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Chapter 13 Fire Patterns and Ungulate Survival in Northern Yellowstone Park: The Results of Two Independent Models

Linda L. Wallace, Michael B. Coughenour, Monica G. Turner, and William H. Romme

Yellowstone National Park (YNP) is renowned for its natural beauty. The original park boundaries were established to contain the geyser basins and hot springs, but they were later altered to include more of the ecosystem, such as watersheds and vegetational communities, within natural boundaries (Haines 1977, Schullery 1997). This was done in an effort to protect habitat for the abundant wildlife found in the park. According to current surveys, one of the reasons park visitors give for their decision to see Yellowstone is the chance to view wildlife in its natural surroundings. Therefore it is not surprising that when the 1988 fires burned a great proportion of the YNP landscape, one concern was how fires affect the wild animals, particularly populations of elk *(Cervus elaphus)* and bison *(Bison bison)*. Concern was so great that in the winter of 1988–1989, feeding programs for elk were proposed, but these were never implemented by the park or the Forest Service (Christensen and others 1989).

Given the large areas utilized by native ungulates and the heterogeneity of habitats, burned areas, and winter conditions across the park landscape, a unique set of tools was needed to explore the effects of the

1988 fires on the elk and bison of YNP. For obvious logistical and ethical reasons, this question could not be addressed using field manipulations of fire and snow. Therefore, computer simulation models needed to be developed that accurately portrayed vegetation, fire, weather, and ungulate population dynamics. These models could then be manipulated to determine what effect fire had on ungulate survival in the park. This was a question that, given its spatial and temporal nature, incorporated issues from population, ecosystem, and landscape ecology. Therefore models needed to recognize the complex nature of this problem.

Two groups independently addressed this issue. Michael Coughenour and Francis Singer of the Natural Resources Ecology Lab at Colorado State University developed a landscape carrying capacity model (LCCM) based on nutritional and energetic requirements of elk. Elk were not treated as individuals in this model, but rather the response of the entire population was assumed based on proportional responses of the landscape to different fire and winter severity scenarios (Coughenour 1994, Coughenour and Singer 1996a). Monica Turner, William Romme, and Linda Wallace developed an individually based, spatially explicit, energetically based model (NOYELP) (Turner and others 1993, 1994, Wallace and others 1995, Wu and others 1996). Both models had a strong landscape component, using spatially explicit and realistic distributions of vegetation, slope, aspect, and fire patterns.

In this chapter, we first compare the assumptions and structures of the two models (Tables 13.1, 13.2). Then we compare the outcomes of the models and the modeling experiments that were conducted and discuss the implications of those results to future fire scenarios in YNP and elsewhere where large populations of native ungulates occur.

MODEL ASSUMPTIONS AND STRUCTURES

The LCCM is a spatially explicit forage-based carrying capacity model, consisting of linked models of forage production, snow cover, elk forage intake, dietary mixing, and elk energy and nitrogen. The model estimates forage biomass based on typical values for a vegetation cover type and the previous year's precipitation. Precipitation at a location is estimated by elevation-corrected spatial interpolation from weather station data (Coughenour 1991). Snow cover is dynamically simulated based on precipitation input and rates of snowmelt derived from temperature. Snow input is corrected for slope and aspect after Farnes and Hartman (1989). Temperature varies with elevation according to an adiabatic lapse rate. Forage intake rate is estimated from a functional response equation

Table 13.1. Comparison of model st
Landscape Carrying Capacity Model
Park (NOYELP) models

Model factor
Pixel size (grain)
Time step
Duration
Area modeled
Vegetation classes
Density dependent effects
Migration outside of park?
Probabilistic responses of ungulates
Normal distribution of forage biomass within different vegetation types

in which intake is a function of fora
ally available, and used in the functi
cover (Table 13.2).

Energy requirements are derived
tabolism, lactation, pregnancy, trave
(1989). An energetic reserve is consic
requirements by the amount of ener
certain level of mortality occurs. Fo
increased by the amount of reserv
(1989), it was assumed that a loss do
in mortality (Table 13.2). Furtherm
from fat. Available reserves are thus
a normal distribution of animal ener
that if 74 percent of the available res
ulation will have overused the availa
is run, the user specifies the energy r
age energy requirements as a fractio
a certain level of mortality in mind.
sumption of 10 percent mortality ar

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Table 13.1. Comparison of model structure and function between the Landscape Carrying Capacity Model (LCCM) and the Northern Yellowstone Park (NOYELP) models

Model factor	LCCM	NOYELP
Pixel size (grain)	25 ha	1 ha
Time step	2 week	Daily
Duration	365 days	180 days
Area modeled	Winter and summer range	Winter range
Vegetation classes	Eleven classes, including 5 forest types	Twelve classes, including 2 forest types
Density dependent effects	No	Yes
Migration outside of park?	Yes	No
Probabilistic responses of ungulates	No	Yes
Normal distribution of forage biomass within different vegetation types	No	Yes

in which intake is a function of forage biomass. The forage biomass that is actually available, and used in the functional response equation, is affected by snow cover (Table 13.2).

Energy requirements are derived from calculations of the costs of basal metabolism, lactation, pregnancy, travel in snow, and thermoregulation as in Hobbs (1989). An energetic reserve is considered by diminishing the over-winter energy requirements by the amount of energy reserves that can be drawn upon before a certain level of mortality occurs. For summer runs, the energy requirements are increased by the amount of reserves that must be accumulated. After Hobbs (1989), it was assumed that a loss down to 67 percent of labile fat reserves results in mortality (Table 13.2). Furthermore, 70 percent of the energy reserves come from fat. Available reserves are thus fat energy times 0.67 divided by 0.7. Using a normal distribution of animal energy reserves with a CV of 0.21, it can be shown that if 74 percent of the available reserves are utilized, then 10 percent of the population will have overused the available reserves and will die. When the LCCM is run, the user specifies the energy reserve level that is to be subtracted from forage energy requirements as a fraction of available reserves. This value is set with a certain level of mortality in mind. Normally, the model was run under an assumption of 10 percent mortality and thus a 74 percent level of reserve use.

Table 13.2. Comparisons of key assumptions made by the two models with respect to population structure and factors limiting population growth

Assumption Factor	LCCM	NOYELP
Population Structure (elk)	12 percent bulls, 77 percent cows	19 percent bulls, 65 percent cows, 20 percent calves,[a] 16 percent calves[b]
Population Structure (bison)	Not modeled	42 percent bulls, 38 percent cows, 18 percent calves[c]
Interaction between bison and elk?	No	No
Landscape factor limiting ungulate survival[d]	Forage on winter range	Forage on winter range
Physiological factor(s) limiting survival	Energy and nitrogen[e]	Energy[f]
Snow limitations on ungulate foraging	[g] $For_{av1} = For_{tot} \times \frac{(1)}{1 + 90\, e^{-0.12Sdep}}$	Snow depth at brisket height, therefore movement of each age class affected differently, SWE over 10 cm starts to limit foraging with a linear feedback
Winter forage availability	Estimated from fall forage values	Refuge of ~15 percent initial forage is unavailable, measured values from fall forage
Maintenance energy requirement	$BW^{0.75}$ [h]	$BW^{0.75}$ [h]
Rates of vegetation recovery to prefire biomass levels	Sagebrush grassland to recover in 25 years, forested to recover in 11 years, meadows recovered in 3 years[a]	Measured biomass levels used from Fall 1990, 1991
Ungulate death[i]	67 percent loss of fat weight	70 percent of fat weight

Notes: LCCM is the landscape carrying capacity model and NOYELP is the Northern Yellowstone Park model.

[a]Coughenour and Singer 1996b
[b]Lemke and Singer 1989
[c]Barmore 1980
[d]Houston 1982
[e]Hobbs and Swift 1985
[f]Turner and others 1994
[g]Cassirer 1990
[h]Thompson and others 1973, Parker and others 1984
[i]Hobbs 1989

Given the energy intake rate, and nitrogen contents, the model cient energy or nitrogen content lated rate of forage intake (Hobb intake rate goes down due to low a higher energy content to meet only a small fraction of the forage high energy content to be able to amount of forage that can meet ber of animals that can be support per ha is calculated as the minim

$$\frac{Tfore}{Frate_{day}}, \frac{Tforn}{Frate_{day}}$$

where Tfore = the total g/m^2 of ments for elk at a given daily feedi of forage required to meet nitroge ing and therefore the nitrogen lin

The model is run over all of th ter range, including areas outside an additional 40,000 ha lie outsid cell, the model runs through tim because snow cover varies over t quirements due to stage of pregna costs of travel in snow. Thus for e the model determines the numbe procedure described above. The r rive a season-long estimate of elk in a given winter.

Fire effects on forage supply ar ing empirical data from each hab addition, it is assumed that the bu age production for a number of y

NOYELP is an individually ba landscape model. It follows the f foraging decisions based upon sn These decisions are probabilistic- of moving when snow depth or

by the two models with respect to
n growth

	NOYELP
	19 percent bulls, 65 percent cows, 20 percent calves,[a] 16 percent calves[b] 42 percent bulls, 38 percent cows, 18 percent calves[c]
	No
	Forage on winter range
	Energy[f]
(1) $0\ e^{-0.12Sdep}$	Snow depth at brisket height, therefore movement of each age class affected differently, SWE over 10 cm starts to limit foraging with a linear feedback
ıge	Refuge of ~15 percent initial forage is unavailable, measured values from fall forage
	$BW^{0.75}$ [h]
recover :o ıeadows	Measured biomass levels used from Fall 1990, 1991
ight	70 percent of fat weight

. NOYELP is the Northern Yellowstone

Given the energy intake rate, the frequency distributions of forage energy, and nitrogen contents, the model calculates what fraction of the forage is of sufficient energy or nitrogen content to meet an animal's requirements at the calculated rate of forage intake (Hobbs and others 1982, Hobbs and Swift 1985). As intake rate goes down due to low forage mass or deep snow, the forage must have a higher energy content to meet requirements. Thus as intake rate decreases, only a small fraction of the forage that is on the landscape would have sufficiently high energy content to be able to meet the animal's requirements. Based on the amount of forage that can meet requirements, the model calculated the number of animals that can be supported at the location and time. Mean animal days per ha is calculated as the minimum value of the following:

$$\frac{\text{Tfore}}{\text{Frate}_{\text{day}}}, \frac{\text{Tforn}}{\text{Frate}_{\text{day}}}$$

where Tfore = the total g/m^2 of forage required to meet daily energy requirements for elk at a given daily feeding rate ($\text{Frate}_{\text{day}}$) and Tforn = the total g/m^2 of forage required to meet nitrogen requirements. Tfore was always more limiting and therefore the nitrogen limitation did not come into play in the model.

The model is run over all of the 25-ha grid cells on the entire northern winter range, including areas outside the park. Although 100,000 ha are in the park, an additional 40,000 ha lie outside of the northern park boundary. For each grid cell, the model runs through time at two-week increments. This is important because snow cover varies over time and space, as do the animal's energy requirements due to stage of pregnancy or lactation, thermoregulatory costs, and costs of travel in snow. Thus for each grid cell and two-week period (Table 13.1), the model determines the number of elk-days that can be supported using the procedure described above. The results are integrated over space and time to derive a season-long estimate of elk-days that can be supported by the landscape in a given winter.

Fire effects on forage supply are simulated as a function of time since fire, using empirical data from each habitat type (Coughenour and Singer 1996a). In addition, it is assumed that the burning off of tree cover results in increased forage production for a number of years, until tree cover is once again established.

NOYELP is an individually based model layered on top of a spatially explicit landscape model. It follows the fate of individual elk (and bison) as they make foraging decisions based upon snow depth and density and forage availability. These decisions are probabilistic—that is, the animal has a greater probability of moving when snow depth or forage amount within a pixel becomes unfa-

vorable. Hence multiple runs of the model could be followed during model experiments and the results could then be statistically analyzed. When an individual animal loses 30 percent of its lean body weight and 70 percent of its fat reserves, it dies (Hobbs 1989) (Table 13.2). This is very similar to the body weight that would result in death that was assumed in the LCCM model (for example, if an average elk bull weighed 292 kg, it would die at 260.56 kg using the LCCM calculations and at 259.3 kg using the NOYELP calculations). Movement is constrained to the winter range within park boundaries, and only the winter range conditions are considered in this model (Table 13.1). The model runs only from November through April, hence there is no opportunity for plant regrowth. However, between-year variation in forage availability can be represented easily by modifying the initial conditions of forage abundance across the landscape for a given simulation. Nutrients were not considered because forage analyses showed no nutritional differences among forage types available during the winter (Wallace and others 1995). Forage availability differs by ungulate age class and is determined by snow water equivalent (SWE), animal brisket height, and vegetation class. Most animals are limited by snow depths deeper than their knees, and movement is severely limited by snow up to the height of the brisket (Parker and others 1984). SWE is the amount of water that snow of a given depth and density would produce if it were melted. Hence the higher the SWE found in an area, the heavier the snow is, making it harder for animals to move about in or dig through the snow to reach forage. Snow conditions across the winter range are modeled based upon snow course data available from one location. Snow is then distributed across the landscape based upon aspect and slope (Turner and others 1994). For example, a flat location has the same amount of snow as would be found at the snow course site. However, on a south-facing steep slope of 15–30 degrees, only 70 percent of the snow found on a flat surface would accumulate. On a north-facing slope of 15–30 degrees, 120 percent of the snow found on a flat surface would accumulate. In unburned forests, 90 percent of the snow found on a flat surface would accumulate. Burned forest areas accumulated the same amount of snow as their nonforested counterparts. Regression equations corrected snow depth for the low-elevation sites of the northern range (areas around Mammoth Hot Springs and Gardiner, Montana).

Sensitivity analysis of the NOYELP model indicated that energy gain is the key process regulating ungulate survival (Turner and others 1994). Thus any factor governing the availability of forage, and the initial body size of the ungulates going into the winter, were critically important to model output. Similarly, en-

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model (Coughenour and Singer

Partially because of its reduce
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MODEL EXPERIMENTATION AND F

Following validation, both mod
NOYELP model was used in a se
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ergy content of forage and forage availability were critical factors in the LCCM model (Coughenour and Singer 1996a).

Partially because of its reduced spatial and temporal scope (winter season and winter range only), the NOYELP model is built at a much finer resolution than the LCCM. However, the reduced spatial scope of NOYELP results in some assumptions about ungulate survival outside of the park that differ from those of the LCCM. If ungulates were forced by snow conditions to the park boundaries, they were assumed to die. However, in reality, some elk survive leaving the park and are not shot by hunters. During the time period these models were built, any bison leaving the park were shot. Therefore this assumption results in an overestimate of elk mortality by NOYELP (Wu and others 1996).

The coarser resolution of the LCCM (25 ha versus 1 ha for NOYELP) results in some potential overestimates of elk mortality as well, with the assumption of 50 percent mortality if the population mean fat reserves are depleted to 67 percent. This reduces the effect of spatial heterogeneity, whereby pockets of resources could result in some elk doing quite well or some elk being "trapped" by winter conditions and doing very poorly.

Forage response to fire is different in the two models, as well. In the LCCM, forage regrowth back to prefire levels takes three years, whereas regrowth to prefire levels can occur in one year in the NOYELP model. This difference could result in an overestimate of ungulate mortality in LCCM if succeeding winters after a fire were mild and would result in an underestimate of ungulate mortality in NOYELP if postfire winters were severe. Both models used different forage amounts for different vegetation classes, with both showing increased forage amounts in burned forests the first year after fire.

This naturally leads to the question, "How do the predictions of these models compare with each other?" Do they identify similar controls on ungulate population size? Both models underwent a validation process where their results were compared to what actually occurred in the system (Table 13.3). Both models simulated elk survival well for years when actual weather data were available for the model run.

MODEL EXPERIMENTATION AND RESULTS

Following validation, both models were used in simulation experiments. The NOYELP model was used in a series of factorial experiments designed to determine the relative importance of winter severity, proportion of the landscape burned, patch structure of the burned areas, and elk population size at the on-

Table 13.3. Model validation results for elk population size during different winters

Year	Observed Mortality	NOYELP mortality	Comments
1987–1988	5%	0%	Prefire winter, mild winter
1988–1989	38–43%	40%	Postfire winter, severe winter
1990–1991	5%	4%	Later postfire winter, mild winter

Year	Observed Population	LCCM Population	Comments
1987	21,000	19,000	Prefire, model had actual weather data
1988	25,000	19,000	Postfire, model had actual weather data
1993	19,000	25,000	Postfire, model run on average weather data

Note: The NOYELP model (Turner and others 1994) examined percent mortality; the LCCM model (Coughenour and Singer 1996) examined total population size.

set of winter. The LCCM model was used in experiments to determine the relative effects of fire, drought, and snow on carrying capacity.

In the LCCM, snow alone in the severe winter of 1988–1989 was found to reduce carrying capacity by 50 percent (Coughenour and Singer 1996a). Drought alone reduced carrying capacity to 66–68 percent of its value for 1988–1989 by reducing forage production during the summer. Similarly the fire alone reduced carrying capacity to 80–84 percent of its value for the same year by consuming plant biomass.

Factorial simulation experiments with the NOYELP model showed that the strongest effect on elk survival the first year after a fire was winter severity, followed by fire size and fire pattern (clumped patches versus dispersed patches) (Turner and others 1994, Wu and others 1996). In these simulations, the initial sizes of the ungulate populations were set at sizes comparable to those observed at the beginning of the 1988–1989 winter. When winter conditions were very mild, even large fires (60 percent of the landscape) had no effect on ungulate population size at the end of the first winter following fire. Effects of fire on ungulate survival became important when winter conditions were average to severe, and effects were observed in both the initial and later postfire winters (Turner and others 1994). In average to severe winters, the spatial pattern of fire also was important: small dispersed burned patches reduced elk survival more than large clumped burned patches for any given total area of fire.

Weather Role in Both Models

Both models focused on forage
survival. The LCCM model fo
tied to annual precipitation an
production during the first tw
model did not examine forage p
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tion of forage biomass within a
increased the first year followin
the data used to parameterize th
cause no differences were found
lace and others 1995), the NOY
to ungulates. The LCCM mod
contents (Singer and Harter 199
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following the fires. Both models
lost its forage in the fires, resulti
ter. Therefore the weather effect
to a combination of several facto
age availability in two ways: fora
forage availability tied to sno
NOYELP model, the forage-re
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Weather also had direct effec
snow accumulated, more energ
the snow to reach forage, and f
needed to move farther to locat
forage intake rate that decreased
intake rate was based on a type
model used a logistic response
thresholds.

Interaction of Fire and Weather with Ungulate Population Size

An extensive factorial simulatio
model to explore the interactio
pattern and winter severity. Th

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ation size during different winters

rtality	Comments
	Prefire winter, mild winter
	Postfire winter, severe winter
	Later postfire winter, mild winter

lation	Comments
	Prefire, model had actual weather data
	Postfire, model had actual weather data
	Postfire, model run on average weather data

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NOYELP model showed that the
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llowing fire. Effects of fire on un-
er conditions were average to se-
initial and later postfire winters
winters, the spatial pattern of fire
atches reduced elk survival more
ven total area of fire.

Weather Role in Both Models

Both models focused on forage biomass production as a critical element in elk survival. The LCCM model found that simulated forage biomass was closely tied to annual precipitation and that burning decreased sagebrush/grassland production during the first two postfire years. Alternatively, the NOYELP model did not examine forage production during the summer months, but used forage biomass measurements at the end of summer to create a normal distribution of forage biomass within a vegetation class. Forage in all vegetation classes increased the first year following a fire rather than having a lag period shown by the data used to parameterize the LCCM model (Singer and Harter 1996). Because no differences were found in wintertime forage quality after the fires (Wallace and others 1995), the NOYELP model focused on forage energy available to ungulates. The LCCM model used a normal distribution of forage protein contents (Singer and Harter 1996) to calculate carrying capacity because during the summer, there were differences in forage quantity and quality in the years following the fires. Both models showed that a large fraction of the winter range lost its forage in the fires, resulting in reduced forage supply the following winter. Therefore the weather effect on elk mortality noted by both models was due to a combination of several factors. For the LCCM model, weather affected forage availability in two ways: forage production tied to summer precipitation and forage availability tied to snow depth and duration in the winter. In the NOYELP model, the forage-related component tied to weather was primarily the availability of forage biomass due to snow depth, density, and duration.

Weather also had direct effects on elk energy expenditure in both models. As snow accumulated, more energy was required for locomotion, digging through the snow to reach forage, and for thermal regulation by elk. Also, elk typically needed to move farther to locate adequate forage supplies. Both models used a forage intake rate that decreased with increasing snow depth. The LCCM model intake rate was based on a type II functional response, whereas the NOYELP model used a logistic response to snow water equivalent with upper and lower thresholds.

Interaction of Fire and Weather with Ungulate Population Size

An extensive factorial simulation experiment was conducted with the NOYELP model to explore the interaction of ungulate population size with fire size and pattern and winter severity. Three winter severities were compared. The most

mild (1976–1977) and most severe (1975–1976) winters recorded during the twentieth century with respect to snow conditions were identified from weather records. Conditions during these winters bracket known weather extremes. In addition, the NOYELP model simulated an "average" winter in which the mean monthly snow conditions were computed across all winters for which data were available. Nine levels were specified for the size of simulated fires by specifying the percentage, p, of the study area burned. In this experiment, p ranged from 10 to 90 in intervals of 10 (the 1988 fires burned ca. 22 percent of the northern range). In addition, two alternative fire patterns—fragmented or clumped in a single patch—were generated for each of the p values to bracket the extremes in spatial patterns of fire. Finally, the initial number of elk in the northern range was simulated at five levels: 6000, 12,000, 18,000, 24,000, and 30,000. Approximately 18,000 elk and 600 bison were present on the northern range at the beginning of the winter of 1988–1989 (Singer and others 1989), and we included both larger and smaller population sizes. Bison population sizes were adjusted simultaneously with the elk, for initial population sizes of 200, 400, 600, 800, and 1000. Simulations were run for both the initial postfire winter, when burned areas contained no forage, and the later postfire winter, when burned areas had enhanced forage quantities. Three replicates with different random number seeds were run for each scenario. Results were analyzed separately for initial and later postfire years using ANOVA (SAS 1990).

Density-dependent thresholds for the effect of fire size on the proportion of elk surviving the winter occurred during the initial postfire winter (Fig. 13.1). When the winter was mild, ungulate survival dropped precipitously from 100 percent to zero or very low levels at different fire sizes, depending on population density. Smaller population sizes survived larger fires, and for the same elk population and fire size, survival was usually greater with clumped fires compared with fragmented fires. For bison, the effects of fire pattern were statistically but not biologically significant (Wallace and others 1994, Fig. 13.2). Note that the difference in percent survival for all age groups was very small. Thresholds of survival were also observed in the average and mild winters and were most pronounced for the smaller population sizes and larger fires. When population densities were high (> 18,000 elk and 800 bison), survival was very low even with the smaller fires if winter conditions were average to severe (Fig. 13.1, Wallace and others 1995). ANOVAs revealed that most of the variation in elk survival during the initial postfire winter was due to variation in winter severity, with ungulate population size and fire size having secondary effects. During later postfire winters, when burned areas generally provided more abundant forage than

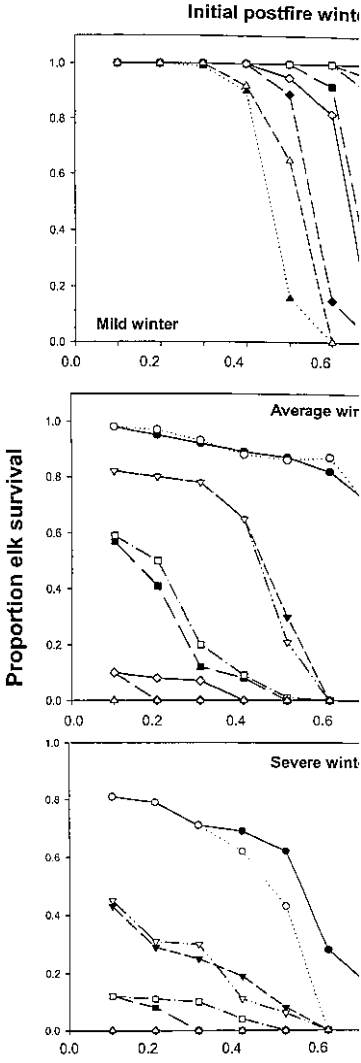

Figure 13.1. Elk survival in the initial pos
mild, average, and severe winter conditio
increasing proportions of the winter ran

comparable unburned sites, elk su
tion densities. When postfire wint
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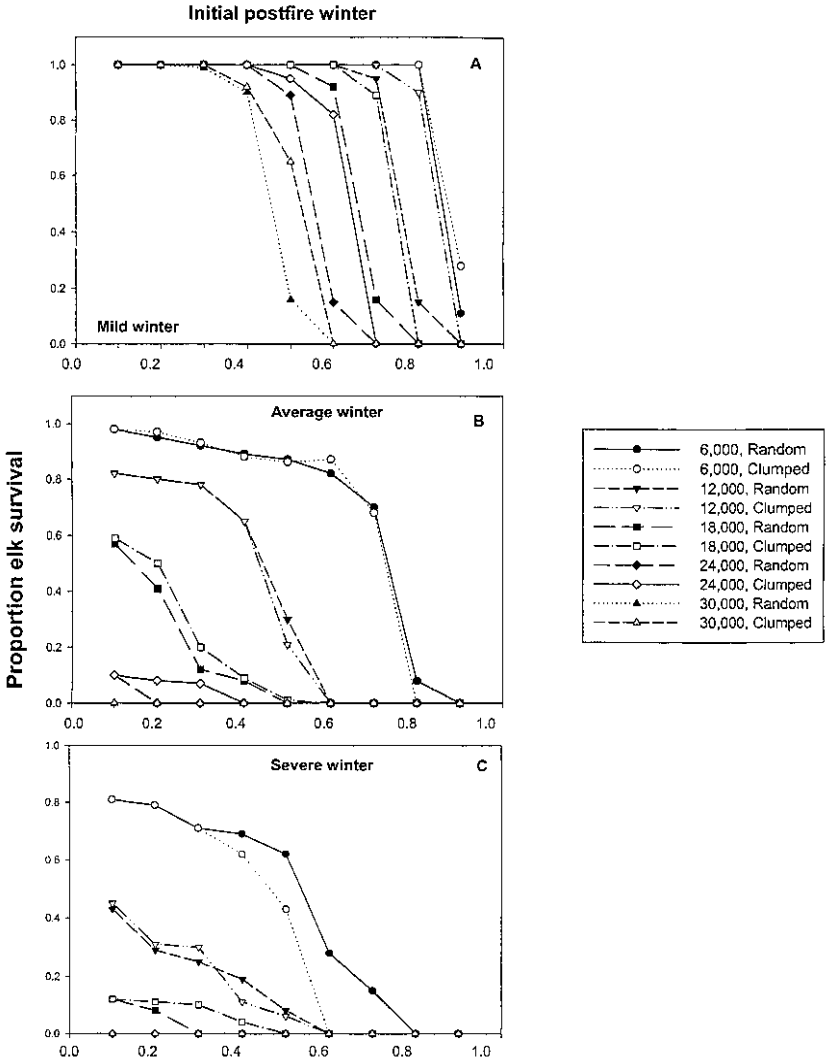


Figure 13.1. Elk survival in the initial postfire winter simulated by the NOYELP model with mild, average, and severe winter conditions under either random or clumped fire patterns with increasing proportions of the winter range landscape being burned indicated on the x-axis.

comparable unburned sites, elk survival was 100 percent at the lower population densities. When postfire winter conditions were average or severe, elk survival increased with fire size (Fig. 13.3). The increase in survival attributable to fire size (and forage enhancement) was most pronounced for the highest population sizes (for example, 24,000 and 30,000 elk and 800 or 1,000 bison during

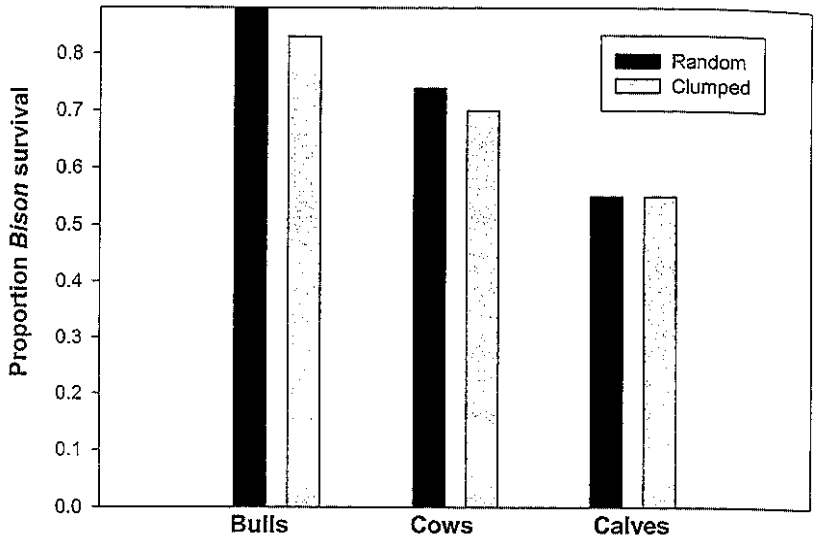
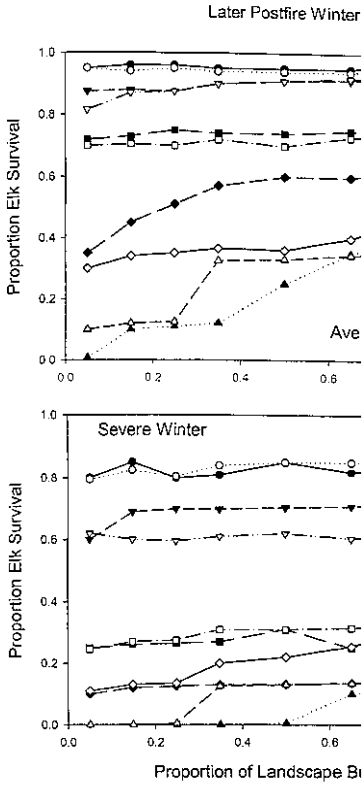


Figure 13.2. Bison survival in different fire patterns averaged over all winter conditions and years.

the average winter). Threshold effects with population sizes were not apparent during the later postfire winters, but there was substantial variation in survival associated with population density (Fig. 13.3). For bison, threshold effects were also minimized, but dramatic effects of winter severity were seen on survival, particularly for calves (Fig. 13.4).

WHAT THESE MODEL RESULTS MEAN FOR FIRE ECOLOGISTS AND LAND MANAGERS

There are substantial differences between the two models in terms of their structure and the objectives for constructing them. The NOYELP model was based on an elk and bison energetics, movement, and spatial variation in winter forage availability and was constructed primarily to investigate the relative importance of fire size and pattern in determining winter survival of ungulates on the northern range. The LCCM model looked at the carrying capacity of the environment (both nutrients and energy) across the entire summer and winter range. Its primary objective was to predict how the carrying capacity of the environment relative to elk changed over time and how quickly the system would return to prefire levels. Given that these models were developed in isolation from each other, it is important to note that both show that weather is the single most important factor governing elk survival in the Greater Yellowstone Ecosystem.



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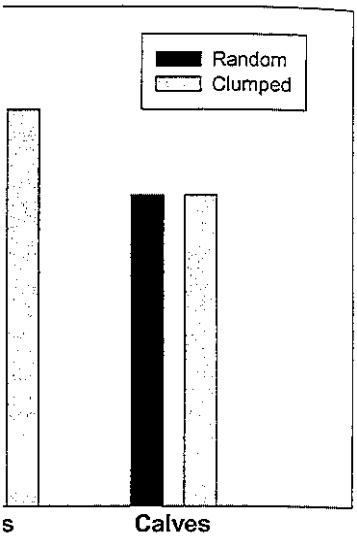

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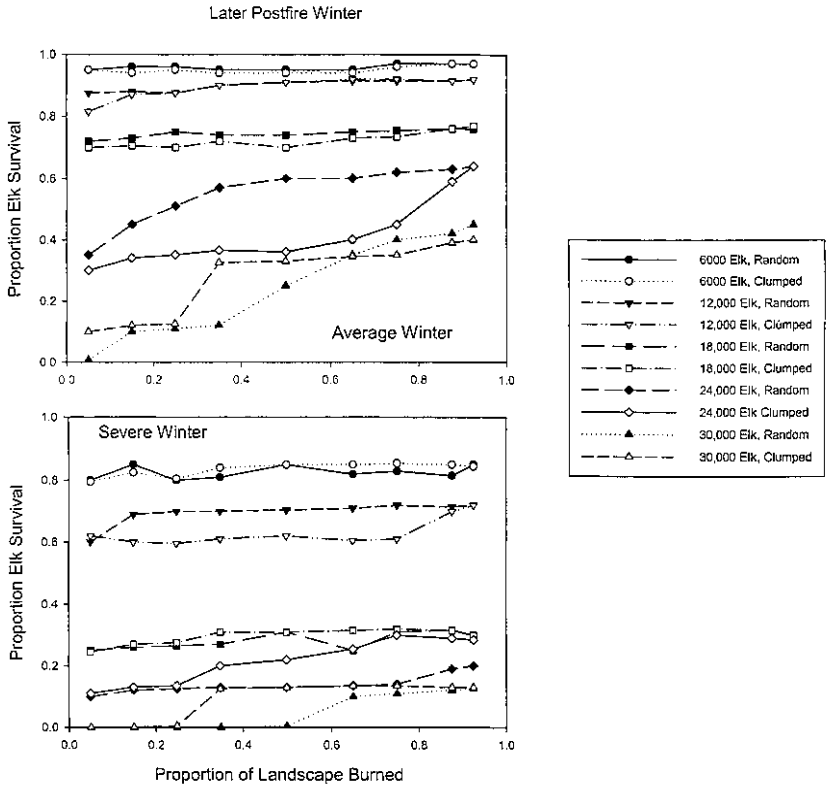

Figure 13.3. Elk survival in the second winter postfire simulated by the NOYELP model with average or severe winter conditions under either random or clumped fire patterns with increasing proportions of the winter range landscape being burned indicated on the x-axis.

Unfortunately, it is also the factor that is the least predictable and under the least control by land managers. Although the fires of 1988 were not under the control of land managers, a future prescribed burn would most likely have little, if any, effects on elk and bison survival in this landscape—unless it occurred under conditions of high ungulate populations and was followed by a severe winter (Coughenour and Singer 1996a, Turner and others 1994, Wallace and others 1994).

Fire patterns had no effects on ungulate survival when fire size was large in NOYELP simulations (Turner and others 1994) with no responses measured in the LCCM model. Fire pattern can be controlled in prescribed fires, which presumably would be much smaller than the large wildfires of 1988. When fire size is small to moderate, more ungulate survival is noted for clumped rather than

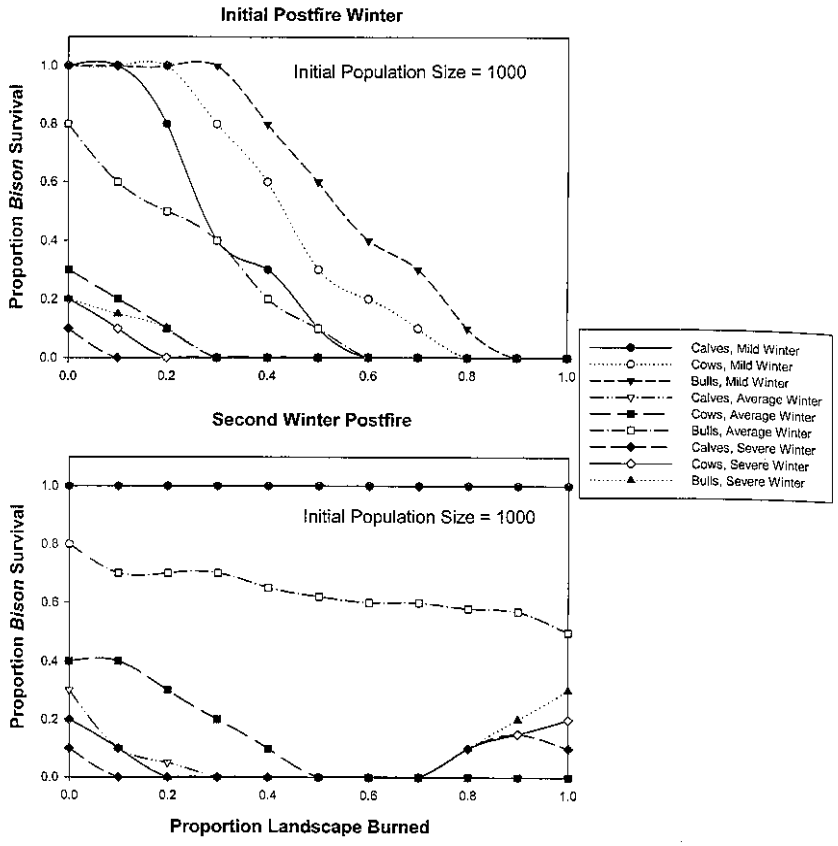

Figure 13.4. Bison survival in both the initial and second winter postfire. Initial population size for these analyses was 1000. Population responses to decreasing initial population size were similar to what was seen for elk.

dispersed fire patterns (Turner and others 1994). Thus managers may enhance survival the first winter postfire as well as subsequent winters by burning clumped rather than dispersed areas. This is more evident for elk than for bison (Wallace and others 1994).

The effects of weather can be readily seen in the LCCM model (Coughenour and Singer 1996a). Coughenour and Singer predicted elk population dynamics under a stochastic set of weather scenarios, by running the model with alternative stochastic weather patterns beginning in 1991 and going through the year 2011 using 1972–1991 weather data. Given the overwhelming importance of weather in determining elk and bison (Wallace and others 1994, Coughenour and Singer 1996a) survival in this ecosystem, it is not surprising that the pre-

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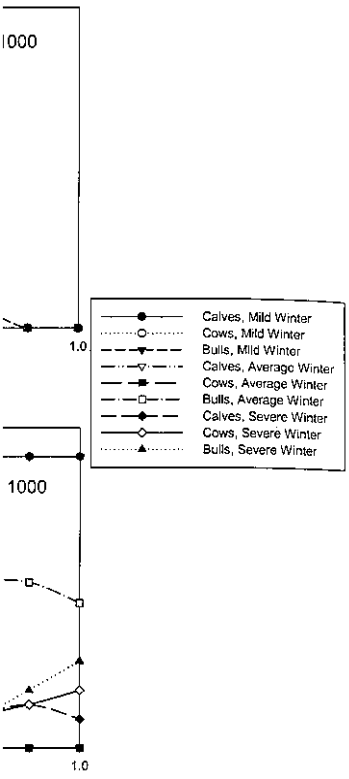

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dicted results of these stochastic runs are very different from the actual observed population sizes for the years 1991–2000. Another factor that cannot be predicted is the success of annual hunting efforts just outside of the park, which were also great during this time frame. When one compares the model results to the actual elk counts obtained by scientists in Yellowstone Park (Lemke and others 1998) for some of these years after the model was run, we see that the model estimates of carrying capacity are larger than observed elk numbers by 20,000 or more animals. However, in some other years, carrying capacity estimates are far below observed numbers of elk. It is important to point out that the LCCM is not predicting population dynamics; it is only predicting forage-based carrying capacity. During 1972–1991, another reason for the seeming discrepancy between model predictions and observed elk populations is that Yellowstone experienced a series of mild winters, a pattern that has not been seen since (Farnes and Hartman 1989, Chapter 10).

Additional simulations with the NOYELP model that explored the implications of spatial heterogeneity at different scales on winter survival of elk and bison demonstrated the critical role of habitat heterogeneity in determining forage availability (Turner and O'Neill 1995). Even though the total amount of forage available on the landscape remained constant in these simulations, removal of spatial variation in forage substantially reduced simulated elk survival. Thus the landscape-level distribution of areas with high and low forage biomass can enhance ungulate survival. Similarly, spatial heterogeneity in snow conditions—especially the maintenance of snow-free or low-snow areas—was demonstrated as being critical for winter ungulate survival. Thus managers should be attentive to maintaining the ecological processes responsible for producing and maintaining spatial heterogeneity in forage resources.

The effects of fire or winter weather on ungulate population size will be modified by the population size at the beginning of the winter. The proportion of animals that survive is density dependent, with survival being higher for lower population densities when conditions produce a reduction in the available forage. Migration out of the park may occur, however, and this was not explicitly simulated in either model.

When predicting ungulate survival in wild land ecosystems in the Northern Rocky Mountains, land managers need to realize that those factors over which they have the most control will be of the least help in their predictions. Weather is the most limiting factor to survival in this environment: summer weather strongly influences forage production, and winter weather largely controls forage availability. Therefore weather conditions will fundamentally determine

whether the environment can support elk and bison well. If it cannot, then those individual animals that find areas of low snow accumulation with adequate forage will survive. Animals elsewhere in the ecosystem will be at risk. Things that managers can control, such as hunting pressure outside protected reserves and prescribed fire within reserves, also may influence elk and bison populations—but the effects of these other controls are constrained by the overarching effects of weather.

In both models, the factor ultimately limiting ungulate survival was energy (Coughenour and Singer 1996a, Turner and others 1994). Why would this limitation yield the responses seen here, the overwhelming effects of climate on survival rather than the effects of fire? As discussed above, the spatial heterogeneity provided by the patch structure of fire may be crucial in forage availability, provided that the total proportion of the landscape burned is not too great (Turner and others 1994, Wallace and others 1994, Turner and O'Neill 1995). The effects of fire in reducing forage availability (energy) are much more localized than the effects of climate in reducing forage availability (energy). Thus it makes sense that both models found energy to be limiting to survival during the winter and that the effects of climate would supercede those of fire.

If land managers wish to predict what will occur in wild land systems in the face of global climate change, they need to consider several factors. The observed values of elk and bison population growth show that both species are capable of rapid population growth, if they experience a series of mild winters. Global change models (Bartlein and others 1997) indicate that conditions will vary across the park but that generally warmer, wetter winters and warmer summers will occur. No change in summer precipitation is called for, a condition that could lead to greater frequency and extent of summer fires. Even then, it would appear, given the results of these separate modeling exercises, that winter weather will be more critical to elk survival than would be the occurrence of fire in this system. However, the survival of elk and bison in this landscape will be difficult to predict if winters are warmer with deeper snows and there is a more widespread occurrence of low-elevation vegetation types (Romme and Turner 1991, Bartlein and others 1997).

Sala and others (2000) suggest that the single greatest factor affecting boreal systems (where Yellowstone Park is classified in their global classification system) will be changes in land use patterns. However, if the park continues to exist, this factor will be of less importance, making climate change the single greatest driver of biodiversity change in this system, followed by nitrogen deposition, biotic exchange and atmospheric CO_2. This assumes that tremendous exurban land-

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scape development does not occur in the areas immediately outside of the park. If such development does occur, then land use change will be a critical factor along with climate change. This corroborates the predictions of Bartlein and others (1997) and again points to how critical it is to understand the effects of weather on ungulate survival in this landscape.

Little work has analyzed how global change will affect fire cycles directly (see Chapter 3). However, if, as Bartlein and others (1997) suggest, we have greater landscape heterogeneity, we may expect the relative severity of fire to be greater when both mesic and xeric elements of the landscape are more juxtaposed (He and Mladenoff 1999). Ungulate survival may be more influenced by changes in plant community structure, phenology, winter weather, and possible changes in land use outside of the park than by changes in fire severity (Price and Waster 1998, Post and Stenseth 1999).

In summary, fire is a critical and recurring element in the ecology of the Greater Yellowstone Ecosystem. Large-scale fires have occurred in the past (Chapters 2, 3) and will probably occur again in the future despite efforts at human intervention (Christensen and others 1989, Pyne 2000). Concern over fires in this landscape will continue to be great as long as humans occupy it. However, in terms of ungulate survival, the scenario popularized by the Disney film *Bambi* is not completely valid. Fire is not the primary driver of ungulate survival. As the landscape is currently structured, weather is the single most important element driving ungulate survival. If landscape use changes as described by Sala and others (2000), then ungulate survival may become more closely tied to habitat loss as we have seen occur in numerous other boreal environments. If Yellowstone Park continues to exist with some buffer zone surrounding it, then the current and long-term variability of winter weather will remain the key to elk and bison survival in this extraordinary environment.

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