Ecological Implications of Fire in Greater Yellowstone, 1996

Yellowstone Elk Population Responses to Fire — A Comparison of Landscape Carrying Capacity and Spatial-Dynamic Ecosystem Modeling Approaches

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Abstract. We used two modeling approaches to examine 1988 fires effects on elk population dynamics, in the winter following the fire, the first three post-fire years and over the long-term. A nutritionally based landscape carrying capacity model (LCCM) indicated that the fires would have little impact in the first winter or the following few years. Over the longer term, the model indicated that the winter range might eventually support 15% more elk and the summer range might support 60% more elk, however both responses would decay over a period of two to three decades as forest canopies regenerate. Winter range was more limiting than summer range. A spatial-dynamic model (SAVANNA) was parameterized to demonstrate the capabilities of ecosystem modeling. The LCCM and ecosystem models provided similar results in the short term - there were negligible fire effects on simulated elk populations in the first few years. Using a historical weather sequence, the ecosystem model predicted an initial drop in elk population size after the fire of 5-10%, followed by recovery after five years, reaching 10-15% higher levels 15-25 years post fire. Confidences in long-term LCCM and ecosystem model predictions were limited by information about long-term herbaceous plant responses to fires of different severities, particularly in sagebrush and forest understories. More information is also needed about the effects of snow and available biomass on winter elk foraging. Spatially explicit ecosystem modeling appeared to provided a more comprehensive and realistic approach to analyses of elk-vegetation-fire interactions compared to nutritionally-based or population-based modeling approaches, but further work is needed to bring it to its potential predictive capacity.

Keywords: Elk; Modeling; Population dynamics.

Introduction

The northern Yellowstone elk herd is hypothesized to be food-limited, particularly during the winter when snow forces the herd to concentrate onto low-elevation winter ranges (Cole 1976, Barmore 1980, Houston 1982, Boyce and Merrill 1991, Coughenour 1994, Coughenour and Singer 1995). Fire potentially alters the degree of food limitation of the elk herd, through its manifold impacts on vegetation and other ecosystem processes. Therefore, the processes and the extent of food limitation must be quantified to assess fire impacts on the population.

The immediate effect of fire is a loss of forage. Thus during the first winter after the fires there was concern that the elk would be severely stressed by the loss of forage in the fires. Although winter feeding was suggested, this was immediately dismissed as inappropriate (Christiansen et al. 1989). Elk moved onto winter ranges 4-6 weeks early in 1988, and more elk migrated out of the park than in prior winters (Singer et al. 1989). The herd declined by about 40% over the winter of 1988/89, however about 37% of the decrease was due to an especially large offtake by hunters (Singer et al. 1989). Other factors could have contributed to the die-off. The drought of 1987-1988 could have reduced winter forage supplies. Deep snows could have reduced foraging area (Farnes 1996) and forage intake rates. Finally, the relatively large herd size could have heightened competition for available forage. A complete assessment must consequently disentangle the effects of snow, fire, and drought in terms of their impacts on forage intake and subsequent mortality.

Over the longer term, fires could improve elk habitats, and thus herd sizes. (Boyce and Merrill 1991). The primary effect of fire, of course, is to convert forests with closed canopies to earlier successional stages dominated by herbaceous plants. There is abundant evidence that there is less forage biomass under closed forest canopies (Basile and Jensen 1971, Collins and Austin 1978, Irwin and Peek 1983, Crouch 1986, Scotter 1980). In Glacier National Park, for example, fires created more favorable habitats comprised of young conifer stands and mosaics of shrub and conifer communities (Martinka 1974). At a larger scale, elk populations declined in much of the Rocky Mountain region over the last 50-70 years due to fire suppression (Scotter 1980). Elk herds expanded in Idaho after the 1910 fires, when burned forests were converted to shrub and brushfields with more abundant browse (Leege 1968). But, as forests regenerated, elk numbers decreased.

The northern Yellowstone elk herd (Houston 1982) is currently comprised of about 20,000 animals that winter in the low-lying valleys of the upper Lamar and Yellowstone Rivers. Most of the winter range is contained in the northern portion of Yellowstone National Park (71%), while the remainder lies just outside of the northern park boundary. Lodgepole and other pine and spruce-fir forests cover 25% of the winter range, Douglas fir covers 20% and the remaining 45% is open grassland and sagebrush grassland. Approximately 283 km^2 or 20% of the 1,400 km^2 winter range burned in 1988. This included about 137 km^2 or 20% of the sagebrush/grasslands and meadows and 146 km^2 or 23% of the forested areas.

The impacts of forest fires on elk forage supply are confounded by elevation. Most of the higher portions of the winter range are forested, while most of the lower portions are non-forested. As snows are deeper at higher elevations, the benefits of forest burning on forage supply may be significantly offset by the low availability, especially during severe winters when snow greatly reduces the size of the winter range and elk foraging efficiency.

About 30% of the ~5,100 km^2 summer range of the northern herd (as delimited by Houston [1982]) burned. However, only 124 km^2 or 15% of the 830 km^2 of meadows and sagebrush/grasslands burned in comparison to 1,500 km^2 or 35% of the forests. The degree of summer range limitation of herd size in Yellowstone has not been evaluated, so it is difficult to predict the consequences of summer range fires. While conditions for foraging are obviously worse during winter, summer foraging determines stored energy (fat) reserves which are important for winter survival. Thus summer ranges could be more limiting than winter ranges if they are relatively small or unproductive.

The objective of this research was to assess the potential effects of the 1988 fires on the "carrying capacity" of winter and summer elk ranges over the short and long-term. The primary approach to this problem is to link a dynamic carrying capacity model with a geographic information system to calculate total energy and nitrogen transfer to the elk herd (Coughenour 1994). We also evaluate the potential for using a more complex, spatially explicit ecosystem model. We point out limitations in current knowledge, and suggest research that would lead to improved understanding of elk-vegetation-fire interactions.

Methods

Comparison of Methods to Estimate Carrying Capacity

Carrying capacity (K) can be derived in several different ways (Caughley 1979, McNab 1985, Coughenour and Singer 1991). (1) "Management" K could be defined as the maximum number of animals to maintain a certain vegetation composition, or other management objective. (2) "Ecological" K can be defined as the size of the animal population when it is at equilibrium with its food supply (Caughley 1979). Equilibrial population size can be derived from empirical relationships between population growth rate and population size (eg. Houston 1982). Boyce (1990) and Boyce and Merrill (1991) relaxed the equilibrial assumption by effectively making K a function of variable weather. (3) "Nutritionally-based" K is the number of animals that can be supported with the available food supply, and can be estimated by dividing forage production (kg) by animal forage requirement (kg/animal) (eg. Hobbs et al. 1982). The area available for foraging varies with snow cover, and the amount of forage per available area varies with precipitation. Consequently, northern elk winter range K varies among years in response to precipitation and the severity of the winter (Coughenour 1994). Nutritonally-based K does not predict how populations will respond to variable K. However, survival rates have been computed by dynamically simulating mean animal energetic status, and applying a statistical relationship between mean energy status and the population survival rate (Hobbs 1989, Coughenour 1994). (4) An"ecosystem modeling" approach to K links nutritional and population approaches. In principle, this was the approach embodied by applying simple predator-prey models to herbivore-plant systems (Caughley 1976), but increased realism is achieved by modeling plant growth responses to weather, landscape variation, and herbivory; herbivore spatial distribution and forage intake rate responses to forage and snow cover; herbivore energetic status, and; consequent ungulate population responses.

In this analysis, we use a spatial-dynamic implementation of a nutritionally-based carrying capacity model (Coughenour 1994), and then demonstrate the potentials of a spatial-dynamic ecosystem modeling approach to K.

Landscape Carrying Capacity Model

Overview

The effects of the 1988 fires on short and long term population dynamics were assessed with a landscape carrying capacity model (Figure 1). This model provides a nutritionally-based estimate of the number of animals that can meet their energy and nitrogen requirements on either the winter or the summer range given the abun-

Landscape Carrying Capacity Model

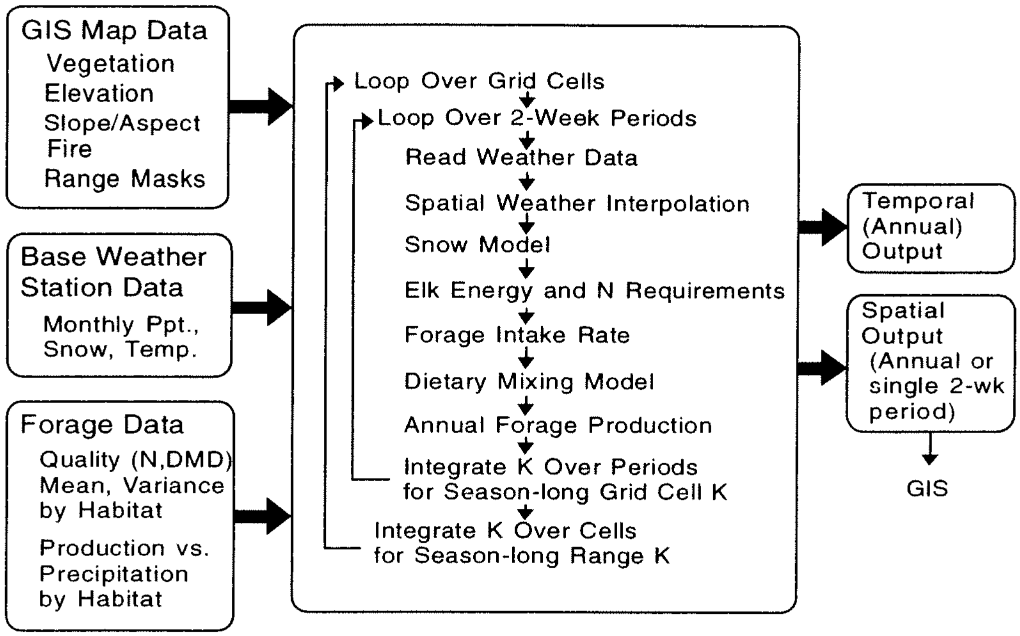

Figure 1. The landscape carrying capacity model.

dance, distribution and quality of the forage. Winter carrying capacity is strongly affected by snow depth and distribution.

Weather and Snow

Precipitation and snowfall were estimated from monthly data collected at five base weather stations (Mammoth, Gardiner, Tower, Cooke City, Lake). Station data are spatially interpolated to derive estimates for each grid-cell. Estimates are corrected for elevation using monthly regressions of precipitation on elevation (Coughenour 1992). Snow is added to the snowpack and it melts at a rate proportional to temperature. Snow model output consists of monthly maps of snow depth on the winter or summer range. Snow depth maps showed characteristic patterns of deeper and longer-lasting snows at higher elevations and in more severe winters.

Elk Ranges

The maximum extent of the winter range of the northern herd was delimited by entering locations of elk group sightings during aerial winter censuses into the GIS. The outermost locations of the sightings were connected to form a polygon of 1,400 km², which is considerably larger than the 1,000 km² winter range size estimated earlier (Houston 1982). Within the maximum extent, the actual winter range extent varies among two-week periods and years in the model in response to simulated snow cover. The model effectively removes burned areas from the range extent where forage is completely lost to fire. The summer range extent was roughly the area proposed by Houston (1982, Figure 4.2), which encompasses about 4,900 km². Calculations were performed for each of the 5,605 25-ha grid-cells on the winter range or 19,178 25-ha grid-cells on the summer range.

Forage Production

Total forage production is calculated on an annual basis for each habitat, based upon water-year precipitation. Snow depth, elk energy requirements and forage intake rates are calculated for two-week periods over the winter or summer season. Spatial variation in forage supply and weather are calculated from digitally mapped data residing in a geographic information system (GIS). The Yellowstone N.P. GIS data base includes the habitat and vegetation cover maps of Despain (1990), topography, geology, roads, streams, annual precipitation, 1988 fires, and other data encoded as maps of 50m x 50m grid cells. For modeling purposes these data were converted to 500m x 500m grid cells. The habitat map was simplified into 11 functional types: (1) dry Douglas fir, (2) moist Douglas fir, (3) wet forests, (4) predominately lodgepole-pine forests with *Vaccinium* dominated understories, (5) lodgepole forests with other types of understories, (6) xeric, (7) dry and (8) mesic sagebrush/grassland, (9) sedge meadow, (10) hairgrass meadow, and (11) the dry valley grasslands near Gardiner.

Forage production responses to water year precipitation in sagebrush/grasslands were estimated from a linear regression model (r^2=0.32, p=<0.0001, n=25) developed from data collected over 18 years between 1935-1950 and 1986-1989 in many different studies (Houston 1982, Coughenour 1991, Frank and McNaughton 1992). Mean production on upper winter range sites was 67 g/m². Regression model predictions were adjusted for other habitat types using empirical scalars, since there were insufficient data to derive precipitation regressions for each. Douglas fir understories are about 65% as productive as sagebrush/grasslands (Houston 1982, Norland and Singer 1994, Singer, Coughenour et al. unpubl. ms.). Lodgepole pine forest understories are about 30% as productive as dry meadows (Basile 1975, Collins and Austin 1978). Hairgrass and sedge meadows produce about 2.5x and 4.5x times more production than sagebrush/grasslands, respectively (Houston 1982, Frank and McNaughton 1992, Mueggler and Stewart 1980). Forage responses to fire are explained below.

Responses of Forage to Fire

A digital map of the 1988 fires was read into the model to delimit burned and unburned areas Fire impacts on forage were applied to burned grid-cells.

The immediate effect of the fire was a loss of forage in the winter of 1988/89. Forage biomass in burned grid-cells was set to zero that winter. Subsequent short-term responses to the fire were mostly based on studies conducted between 1989-1991 (F. Singer and J. Norland, unpubl. data, Singer, Coughenour et al. unpubl. ms., Singer and Harter 1995). In the summer of 1989, there was 77% as much forage on burned as on unburned sagebrush/grasslands, while in 1990 burned forage production was 90% of unburned. We hypothesized complete recovery by summer of 1991, in accordance with findings of Antos et al. (1983) and Hobbs and Spowart (1984). In Douglas fir understory there was 43% as much forage on burned as on unburned sites in 1989 (mean of lightly and moderately burned sites) and 70% as much on burned sites as on unburned sites in 1990 (Singer, Coughenour et al. unpubl. ms.). In the lodgepole pine understory there was 29% as much forage on burned as on unburned sites in 1990, and 70% as much in 1991. On a mesic summer range meadow, forage mass on a burned site was 112% of that on an unburned site in 1991. We hypothesized that burned and unburned productivities would be equal in the third post-fire year in all habitats.

We based our hypotheses of longer term responses on observations from similar systems elsewhere. Long-term responses result initially from an increase in basal cover, number of plants, and sizes of perennial plants over years. Later, it is influenced by the reestablishment of tree canopies. Thus, it is related to vegetal succession. We estimated that forage production would increase by 20% on burned sagebrush grasslands after a decade based on forage productivities of habitats with and without sagebrush (Mueggler and Stewart 1980). Forage production will then decrease to prefire levels after 25 years of sagebrush regrowth. Although Crouch (1986) found that understory production in thinned lodgepole stands equaled or surpassed that in unthinned stands in year two and had doubled in year five in stands thinned to 17% tree cover, we modeled a gradual increase to a maximal three-fold stimulation of understory production in burned subalpine forest by year 11, and a decrease to pre-fire levels by year 25 (Basile 1975). In Douglas fir burned understory, we gradually increased forage production to 154% of that in unburned understories in year 11.

Changes in forage quality were based on sampling during summers of 1989-90 and winters of 1990/91 and 1991/92 (Singer, Coughenour et al. unpubl. ms.). Within winter feeding craters, dry matter digestibility (DMD) was lower in burned than unburned Douglas fir, but was unaffected in sagebrush/grassland. There were no fire effects on protein. Fire had few impacts on winter forage quality outside of feeding craters in 1990/91 - protein was slightly lower on burned than unburned sedge meadows, DMD was lower in burned than unburned lodgepole pine, moist Douglas fir understory and xeric sagebrush/grassland. In feeding craters, protein was higher in burned sagebrush/grassland and Douglas fir, while DMD was higher under burned Douglas fir. Fall forage qualities were higher in burned winter range grasses in 1989 and 1990. In summer, protein and DMD concentrations were higher in burned than unburned lodgepole pine understories in 1989 and 1990. On a summer range moist meadow, protein was elevated in 1989 but DMD was unaffected. Generalized short-term fire impacts were developed for each habitat based on these data. We assumed there were no fire impacts on forage qualities in unforested habitats after three years (e.g. Hobbs and Spowart 1984). Normal frequency distributions of forage N and DMD were generated for the dietary mixing model from observed means and variances.

Elk Energetics and Foraging

Elk energy requirements are derived from equations for thermoregulatory costs (Parker and Robbins 1985), travel costs as a function of snow depth (Parker et al. 1984), and gestation (Hobbs 1989, Robbins 1983), after Hobbs (1989). The equations were parameterized for elk from values published in the literature. Costs are calculated in terms of kcal per animal per minute, and these are multiplied by time spent in different activities. Seasonal activity budgets were based on data of Craighead et al. (1972). Although activity patterns vary in response to weather and location, the seasonal activity data captures much of the variation and a detailed behavior model was beyond our objectives.

Energy reserves are depleted during the winter and replenished during the summer. For winter model runs, energy reserves are subtracted from demands. For summer runs, energy reserves must be added to total demands. Maximum fat reserves of 16% and 11% of body weight were assumed for cows and bulls based on data from deer and elk (Torbit et al. 1988, Schwartz et al. 1988, Cassier and Able 1990). Fat reserves were assumed to be normally distributed in the population with a coefficient of variation of 0.21, and individual animals were assumed to die when 67% of their reserves are depleted (Torbit et al. 1985, Hobbs 1989). Based on this distribution, a mean depletion of 26% of total reserves would result in about an 10% overwinter mortality rate. This would be a reasonable long-term mean annual mortality rate for adult elk (Houston 1982, Coughenour and Singer 1995). For example, mean mortality rates of cows aged 1-20 is 0.072, and for bulls aged 1-14 it is 0.21 (Houston 1982, Tables 5.8,5.9). If bull:cow ratio is 25, the mean adult mortality rate is 0.1.

Calculated energy requirements ranged between 42 and 52 kcal/kg/d on the entire winter range, with a mean of 43 kcal/kg/d. On snow depths that are more likely to be used by the elk, energy requirements were only 40-42 kcal/kg/d. Total requirements for the mean 254 kg animal in winter ranged between 10,414 and 10,922 kcal/d over winter. During summer, requirements were only 38-39 kcal/kg/d, including the energy needed to replenish reserves.

Nitrogen requirements are calculated after Hobbs et al. (1982). Metabolic fecal nitrogen requirements are proportional to forage intake rate. Endogenous urinary nitrogen requirements are scaled to metabolic body weight.

The effect of forage quality on elk carrying capacity is calculated using the dietary mixing model of Hobbs and Swift (1985). Forage energy contents (%DMD) and protein contents are assumed to be normally distributed based on observed means and standard deviations in different habitats and seasons (Singer, Coughenour et al. unpubl. ms.). The mixing algorithm progressively adds forage quality classes to the diet beginning with the highest quality items until the quality of the mix just satisfies requirement. The quality of the mix must increase as forage intake rate declines, thus reducing the fraction of plant tissues that can meet elk requirements.

Forage intake rate was allowed to vary in response to forage density and snow depth. Hobbs (1982) used a fixed intake rate, which was appropriate since that model was static. Coughenour (1994) used a fixed intake rate in the dynamic model, but estimates of K were inflated. Modeled intake rate increases asymptotically with forage biomass in a Type-II functional response, parameterized with data of Collins and Austin (1978), Wickstrom et al. (1984), and Hudson and Watkins (1986). Available forage is reduced by increasing snow depth according to a function suggested by Cassirer and Ables (1990).

Carrying Capacity

Each season, carrying capacity is estimated from the mean animal days per ha (*Andha*) that can be supported in each grid-cell (*nc*) in each two-week period (*np*) during the season, which is

$$Andha_{nc,np} = \mathrm{Min}\ [\ \frac{Tfore}{Frate_{day}}, \frac{Tforn}{Frate_{day}}]\ \times\ 10^4$$

where *Tfore* and *Tforn* are total g/m² of forage that meet energy and nitrogen requirements respectively, at a daily forage intake rate of $Frate_{day}$ g/d/animal and where 10^4 is m²/ha.

The number of elk that can be supported that year is

$$\mathrm{Elk} = \frac{Andha_{mn} \times Ha}{Days_{sn}}$$

where $Andha_{mn}$ is mean animal-days per ha supportable over all grid-cells and all two-week periods, *Ha* is total ha on the seasonal range, and $Days_{sn}$ is number of days in the season.

The number of elk that could be supported on winter or summer ranges was calculated for each year 1968-2012. Observed weather data were used over the period 1968-1991. After 1991, weather years were chosen at random from the 1968-1992 data set. Six runs of the model were conducted on winter and summer range using different random weather sequences 1992-2012; three with fires in 1988 and three without fires in 1988.

Spatial-Dynamic Ecosystem Modeling

An ecosystem model was used to make provisional predictions of elk population responses to forage supply and the 1988 fires. The SAVANNA model (Coughenour 1992, 1993) simulates ecosystem processes that influence plant-ungulate interactions (Figure 2). Ecosystem dynamics are simulated on a weekly basis over 5-100 year time spans. Grid-cells on the landscape are simulated in parallel, so organisms, as well as water or other materials can move or be spatially redistributed during a model run. Spatial (GIS) data are converted to model inputs at the beginning of a simulation. Spatial model output are passed to a GIS for display and analyses. A preliminary parameterization of the SAVANNA model was developed for the total annual range of the northern Yellowstone elk herd. The annual range was divided into 1,650 2 km x 2 km grid-cells. Coniferous trees, open herbaceous plants, understory herbaceous plants, and shrubs were simulated.

Weather data are converted to dynamic maps using topographically corrected spatial interpolation. The water balance on each grid-cell is simulated: including precipitation, runoff, infiltration, evapotranspiration, snow accumulation and snowmelt. Available soil moisture affects plant growth rate, along with temperature, light and

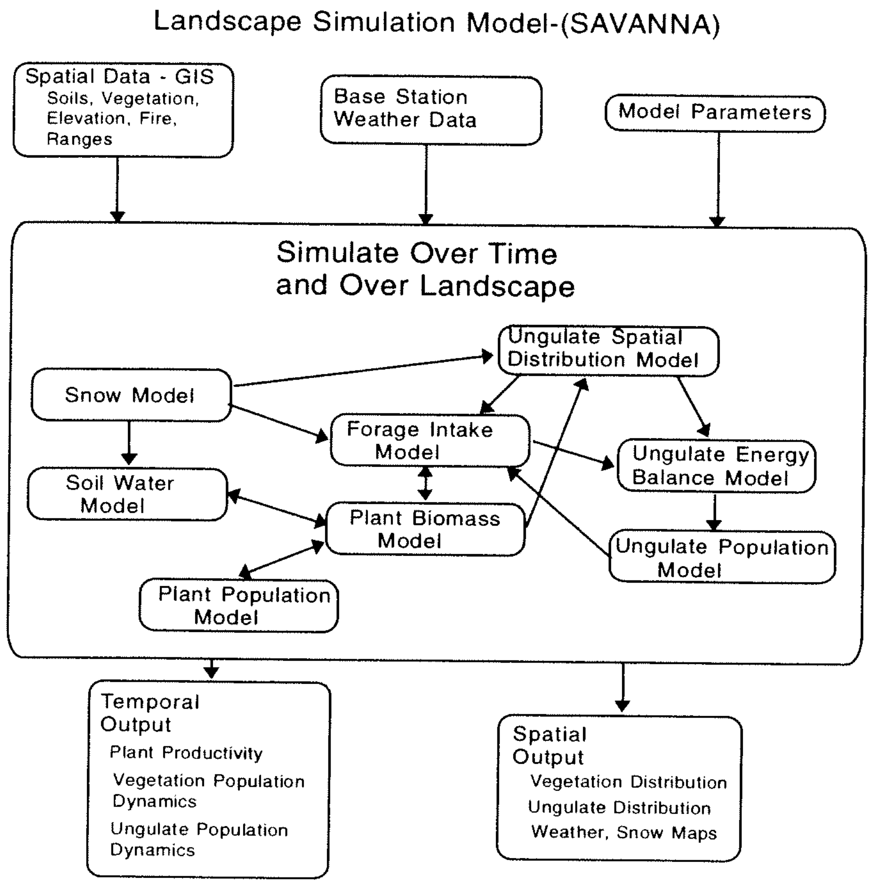

Figure 2. The SAVANNA spatial-dynamic ecosystem model.

herbivory. Plant growth is partitioned above and belowground. When aboveground plant tissues senesce, they are transferred to litter and become unavailable to herbivores. Nitrogen is taken up by roots and distributed in the plant. Leaf N concentration declines with advancing phenology.

A tree population model represents establishment, transfer among size classes, and mortality. Tree number and size dynamics determine tree cover on the landscape. Trees affect herbaceous understories through competition for light and water. Competition between trees and grasses only occurs on those portions of grid-cells where trees are rooted.

Elk are distributed over the simulated landscape in response to forage, snow, topography and tree cover on a monthly basis. Forage intake in each grid-cell depends upon forage biomass in the functional response, as well as snow depth. The energy balance of the mean animal in the population is simulated as the difference between energy intake and energy expenditures. Resultant mean body weight is converted to an index of animal condition, which then affects reproduction and survival. Elk population dynamics are simulated with a simple age/sex class model. This scheme provides an explicit and mechanistic linkage from spatially and temporally variable forage abundance to elk population responses. Resultant elk herbivory affects plant growth and vegetation dynamics.

The 1988 fires map was read into the model and fire impacts were simulated for each plant functional group in each fire intensity class. Parameterized fire responses included fractions of aboveground tissues lost and fractions of plants that died in each fire severity class. Subsequent plant growth after the fire was affected by changes in tree cover, which increased light and water in former understory. Decreased shrub cover also provided more opportunities for herbaceous plant growth. Trees reestablished through seedlings, with subsequent increases in tree size and stand thinning.

Results

Landscape Carrying Capacity Modeling

Simulated forage biomass varied with annual precipitation between 37 and 81 g/m^2 on the winter range (66±8 g/m^2) and 37-73 g/m^2 on the summer range (55±8 g/m^2). Forage was less abundant on the summer range due to greater forest cover. Burning decreased sagebrush/grassland production during the first two post-fire years and decreased forage production in simulated forest understories for the first three post-fire years. Subsequently, forage biomass was stimulated by burning -maximally in the 11th post-fire year. Sedge meadow production was not affected in the first year. It was stimulated in the next two years, and there were no fire effects after that. Forage biomass returned to unburned levels by the 25th post-fire year in all habitats. The fires enhanced total forage on the winter range by about 30% in the 11th post-fire year (1999), and by over 20% between 1994-2001.

Only a fraction of the total forage biomass could meet elk energy or nitrogen requirements, given the forage quality distribution on the range and the forage intake rate of the elk. Energy was always more limiting than nitrogen in that the supply of forage with sufficiently high energy content was smaller than the supply of forage with sufficiently high N content (*Tfore<Tforn*).

Model calculations indicated that the fires had little effect on winter or summer range carrying capacities in the year of the fire (Figure 3a). In the first three post-fire years winter range K was essentially unaffected, while the fires decreased summer range K by 4-8% (Figure 3b). In the first winter after the fire (1988/89), the model indicated that drought reduced total forage biomass to 37 g/m^2, or 56% of the long-term mean. The 1988 fires reduced total forage biomass on the winter range by another 20%. However, the fraction of total forage that could meet elk energy requirements with only 10% mortality that winter was very low - about 10%. This was a consequence of two factors. The functional response predicted a low forage intake rate that winter in response to low forage biomass densities and heavy snows reduced forage intake rates further. Given the resultant low forage intake rates, high forage energy contents were needed for elk to meet their energetic requirements. After accounting for these stresses, the fires only reduced the supply of adequate quality forage by an additional 12%.

The model indicated that the 1988 fires had little effect on winter range carrying capacity in post-fire winters 1989/90-1991/92 (Figure 3a). However the 1988 fires gradually increased carrying capacity until the 11th post-fire year, when the total stimulation was 16%. Fires depressed summer range K by 8% during the first two summers after the fires (Figure 3b). An increase in summer range K of over 62% was predicted by the 11th year post-fire. Winter and summer range K's decreased to unburned levels by the 25th year post-fire.

Estimates of winter and summer range K's made with the current version of the LCCM were considerably lower than those made with an earlier version (Coughenour 1994). Lower estimates were due to two changes in model assumptions. First, forage intake rate in the earlier version was set at a fised value, as elsewhere (Hobbs et al. 1982, Hobbs and Swift 1985). In the current version, intake rate

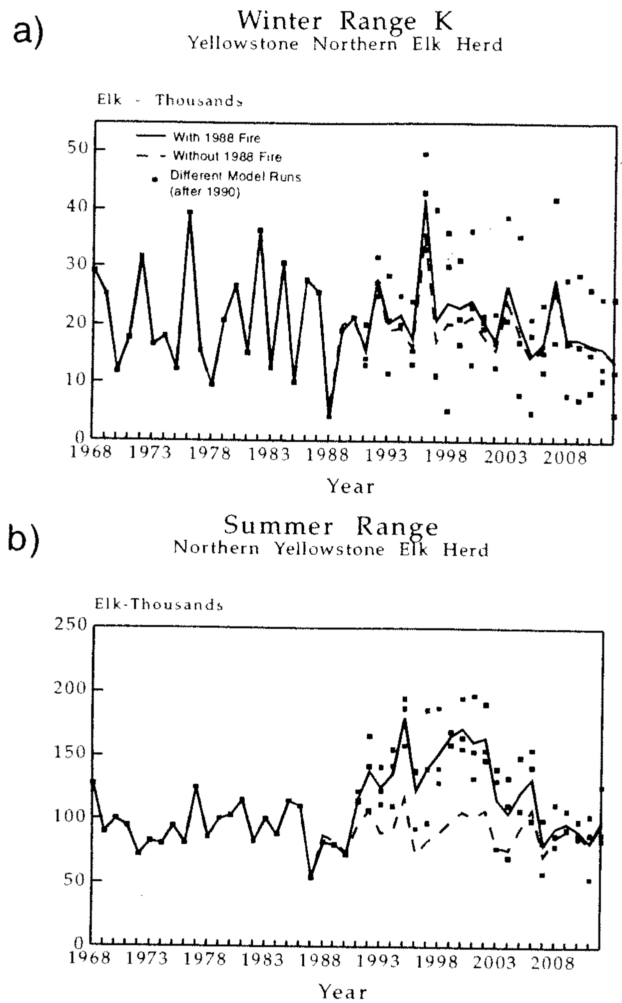

Figure 3. Carrying capacity model output for (a) winter range and (b) summer range; number of elk that can meet energy requirements while maintaining an adult mortality rate of 10%. Three burned and three unburned simulations were conducted in which weather years were randomly selected from 1968-1991 weather data during 1992-2011. Lines during 1968-1991 represent the means of three stochastic simulations.

is affected by forage biomass, so low production habitats, like lodgepole pine, support fewer elk the current model. Second, available forage biomass on any land area declines gradually from 25 cm to 50 cm of snow in the current model, while a simple threshold of 40 cm depth was used to exclude land area earlier. The decreased forage biomass then enters into the functional response.

Populations would be more likely to reflect winter rather than summer range responses to the fires, since winter range appears to be more limiting. Summer range K's would appear to be about 4 times greater than winter range K's on average. Energy-limited forage comprised about 60% of total forage. Conservatively, if the 60% was limited to a few species or the most productive plant tissues, then perhaps 50% of the 60% offtake would be sustainable. The summer range is shared with about 5,000 elk from three other herds, and perhaps 2,000-2,500 bison. Offtake from other herbivores like small mammals is unknown. Assuming an allowable use factor of 50% of the forage, the summer range may sustain about 50,000 elk. After subtracting at least 9,000-10,000 elk equivalents from other herds, this reduces the number to nearly 40,000 for the northern herd, which is still 1.6x mean winter range K. Furthermore, winter range K is much more variable than summer range K, due to the variability of winter weather. Periodic severe winters are highly limiting "bottlenecks" for the population.

Ecosystem Modeling

The level of verification achieved for most aspects of model behavior was judged sufficient for the model to be used for demonstration purposes here. Further parameterization would be required to use the model as predictive tool. The preliminary parameterization produced reasonable simulations of herb, shrub and tree biomass and population dynamics values fell within observed ranges, and the model responded realistically to weather, herbivory and fire.

The model successfully simulated population dynamics 1968-1991 (Figure 4a). The gradual increase after cessation of artificial herd reductions in 1968 was adequately simulated, indicating that long-term population recovery rate was correctly represented. The population ceased its growth with a die-off in winter 1975/76. The die-off was caused by reduced winter range area and negative effects of snow on forage intake rate. The simulated population grew again in 1977-78, followed by another winter die-off in 1978/79. The pattern was repeated a third time, ending in a die-off in winter 1981/82. During 1974-84, the population fluctuated around 15,000, which is the carrying capacity that was estimated using population data from 1968-1978 (Houston 1982, Boyce and Merrill 1991). However, the population gradually recovered from the three die-offs after 1980, growing to a transient high of over 25,000. The large die-off in winter of 1988/89 was correctly simulated. The magnitude of the predicted die-off corresponded with the sightability-corrected estimates of 22,000 elk in January and 13,000 elk in April 1989 (Singer, Coughenour et al. unpubl. ms.).

There was essentially no difference between with-fire and without-fire simulations with respect to elk population dynamics through 1991 (Figure 4b). Immediately after the fire in fall-winter 1988, the model simulated a 17% drop in forage biomass. During January-April there was a substantial transfer of standing dead forage to litter. Forage was below normal due to drought, and this was exacerbated by the transfer to litter. Deep snow conditions further contributed to reduced intake. Snow concentrated elk onto low elevations where there was intense competition for available forage. Reduced forage intake

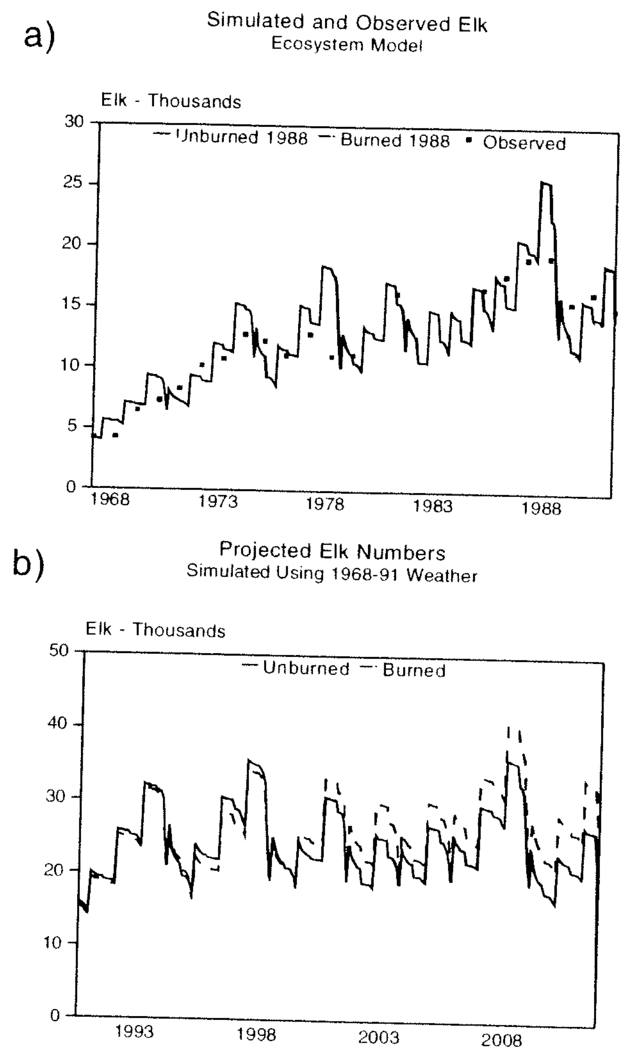

Figure 4. (a) Ecosystem model prediction of elk population dynamics 1968-1991, with and without fires in 1988. Observed data are calculated elk population sizes in early October, prior to annual hunts. (b) Ecosystem model predictions of elk population dynamics for 1992-2011 using 1972-1991 weather data (preliminary parameterization).

caused rapid weight loss, which resulted in a high rate of mortality.

The dynamics of the northern Yellowstone elk herd were simulated over the following 21 years, with and without fires in 1988 (Figure 4b) using 1972-1992 weather data. Many of the same dynamics occurred in the 1992-2011 and 1968-1992 simulations, which was a result of using the same weather sequence. The model simulated slightly depressed herd sizes in the first decade after the fire. It was not until then that elk herd size in the burned scenario surpassed that in the unburned scenario. The herd remained about 10% higher in the burned scenario for the duration of the simulation. Herd size fluctuated, but the long-term trend was a leveling off at a mean of about 25,000 animals. If this were to be taken as the effective carrying capacity, it would be concordant with both the nutrition- and population-oriented definitions of the term.

Discussion

Landscape carrying capacity (LCCM) and ecosystem modeling results both indicated that the winter 1988/89 die-off was mainly a result of the combined effects of drought and deep snow. Loss of forage due to burning 20% of the winter range probably increased elk mortality by less than 5%. Much of the burned winter range was situated at disproportionately high elevations. Deeper snows at higher elevations drove elk down to less fire-impacted portions of the landscape. The effects of drought on elk were larger than the effects on plants. While drought reduced forage mass to 56% of the long-term mean, forage intake rate was reduced more, due to the non-linear shape of the foraging functional response. Heavy snows further reduced effective forage biomass density.

Another experiment with the LCCM indicated that the 1988/89 snow alone would have caused a 50% drop in K without fire, and a 48% drop with fire (Singer, Coughenour et al. unpubl. ms.). Drought alone reduced K's to 32-34% of the values with no drought or severe winter weather. Drought and severe winter weather together resulted in K's that were 16-18% as high as K with neither factor. Fire alone reduced K's to 80-84% of the values with no fire. Since K was reduced so greatly by drought and winter weather, the added effect of fire was negligible.

Although drought and fire are correlated, it was coincidental that deep and hardened snow and drought occurred during the same year. The result was a uncommonly large die-off, probably similar in magnitude to the one observed in the winter of 1919/20, which was also preceded by drought (Houston 1982). However, the ecosystem model suggested that the herd will return to pre-fire levels within 6-7 years. After that, the herd was predicted to fluctuate between 20,000-35,000 elk.

The LCCM and the ecosystem models both suggested that the 1988 fires would have little impact on the herd in the first three post-fire years. This was mainly due to the rapid recovery of herbaceous vegetation on non-forested habitats on the winter range (Singer, Coughenour et al. unpubl. ms., Singer and Harter 1994). Antos et al. (1983) documented a similar rapid recovery after fire. Late summer fires generally cause much less plant mortality than early season fires (Wright and Klemmedson 1965, Owensby and Anderson 1967). While forage was slightly depressed on burned sagebrush/grasslands in the first two years, less than 20% of these habitats burned. The depression was greater in burned forests, but these habitats have little forage value. Greater fractions of the summer range burned, but summer range appears to be much less limiting to the elk herd.

After three years, both models predicted small increases in herd size. The magnitude and dynamics of these responses were strongly influenced by modeled vegetation responses to the fires, particularly forest understory regrowth, and the rate of forest canopy regeneration. Although the carrying capacity model represented a three-fold increase in forage production in burned lodgepole pine, winter K increased by only 5-10% (Figure 3a). Burned lodgepole pine comprised only about 10% of the winter range, and the most of the burned area was situated in areas of deeper snow. Furthermore, forage biomass was very low to begin with. Thus, the net effect of the fires was small. The increase in summer range K was much larger because burned forest comprised a much larger fraction of the summer range, and there were no confounding effects of elevation or snow.

The models differed in their predictions of the rate of return to pre-fire conditions. The carrying capacity model represented a peak response in 11 years, based on observations of Basile (1975). The ecosystem model response had not peaked after 25 years. For the first 50 years following fire, lodgepole pine forests are expected to remain relatively open and sunny, which will elevate herbaceous productivity (Romme and Despain 1989). Canopy closure is expected between 50-150 years post-fire. However, some forests could become permanent meadows where conditions are marginal for tree growth (Stahelin 1943, Knight and Wallace 1989).

Long-term predictions of elk population responses to fire were clearly limited by a lack of vegetation fire response data. The effects of fire on sagebrush/grasslands depends on herbaceous responses to sagebrush removal and sagebrush regeneration rate, yet neither is well understood. Forest understory production has received very little study apart from a few studies that have been conducted in patch-cut and clear-cut lodgepole pine forests in Montana (Basile and Jensen 1971) and Colorado (Crouch 1986). Long-term responses of herbaceous plants to forest canopy burning seem to be very poorly known. Thus, further understanding of the long-term responses of elk populations to the 1988 fires will require long-term studies of forage production on burned and unburned habitats, particularly forests and sagebrush stands.

Plant responses to fire are highly variable with burn intensity. Ideally, a fire severity map could be used to predict these variations. Unfortunately, we were not aware of any data which demonstrated differences in herbaceous plant responses in different fire severity classes. Thus, it would be useful in future studies to collect these data 1-3 years post fire. It would still be worthwhile to document responses to different fire severities 10 years post fire.

Predictions of elk population responses to fire were also limited by information about elk forage intake processes. Both models were quite sensitive to forage intake rate responses to forage biomass and snow depth during winter. There have been few, if any, studies of elk foraging during winter, especially of snow impacts on forage intake rate.

The combined approach of landscape carrying capacity and spatially explicit ecosystem modeling provided quantitative and explanatory predictions, and identified important knowledge gaps. The ecosystem modeling approach unified the nutritional and population approaches to carrying capacity: linkages between forage abundance, forage intake, energy balance, and population response were explicit. Feedback effects of herbivory on plants were modeled, but these were not given much attention here as they were somewhat peripheral to our objectives. It was clear that spatial heterogeneity must be considered in any analysis, particularly the dynamic distributions of vegetation, snow and elk. Further efforts are required, but it is clear that a spatially explicit systems approach is needed to determine plausible outcomes of the many processes and feedbacks involved in plant-fire-herbivore interactions.

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