Elk Survival Following the 1988 Yellowstone Fires: A Simulation Experiment

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ABSTRACT: Extensive fires in 1988 burned 22% of the northern winter range in Yellowstone National Park, which provides critical winter habitat for one of the largest free-ranging herds of elk *(Cervus elaphus)* in North America. The winter of 1988–89 was moderately severe, and the combination of forage loss due to fire plus deep snows led to high elk mortality (-40%). We designed a simulation experiment to explore how elk mortality that winter might have been different under alternative weather conditions, spatial patterning of the burn, and initial elk numbers. The simulations were performed with the Northern Yellowstone Park model (NOYELP), a spatially explicit model of forage availability, snow conditions, elk movement and foraging, and elk energetics. Results supported earlier findings indicating that snow depth and water equivalent were major determinants of elk survival: in a mild winter scenario, there was almost no mortality even with forage loss from the fire, but when the most severe winter in recent history was simulated, calf mortality approached 100%. Under moderate to severe winter conditions, fire pattern and initial elk density also were important. Burning 22% of the northern range at random or in single large patches produced higher mortality than did the actual burn pattern. This study also showed that mortality increased nonlinearly as initial elk density increased, with thresholds in density at which mortality went up sharply. Modeling experiments of this kind can help managers of natural areas similar to Yellow-stone National Park anticipate the effects of future large-scale fires, and can provide insights into likely effects of management activities such as prescribed fire.

Index terms: elk, fire, Yellowstone National Park, spatially explicit population models, NOYELP

INTRODUCTION

The northern winter range in Yellowstone National Park (YNP) provides critical win-ter habitat for some of the largest free-ranging herds of elk, bison, and other ungulates in North America (Houston 1982). Management of these animals has long been controversial, in part because of uncertainty about the broad-scale interactions of fire, vegetation, and ungulate population dynamics in this area. The northern winter range burned at intervals of 20–25 years prior to European settlement of the region (Houston 1973), but no large f i ʳes occurred in the twentieth century until the extensive fires of 1988. In that year, fires affected 22% of the northern winter range, as well as other portions of the park (Despain et al. 1989), and created excellent opportunities to answer some fundamental questions about limiting factors on the winter range (Wallace and Knight 1989). In this paper, we examine the relative importance of fire pattern, winter weather, and initial ungulate densities in control-ling the behavior and survival of elk during the first winter after large fires such as the ones that occurred in 1988.

One important effect of fire is removal of forage from the burned areas. Thus, fire is expected to increase mortality of ungulates during the first postfire winter. The spatial pattern of burning may be as important as the total extent of burned area, since differ-ent portions of the northern winter range differ in forage production and other impor-tant parameters, and because animal forag-ing behavior may be influenced by the spa-tial distribution of resources (Westoby 1974, Owen-Smith and Novellie 1982, Senft et al. 1987, Turner et al. 1993, Wallace et al. 1995). In addition to fire effects, deep or dense snow conditions impair ungulate for-aging and travel. Historically, these snow conditions have produced high mortality in YNP even in the absence of fire, whereas light snow conditions usually have been associated with low mortality (Houston 1982). The initial population density of ungulates going into the winter also is expected to influence survival rates, especially in severe winters, because of competition for limited forage resources.

We used a modeling approach to identify the relative contributions of fire pattern, winter snow conditions, and initial ungulate densities to ungulate survival on the northern winter range of YNP following the fires of 1988. The development and validation of our model for Northern Yellowstone Park (NOYELP) are documented in detail in Turner et al. (1994). That paper reports on a factorial simulation experiment using NOYELP that explored the effects on ungulate survival of fire size, fire pattern, and winter severity. Initial ungulate densities were held constant, and fire size ranged from no fire to three times the size of the actual 1988 fires. The results showed that winter severity played a dominant role in survival of elk and bison. Under extremely mild winter conditions, there was little mortality in the first postfire winter even when 60% of the landscape was burned. Fire effects were important in average or severe winters, how-ever, with ungulate survival decreasing as area burned increased. Fire pattern also was important under average or severe winter conditions; ungulate mortality was substantially higher with a random pattern than with a clumped dispersion of burned sites (Turner et al. 1994).

In this paper we extend the results of Turner et al. (1994) by using the same model and database to address additional questions that were not asked in the original study. In particular, we examine the effects of varying (1) initial elk numbers, (2) the geographic location of a single burned patch representing the total acreage actually burned in 1988, and (3) the weather that occurred in the initial postfire winter using actual areas burned in 1988. Turner et al. (1994) held initial elk numbers constant in all simulation experiments, simulated a single large burned patch only at one location near the center of the winter range, and simulated alternative spatial patterns for the actual area burned in 1988 only under actual weather conditions that occurred that winter. Whereas the objective of Turner et al. (1994) was to examine the effects of a broad range of fire size, fire pattern, and winter weather on elk survival, the focus of the present paper is on the actual fire that occurred in 1988 and how its effects might have been different under different initial conditions. Some of those initial conditions could have been altered by management, for example, initial elk density and geographic location of burned patches (i.e., with a prescribed fire program instead of a natural fire). The actual winter of 1988–89 had moderately severe snow conditions, elk density was high at the outset (–18,000), and elk mortality was high (–40%) (Singer et al. 1989).

There has been much debate about management of the northern Yellowstone elk, and much speculation on how the population structure and dynamics would differ if there were changes in elk numbers, in the vegetation on the northern range, or in winter weather conditions (e.g., Beetle 1979, Houston 1982, Despain et al. 1986, Kay 1990). Most of these speculations cannot be tested empirically because of the complexity of the interactions among the various parameters and the impossibility of controlling weather or creating meaningful replication of treatments at such a broad scale. A modeling approach provides a way of varying the important parameters in a controlled fashion and of replicating treatments (Dunning et al. 1995, Turner et al. 1995). Be-cause large fires will undoubtedly occur in YNP again in the future, the results of this type of study may be useful to managers in anticipating the effects of large fires under different conditions than those that happened to occur after the fires in 1988. Additionally, by varying the size and spatial pattern of burned patches in our simulation experiments, we provide some insights into the effects that might be expected from introducing a prescribed fire program in the Yellowstone northern winter range. Al-though we focus specifically on YNP, our general results and conclusions may be applicable to many other important elk winter ranges in national parks, forests, and other lands in the Rocky Mountain region.

We dealt only with elk *(Cervus elaphus)* in this study, because they are the most numerous ungulates in YNP and are the species for which we had the best empirical data for building and testing our model. We tested four specific hypotheses.

1. Winter mortality in 1988–89 would have been high even if the fires had not occurred, because of the high elk density and severe snow conditions of that winter.
2. Winter mortality would have been high even if snow conditions had been more moderate, because of the loss of forage **in burned areas and the high elk density.**
3. Winter mortality would have been different, either higher or lower, if the fire **had** burned in a different pattern than actually occurred, that is, if the 22% of the winter range that burned had been distributed randomly or had been clumped in a particular geographic area.
4. Winter mortality would have been substantially lower if initial elk density had been lower, even with the fire and severe snow conditions.

STUDY AREA

Yellowstone National Park is located in the northwest corner of Wyoming and adjacent parts of Montana and Idaho. The northern winter range lies along the major river valleys in the northern portion of YNP (Figure 1). Elevations here are lower than in most of the rest of the park, and the climate is warmer and drier (Dirks and Martner 1982). Meagher (1973), Barmore (1980), Houston (1982), and Despain (1990) provide general descriptions of the physiography, soils, and vegetation of the northern winter range.

We identified six vegetation types in the northern range (vascular plant nomenclature follows Dorn 1992): (1) dry grass-lands, dominated by big sagebrush *(Artemisia* ***tridentata),*** **bluebunch** wheatgrass ***(Agropyron spicatum),*** **and Idaho fescue** *(Festuca* ***idahoensis);*** (2) mesic grasslands, with sagebrush, awned wheatgrass *(Agro****pyron caninum),*** **and bluebunch wheat-**grass; (3) moist grasslands, dominated by sagebrush, California brome *(Bromus car****inatus),*** **and sticky geranium *(Geranium viscossisum);*** (4) wet **grasslands, with** tufted **hairgrass *(Deschampsia*** *caespitosa),* sedges *(Carex spp.),* and reedgrass *(Calamagrostis* spp.); (5) aspen forests *(Pop****ulus tremuloides)*** **with variable herbaceous** understory composition; and (6) conifer **forests, dominated** by **Douglas-fir** *(Pseudotsuga menziesii)* and lodgepole pine *(Pinus contorta* var. *latifolia),* with variable understory composition of shrubs and herbs. Forage biomass at the onset of

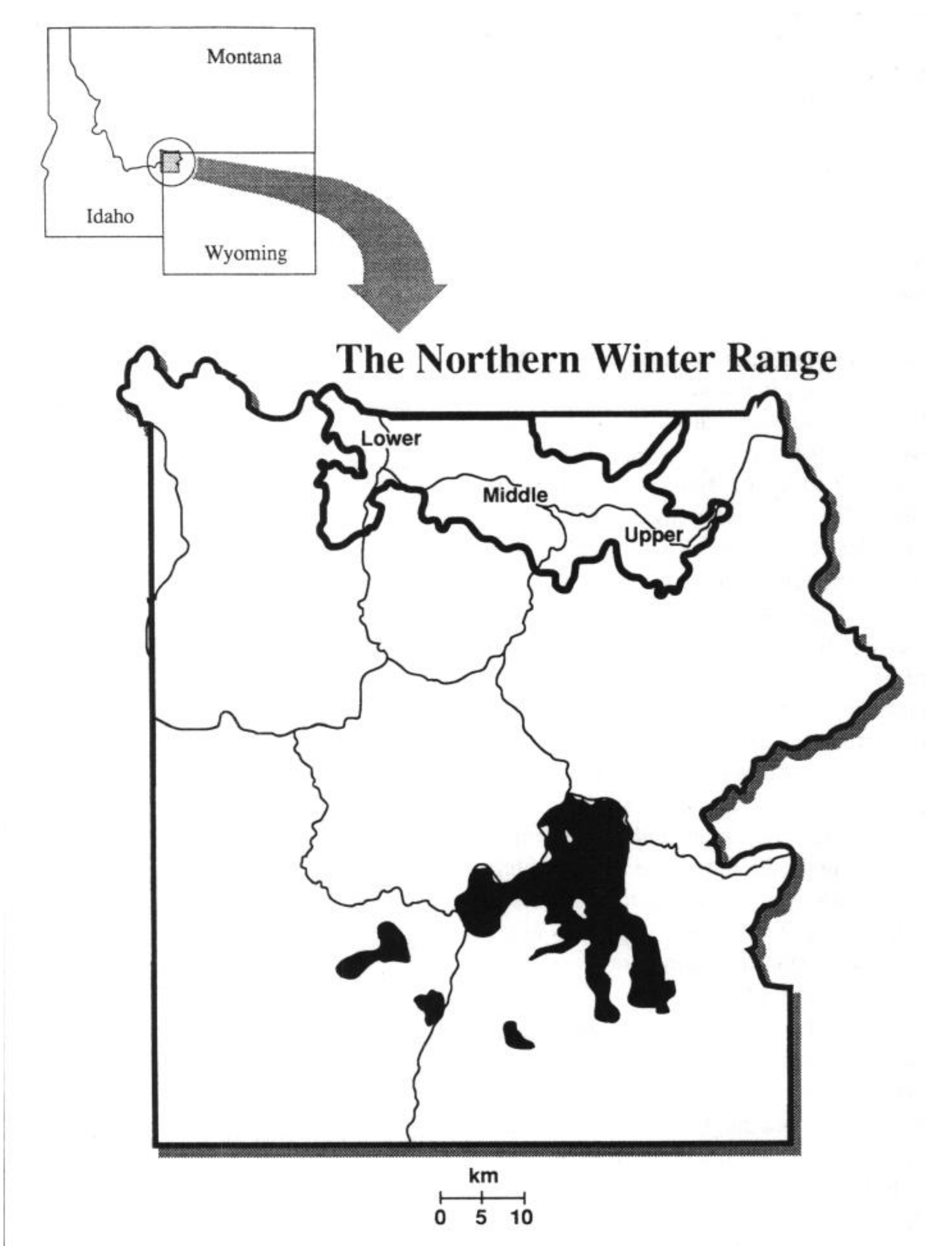

Figure 1. The northern winter range in Yellowstone National Park, and the locations of the upper, middle, and lower portions of the winter range.

winter in the grassland types increases along the moisture gradient from dry grass-lands (520 kg/ha) to mesic, moist, and wet grasslands (2260 kg/ha); see Despain (1990), Turner et al. (1994), and Wallace et al. (1995) for details. All of these vegetation types burned readily under the severe fire conditions of 1988.

The northern range can be subdivided into three relatively distinct portions on the basis of winter snow conditions, vegetation, and ungulate distribution throughout the win-ter (Figure 1). The upper winter range lies in the eastern portion and is relatively mesic. Extensive wet and moist grasslands provide excellent forage, but the area of-ten becomes inaccessible to ungulates in late winter because of deep snow. The lower winter range, in the western portion, is more xeric. Ungulates often accumulate here in late winter, when snow conditions become severe in the upper range, and forage in extensive dry and mesic grass-lands. The middle winter range lies between the other two and is characterized by intermediate snow and forage conditions (Meagher 1973, Barmore 1980, Houston 1982).

METHODS

NOYELP is a spatially explicit, individu-al-based model that simulates the search, movement, and foraging activities of elk and bison in the 77,020-ha northern winter range of YNP (see Turner et al. 1994 for details of model structure and validation). The model is initialized with forage dis-tributed among the various vegetation types described above and animals distributed across the landscape in their actual pat-terns of early winter. The actual spatial distribution of vegetation types and topo-graphic features are built into the model by use of the park's geographic information system (GRASS). Over the course of a 180-day winter, the model simulates snow depth, density, and forage availability at a resolution of 1 ha and monitors energy gains, losses, and movement by each small group of ungulates. Animals die when they lose 70% of their initial fat and 30% of initial lean body weight. Initial values for forage, ungulate distribution, and the snow simulation were derived from field data collected in YNP; values for calculations of animal energetics were obtained from the literature (Turner et al. 1994).

When the model was run using actual val-ues for snow conditions, initial ungulate densities, and burn patterns from three different recent winters in YNP, the simu-lated survival of elk and bison was very close to observed survival in each year (see Turner et al. 1994 for details of model validation and sensitivity analysis). For example, one of the simulated years was 1988-89, in which simulated elk mortality was 40% and observed mortality was 38-43%. (Actual mortality estimates were based on aerial and ground-based census-es conducted in YNP by an interagency team each year; see Houston 1982 and Singer et al. 1989 for details of methodology and reliability of elk density and mortality estimates.) We therefore felt confident about using the model for further experiments designed to explore alternative scenarios that could occur in YNP.

For the present study, we simulated 31 combinations of winter conditions, initial elk densities, and fire patterns (Table 1). Be-cause the model is stochastic, we ran each simulation three times and calculated mean survival of elk cows, calves, and bulls. One of the simulations depicted the actual situation in the winter of 1988-89, that is, actual number of animals, burn pattern, and snow conditions. The other simulations all represented hypothetical but possible scenarios for the northern range following a fire of the size that occurred in 1988.

We examined a range of winter snow conditions as follows (Figure 2). First we simulated actual snow depths and densities recorded for the most severe winter (1975-76) and for the mildest winter (1976-77) experienced in northern YNP in the last half-century (Diaz 1979). Win-ter severity was defined in terms of snow depth and snow water equivalent. We also simulated snow conditions in the winter of 1988-89, and in the winter of 1972-73. This latter winter had total snow accumulations comparable to those of 1988-89, but more of the snow came in late winter in 1972-73 and persisted longer than in 1988-89. Finally, we calculated mean monthly snow depth and water equivalent over all winters for which data were avail-able and called this an "average" winter.

We varied initial elk numbers from 6,000 to 30,000, and did simulations with the actual number in 1988-89 (19,270 elk). Actual numbers of elk wintering in northern YNP increased from ca. 3200 in 1968 to ca. 20,000 throughout the 1980s, in response to elimination of artificial elk reductions beginning in 1969 and a series of mild winters in the 1980s (Houston 1982, Singer 1989). We simulated the actual burn pattern in 1988, as well as the same total area distributed either randomly across the winter range or in a single patch located in the upper range, middle range, or lower range (Figure 3). We also simulated a no-fire scenario. We tested for significant differences in elk survival between simulations by use of ANOVA (SAS Institute 1990).

RESULTS

Effects of the 1988 Fires

A comparison of mortality rates in 1988-89, using actual elk numbers and winter conditions but with and without the fires, shows that calf mortality was about a third lower without the fires (Figure 4). However, there was no significant difference ($P<0.05$) in mortality of cows or bulls between the burn and no-burn simulations (Figure 4). For all age and sex classes combined, mortality was significantly higher in the burn scenario, but the difference was small: 39% with the fire and *32%* without (Figure 4). Thus, the 1988 fires caused a 7% increase in overall elk mortality compared to the expected mortality in the absence of fire, with most of the increased mortality occurring in calves.

Effects of Winter Conditions Following the 1988 Fires

The simulations using the actual burn pat-tern and elk numbers in 1988-89 under a range of snow conditions showed that mortality was substantially different under different winter weather conditions (Table 2). Under extremely mild conditions, there was no mortality even though the fires had

Table 1. Simulation experiments for the northern winter range In Yellowstone National Park, listing winter conditions, initial elk number, fire location, and fire pattern used as Input in the scenarios.

Experiment	Winter	**Elk No.**	**Fire Location**	**Pattern**
1988 Fires	1988-89	19,270	1988	1988
No Fires	1988-89	19,270	No Fires	No Fires
Mild Winter	1976-77	19,270	1988	1988
Average Winter	Average	19,270	1988	1988
Severe Winter	1975-76	19,270	1988	1988
Even Winter	1972-73	19,270	1988	1988
Random I	1988-89	19,270	Random	Random
Random II	Average	19,270	Random	Random
Random III	1975-76	9,270	Random	Random
Upper I	1988-89	19,270	Upper Range	One Patch
Upper II	Average	19,270	Upper Range	One Patch
Upper III	1975-76	19,270	Upper Range	One Patch
Middle I	1988-89	19,270	Middle Range	One Patch
Middle II	Average	19,270	Middle Range	One Patch
Middle III	1975-76	19,270	Middle Range	One Patch
Lower I	1988-89	19,270	Lower Range	One Patch
Lower II	Average	19,270	Lower Range	One Patch
Lower III	1975-76	19,270	Lower Range	One Patch
Elk 6K	1988-89	6,000	1988	1988
Elk 8K	1988-89	8,000	1988	1988
Elk 10K	1988-89	10,000	1988	1988
Elk 12K	1988-89	12,000	1988	1988
Elk 14K	1988-89	14,000	1988	1988
Elk 16K	1988-89	16,000	1988	1988
Elk 18K	1988-89	18,000	1988	1988
Elk 20K	1988-89	20,000	1988	1988
Elk 22K	1988-89	22,000	1988	1988
Elk 24K	1988-89	24,000	1988	1988
Elk 26K	1988-89	26,000	1988	1988
Elk 28K	1988-89	28,000	1988	1988
Elk 30K	1988-89	30,000	1988	1988

removed forage from 22% of the winter range. In contrast, 100% of the calves died under the severe winter scenario, as did 85% of cows and 80% of bulls (Table 2). Mortality in all groups under actual 1988–89 conditions was lower than for any of the other simulations except the extremely mild winter. In all of the scenar-ios except the mild winter, mortality was substantially higher in calves than in adults, and differences between cows and bulls were small (Table 2).

Effects of Fire Pattern and Location

When the 22% of the winter range that burned in 1988 was distributed randomly or in a single patch, rather than in the actual burn pattern, elk mortality was sub-stantially higher than actually occurred (Table 3). The highest mortality was seen with a single burned patch in the lower winter range (Figure 3, Table 3). Mortality with any of the burn patterns was higher in the "average" winter than in the actual winter of 1988–89, and was highest in the severe winter when no elk survived with any of the random or single patch patterns.

With the extremely mild winter there was negligible mortality under any burning pattern. ANOVA on mortality produced by all of the simulations that varied fire pat-tern and winter severity revealed the strong interaction between these two variables (Table 3).

Effects of Initial Elk Density

Simulations of actual 1988–89 burn pat-terns and winter conditions showed that mortality rates in all age and sex classes increased with increasing initial elk density (Figure 5), as would be expected. Inter-estingly, however, there appear to be thresh-olds at which mortality rates increase sharply. The threshold for calf mortality occurred at around 17,000 total elk, for cows at around 23,000, and for bulls at about 25,000 animals (Figure 5). For all age and sex classes combined the thresh-old was around 23,000 elk. Calf mortality was higher than adult mortality at all densities except the maximum of 30,000 animals, at which point mortality reached 100% for all age classes.

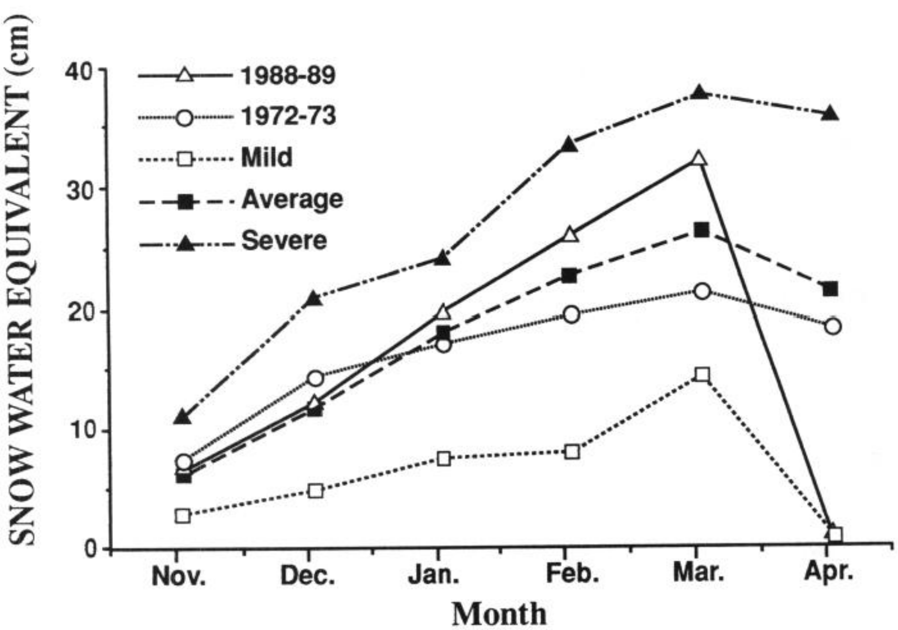

Figure 2. Monthly snow conditions in the five winters that were simulated in this study. The winters of 1988-89 and 1972-73 both had moderate total amounts of snow, but the temporal distribution of the snow differed (see text). The winters of 1976-77 and 1975-76 were the mildest and most severe on record, respectively, and were simulated to represent "mild" and "severe" winters in this study. The "average" winter represents the arithmetic average of monthly snow water equivalent on the northern range from 1938 to 1991 (Diaz 1979).

The number of elk surviving winter in-creased with increasing initial population, until initial density reached 17,000, and remained relatively constant through initial densities up to 23,000 (Figure 6). As initial density increased beyond that level, number of survivors fell precipitously (Figure 6). The various age and sex classes showed similar patterns, except that the number of surviving calves began to drop at lower initial densities (around 17,000).

DISCUSSION

The simulation experiments reported here and in Turner et al. (1994) allow us to evaluate the relative contributions of weath-er, fire pattern, and initial animal numbers in determining elk winter survival in north-ern YNP. Results of both studies show clearly that winter snow conditions are a powerful controlling variable, and this is borne out by field studies as well (e.g., Meagher 1973, Barmore 1980, Houston 1982). If snow conditions are extremely mild, then fire—even extensive fire—has little effect on elk survival rates. Had the winter of 1988–89 been unusually mild rather than normal, we would not have seen the abundant carcasses that were so conspicuous the following spring. Thus, we reject our second hypothesis that mortality in 1988–89 would have been high even if the winter had been mild. However, if snow conditions are severe, then mortality will be high—regardless of the occurrence or pattern of burning. Thus, we conclude that our first hypothesis is correct: many elk would have died in 1988–89 even if the northern range had not burned, because the moderately severe snow conditions of that winter reduced forage avail-ability and increased the energetic costs of travel over a large portion of the winter range. What if the winter range had burned in 1988 as it did, but then the next winter had brought even more severe snow conditions, e.g., like those in the extremely severe winter of 1975/76? Our simulations indicate that almost no calves would have survived such a combination of fire and harsh winter, and even adult survival would have been extremely low (Table 2).

The spatial pattern and location of burned areas had significant effects on elk survival,

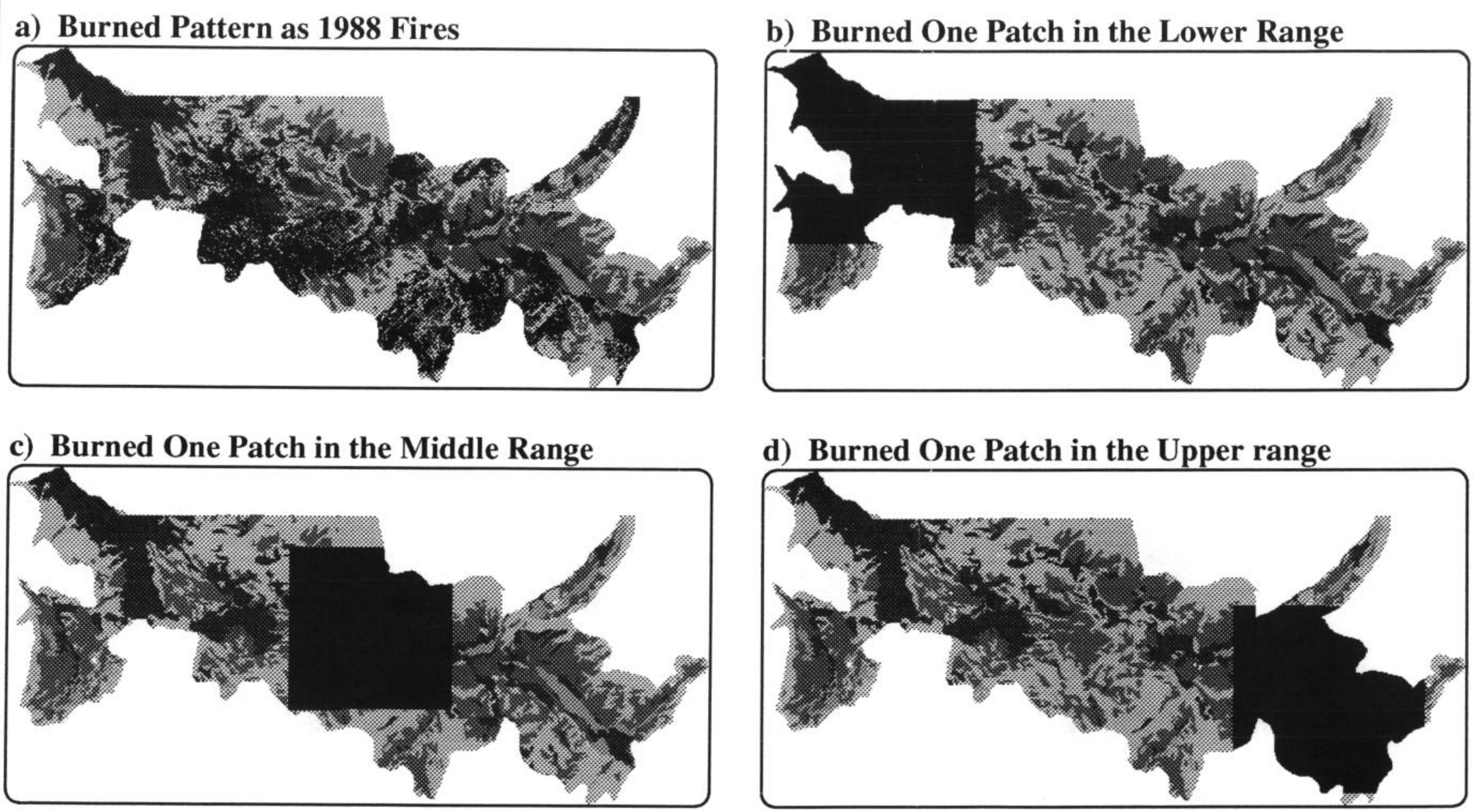

Figure 3. Simulated burn patterns on the northern winter range of Yellowstone National Park: (a) the actual burn pattern produced by the fires in 1988, and (b-d) hypothetical single patches in the lower, middle, and upper winter range that each burned the same number of hectares as actually burned in 1988 (-17,000 ha or 22% of the winter range). Black patches indicate burned areas; greys are various vegetation types.

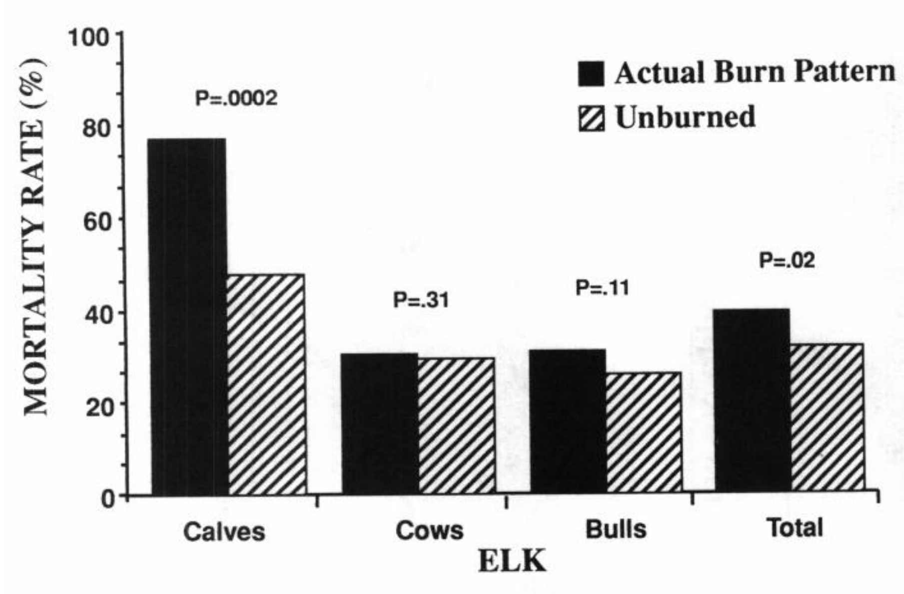

Figure 4. Simulated mortality rates of elk calves, cows, bulls, and all age/sex classes combined, with the actual burn pattern, Initial elk densities, and winter conditions of 1988-89, and with the actual winter conditions and initial densities but without the fire.

Table 2. Results of a one-way ANOVA and Tukey's Studentized Range test for the elk mortality rates under alternative winter severities, simulation experiments, northern winter range, Yellow-stone National Park.

Winter	N	Mean	SE	TG'	$F_{(4,14)}$	Pro>F
All **Elk**					42.21	0.0001
1988—89	3	0.393	0.0142	A		
1972—73	3	0.539	0.0142	B		
Mild	3	0.000	0.0000	C		
Average	3	0.620	0.0518	B		
Severe	3	0.865	0.0226	D		
Calves					412.98	0.0001
1988—89	3	0.762	0.0127	A		
1972—73	3	0.947	0.0372	B		
Mild	3	0.000	0.0000	C		
Average	3	0.937	0.0237	B		
Severe	3	1.000	0.0000	D		
Cows					71.15	0.0001
1988—89	3	0.308	0.0029	A		
1972—73	3	0.496	0.0278	B		
Mild	3	0.000	0.0000	C		
Average	3	0.598	0.0706	B		
Severe	3	0.852	0.0376	D		
Bulls					212.76	0.0001
1988—89	3	0.309	0.0061	A		
1972—73	3	0.343	0.0131	A C		
Mild	3	0.000	0.0000	B		
Average	3	0.429	0.0403	C		
Severe	3	0.797	0.0092	D		

[a] TG = **Tukey grouping; there are no significant differences in means with the same letter.**

as predicted by **hypothesis** 3. Interestingly, the actual burn pattern in 1988 resulted in lower mortality than was observed in any of the four alternative patterns that we simu-lated (Table 3). There also was an important interaction between burn pattern, geographic location of burned patches, and winter se-verity. In all three weather scenarios, highest elk mortality was seen when the fire burned a single patch in either the upper or lower winter range. This is because the upper range contains most of the high-forage wet grasslands, and the lower range contains most of the forage that remains available to elk under the deep snow conditions of late winter; loss of either of these important forage resources leads to higher mortality. The random burn pattern also increased mor-tality compared to the actual burn pattern because with random elimination of forage, animals must travel farther and expend more energy to find resources (Turner et al. 1993, 1994). It is apparent, then, that the total area burned is only one determinant of elk sur-vival in the following winter: the geograph-ic location of the burn, the pattern of the burn, and the winter snow conditions also have powerful effects.

The simulations also supported hypothesis 4. Mortality rates increased as initial elk density increased, but the trends were not linear (Figure 5). There appear to be thresh-olds in elk density beyond which survival decreases sharply because of competition for forage (Figure 6). The threshold for high calf mortality is lower than that for adults, a result of the lower initial energy reserves of the smaller calves. Figures 5 and 6 show where these thresholds occurred for the burn pattern produced in 1988 and the weather conditions of 1988—89. The actual number of elk at the beginning of the 1988—89 winter was ca. 19,000, above the threshold for calves but below the thresholds for adults. Figure 6 suggests that if initial elk numbers had been greater than 23,000, the number of surviving elk at the end of the winter would have been substantially lower than it actually was with 19,000 animals. The elk density in 1988 apparently was within a range (ca. 17,000–23,000) that would result in maximum numbers of survivors (though not maximum survival rates) under the fire and weather conditions that occurred in

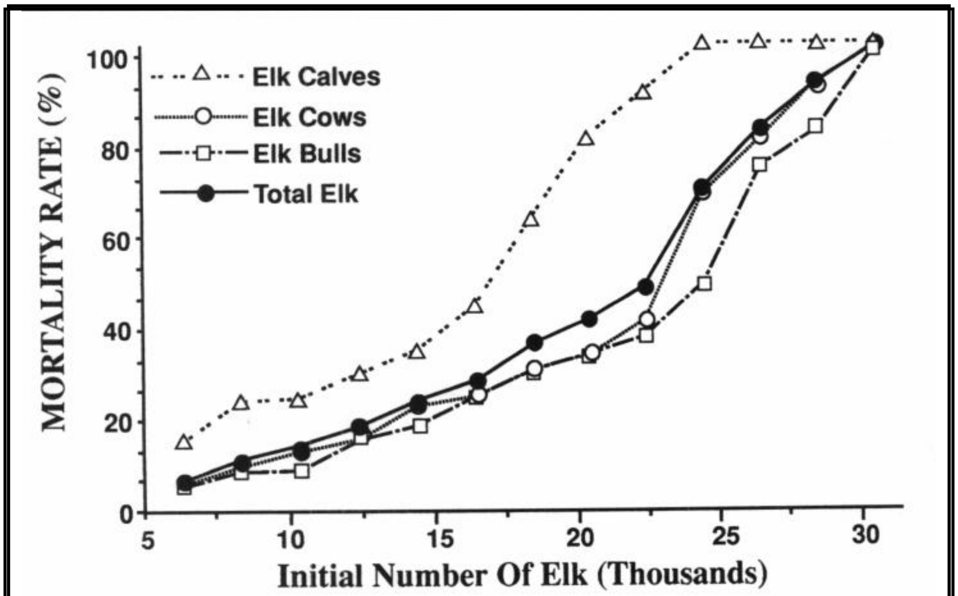

Figure 5. Simulated mortality rates of elk calves, cows, bulls, and all age/sex classes combined, under actual fire and winter conditions of 1988-89, and as a function of initial total elk density.

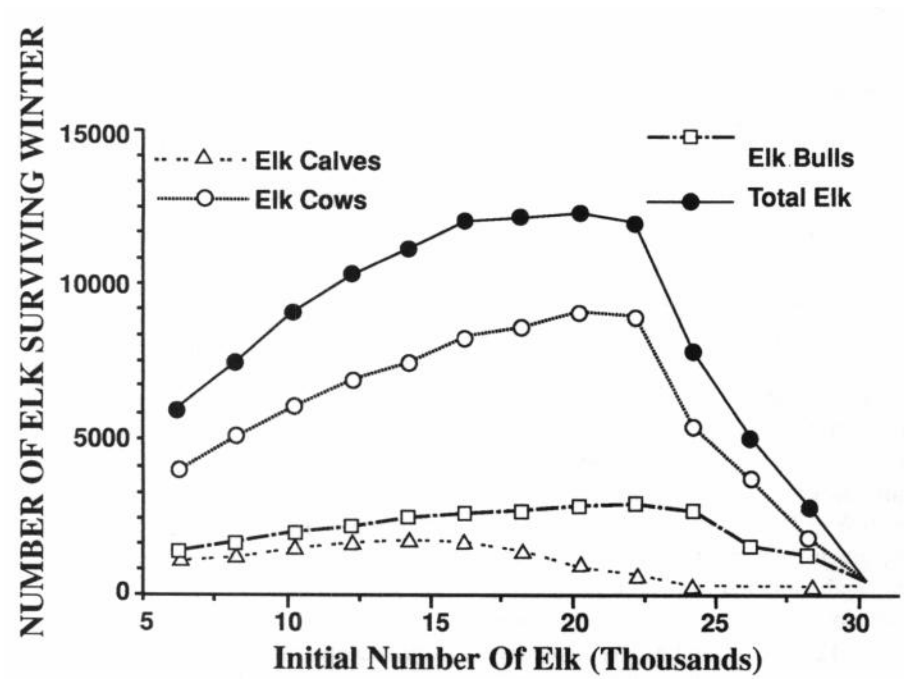

Figure 6. Simulated numbers of elk calves, cows, bulls, and all age/sex classes combined at the end of winter, under actual fire and winter conditions of 1988-89, as a function of initial total elk density.

that year (Figure 6). In other winters or with other burn patterns, the survival thresholds would likely occur at different initial densities. Because so many combinations of fire size, pattern, and winter weather are possible, the particular thresh-olds identified in these figures are not especially significant. What is important is to recognize that responses to the driving abiotic variables of fire and weather may be interactive and nonlinear: hence we must be cautious in making predictions about what will happen in any particular situation.

A patently unrealistic feature of our NOYELP model is that it restricts the animals to the 77,000-ha portion of the north-ern range that lies within the borders of YNP. In the model, animals either find sufficient forage within the park or they die. In reality, large numbers of elk and bison may migrate out of YNP onto other public and private lands, especially in severe winters when the forage of the upper winter range in YNP becomes buried by snow. Consequently, actual mortality rates under severe snow conditions may be less than predicted by the model; instead of dying, the animals exit the park. Once they leave the park they may be subjected to human hunting, however, so the dynamics of the entire northern elk herd are complex. We did not have an adequate geographic database to simulate elk foraging and survival outside the park in this study. Nevertheless, our simulations do reveal some of the limits imposed by the interactions of fire pattern, snow conditions, and initial elk numbers within that portion of winter habitat that lies inside YNP. Ironically, the single most important determinant of elk winter survival appears to be the weather, over which managers have no control. Those factors that can be con-trolled to some degree—fire pattern and initial elk numbers—are important, but their effects interact with the effects of winter weather conditions and may be completely overshadowed by the influence of snow depth and snow water equivalent.

In what ways does a modeling exercise of this kind aid managers of a natural area such as YNP? One could argue that the importance of winter weather in determining elk survival is obvious even without elaborate simulation experiments. However, the simulations also revealed more subtle patterns that were not so apparent, al-though they made sense once the modeling experiments were conducted. Some of these patterns may have important management implications. For example, our results suggest that a prescribed fire program that produced numerous, randomly dispersed, small burned patches would likely lead to greater elk mortality if it were followed by a severe winter, than would a program producing a single large burned patch of the same total acreage—unless,

Table 3. Effects of simulated fire patterns and locations on elk mortality in the northern winter range of Yellowstone National Park using one-way ANOVA and Tukey's Studentized Range test.

Winter	Fire	N	Mean	SE	TG[a]	$F_{(414)}$	Pro>F
1988–89						24.65	0.0001
	1988	3	0.393	0.0142	A		
	Random	3	0.472	0.0038	B		
	Middle	3	0.487	0.0122	B D		
	Upper	3	0.534	0.0210	C D		
	Lower	3	0.562	0.0127	C		
Average						33.80	0.0001
	1988	3	0.620	0.0518	A		
	Random	3	0.799	0.0082	B		
	Middle	3	0.740	0.0035	B		
	Upper	3	0.756	0.0050	B		
	Lower	3	0.998	0.0015	C		
Severe						35.56	0.0001
	1988	3	0.865	0.0226	A		
	Random	3	1.000	0.0003	B		
	Middle	3	1.000	0.0000	B		
	Upper	3	1.000	0.0003	B		
	Lower	3	1.000	0.0000	B		

"TG = **Tukey grouping; there are no** significant differences **in means with the same letter.**

of course, the single large patch was in a critical geographic location such as the limited lower elevation area that remains snow-free during a severe winter. Another example of nonintuitive results is the thresholds in density effects that were demonstrated in this study (Figures 5 and 6): anyone familiar with YNP would expect increased mortality in a severe winter with increased initial numbers of animals, but the nonlinear responses to initial elk density are not so obvious and could lead to otherwise unexpectedly high mortality under conditions of high density and severe winter weather.

There is growing interest among ecologists and managers in spatially explicit population models, of which NOYELP is an example (e.g., Dunning et al. 1995, Turner et al. 1995). These models have great potential both to enhance our under-standing of the basic ecological processes that operate in natural areas and to fore-cast the specific consequences of alternative management decisions (Conroy et al. 1995). The models must be used appropriately, with due attention to issues of spatial extent, resolution, structure, and sensitivity analysis of the model, as well as accuracy and suitability of the data used to parameterize and validate the model (Conroy et al. 1995, Turner et al. 1995). It is impractical to develop a complex model like NOYELP for every individual natural area, given costs of databases, programming, and computer time, but the general conclusions of this study and of Turner et al. (1994) probably can be extrapolated to other natural areas and public lands in the western United States where ungulate win-ter range is a key issue. Alternatively, the basic NOYELP model could be readily adapted to accommodate new spatially explicit databases or new values for model parameters that would represent unique conditions in other natural areas that are otherwise ecologically similar to northern YNR

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