a wet year; (d) Elk population effects on cattle condition index, where columns represent means of 30-year simulation runs for each elk population level, and error bars represent 95% confidence intervals. Condition index measures animal body weight expressed as a proportion of maximum weight, such that 1.0 is maximum and 0.0 is minimum.

Cattle intake and condition were reduced at higher elk populations only slightly (Figures 6c, d). For example, mean cow weights at the end of September averaged 477 kg and 471 kg at the 0 elk and 12 000 elk population levels, respectively. However, effects of higher elk populations on cattle condition were cumulative, and amplified over time.

### Utilization of plant production

Utilization of herbaceous production on elk winter range was about 20% at current elk population levels (4000), only a small fraction of which was attributable to elk grazing (Figure 7). Most was due to cattle (45 000) consumption. Even tripling the elk population added only about 3% to the total utilization by all ungulate species. The effect of elk population level on ungulate utilization of total (herbaceous + shrubs + trees) production was also small. Total utilization varied from about 14% at current elk population levels to about 16% at three times the current elk population.

On sagebrush grassland areas of heavy winter elk use, utilization of herbaceous production varied from 29% at current elk population levels to 32% at three times the current elk population. Utilization of total plant production varied from 14% at current elk population levels to 15% at three times



**Figure 7.** Elk population effects on utilization of herbaceous biomass, averaged over elk winter range, including all four herbivore species simulated. Utilization is calculated for each grid-cell as total annual intake divided by peak standing crop, for all herbaceous plant functional groups. In the case of cattle, total annual intake refers only to the six months of the year when they were on the range. Columns represent means of 30-year simulation runs for each elk population level, while error bars represent 95% confidence intervals. These are results from the Historical Climate experiment.

the current elk population. The relationship between elk population and utilization of total production was asymptotic, nearing a plateau at a population level of 6000 elk, where the availability of palatable browse had been reduced to very low levels.

### Stochastic climate experiment

Results from stochastic climate runs (Table 3) were similar to those from the historical climate experiment for several output variables, but differed in interesting ways for certain others. On elk winter range, the magnitude of the decrease in herbaceous ANPP with increasing elk population was about double that from the historical experiment, although still only about 4% from 0 elk to 4000 elk (Table 3). This decline was about the same for high density range as for all elk winter range, although production was lower, but more variable, on high density range. Increases in utilization of herbaceous production were of similar magnitude between historical and stochastic experiments, and between elk winter range and high density range within the stochastic experiment (Table 3). Changes in plant community composition with increasing elk population level, reflected by decreasing palatable herbaceous root biomass and palatable shrub leaf biomass, and increasing unpalatable shrub leaf biomass, were similar for historical and stochastic experiments. Changes in unpalatable herbaceous root biomass were minor and non-significant (Table 3).

The stochastic experiment results do not show a threshold for elk forage intake and elk condition at between 4000 and 5000 animals (Figures 8a, b), as do the historical experiment results (Figures 6a, b). Rather, the magnitude of decline across all levels of increasing elk population was similar, particularly for forage intake (Figure 8a). This is because thresholds occur at different elk population levels, for particular climate scenarios associated with individual model runs for the stochastic experiment. For a model run with a generally favorable climate, thresholds in a particular density-dependent response of elk population may occur at a lower level of elk population than for a model run of less favorable climate. Results averaged over replicate runs for the stochastic experiment are therefore not well-suited for identifying threshold effects associated with elk population level. However, a minor threshold effect is evident for elk condition, which declined a relatively great amount (73%) between 8000 and 10 000

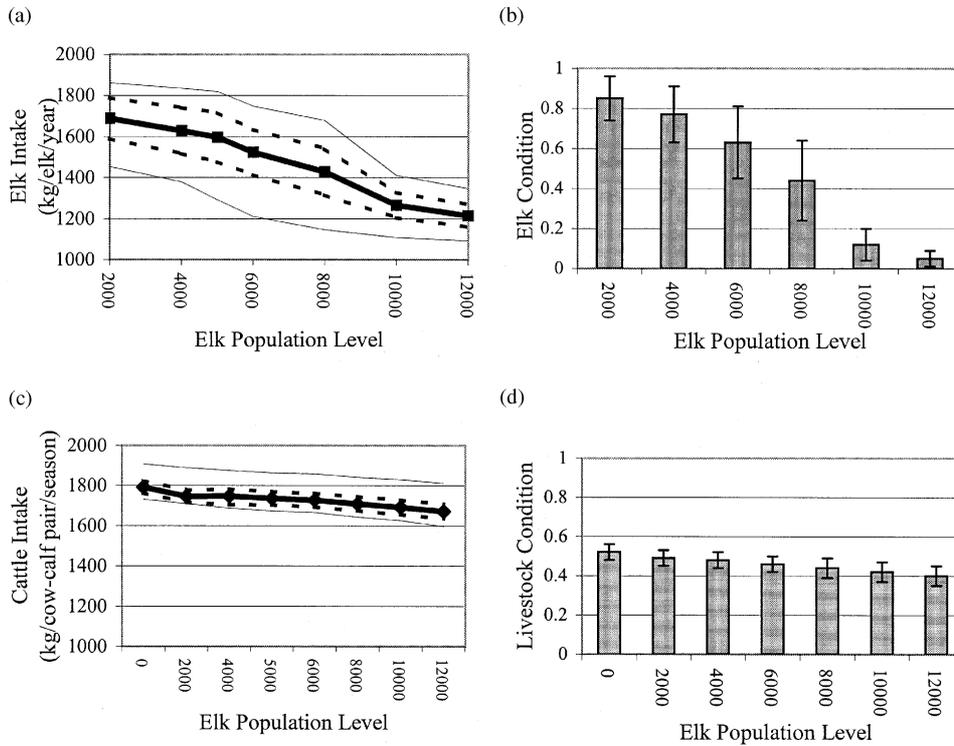
**Table 3.** Results from the stochastic climate runs over 7 elk population levels, for selected ecosystem variables on elk winter range, and on high density elk winter range. Mean values shown are averaged over 10 random model runs. Letter codes (a–e) indicate whether means are significantly different, using ANOVA and the Bonferroni Multiple Comparisons Procedure, with  $\alpha = 0.05$

Variable	Elk population	Winter range	High density range
Herbaceous Aboveground NPP (g/m <sup>2</sup> )	0	52.32 a	32.95 a
	2000	51.13 ab	32.19 ab
	4000	50.30 ab	31.42 ab
	6000	49.90 bc	30.79 ab
	8000	48.35 bc	29.93 ab
	10 000	47.46 bc	29.62 b
	12 000	46.69 c	29.14 b
Herbaceous Utilization (All Herbivore Species) (%)	0	18.9 a	28.2 a
	2000	20.1 b	28.8 ab
	4000	20.9 b	29.4 abc
	6000	21.8 bc	30.1 abc
	8000	22.5 c	30.4 bc
	10 000	22.9 cd	30.9 bc
	12 000	23.7 d	31.4 c
Unpalatable Herbaceous Root Biomass (g/m <sup>2</sup> )	0	7.37 a	7.66 a
	2000	7.37 a	7.63 a
	4000	7.36 a	7.60 a
	6000	7.35 a	7.59 a
	8000	7.35 a	7.58 a
	10 000	7.36 a	7.58 a
	12 000	7.36 a	7.59 a
Palatable Herbaceous Root Biomass (g/m <sup>2</sup> )	0	53.10 a	24.21 a
	2000	51.30 ab	23.16 ab
	4000	49.86 bc	22.29 abc
	6000	48.25 bcd	21.57 bc
	8000	47.11 cd	20.83 bc
	10 000	45.92 d	20.31 c
	12 000	44.80 d	19.70 c
Unpalatable Shrub Leaf Biomass (g/m <sup>2</sup> )	0	36.11 a	78.92 a
	2000	37.43 ab	80.77 ab
	4000	38.73 abc	82.91 ab
	6000	39.99 bcd	85.13 ab
	8000	41.11 cd	87.20 ab
	10 000	42.14 cd	88.96 ab
	12 000	43.22 d	90.76 b
Palatable Shrub Leaf Biomass (g/m <sup>2</sup> )	0	26.80 a	32.91 a
	2000	25.54 ab	30.73 ab
	4000	24.31 bc	28.61 abc
	6000	23.00 bcd	26.41 bcd
	8000	21.83 cde	24.15 cd
	10 000	20.83 de	22.21 d
	12 000	19.74 e	20.40 d

animals, while successive declines for 2000-animal increments in elk population level from 2000 to 8000 animals were 9, 19 and 30% (Figure 8b).

As for the historical climate experiment, cattle forage intake was reduced slightly with increasing elk population level, with the greatest decline occurring from 0 to 2000 elk (Figure 8c). The current elk population (about 4000) would have to triple before

cattle intake rates would decline significantly, suggesting that variation in available forage for cattle may be associated far more with climate variability than with elk effects. Results for cattle condition are similar, in that effects of climate variability were more important than the effects of varying elk population levels over reasonable ranges (Figure 8d). However, the overall magnitude of cattle condition



**Figure 8.** Results for animal intake rates and body condition, from the Stochastic Climate experiment: (a) Elk population effects on mean elk annual intake; (b) Elk population effects on mean elk condition index; (c) Elk population effects on mean annual intake for a cow-calf pair; and, (d) Elk population effects on cattle condition index. For (a) and (c) the thick solid line represents the mean, the dashed lines the 95% confidence interval, and the thin solid line the minimum and maximum values, at Year 30 of 10 random climate simulation runs. For (b) and (d), columns represent means at Year 30 of 10 random climate simulation runs, and error bars represent 95% confidence intervals. Condition index measures animal body weight expressed as a proportion of maximum weight, such that 1.0 is maximum and 0.0 is minimum.

decline was greater for the stochastic experiment, where the average cow lost 11 kg (a 2% decline) as elk population increased from 0 to 12 000 animals, compared to a loss of 6 kg (a 1% decline) for the historical climate experiment.

## Discussion

### *Elk effects on the ecosystem and other wild ungulates*

Simulation results based on historical climate scenarios suggest that elk populations in excess of 6000 reduce herbaceous root and shoot biomass, and alter vegetation composition by promoting unpalatable shrub and herbaceous species over palatable ones. These effects were greater for localized wintering areas of heavy use. In particular, the decrease in palatable shrub biomass was 2.5 times greater on areas of high elk density than when averaged over

all elk winter range. Despite observed effects on belowground and aboveground biomass, net primary productivity changed little between elk population levels.

These results are supported by field studies in some areas, but are in disagreement in others. Elk winter grazing over a 30-year period in Yellowstone National Park reduced standing dead and litter biomass without altering plant productivity (Coughenour, 1991). Coughenour (1991) also reports mixed effects on live herbaceous biomass, no effect on herbaceous root biomass, and no change in plant species composition. In northwestern Colorado, increasing levels of winter elk herbivory on sagebrush grassland were associated with decreased spring forage for cattle, mainly because standing dead grass biomass was reduced (Hobbs *et al.*, 1996a), although reductions in biomass of live perennial grass also approached significance. This is in agreement with our results. Canopy cover of sagebrush was least, and grass cover greatest, at an intermediate level of elk density. Since the intermediate level (15 elk/km<sup>2</sup>) of Hobbs *et al.* (1996a)

corresponds to a high elk population level in this study, this trend opposes our simulated results for North Park, where elk grazing reduced competition from grasses, allowing the relatively unpalatable sagebrush to increase in biomass. Results agree where Hobbs *et al.* (1996a) report insignificant or minor effects of elk grazing on herbaceous above-ground NPP, as does Coughenour (1992). However, a study in Yellowstone National Park has reported the aboveground NPP of grazed herbaceous vegetation to be 47% higher than that of ungrazed vegetation (Frank and McNaughton, 1993).

Simulated effects of elk herbivory on plant species composition may be overestimated, since the SAVANNA model does not allow plants to respond through increased fruit and seed production. Such compensatory responses may not involve increased growth or productivity, but can lead to increased plant fitness, and have been observed for annual and biennial species following herbivory by vertebrates, insects, and experimental clipping (Hendrix, 1979; Paige and Whitham, 1987; Maschinski and Whitham, 1989).

Ecosystem responses to elk population levels were not static, but were amplified over the course of 30-year simulation runs. These effects were likely cumulative because simulated plant production at any one time step is influenced by plant production at the previous time step. Plants that do not perform well are not able to store ample reserves of photosynthate for the next growing season, nor are they able to reproduce as successfully. Time series plots of predicted biomass responses to the higher elk population levels (Figures 4d, 5c) resemble the hypothetical model of rangeland degradation postulated by Walker (1988), where a measure of rangeland quality oscillates cyclically over time according to rainfall.

It was surprising that elk population levels did not influence forage or condition of deer, given that dietary overlap between elk and mule deer has been well-documented in field studies (Hansen and Reid, 1975; Collins and Urness, 1983; Kirchoff and Larsen, 1998). This lack of effect likely results from two mechanisms of resource segregation: dietary partitioning, and habitat partitioning. There is not much forage competition between the species in the summer, since elk do not eat much browse, while moose and deer eat mainly browse. In winter, when diets of the three species overlap to a greater extent, winter ranges of deer, elk, and moose do not overlap completely. The overlap between elk and deer winter ranges is about 30% of the total combined area, or 66% of elk winter range, or 53% of deer winter range. Moose remain at higher elevations during

winter, compared to the other two species. The overlap between elk and moose winter ranges is about 10% of the total combined area, or 32% of elk winter range, or 15% of moose winter range. Segregation of elk, deer, and moose winter ranges by spatially heterogeneous snow depths has been observed elsewhere in the western US (Murie, 1951; Harrington, 1978; Hayden-Wing, 1980). Hayden-Wing (1980) goes as far as to suggest that coevolution has resulted in ecological separation of the three species, and that cases of intense competition may result from human interventions.

### **Elk effects on cattle forage and condition**

Although cattle forage and condition were reduced at greater elk population levels, this effect was small compared to effects from climate variability. Cattle forage was markedly reduced in areas where elk concentrated in severe winters, but was reduced much less, or even improved, elsewhere. Our results showing minor effects of elk population level on cattle (a difference of 6 kg, or 1%, in cow weights for the historical experiment, and 11 kg, or 2%, for the stochastic experiment) were surprising because a field experiment for a nearby area found far greater effects (Hobbs *et al.*, 1996b). In their study, Hobbs *et al.* (1996b) report delayed calf birth dates, decreased calf body mass at the end of the growing season, and decreased total cattle production, as elk population density increased in a controlled experiment. However, decreases in cow body mass, the variable reported here, were not significantly associated with increasing elk population density (Hobbs *et al.*, 1996b).

Minor negative effects on cattle condition may have resulted from interactions involving decreases in forage quantity, and increases in forage quality associated with an increased live/dead ratio of spring forage. However, we believe this was a very conservative test because of two simplifying assumptions in model implementation: (1) simulated cattle distributions were overly flexible, since individual herds were not confined to allotment boundaries, allowing cattle to redistribute themselves to avoid areas of relatively severe elk impact; and, (2) our use of fixed population levels, instead of dynamic ungulate population modeling, did not allow emergence of potentially important effects of elk consumption on delayed birth dates and reduced birth weights of cattle (Hobbs *et al.*, 1996b).

## Management implications

Simulation results based on historical climate suggest that elk population levels on the order of 4000–5000 elk are compatible with current levels of livestock utilization in North Park. At population levels of 5000 or greater, elk intake rates declined, and body condition declined following a severe winter. The availability of palatable browse on critical winter range appears to be the limiting factor. We did not simulate elk use of cattle feed (i.e. hay in haystacks) in winter, which could increase the number of elk North Park could support. On the other hand, increasing the number of elk much above 5000 might increase the undesirable use of haystacks by elk.

Model experiments based upon stochastic climate scenarios did not reveal the 5000 elk threshold, but suggest that density-dependent effects on elk may occur at population levels between 2000 and 10 000, depending on climatic variability. Elk population levels from 4000–5000 animals may represent a conservative population objective for wildlife managers. Population levels that are much greater might exhibit significant ecosystem effects or density-dependent feedbacks under conditions of unfavorable climate (cold and snowy winters, hot and dry summers), but not under more favorable climatic conditions.

We suggest that efforts to resolve elk-cattle conflicts are likely to be facilitated by managing the distribution of elk, rather than overall population levels. Our basis for this recommendation is the relatively minor effect of changing overall elk population levels on cattle forage and condition, even though elk population levels were varied over a broad range. Increasing elk population levels appears to intensify intraspecific competition among elk far more than interspecific competition with cattle.

The SAVANNA model provides ecosystem analyses at spatial and temporal scales relevant for ungulate population management decisions. Clearly, real-world problems must be solved using real-world data, and it may be difficult to determine the level of prediction uncertainty associated with a complex ecosystem model such as SAVANNA. However, the modeling framework provides a useful tool for integrating data from a variety of sources into a cohesive representation of system dynamics, where causal relationships between ecosystem components (e.g. elk numbers and willow biomass) can be explored dynamically. For example, data utilized in this study included: plant species composition;

plant production; shrub height and cover; historical climate; historical animal numbers; soils maps; field soil survey data for texture, depths, and nitrogen levels; maps for vegetation, topography, hydrology, animal ranges, and land ownership; satellite imagery for NDVI data; and many literature-derived parameters from fields of study such as animal energetics and plant physiology. Simply providing all of these data to a wildlife scientist would be unlikely to contribute to good wildlife management decisions. An ecosystem simulation model is useful for organizing the information within a logical, unified framework. Although we tested a simple set of management options, more complex simulation experiments could be conducted to explore the effects of more realistic management decisions.

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