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Author(s): Monica G. Turner, Yegang Wu, Linda L. Wallace, William H. Romme, Antoinette Brenkert
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SIMULATING WINTER INTERACTIONS AMONG UNGULATES, VEGETATION, AND FIRE IN NORTHERN YELLOWSTONE PARK[1]

MONICA G. TURNER AND YEGANG WU
Environmental Sciences Division, Oak Ridge National Laboratory, P. O. Box 2008, Oak Ridge, Tennessee 37831-6038 USA

LINDA L. WALLACE
Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma 72019 USA

WILLIAM H. ROMME
Biology Department, Fort Lewis College, Durango, Colorado 81301 USA

ANTOINETTE BRENKERT
Environmental Sciences Division, Oak Ridge National Laboratory, P. O. Box 2008, Oak Ridge, Tennessee 37831-6038 USA

Abstract. The interaction of large-scale fire, vegetation, and ungulates is an important management issue in Yellowstone National Park. A spatially explicit individual-based simulation model was developed to explore the effects of fire scale and pattern on the winter foraging dynamics and survival of free-ranging elk (*Cervus elaphus*) and bison (*Bison bison*) in northern Yellowstone National Park. The Northern Yellowstone Park (NOYELP) model simulates the search, movement, and foraging activities of individuals or small groups of elk and bison. The 77 020-ha landscape is represented as a gridded irregular polygon with a spatial resolution of 1 ha. Forage intake is a function of an animal's initial body mass, the absolute amount of forage available on a site, and the depth and density of snow. When the energy expenditures of an animal exceed the energy gained during a day, the animal's endogenous reserves are reduced to offset the deficits. Simulations are conducted with a 1-d time step for a duration of 180 d, ≈1 November through the end of April. Simulated elk survival for three winters (1987–1988; 1988–1989; 1990–1991) agreed with observed data.

A factorial simulation experiment was conducted to explore the effects on ungulate survival of fire size, fire pattern, and winter severity during an initial postfire winter (when no forage is available in burned areas) and a later postfire winter (when forage is enhanced in burned areas). Initial ungulate population sizes were held constant at 18 000 elk and 600 bison. Winter severity played a dominant role in ungulate survival. When winter conditions were extremely mild, even fires that affected 60% of the landscape had no effect on ungulate survival during the initial postfire winter. The effects of fire on ungulate survival become important when winter conditions were average to severe, and effects were apparent in both the initial and later postfire winters. The spatial patterning of fire influenced ungulate survival if fires covered small to moderate proportions of the landscape (e.g., 15% or 30%) and if winter snow conditions were moderate to severe. Ungulate survival was higher with a clumped than with a fragmented fire pattern, suggesting that a single, large fire is not equivalent to a group of smaller disconnected fires. The interaction between fire scale and spatial pattern suggests that knowledge of fire size alone is not always sufficient to predict ungulate survival.

Key words: *bison;* Bison bison; Cervus elaphus; *elk; fire; landscape ecology; simulation modeling; snow; spatial scale or pattern; ungulates; winter severity; Yellowstone National Park.*

INTRODUCTION

Native ungulate populations may be strongly influenced by spatial and temporal heterogeneity at the landscape scale (Houston 1982, McNaughton 1985, Senft et al. 1987, McNaughton et al. 1988). Understanding the relationship between environmental heterogeneity and organism function remains a high priority for ecology (Lubchenco et al. 1991), but it often is simply not possible to manipulate the environment at the appropriate scales (Turner et al. 1989). For example, it is likely that the effect of large-scale fire on ungulates depends on winter conditions and ungulate densities, but a factorial experiment in which these factors are varied systematically across a landscape is logistically impossible. Natural events (e.g., fires, storms, droughts, land use changes) offer valuable insight into ungulate responses to broad-scale distur-

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bances, but even natural experiments often do not encompass a wide range of conditions. Consequently, models linking the responses of ungulates to environmental heterogeneity are needed.

The interaction of large-scale fire with the large assemblage of native ungulates and vegetation dynamics in the landscape is an important management issue in Yellowstone National Park (YNP), and the 1988 fires in YNP provide a unique opportunity to study this interaction. These fires were unusual in both their scale and heterogeneity (Christensen et al. 1989), and although fires of this magnitude may occur in YNP only every 100–300 yr (Romme and Despain 1989), some ecological effects will persist for centuries (Christensen et al. 1989, Knight and Wallace 1989, Minshall et al. 1989). Along with affecting the extensive coniferous forests, the 1988 fires also burned in the lower elevation sagebrush-grasslands, which are important winter range for the native ungulate populations. Previous research has not explicitly addressed the ecological implications for native ungulates of large, infrequent fires, such as occurred in 1988, compared with smaller, more frequent fires. Of particular interest is an understanding of the relative importance of fire as compared to other factors that might limit the ungulate population in Yellowstone.

This paper describes a spatially explicit individual-based simulation model developed to explore the effects of fire scale and pattern on the winter foraging dynamics and survival of free-ranging elk (*Cervus elaphus*) and bison (*Bison bison*) in northern Yellowstone Park. Our objectives were to (1) quantify the specific effects of fire size and pattern on ungulate dynamics; and (2) delimit the conditions under which fire size and heterogeneity are important—that is, identify when other environmental constraints (such as winter snow conditions) may overshadow the effects of spatial pattern. The model is used to project ungulate survival on the winter range under different fire regimes and winter weather scenarios.

We focus on elk and bison because these are the most numerous ungulates in the area (Houston 1982), and we have chosen to examine winter foraging for several reasons. Winter range conditions are the primary determinant of ungulate survival and reproduction in Yellowstone, and winter utilization of the vegetation by ungulates appears to be intense in some areas. Ungulates make distinct foraging choices in the winter as in the rest of the year, and burn patterns may influence those choices. In addition, the activities of animals can be readily monitored in the winter.

The responses of wintering ungulate populations to fire is complicated by temporal changes in fire effects. Initially, fire consumes plant biomass and reduces forage supply for ungulates. This loss of forage, which may be accompanied by reduced forage production in unburned areas because drought conditions usually accompany a large fire, can lead to substantial ungulate mortality during the first winter after the fire, as occurred during 1988 (Singer et al. 1989). In subsequent years, however, fire may stimulate primary productivity, resulting in improved forage quantity and palatability (Harniss and Murray 1973, Gruell 1980, Hobbs and Spowart 1984, West and Hassan 1985, Coppock and Detling 1986). Boyce and Merrill (1991) hypothesized that the fire-enhanced forage base should enhance recruitment and population size for several years following the 1988 fires, but the extent to which the ungulates would use burned areas was not known. We distinguish between these two different effects of fire in our simulations, and will refer to these as the "initial postfire" and "later postfire" winters.

Study Area

Yellowstone National Park (YNP) was established in 1872 and encompasses 9000 km^2 in the northwest corner of Wyoming and adjacent parts of Montana and Idaho. Elevations in the Park range from 1500 to >3000 m, and much of the area is covered by Quaternary volcanic deposits that underwent at least three extensive glaciations (Houston 1982). General descriptions can be found for park geology (Keefer 1972), and for physiography, soils, and vegetation (Meagher 1973, Barmore 1980,[2] Houston 1982, Despain 1991). The climate of YNP is characterized by long, cold winters and short, cool summers (Diaz 1979, Dirks and Martner 1982). Our study focused on the northern 20% of the park, which is primarily a lower elevation grassland or sagebrush steppe (Fig. 1). The northern Yellowstone elk and bison migrate seasonally between a high-elevation summer range and this lower elevation winter range (Craighead et al. 1972, Barmore 1980,[2] Houston 1982).

The northern range extends ≈80 km down the Lamar, Yellowstone, and Gardner river drainages (Houston 1982). Approximately 83% of the winter range for elk is included within YNP (Houston 1982), comprising nearly 80 000 ha, and has a warmer, drier climate than the rest of the Park (Diaz 1979, Dirks and Martner 1982). We focused solely on the winter range within the Park boundaries. Most of the soils derive from glacial till deposited during the Pinedale glaciation (Houston 1982) and tend to be higher in silt, clay, and organic matter than soils derived from rhyolite, the parent rock of most of YNP (Despain 1991). The drier grasslands are dominated by big sagebrush (*Artemisia tridentata*), bluebunch wheatgrass (*Agropyron spicatum*), and Idaho fescue (*Festuca idahoensis*). Wet sites are dominated by bearded wheatgrass (*Agropyron caninum*), sedges (*Carex* spp.), and introduced graminoids such as Kentucky bluegrass (*Poa pratensis*). More continuous forest occurs at high elevations and on north slopes (see detailed descriptions in Houston 1982 and

[2] W. J. Barmore, *unpublished report* [1980] to Research Division, Yellowstone National Park, Wyoming, USA.

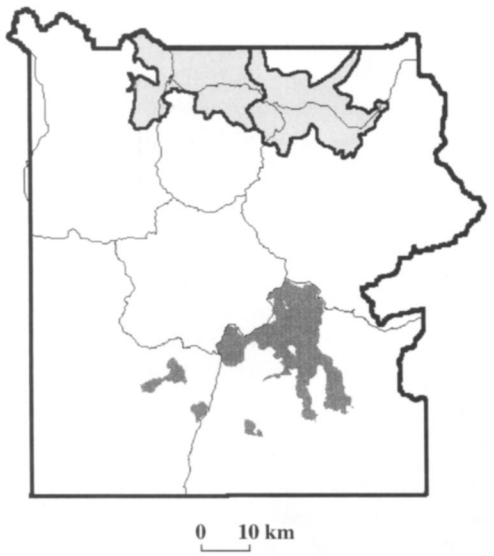

FIG. 1. Map of Yellowstone National Park showing the northern range outlined in black and shaded in light grey. The upper (right) and lower (left) range indicated were used in specifying the initial locations of bison. Major lakes are shaded in dark grey and major roads are shown. Yellowstone is primarily in Wyoming, but also partly in Montana (to the north) and Idaho (to the west); the southeast (lower right) corner of Yellowstone is at 44°08′ N, 110° W.

Despain 1991). At lower elevations, the sagebrush-grasslands are interspersed with coniferous forest, primarily Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta* var. *latifolia*); aspen groves (*Populus tremuloides*); and riparian willow (*Salix*) communities.

Natural fires have influenced plant succession on the winter range for a long time (Houston 1973). Tree-ring evidence suggests that 8–10 extensive fires occurred in the area during the last 300–400 yr, but no large fires had occurred previously in this century (Houston 1973). Approximately 34% of the winter range burned during the 1988 fires, including 22% of the grasslands (D. Despain, A. Rodman, P. Schullery, and H. Shoric, *unpublished report* [1989] to Research Division, Yellowstone National Park, Wyoming, USA). The vegetation has been dynamic during the past century (Houston 1982). Forest cover has increased, mostly on north slopes, and forests have recolonized burned areas, although aspen appears to have declined from 4–6% to 2–3% of the winter range. Sagebrush increased in extent on many slopes and exposures. Willows and associated riparian vegetation have shown a net decrease. The production of herbaceous vegetation on the northern range shows substantial annual fluctuations resulting from varied growing conditions, primarily precipitation (Houston 1982; E. H. Merrill, M. S. Boyce, R. W. Marrs, and M. K. Bramble-Brodahl, *unpublished report* [1988] to Research Division, Yellowstone National Park, Wyoming, USA).

MODEL DESCRIPTION

The Northern Yellowstone Park (NOYELP) model is a spatially explicit simulator of small groups of individual elk and bison in a multi-habitat landscape influenced by different fire disturbances and winter severities. The model simulates the search, movement, and foraging activities of individuals or small groups of elk and bison. Forage intake is a function of an animal's initial body mass, the absolute amount of forage available on a site, and the depth and density of snow. When the energy expenditures of an animal exceed the energy gained during a day, the animal's endogenous reserves are reduced to offset the deficits.

The 77 020-ha landscape is represented as a gridded irregular polygon with a spatial resolution of 1 ha. Simulations are conducted with a 1-d time step for a duration of 180 d, ≈1 November through the end of April. Simulations are conducted anew for each winter season, as the model does not project ungulate reproduction or plant regrowth during the spring and summer. Sequential years can be simulated by specifying the number of ungulates present at the beginning of the winter and the appropriate amount of initial forage in each habitat category.

The values of all parameters used in the model were obtained from our field data or from published literature, or by consulting with appropriate experts. Initial runs of the model were made for three known winters in Yellowstone, and the model was calibrated by adjusting the values of only two parameters for which we were unsure of our estimates (maintenance energy and the upper threshold of snow water equivalent at which foraging is precluded). We now describe each major component of the simulation model.

Landscape representation

The landscape is represented as a grid with a resolution of 1 ha. The grid cell structure is useful because (1) it is compatible with remotely sensed imagery and geographic information system data, (2) the structure is easy to work with conceptually and mathematically, and (3) a variety of quantitative measures are available to analyze the spatial patterns in raster landscape data (e.g., Turner and Gardner 1991). Because of the irregular shape of the northern range (Fig. 1), we use a 290 row by 592 column matrix that contains the 77 020 grid cells encompassed by the study area. Spatial heterogeneity across the landscape is represented by a series of data layers obtained from the YNP geographic information system (GIS).

First, we aggregated the habitat types defined by Despain (1990) into six habitat types (Table 1). Despain (1990) uses a complex classification scheme that recognizes many community types. However, because ungulate foragers appear to respond primarily to forage quantity rather than quality or subtle community differences (Wallace et al., *in press*), we aggregated Des-

TABLE 1. Habitat categories used in the NOYELP (Northern Yellowstone Park) model and their common species. The habitat maps were created by aggregating Despain's (1990) habitat types (i.e., potential natural vegetatioon) into the four grassland classes and the single forest class; aspen stands were used directly from the Park GIS.

Habitat	Common species
Wet grassland	*Poa pratensis, Phleum pratense, Agropyron caninum, Deschampsia caespitosa, Carex* sp., *Calamagrostis* sp.
Moist grassland	*Artemisia tridentata, Phleum pratensis, Bromus carinatus, Agropyron caninum, Geranium viscoscisimum, Potentilla* sp., *Carex* sp.
Mesic grassland	*Artemesia tridentata, Agropyron caninum, Agropyron spicatum, Bromus* sp., *Potentilla* sp., *Stipa* sp.
Dry grassland	*Artemisia tridentata, Agropyron spicatum, Koeleria cristata, Festuca idahoensis, Chrysopsis villosa, Stipa comata, Danthonia* sp., *Poa* sp., *Sedum* sp.
Aspen stands	*Populus tremuloides* sprouts plus herbaceous vegetation
Canopy forest	*Pinus contorta* or *Pseudotsuga menziesii* understory

pain's sagebrush-grassland community types based on average annual precipitation to obtain four grassland types (Table 1). Coniferous forest and aspen stands were also separated because of the differential production of browse in these forest types. Second, we identified burned and unburned areas. The 1988 fire pattern was obtained from the Park GIS, but we also simulated other fire patterns by specifying the size, number, and locations of burned areas. The combination of a fire pattern overlaid on the habitat pattern results in a landscape map of 12 vegetation classes. Third, we used slope, aspect, and elevation arrays from the YNP GIS. Slopes were assigned to one of four categories: <3°, 3–15°, 15.1–30°, and >30°. Aspects also were grouped into four categories, approximating differences in moisture availability: flat (no aspect); northerly (north, northeast, and northwest); southerly (south, southeast, and southwest); and intermediate (east and west). Slope and aspect classes are used in the snow simulation (described below), and elevation is used to initialize bison locations at the beginning of a simulation (also described below, see *Ungulate initial conditions . . .*).

Forage distribution

Each grid cell is assigned an initial quantity of available forage (mass per unit area) based on its habitat type and burn status. Pre-winter forage was sampled in the burned and unburned grassland habitats and canopy forest during October 1990 (Wallace et al., *in press*), and aspen sprouts in burned and unburned stands were counted and weighed in September 1990 (W. H. Romme, M. G. Turner, L. L. Wallace, and J. Walker, *unpublished manuscript*). Thus, our field data represent the forage available in unburned habitats and in burned habitats during the second postfire winter. When simulating the initial postfire winter, we assumed there was no available forage in burned areas. When simulating a later postfire winter, we used the fall 1990 data for burned areas. We did not incorporate the range of pre-winter available forage that may result from variation in weather during the growing season. Total available forage in aspen grid cells included both woody and herbaceous forage and was computed by summing the forage biomass of aspen sprouts (number of sprouts per hectare × mean sprout mass) and the mean herbaceous forage available in the nonforest grid cells immediately adjacent to an aspen site.

Initial forage was distributed within each vegetation class by assigning to each grid cell a forage value obtained from a normal distribution based on a 95% confidence interval (equal to approximately ± 2 standard errors) around the mean of its vegetation class (Table 2). The 1990 forage data were tested for normality using a G test for goodness of fit (Sokal and Rohlf 1981) and were found not to differ from a normal distribution (Wallace et al., *in press*). This method of initialization eliminates the artificial synchronization of grazing and movement dynamics that may result when all grid cells in a vegetation class contain the average forage value (Turner et al. 1993).

The absolute abundance of forage on each grid cell is decremented as ungulates graze the forage. Because the vegetation is dormant during the simulated time period, no regrowth occurs. Therefore, forage abundance can either remain constant or decline during the simulation. Vegetation loss due to factors other than grazing (e.g., decomposition) is not included in the model.

Ungulate initial conditions and spatial distribution

The model includes six ungulate classes: cows, calves, and bulls for both elk and bison. The initial numbers of elk and bison used to simulate actual years were obtained from early and late winter censuses conducted in the Park (Table 3). The northern elk herd has ranged

TABLE 2. Available forage (kg/ha) during the second postfire winter in burned and unburned areas of each habitat type used in the model. Data were collected during October 1990; methods are described in Wallace et al. (*in press*).

Habitat	Burned		Unburned	
	Mean	SE	Mean	SE
Dry grassland	No data*	No data*	520	59
Mesic grassland	1230	217	631	139
Moist grassland	1503	297	1122	166
Wet grassland	2413	296	2259	266
Canopy forest	701	396	333	85
Aspen	1867	352	659	101

* Burned dry grasslands were very rare and not sampled; we assigned the unburned biomass values to burned dry grasslands when they occurred.

TABLE 3. Values of the parameters used in the simulation model.

Description	Parameter Code	Value	Units	Source
Maximum daily moving distance				
Elk	MDISTM(1)	4 40	km Pixels	Our estimate based on Green and Bear (1990)
Bison	MDISTM(2)	2 20	km Pixels	M. Meagher [Yellowstone National Park, YNP], *personal communication*
Elk—initial number				
1987–1988	NELK	21600	Individuals	J. A. Mack and F. J. Singer, *unpublished manuscript*
1988–1989		19270	Individuals	Singer et al. (1989)
1990–1991		18000	Individuals	J. Mack [YNP], *personal communication*
Bison—initial number				
1987–1988	NBISON	697	Individuals	M. Meagher [YNP], *personal communication*
1988–1989		699	Individuals	
1990–1991		456	Individuals	
Animals/group				
Elk calves	NPG(1)	4	Individuals	Our data
Elk cows	NPG(2)	4	Individuals	Our data
Elk bulls	NPG(3)	4	Individuals	Our data
Bison calves	NPG(4)	9	Individuals	M. Meagher [YNP], *personal communication*
Bison cows	NPG(5)	9	Individuals	M. Meagher [YNP], *personal communication*
Bison bulls	NPG(6)	2	Individuals	M. Meagher [YNP], *personal communication*
Sex ratio (proportion of population)				
Elk calves	SXRT(1)	0.16	Unitless	Lemke and Singer 1989*
Elk cows	SXRT(2)	0.65	Unitless	Lemke and Singer 1989*
Elk bulls	SXRT(3)	0.19	Unitless	Lemke and Singer 1989*
Bison calves	SXRT(4)	0.18	Unitless	Barmore 1980†
Bison cows	SXRT(5)	0.38	Unitless	Barmore 1980†
Bison bulls	SXRT(6)	0.42	Unitless	Barmore 1980†
Proportion body fat				
Elk calves	FTRT(1)	0.08	Unitless	Based on Torbit et al. 1985
Elk cows	FTRT(2)	0.16	Unitless	Based on Torbit et al. 1985
Elk bulls	FTRT(3)	0.15	Unitless	Our estimate
Bison calves	FTRT(4)	0.10	Unitless	R. Dineen [Rocky Mountain Meat Company], *personal communication*
Bison cows	FTRT(5)	0.11	Unitless	R. Dineen [Rocky Mountain Meat Company], *personal communication*
Bison bulls	FTRT(6)	0.085	Unitless	R. Dineen [Rocky Mountain Meat Company], *personal communication*
Initial body mass				
Elk calves	$BM_i(1)$	116	kg	Murie 1951
Elk cows	$BM_i(2)$	179	kg	Murie 1951
Elk bulls	$BM_i(3)$	236	kg	Murie 1951
Bison calves	$BM_i(4)$	159	kg	Meagher 1973
Bison cows	$BM_i(5)$	409	kg	Meagher 1973
Bison bulls	$BM_i(6)$	909	kg	Meagher 1973
Brisket heights				
Elk calves	SDM(1)	65	cm	Based on Hobbs 1989 and Bubenik 1982
Elk cows	SDM(2)	86	cm	Parker et al. 1984
Elk bulls	SDM(3)	86	cm	Parker et al. 1984
Bison calves	SDM(4)	52	cm	Van Camp 1975‡
Bison cows	SDM(5)	70	cm	Van Camp 1975‡
Bison bulls	SDM(6)	70	cm	Van Camp 1975‡
Maximum feeding rate				
Cows and bulls	FGB	0.025	kg/kg§	N. T. Hobbs, *personal communication*

TABLE 3. Continued.

Description	Parameter Code	Value	Units	Source
Calves		0.030	kg/kg§	
Fat energy	FATEN	39330	kJ/kg	Torbit et al. 1985
Lean energy	BWLEN	22175	kJ/kg	Torbit et al. 1985
Ratio of lean body lost during mass loss	RLBWL	0.30	unitless	Hobbs 1989
Ratio of fat lost during mass loss	RFATL	0.70	unitless	Hobbs 1989
Maintenance energy‖				
Elk calves	ME(1)	510	$kJ/BM^{0.75}$	Calibrated
Elk cows	ME(2)	418	$kJ/BM^{0.75}$	Calibrated
Elk bulls	ME(3)	418	$kJ/BM^{0.75}$	Calibrated
Bison calves	ME(4)	502	$kJ/BM^{0.75}$	Calibrated
Bison cows	ME(5)	376	$kJ/BM^{0.75}$	Calibrated
Bison bulls	ME(6)	376	$kJ/BM^{0.75}$	Calibrated
Lower SWE [snow water equivalent] when foraging limitation begins				
Elk	SWLO(1)	5.0	cm	P. Farnes and M. Meagher, *personal communication*
Bison	SWLO(2)	5.0	cm	P. Farnes and M. Meagher, *personal communication*
Upper SWE when foraging stops				
Elk calves	SWHI(1)	14.0	cm	Calibrated
Elk cows	SWHI(2)	15.0	cm	Calibrated
Elk bulls	SWHI(3)	16.0	cm	Calibrated
Bison calves	SWHI(4)	16.0	cm	Calibrated
Bison cows	SWHI(5)	18.0	cm	Calibrated
Bison bulls	SWHI(6)	18.0	cm	Calibrated
Forage energy content	ENPK	5648	kJ/kg	Cassirer et al. 1992, Hobbs and Robin 1983, and our data

* T. Lemke and F. Singer, *unpublished report* [1989] to Research Division, Yellowstone National Park, Wyoming, USA.
† W. J. Barmore, *unpublished report* [1980] to Research Division, Yellowstone National Park, Wyoming, USA.
‡ J. Van Camp, *unpublished manuscript* [1975], Canadian Wildlife Service, Edmonton, Alberta, Canada.
§ Dry forage mass/wet body mass.
‖ The numerical values for ME and for SWHI were calibrated within an acceptable range during model testing.

in number from 3000 to >17 000 during the past 50 yr (Houston 1982, Garton et al. 1990, Singer 1991), and the bison population has ranged between 200 and 1000 animals (Meagher 1971, *personal communication*). Sex and age ratios for elk and bison in Yellowstone National Park (Meagher 1971, Barmore 1980,[3] Lemke and Singer 1989[4]) were used to allocate the appropriate number of animals to each of the six ungulate classes. We fixed the sex ratios used in the simulation based on long-term records of population composition from the Park (Table 3). Each ungulate class also was assigned an initial body mass (Table 3). We assumed all animals within a class (i.e., calf, cow, or bull) had the same initial body mass.

The movement, foraging, energetics, and survival of ungulates were simulated for small groups of individuals assumed to be of the same ungulate class (i.e., calves, cows, or bulls) and identical. The groups remained intact throughout the simulation. Calf groups were always associated with a cow group and moved accordingly to the same sites. The use of ungulate groups is reasonable biologically (Meagher 1973, Franklin and Lub 1979, Telfer and Cairns 1979, Geist 1982), is appropriate for the 1-ha spatial resolution of the model and also reduces computational intensity. The equations described later (e.g., see *Ungulate foraging, Ungulate energetics*) apply to individual animals, and group size is used as a multiplier in the model. For elk cows, calves, and bulls, the group size was four animals. Field observations during the winter of 1990–1991 indicated that 94% of elk cow/calf groups and 78% of bull groups contained >4 individuals (*unpublished data*). For bison, we simulated groups of 9 cows and 9 calves, and bull groups included 2 animals. M. Meagher (*personal communication*) reported a mean group size for bison of 37 animals during the winters of 1989–1990 and 1990–1991, and suggested that if group size dropped below 18 the group would fragment completely as animals seek other groups. Because calf groups associate with cow groups in the model, we effectively simulate herds of 18 bison cows and calves. Actual herd sizes

[3] See footnote 2.

[4] T. Lemke and F. Singer, *unpublished report* [1989] to Research Division, Yellowstone National Park, Wyoming, USA.

of elk and bison in the model can be large because there is no constraint (other than food limitation) on the number of groups that can occupy a grid cell simultaneously. Because the group size parameter acts multiplicatively, group size is flexible and could be set to one to allow the simulation of individual behavior. A comparison between simulating single animals and groups of four showed no significant differences in projected ungulate survival. For simulation of 18 000 elk, the model tracks 4500 individual groups.

The initial spatial distribution of ungulates is specified as follows. Elk are distributed randomly on resource sites (i.e., grid cells that contain forage) across the entire landscape. This pattern is in agreement with observed locations of elk during the autumn (Barmore 1980,[5] Houston 1982); animals migrate from summer to winter range, but in fall and early winter appear not to select among grassland communities or landscape positions. Bison are distributed randomly in nonforest habitats at elevations <2100 m. In addition, based on Park data,[5] 90% of the bison population is located initially in the eastern portion of the range and the remaining 10% is located in the western half (see Fig. 1). More than one group of elk or bison can simultaneously occupy the same grid cell, both initially and throughout the simulation.

Snow simulation

The model simulates the spatial and temporal heterogeneity of snow conditions across the northern range. Snow conditions are an extremely important determinant of winter ungulate dynamics (e.g., Houston 1982, Parker et al. 1984, Telfer and Kelsall 1984, and many others), but snow may have different effects on foraging and travel. For example, in coniferous forests of southeastern Alaska, 20 cm of snow depth can reduce available forage by 60% but have little effect on travel costs (Wickstrom et al. 1984). The northern range was subdivided into two subregions for the snow simulation. The northwestern portion of the range in the vicinity of Mammoth Hot Springs and Gardiner, Montana, occurs within a rain shadow created by high mountains on all sides. We demarcated the approximate boundaries of this low-precipitation area and treated the Mammoth–Gardiner area separately from the rest of the northern range. Snow simulation was then a two-step process.

First, baseline snow depth and snow density were projected within each of the two qualitatively different snow regions assuming a flat area with no slope or aspect. Monthly data for snow depth, snow water equivalent, and weather were used for the baseline snow projections. For most of the study area, we directly used monthly data for snow depth and snow density collected over many years at the Lupine Creek Snow Course, located in the south–central portion of the northern range (data were obtained from the Snow Survey Program, Soil Conservation Service, Portland, Oregon). For the Mammoth–Gardiner area, where no snow survey data sites are located, we developed regressions for snow depth (Table 4A) based on weather data recorded at Mammoth Hot Springs, and we assumed snow density at Lupine could be extrapolated to the Mammoth region. Snow conditions between the monthly values were interpolated by assuming a constant linear change (e.g., if snow depth was 30 cm on 1 January and 50 cm on 1 February, we assumed a linear increase of 20 cm during that month). The model permits the user to specify the time interval for updating snow conditions across the landscape. A 3-d interval was used in the simulations presented in this paper.

The second step in the snow simulation was to distribute snow to each grid cell every 3 d by modifying the baseline projection by the slope and aspect of each grid cell. Multipliers based on slope and aspect were determined by sampling snow depth and snow water equivalent (SWE) using standard techniques (Goodison et al. 1981) at five sites on the northern range during February 1992 (unpublished data). At each site, sampling was conducted on an open, flat area, comparable to the sites where snow course measurements are made and on a variety of slope–aspect combinations. Analysis of these data produced a set of coefficients (Table 4B and C) by which we could multiply the baseline projections to predict the snow depth and SWE in any grid cell on the landscape.

There is a simple relationship between snow water equivalent, snow depth, and snow density:

$$\mathrm{SWE} = \mathrm{SD} \times \mathrm{SN}, \quad (1)$$

where SWE = snow water equivalent (in centimetres), SD = snow depth (in centimetres), and SN = snow density (as percentage), which permitted us to use any of these three snow parameters in the model. Snow depth and snow density are used to determine the energy cost of travel and the maximum daily moving distance. SWE, an integrated measure of snow mass, is used to influence daily forage intake.

Ungulate foraging

Ungulates located on suitable sites (i.e., there is some amount of forage available) graze. The daily intake of forage by each ungulate follows Wiegert (1979) and is represented as:

$$I = \sum_{i,j} [\mathrm{FGB} \cdot \mathrm{BM}_i \cdot \mathrm{minimum}(\mathrm{FB}_{\mathrm{snow}(i,j)}, \mathrm{FB}_{\mathrm{forage}(i,j)})], \quad (2)$$

where I = daily forage intake (in kilograms) per ungulate, FGB (i.e., foraging baseline) = maximum daily foraging rate (in kilograms dry mass of forage eaten per kilogram ungulate body mass), BM_i = initial un-

[5] See footnote 2.

TABLE 4. Relationships used to simulate snow conditions across the landscape. All snow depths are in centimetres.

A. Regression equations used to simulate baselne snow depths in the Mammoth–Gardiner region.

Month	Equation for snow depth (SD) in cm)	r^2	P
November	$SD_{Nov} = -6.467 + 0.525 \cdot$(Nov. snowfall)	0.79	0.0001
December	$SD_{Dec} = -6.5 + 0.282 \cdot (\Sigma$ Nov., Dec. snowfall)	0.62	0.0024
January	$SD_{Jan} = -8.951 + 0.849 \cdot$(Jan. snowfall) $+ (1.165 \cdot SD_{Dec})$	0.84	0.0007
February	$SD_{Feb} = -7.14 + 0.327 \cdot$(Feb. snowfall) $+ 0.758 \cdot SD_{Jan}$	0.90	0.0001
March	$SD_{Mar} = -23.952 + 0.164 \cdot (\Sigma$ Nov. through Mar. snowfall)	0.55	0.0088
April	No data; SD_{Apr} assumed to be zero.	...	...

B. Effects of slope and aspect of snow depth

Aspect class	Slope (°)	Multiplier
	Nonforest and burned forest	
All	0–15	1.0
E, SE, W, SW	All	1.0
S	15–30	0.7
	>30	0
N, NW, NE	15–30	1.2
	>30	1.4
	Unburned forest	
All	All	0.90·(nonforest multiplier)

C. Effects of slope and aspect on snow water equivalent

Aspect class	Slope (°)	Multiplier
	Nonforest and burned forest	
E, W	All	1.0
S, SE, SW	0–15	1.0
	15–30	0.7
	>30	0
N, NW, NE	<3	1.0
	3–15	1.1
	15–30	1.2
	>30	1.3
	Unburned forest	
All	All	0.90·(nonforest multiplier)

gulate body mass (in kilograms), $FB_{snow(i,j)}$ = feedback due to snow depth and density on cell i,j (unitless), $FB_{forage(i,j)}$ = feedback due to biomass availability on cell i,j (unitless), and i,j = locations of each grid cell visited per day.

We assumed that the maximum daily intake was a function of the initial body mass of the ungulates at the beginning of the winter, and that gut fill essentially limits daily intake (Hobbs 1989). That is, animals attempt to obtain a maximum amount of forage even as they lose body mass during the winter. The value of FGB was set to 0.025 for cows and bulls and to 0.03 for calves of each species. Based on the initial body masses of the animals (Table 3), this generates a maximum daily forage intake of 3.48, 4.48, and 5.90 kg for elk calves, cows, and bulls, respectively; and 4.78, 10.15, and 22.73 kg for bison calves, cows, and bulls, respectively. These values are within the ranges reported in the literature (e.g., Richmond et al. 1977, Reynolds et al. 1978, Skovlin 1982, Wickstrom et al. 1984, Baker and Hansen 1985, Hudson and Frank 1987).

Two negative feedback terms were included in the model. Each feedback returns a unitless number ranging from 0 to 1 such that the maximum forage intake is achieved when there is no limitation (i.e., the feedback is 1), and no forage intake occurs when there is complete limitation (i.e., the feedback is 0). We assumed no interaction between the feedback terms and allowed the term with the lower value to operate.

The first feedback represents the effect of a reduction in the amount of available forage on the rate of forage intake. The forage present on a grid cell is modified during the simulation as grazing removes biomass. Numerous empirical studies (e.g., Wickstrom et al. 1984, Hudson and Neitfeld 1985, Hudson and Frank 1987, McCorquodale 1991) have demonstrated a hyperbolic decrease in the instantaneous rate of feeding as forage is reduced. Spalinger and Hobbs (1992) note that a hyperbolic curve can be obtained through a variety of mechanisms, and several alternative equations are often used to represent the response. We used a simple hyperbolic feedback term, modified so that it does not pass through the origin by including a refugium value for the forage:

$$FB_{forage} = 1 - \frac{REF}{BIO}, \quad (3)$$

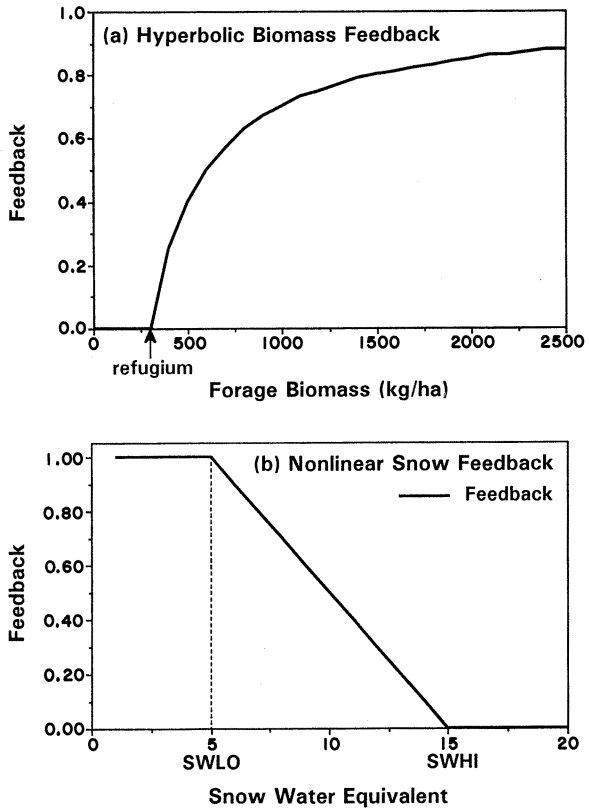

FIG. 2. Forms of the feedback terms used to influence grazing: (a) a hyperbolic feedback based on forage limitation with a refugium, and (b) a nonlinear feedback based on snow water equivalent with two thresholds. SWLO = the snow water equivalent value at which limitation to foraging begins (i.e., lower threshold).

where FB_{forage} = value ranging from 0 to 1 (unitless), REF = refuge value of biomass not available to ungulates (in kilograms per hectare), and BIO = actual biomass in that grid cell (in kilograms per hectare). The value of the feedback term is zero when biomass on the site is less than or equal to the refugium value, then asymptotically approaches 1 as biomass increases (Fig. 2a). A refugium was included for the following reasons. Elk and bison paw through the snow or use headswings to move snow to obtain forage. After an animal grazes in the cleared area and moves on, the snow forms a hard crust or ice layer that precludes regrazing until after a significant warming event has occurred and the ice layer thaws. Brown and Theberge (1990) note that weather conditions that promote hardening of the snow after a feeding event will discourage reuse of feeding areas. This implies that although some forage may be present, there is an amount of forage that will not be available to the ungulates. We incorporated this phenomenon by designating a forage refuge level.

To estimate this refugium, we sampled paired grazed and ungrazed plots in four habitat types. Although the absolute value of the biomass remaining in grazed plots varied among the habitat types, the percentage of the ungrazed biomass did not vary among habitats and was ≈13% (Table 5). Therefore, we assigned the refugium value of forage for each habitat type to be 13% of the initial biomass.

The second feedback represents the effect of snow on the ability of an animal to obtain forage. Foraging may be limited by snow depth; animals generally cannot forage in snow that exceeds their brisket height, even if the snow is quite powdery. However, snow density also influences foraging; shallow dense snow may effectively preclude foraging. Therefore, we used snow water equivalent (SWE), which integrates both depth and density, in a feedback that incorporates two thresholds:

$$FB_{snow} = \left[1 - \frac{(SWE - SWLO)}{SWHI - SWLO} +\right] +, \qquad (4)$$

where FB_{snow} = value ranging from 0 to 1 (unitless), SWE = actual snow water equivalent in that grid cell, SWLO = the SWE value at which limitation to foraging begins, SWHI = the SWE value at which feeding goes to zero, and "+" indicates that the term must remain positive, i.e., it is set to zero if negative.

Eq. 4 assumes that there is a threshold value of snow water equivalent below which there is no limitation on foraging. That is, below SWLO an animal can forage at its maximum rate. At some other threshold value, SWHI, foraging is precluded by the mass of the snow. Between the two thresholds, there is a linear decline in the value of the feedback (Fig. 2b). Cassirer et al. (1992) and Hobbs (1989) have also assumed linear decreases in forage availability within increasing snow depth, although snow density was not included. We estimated the values of these thresholds (Table 3), and adjusted the SWHI values during model calibration.

Search and movement rules

A simple rule-based algorithm was selected from several alternative approaches to simulate an ungulate's search-and-movement strategy (Turner et al. 1993). If an animal is located on a grid cell that contains available forage, it grazes as described by Eq. 2. If the animal has not obtained its maximum forage intake for the day, the animal searches the landscape to move

TABLE 5. Forage in paired plots where one plot sampled biomass remaining in grazed "craters" and the other was in an adjacent ungrazed plot. Grazed biomass was used to estimate the refugium value used in the feedback term that influenced grazing (Eq. 3). The percentage of the ungrazed biomass remaining did not differ among habitats.

Habitat	Initial (kg/ha)	Refuge (kg/ha)	% of initial
Moist unburned	1120	168	15
Moist burned	1503	240	16
Wet unburned	2250	216	10
Wet burned	2413	396	16

to another site. Successive concentric rings of grid cells up to a radius equal to the maximum daily moving distance under present snow conditions are examined. The ungulate's search is based on the feedback term because it integrates both the absolute abundance of forage and the snow conditions on the cell. Once nonzero feedback terms are found within one of the concentric rings, the ungulate simply moves to the grid cell that has the highest value. If there is a tie for the highest value, then the ungulate selects among them at random. If an ungulate is not located on a grid cell containing forage, it uses the same search-and-movement algorithm to find a suitable site. If no resource sites are available within the search radius, then the animal moves its maximum distance in a random direction. Note that even though we refer to "an animal," each group will move according to these rules.

A simple self-avoidance rule was also added to prevent artificial movements between the same pair of grid cells. This rule prohibits an ungulate from returning to the grid cell from which it just came. Ungulates also are not permitted to leave the Park boundaries during the simulation, and thus they are reflected back into the Park if they reach the border. The foraging process is iterative, and the daily foraging bout of an ungulate is completed in the model when either of two conditions is met: (1) the maximum daily intake is obtained, and the animal is satiated for the day; or (2) the maximum daily movement distance (described below) has been reached. If condition 2 is met, no more foraging can occur that day even if the animal is not satiated. The next ungulate group is then located and the procedure repeated until all ungulate groups have completed foraging for the day.

The mean maximum daily movement distance for elk (4 km, Table 3) was estimated from Green and Bear's (1990) data. They followed the activity patterns of female elk in Rocky Mountain National Park, Colorado, over a 2-yr period. During winter the elk spent 45% of their day feeding, 46% resting, and ≈10% travelling. We assumed moving rates of 4 m/min while feeding and 10 m/min while moving at relatively low speed (Wickstrom et al. 1984; N. T. Hobbs, *personal communication*) to estimate a daily travel distance of 3882 m, which we rounded up to 4.0 km. The mean maximum daily movement distance for bison was estimated to be 2 km (M. M. Meagher, *personal communication*). The model does not simulate occasional long-distance movement events.

The maximum daily movement distance is modified by snow conditions. This is done by using the relative increase in travel costs in snow (Y from Eq. 12, defined in the next section) to reduce the maximum daily movement distance as follows:

$$\text{DIST} = \frac{\text{MDISTM}}{1 + (\mathbf{Y}/100)}, \tag{5}$$

where DIST = the modified maximum daily movement distance in snow, MDISTM = the initial maximum daily movement distance for that ungulate class, and Y = the relative increase in energy costs of travel in snow. This equation is used to constrain animal movement so that elk or bison move a shorter distance when snow conditions are severe.

Ungulate energetics

Daily energy balances are computed at the end of each day for each ungulate group. The equations again are parameterized separately for each of the six ungulate classes (see Table 3 for the numerical values we used). Energy balance is simply the difference between daily energy gain and cost. The three general equations for daily energetics are:

$$E_{\text{balance}} = E_{\text{gain}} - E_{\text{cost}} \tag{6}$$

$$E_{\text{gain}} = I \times \text{ENPK} \tag{7}$$

$$E_{\text{cost}} = E_{\text{maint}} + E_{\text{travel}}, \tag{8}$$

where I = total intake of forage (in kilograms), ENPK = forage energy content (in kilojoules per kilogram), E_{maint} = metabolizable energy needed for zero energy balance, excluding travel (in kilojoules), and E_{travel} = energy cost of travel (in kilojoules).

Energy gain is a direct function of the total amount of forage consumed per day, which is computed for each ungulate group. Field studies conducted in October 1990 across all 12 vegetation classes showed no difference in the energy content or nutrient quality of herbaceous forage (Wallace et al., *in press*). The energy content of the forage followed Cassirer et al. (1992) and is based on Hobbs et al. (1981) and Robbins (1983):

$$\text{ENPK} = \text{GE}\cdot\text{IVDM}\cdot\text{MC}, \tag{9}$$

where ENPK = forage energy content (in kilojoules per kilogram), GE = gross energy (18 410 kJ/kg), IVDMD = in vitro dry matter digestibility (0.374 from our October 1990 forage samples), and MC = metabolizable energy coefficient (0.82). From Eq. 9 we obtain a value of 5648 kJ/kg dry mass as the energy content of forage, and we assume this value to remain constant throughout the simulation for all vegetation classes.

Energy costs include the energy required for maintenance plus the energy required for travel. Maintenance energy is a power function of body mass (e.g., Thompson et al. 1983):

$$E_{\text{maint}} = \text{ME}\cdot\text{BM}^{0.75}, \tag{10}$$

where ME = metabolizable energy needed per kilogram of body mass (in kilojoules), and BM = present body mass (in kilograms) of the ungulate. As used in our model, maintenance energy includes the energy costs of all the animal's daily activities (e.g., standing, resting, grazing, ruminating, thermoregulating) within the spatial extent of 1 ha. Therefore, our ME values had

to be higher than values reported in the literature calculated for an animal at rest (e.g., Osuji 1974, Christopherson et al. 1979). We did not account separately for thermoregulatory energy costs in the model. In Rocky Mountain National Park, female elk were most active during the colder parts of the day and frequently used cooler, north-facing slopes to rest, suggesting little response to the thermal environment (Green and Bear 1990). Hobbs (1989) also found that thermoregulatory costs were a small fraction (<1%) of total energy expenditure for wintering mule deer, even during a severe winter. We assume that the maintenance energy parameter employed in the model incorporates thermoregulatory costs. Initial parameter estimates were obtained from the literature (e.g., Christopherson et al. 1978, 1979, Bubenik 1982, Parker et al. 1984, McCorquodale 1991) but were adjusted during model calibration.

The energy cost of travelling was computed following Parker et al. (1984) using a two-step process. First, the energy cost of horizontal travel for a given distance in the absence of snow as reported by Parker et al. was computed:

$$E_{\text{travel}}(\text{no snow}) = [2.97\ \text{kJ/kg}\cdot\text{BM}^{-0.34}]\cdot\text{BM}\cdot S, \quad (11)$$

where S = distance travelled (in kilometres), and BM = present body mass of the animal (in kilograms). By using the value for horizontal travel, we assume that the costs of upslope and downslope travel average out. Next, the relative increase in travel costs in snow relative to no-snow conditions is computed as a function of relative sinking depth and snow density. In this calculation, we use the snow conditions on the grid cell on which an animal is located before it moves to the next site, and we do not integrate snow conditions across the travel path. We used the empirical relationship developed by Parker et al. (1984):

$$Y = [0.71 + 2.6(\rho - 0.2)]\cdot\text{RSD} \cdot e^{[0.0191 + 0.016(\rho - 0.2)]\cdot\text{RSD}}, \quad (12)$$

where Y = relative increase in energy costs for travel in snow (in percent), ρ = snow density (in grams per cubic centimetre), and RSD = relative sinking depth [(sinking depth/brisket height) × 100]. The depth to which an animal sinks in snow is the most appropriate measure of "effective" snow depth (Parker et al. 1984). Sinking depth is a function of snow depth, snow density, and snow hardness (i.e., Parker et al. 1984, Bunnell et al. 1990), but no published values were found for either elk or bison. Therefore, we assumed that sinking depth was equal to the depth of the snow on that grid cell. The relative increase in the net cost of locomotion increased exponentially as a function of relative sinking depth. Although elk have been observed to travel with relatively little difficulty in powdery snow as deep as 102 cm, free-ranging herds are generally restricted in distribution by snow depths >46 cm (Van Camp 1975,[6] Parker et al. 1984 [with citations to Beall 1974, Leege and Hickey 1977, Adams 1982], Sweeny and Sweeny 1984).

The body mass of the ungulates is adjusted after the daily energy balance is computed. If energy balance is positive (i.e., energy gain exceeds energy cost), we do not permit this in the model, i.e., we assume that ungulates do not gain body mass during winter. Ungulates can only maintain or lose body mass during the simulation. If energy balance is negative, we calculate an animal's mass loss as follows (Hobbs 1989:15, based on Torbit et al. 1985):

$$\text{LOSS} = [\text{RFATL}\cdot(E_{\text{balance}}/\text{FATEN})] + [\text{RLBWL}\cdot\text{GWP}\cdot(E_{\text{balance}}/\text{LEAN})], \quad (13)$$

where E_{balance} = daily energy balance (in kilojoules), RFATL = proportion of total energy catabolized from fat, set to 0.70, FATEN = kilojoules per kilogram of fat catabolized, RLBWL = proportion of total energy catabolized from protein, set to 0.30, GWP = mass of water per unit mass of protein catabolized, set to 4.0, and LEAN = kilojoules per gram of protein catabolized. This equation incorporates the differential rates of tissue loss and energy obtained from fat and protein. Under starvation conditions, ungulates do not catabolize all fat reserves prior to catabolizing protein, and even animals who obtain relatively high forage intake deplete both fat and protein (Torbit et al. 1985). In our model, simulated ungulates died when they lost both 70% of their fat and 30% of their lean body mass.

Technical details

Because the model is stochastic, the number of replicate simulations for a given parameter set is specified in the input file. Results can then be summarized statistically over the replicates. A variety of outputs are provided by the model: daily and total forage consumed; daily and total survival for each ungulate category; and the mean amount of biomass (in kilograms per hectare) remaining in each vegetation class. Outputs can be either in tabular form, written to a file, or in graphs on the screen. Maps (e.g., ungulate locations, snow conditions, forage availability, etc.) can also be output to the screen or to a color printer.

Model Testing and Uncertainty Analysis

Calibration and testing

To calibrate and test the model, we selected three recent winters that represented alternative fire conditions (unburned, initial postfire winter, and later postfire winter) and both mild and average winter severities (Table 6). In each case, we used the weather data and

[6] J. Van Camp, *unpublished manuscript* [1975], Canadian Wildlife Service, Edmonton, Alberta, Canada.

TABLE 6. Observed and simulated elk and bison mortality in northern Yellowstone National Park (YNP) for three years selected to represent alternative conditions simulated in the model. These simulations were used to test the model before exploring alternative scenarios.

Winter	Fire status	Winter severity	Fall elk count	Elk mortality (%)		Fall bison count	Bison mortality (%)	
				Observed	Simulated		Observed	Simulated
1987–1988	Unburned	Mild	21 491 to 21 706*	<5†	0	697‡	0‡	0
1988–1989	Postfire winter	Normal	17 207 to 19 059†	38–43†	40	577‡§	20‡	18
1990–1991	Later postfire winter	Mild	18 000‖	<5¶	4	456‡	No data	0

* J. A. Mack and F. J. Singer, *unpublished manuscript*:41:Table 19; ranges reported here reflect the variation in estimates based on three different kinds of sightability corrections.
† Singer et al. (1989):721:Table 2.
‡ M. M. Meagher [YNP], *personal communication.*
§ Although 577 bison were counted, 222 had already been shot and killed outside YNP.
‖ J. Mack [YNP], *personal communication.*
¶ F. J. Singer [YNP], *personal communication.*

initial ungulate densities for the particular year simulated. Both observed and simulated elk and bison survival were used for model calibration and testing. Because bison and elk are subjected to winter hunting pressure when they leave the Park boundaries (e.g., 577 bison were counted during 1988–1989, but 222 had already been shot outside the Park), we recognize that our survival rates could potentially be greater than actually observed.

The model was calibrated using only the 1988–1989 winter data by adjusting the values of the two parameters in which we had the least confidence in our initial estimates: maintenance energy (ME) and the upper threshold of snow water equivalent (SWHI) for each ungulate category. Maps of the simulated snow conditions were examined periodically during the simulation, and no anomalies were observed. We also observed the locations of ungulates during the simulations and, again, no anomalies were observed. During mid-to-late winter, simulated ungulates were congregating on south-facing slopes and other areas in which snow conditions were less severe. Following calibration, simulated and observed ungulate survival at the end of the winter were then compared for each of the three winters and showed good agreement (Table 6).

Sensitivity and uncertainty analyses

Sensitivity analysis and uncertainty analysis were conducted by performing independent sets of 100 Monte Carlo iterations using Latin hypercube sampling methods (Gardner et al. 1983) applied to 43 parameters (Table 7). Sensitivity analysis relates the variability of the model predictions to small variances (CV = 1%) in parameters of interest and can be used to identify parameters that exert a strong influence on simulation results. Of equal importance, however, is to understand how the uncertainty in our empirical estimates of parameters can influence model projections (Gardner et al. 1981). For example, if reported values for a parameter vary over a range, how may this inherent uncertainty in the parameter value influence model results? To explore these effects, an uncertainty analysis was conducted. Uncertainty analysis relates the variability in model predictions to larger variances in the parameters and involves specifying a potential reasonable range for each parameter.

In both sets of simulations we used the 1988–1989 weather (a winter of "average" severity) and landscape for the initial postfire year and simulated 18 000 elk and 600 bison. Initial conditions were held constant, and the same sequence of random numbers was used in all simulations. The model remains stochastic, however, because movement trajectories for any ungulate group will vary between runs as parameters vary. The output variables examined were: percentage survival of elk calves, cows, and bulls; percentage survival of bison calves, cows, and bulls; biomass remaining in six habitats (note that burned areas contain no forage during the postfire winter); and total biomass across the entire landscape at the end of each month.

Simple Pearson correlation coefficients (r) were calculated between each of the parameters and the model predictions. The squared Pearson correlation coefficients (r^2) were used as measures of the percentage of the total variance in the model prediction that was explained by the variability of each of the parameters. If the parameters used in the Monte Carlo simulations are independent of each other, the squared Pearson correlation coefficients can be used as a sensitivity measure (Rose et al. 1991). The sum of the sensitivity measures quantified the portion of the total variance of the model prediction that relates linearly to the parameter variation (Bartell et al. 1988).

Sensitivity analysis.—The sensitivity analysis selected all parameters from the normal distribution with means equal to the nominal values and coefficients of

TABLE 7. Parameters used for sensitivity and uncertainty analyses done by using Monte Carlo simulation methods. In the sensitivity analysis, parameters were varied within 1% of their nominal value. In the uncertainty analysis, parameters were varied within the minimum and maximum values shown here under the assumption of a uniform distribution.

Parameter Code	Description	Value		
		Nominal	Minimum	Maximum
PSN(1)	Snow depth (SD) on nonforested sites, all aspects, <15° slope	1.0	0.7	1.3
PSN(2)	Snow depth on nonforested sites, south aspect, 15–30° slope	0.7	0.4	1.0
PSN(3)	Snow depth on nonforests sites, south aspect, >30° slope	0.0001	0.0001	0.0001
PSN(4)	Snow depth on nonforested sites, north aspects, 15–30° slope	1.2	0.9	1.5
PSN(5)	Snow depth on nonforested sites, north aspects, >30° slope	1.4	1.0	1.8
PSN(6)	Snow water equivalent (SWE), nonforested sites, flat aspect, 0° slope	1.0	0.7	1.3
PSN(7)	Snow water equivalent, nonforested sites, north aspect, <15° slope	1.1	0.8	1.4
PSN(8)	Snow water equivalent, nonforested sites, north aspect, 15–30° slope	1.2	0.9	1.5
PSN(9)	Snow water equivalent, nonforested sites, north aspect, >30° slope	1.3	1.0	1.6
PSN(10)	Snow water equivalent, nonforested sites, east-west aspect, all slopes	1.0	0.7	1.3
PSN(11)	Snow water equivalent, nonforested sites, south aspect, <15° slope	1.0	0.7	1.3
PSN(12)	Snow water equivalent, nonforested sites, south aspect, 15–30° slope	0.7	0.4	1.0
PSN(13)	Snow water equivalent, nonforested sites, south aspect, >30° slope	0.0001	0.0001	0.0001
PSN(14)	Snow depth, nonforested sites, Mammoth–Gardiner area, east-west-south aspects, >30° slope	0.0001	0.0001	0.0001
PSN(15)	Snow depth, nonforested sites, Mammoth–Gardiner area, north aspect, <15° slope	1.0	0.7	1.3
PSN(16)	Snow depth, nonforested sites, Mammoth–Gardiner area, north aspect, 15–30° slope	1.2	0.9	1.5
PSN(17)	Snow depth, nonforested sites, Mammoth–Gardiner area, north aspect, >30° slope	1.4	1.0	1.8
PSN(18)	Snow depth, nonforested sites, Mammoth–Gardiner area, flat aspect, no slope	1.0	0.7	1.3
PSN(19)	Snow water equivalent, nonforested sites, Mammoth–Gardiner area, flat aspect, no slope	1.0	0.7	1.3
PSN(20)	Snow water equivalent, nonforested sites, Mammoth–Gardiner area, north aspect, <15° slope	1.1	0.8	1.4
PSN(21)	Snow water equivalent, nonforested sites, Mammoth–Gardiner area, north aspect, 15–30° slope	1.2	0.9	1.5
PSN(22)	Snow water equivalent, nonforested sites, Mammoth–Gardiner area, north aspect, >30° slope	1.3	1.0	1.6
PSN(23)	Snow water equivalent, nonforested sites, Mammoth–Gardiner area, north aspect, >30° slope	0.0001	0.0001	0.0001
PSN(24)	Snow depth in unburned forest, proportion of nonforested equivalent site	0.9	0.7	1.1
PSN(25)	Snow water equivalent in unburned forest, proportion of nonforested equivalent site	0.9	0.7	1.1

TABLE 7. Continued.

Parameter Code	Description	Value		
		Nominal	Minimum	Maximum
$MDISTM_e$	Maximum daily movement distance for elk	40 grid cells	20	80
$MDISTM_b$	Maximum daily movement distance for bison	20 grid cells	10	30
ENMOVC	Multiplier for the energetic cost of movement calculated in the model	1.0	0.6	1.4
ME	Multiplier for the maintenance energy (ME) values assigned to each ungulate class	1.0	0.7	1.3
SWLO	Threshold above which snow water equivalent begins to influence forage intake	5.0	2.0	8.0
SWHI	Multiplier for the threshold snow water equivalent at which forage intake goes to zero for each ungulate class	1.0	0.6	1.4
FTRTC	Multiplier for the percentage of body fat for each ungulate category	1.0	0.2	1.8
BM_i	Multiplier for the initial body mass for each ungulate category	1.0	0.6	1.4
RLBWL	Percentage loss of lean body mass at which ungulates die	0.3	0.2	0.4
RFATL	Percentage loss of body fat at which ungulates die	0.7	0.4	1.0
GWP	Water content per kilogram of protein	4.0	2.0	6.0
FATEN	Energy gained (in kilojoules) from catabolizing 1 kg body fat	39330	20083	50208
LEAN	Energy gained (in kilojoules) from catabolizing 1 kg lean tissue	22175	12552	25104
SDMC	Multiplier for brisket height in each ungulate category	1.0	0.6	1.4
FGB	Forage intake (in kilograms) per kilogram of initial body mass	0.025	0.015	0.035
REF	Multiplier (unitless) for the refugium value of forage in each habitat	1.0	0.4	1.6
ENPK	Multiplier (unitless) for the energy gain per kilogram of forage intake	1.0	0.6	1.4
RANDX	Parameter substituted for the random number used in the movement rule	0.5	0.001	0.999

variation of 1%. When groups of parameters were expected to vary simultaneously (e.g., initial body fat content might increase or decrease in all ungulate categories as a function of summer range conditions), multipliers were used to vary the group of parameters simultaneously in the same way (Table 7). Correlation analysis among the parameters in the sensitivity analysis indicated that the parameters were relatively independent, as all r^2 values were <0.09 between pairs of parameters.

Variance in ungulate survival was explained primarily by four parameters, each of which explained $\geq 10\%$ of the variance (Fig. 3a). Survival of elk and bison calves was sensitive to their initial body mass (BM_i) and the upper snow water equivalent threshold at which foraging is precluded (SWHI), suggesting that small differences in these estimates can have relatively large effects on calf survival. Bison calf survival also showed sensitivity to the snow depth in forests [PSN(24)], as did bison cows and elk bulls. Survival of bison cows was also sensitive to snow water equivalent in forests [PSN(25)], and to the upper threshold of snow water equivalent at which foraging stops (SWHI). These results might indicate that survival of bison cows and calves partly hinges on snow conditions in forested areas. Note that a predetermined amount of mass loss results in ungulate death during the simulation. Mass loss is offset by foraging. Mass gain, however, is not permitted in the model. This may cause a nonlinear relationship between the foraging parameters and survival, explaining why the sum of the sensitivity measures is relatively low. In addition, stochasticity in a model (ungulate movement in this model) also is likely to contribute considerably to the variance in model output (Bartell et al. 1986).

Variance in the amount of biomass remaining at the end of the winter in each habitat was explained by a number of parameters (Fig. 3b), all of which were re-

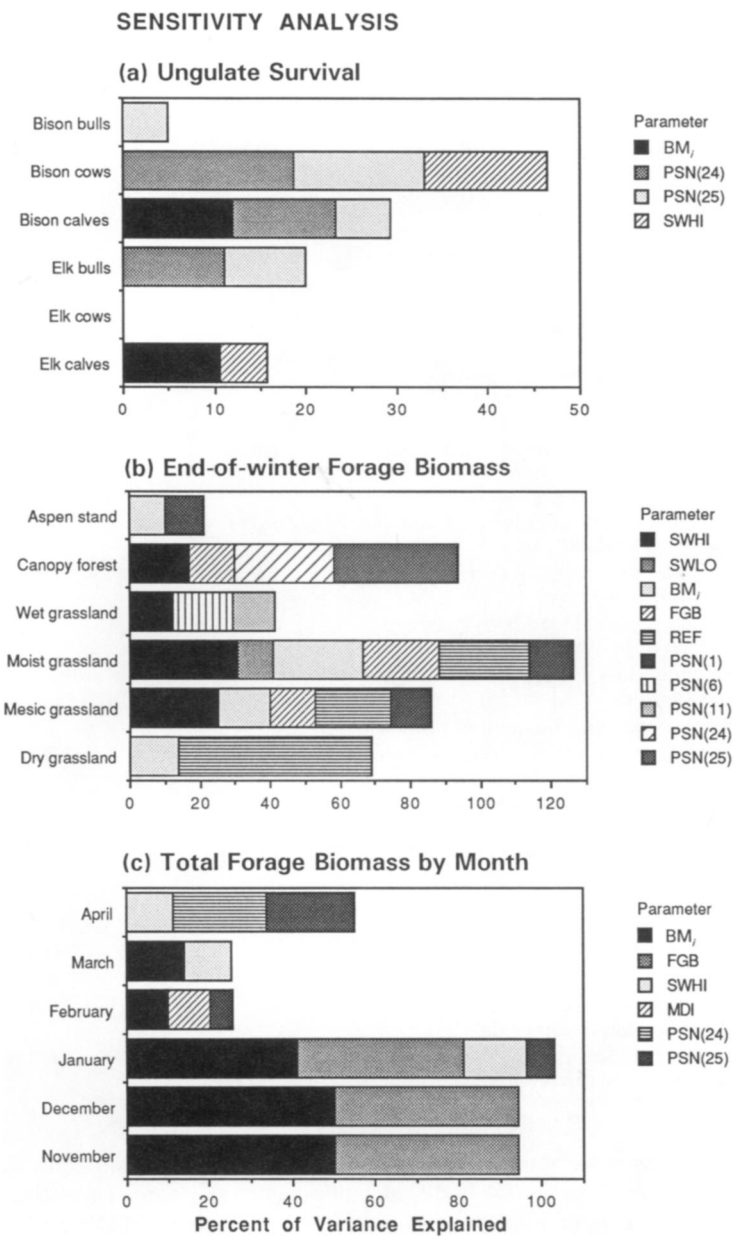

FIG. 3. Results from sensitivity analysis of the NOYELP model during the 1988–1989 winter for (a) survival in each ungulate class, (b) forage biomass remaining in each habitat at the end of the winter, and (c) total forage biomass across the landscape at the end of each month. Parameters were varied by 1% of their nominal values. See Table 7 for parameter definitions and values.

lated to biomass removal by ungulates. Parameters associated with snow conditions (PSN(x)) and snow effects on foraging (SWHI, SWLO) were important for most habitats. The initial body masses of the animals (BM_i) and their feeding rate (FGB), both of which control how much forage is removed from the landscape, were also important, similar to the results of Owen-Smith and Novellie (1982). In addition, there was sensitivity in moist, mesic, and dry grasslands to the value of the refuge biomass (REF). The sum of the sensitivity measures exceeds 100% for moist grassland, indicating that interaction effects among parameters and nonlinearities in the model play a role in the calculation of sensitivity measures.

The low sum of sensitivity measures for aspen biomass at the end of the winter might be due in part to its spatial extent and distribution. Aspen stands are sparsely represented in the landscape ($\approx$1% of the landscape) and are dispersed spatially. The initial biomass of aspen and the initial ungulate masses explain part of its variance. The squared Pearson correlation coefficient between the aspen biomass and the maximum

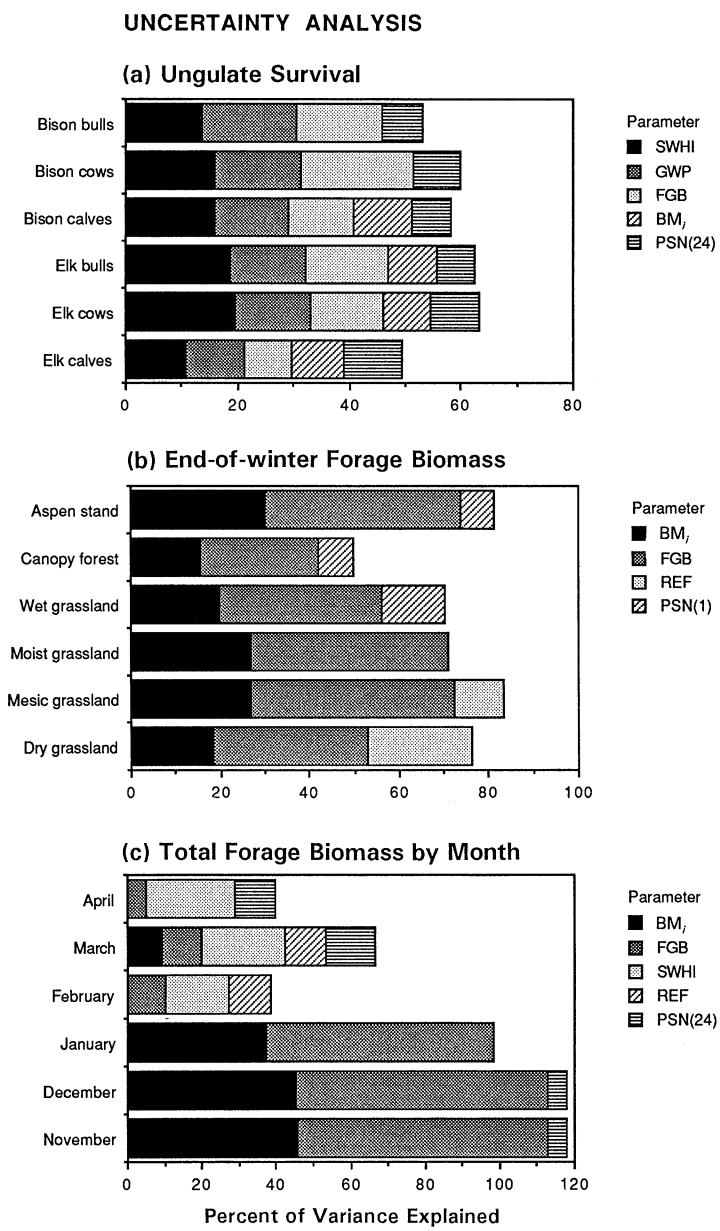

FIG. 4. Results from uncertainty analysis of the NOYELP model during the 1988–1989 winter for (a) survival in each ungulate class, (b) forage biomass remaining in each habitat at the end of the winter, and (c) total forage biomass across the landscape at the end of each month. Parameters were varied across the ranges shown in Table 7. See Table 7 for parameter definitions and values.

daily moving distance (MDISTM) indicates that MDISTM explains an additional 7.8% of the variance.

There was a marked change in sensitivities with time for the total biomass remaining on the landscape (Fig. 3c). The initial ungulate body masses (BM_i) and the ungulate feeding rate (FGB) were the only parameters affecting biomass in November and December, and the summed sensitivity measures explained 95% of the variance in the predictions. In January the snow water equivalent at which foraging stops (SWHI) and the snow density in forests (PSN(25)) contributed to the variance. In late winter (February and March) the importance of the initial ungulate parameters was greatly diminished, and by April snow conditions dominated.

Uncertainty analysis.—The second set of 100 simulations (uncertainty analysis) selected all parameters from uniform distributions with upper and lower limits as shown in Table 7. This set of simulations represents the situation where estimates of the true values of model parameters are uncertain, and we wish to explore the relative responses of the ouput variables from varying the parameters within an acceptable range and as-

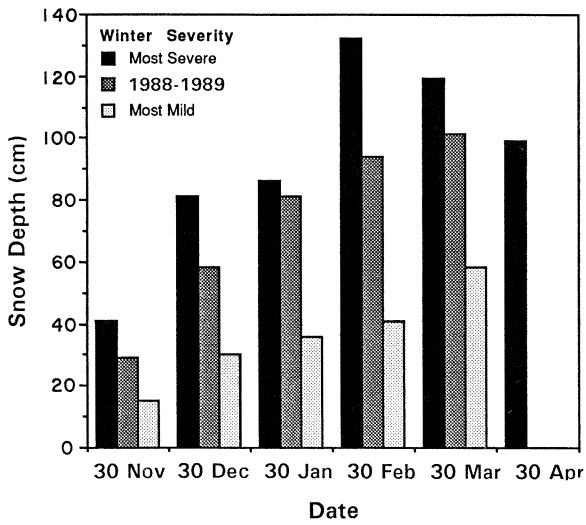

FIG. 5. Monthly snow depths from the Lupine Creek Snow course for the winters of mild (1976–1977), "average" (1988–1989), and severe (1975–1976) snow conditions.

suming a uniform distribution. The variances in the parameters ranged from 13% to 48% of their mean values (Table 7). Variances in projected ungulate survival ranged from 54% (for bison bulls) to 140% (for elk calves) of their mean values. Variance in total biomass remaining in each habitat ranged from 29% (for dry grasslands) to 69% (for wet grasslands) of their mean values.

Explanation of the variance in ungulate survival is improved considerably in the uncertainty analysis as compared to the sensitivity analysis (Fig. 4). Approximately 60% of the variance in ungulate survival is explained by five parameters, each of which contributes toward explaining at least 5% of the variance in the outputs (Fig. 4a). The upper threshold of snow water equivalent at which foraging stops (SWHI), the ratio of water to protein (GWP) (Eq. 13) to calculate mass loss, and the ungulate feeding rate (FGB) are consistent contributing parameters. As in the sensitivity analysis, initial body mass (BM_i) plays a role for elk and bison calf survival and a lesser role for elk cows and bulls. The snow depth in the forest habitat (PSN(24)) also was consistently important, although the r^2 value was lower.

Variation in the end-of-winter biomass by habitat was explained by four parameters in the uncertainty analysis (Fig. 4b). The initial ungulate body masses (BM_i) and feeding rates (FGB) were consistently important, and, combined, they explained from 45% to 75% of the variance in each habitat. In addition, the refuge value for the forage (REF) was important in both dry and mesic grasslands, and the snow depth in relatively flat nonforested sites (PSN(1)) contributed to the biomass remaining in aspen stands, canopy forests, and wet grasslands.

There was again a marked change in the contribution of different parameters to variation in total biomass across the landscape through time (Fig. 4c). As in the sensitivity analysis, the initial ungulate body masses (BM_i) and feeding rate (FGB) were important during the first three winter months. During late winter the contributions of these parameters diminished, and the importance of snow conditions (SWHI, PSN(24)) and the refuge value of the forage (REF) increased.

The combination of sensitivity and uncertainty analysis through Monte Carlo simulations demonstrated a direct response of early-winter and total remaining biomass to ungulate feeding activities as controlled by both ungulate parameters and snow conditions. Finally, results suggest that the variability of model predictions would decline most in response to better estimates of the initial ungulate body masses (BM_i), ungulate feeding rates (FGB), the ratio of water to protein (GWP), and the upper threshold of snow water equivalent at which foraging stops (SWHI).

SIMULATION EXPERIMENTS

Winter severity, fire size, and fire pattern

To examine the interaction between fire patterns and weather conditions on ungulate survival, a factorial simulation experiment was conducted. The most mild (1976–1977) and most severe (1975–1976) winters recorded during this century with respect to snow conditions were identified from weather records to bracket known weather extremes (Fig. 5). We used only snow conditions to indicate winter severity because temperature is not included explicitly in the model. Three levels then were specified for the scale of simulated fires by specifying the percentage, p, of the study area burned: 15%, 30%, and 60% (the 1988 fires burned 22% of the northern range). Two alternative fire patterns were generated for each of the p values to bracket the extremes in fire heterogeneity. A fragmented burn pattern was generated by distributing burned grid cells at random across the landscape (Fig. 6a–c). A clumped pattern was generated by generating a single patch of burned cells centered on an arbitrary location in the west–central portion of the study area (Fig. 6d–f) (Universal Transverse Mercator projection values of 529675 east and 4973175 north). Finally, we simulated both the initial postfire winter, when burned areas contained no forage, and the later postfire winter, when burned areas had enhanced forage quantities. This factorial simulation resulted in 24 different scenarios. In the simulations presented here, we fixed the initial numbers of elk at 18 000 and bison at 600, approximating the population size during the fall of 1988 (Singer et al. 1989, Singer and Norland, *in press*; M. M. Meagher, *personal communication*) (Table 3). Each scenario was replicated three times using different random number seeds.

Mild winter.—No ungulate mortality occurred in any of the simulations (15%, 30%, and 60% of the land-

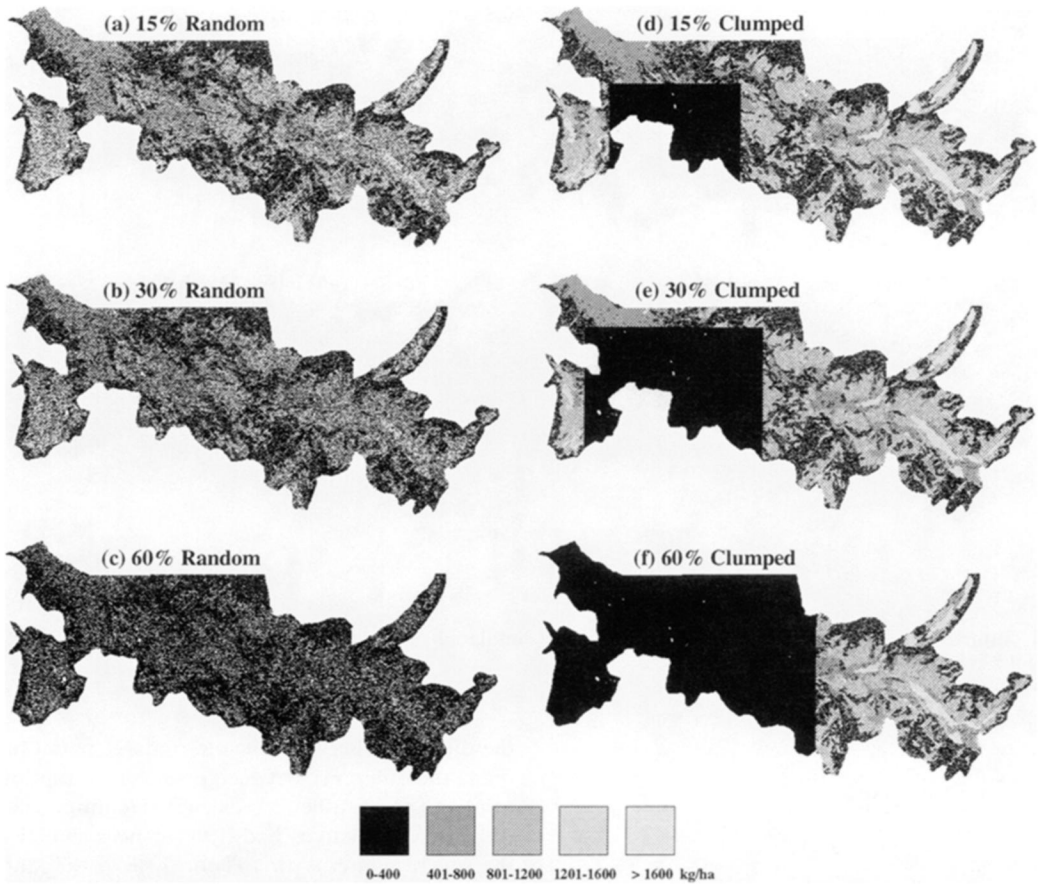

FIG. 6. Spatial patterns of initial forage biomass with simulated fires (15%, 30%, and 60% of the landscape) used in the factorial simulation experiment: (a–c) fragmented patterns, in which burned grid cells are distributed at random across the landscape, and (d–f) clumped patterns, in which burned grid cells are distributed as a single contiguous fire.

scape burned). When winter conditions were mild (the 1976–1977 winter), simulated snow conditions reflected the low winter severity. During early winter, snow depths were generally <20 cm (Fig. 7a). Even during late winter, snow depths were <60 cm across most of the landscape (Fig. 7b). All elk and bison survived during the initial postfire winter even when fire covered as much as 60% of the northern range. Forage augmentation during the later postfire winter produced no population-level response because access to forage was not limiting.

Severe winter.—When winter conditions were severe (the 1975–1976 winter), simulated snow conditions differed dramatically from the mild winter. During early winter, only south-facing slopes had ≤ 20 cm of snow accumulation (Fig. 7c). By 30 March, snow depths exceeded 100 cm across most of the landscape, and only the low-elevation Mammoth–Gardiner area and south-facing slopes had minimal snow depths (Fig. 7d). The spatial locations of ungulates during the simulation reflected the snow accumulation patterns. During the postfire winter simulation when 60% of the landscape burned in a single patch, ungulates congregated on south-facing slopes during early winter, then spread out across the landscape as conditions worsened and accessible resources were depleted (Fig. 8); in this scenario, all elk and bison died before the simulation was completed.

1. *Initial postfire winter.*—Ungulate survival varied with both fire size and fire pattern during the severe winter. During the initial postfire year (when no forage was available in burned areas), ungulate survival always decreased as the proportion of the landscape burned increased (Fig. 9). No elk or bison survived the winter when 60% of the landscape was burned. The survival of cows and bulls was always greater than calf survival for both elk (Fig. 9a) and bison (Fig. 9b). For elk, the cows and bulls generally showed similar survival patterns with the exception of the 15% random burn, where cow survival was 19% and bull survival $\approx 36\%$ (Fig. 9a). For bison, survival of bulls substantially exceeded the survival of cows (Fig. 9b) for each fire size (p).

Within a given fire size, ungulate survival was always greater with the clumped burn pattern than with the random burn pattern (Fig. 9). For elk and bison calves

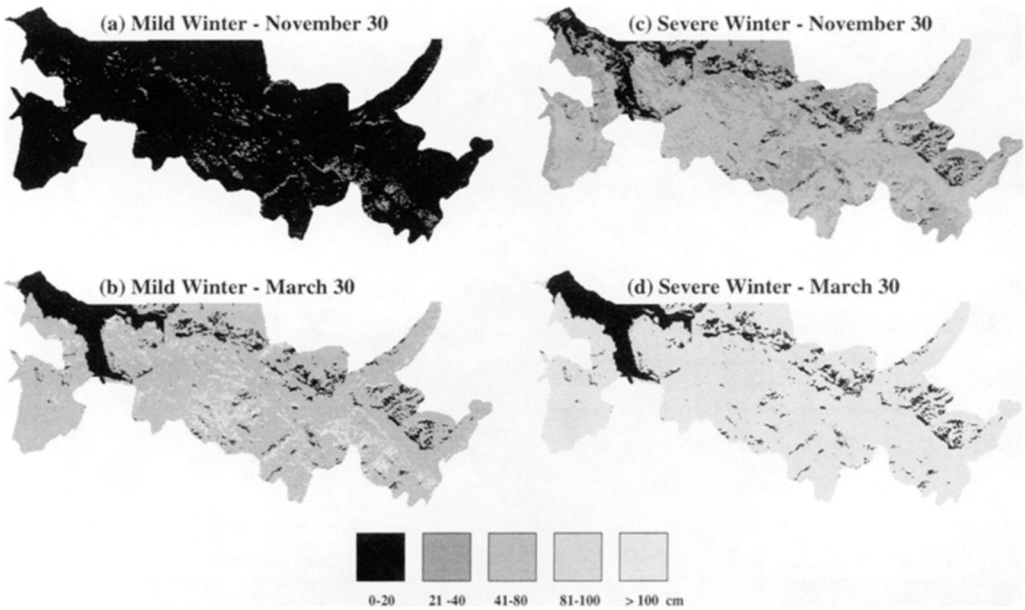

FIG. 7. Simulated snow conditions at two dates during the simulations for (a, b) the mild winter conditions of 1976–1977, and (c, d) the severe winter conditions of 1975–1976.

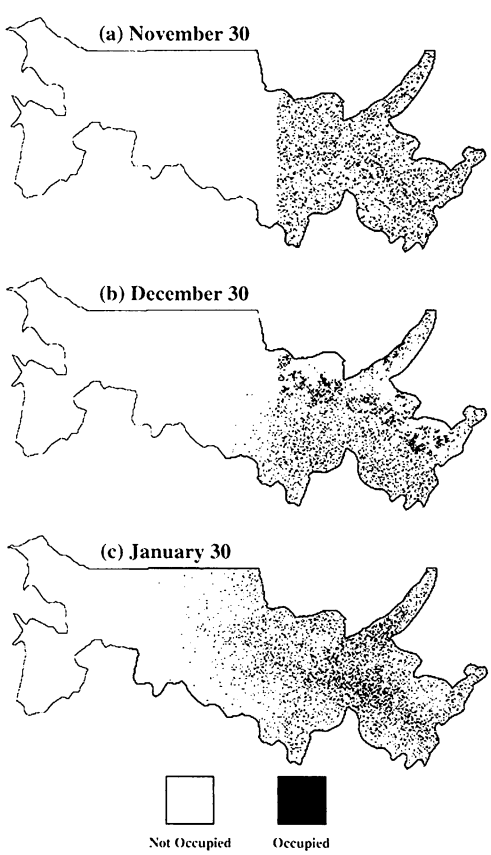

FIG. 8. Simulated locations of ungulates during a postfire severe winter in which 60% of the landscape was burned as a single patch. By 30 March, all simulated ungulates had died.

the difference between the alternative spatial patterns made the difference between no survival (random pattern) and some, albeit low, survival (clumped pattern). Bison and elk calves had little or no survival during the severe winter with 15% or 30% of the landscape burned at random, but some calves survived if the burn was clumped. With the smaller fire ($p = 0.15$), survival of elk cows increased from 18% with a random burn to 43% with a clumped burn. Ungulate survival was clearly influenced by both fire size and pattern. For example, a fragmented fire that affected 15% of the landscape and a clumped fire that affected 30% of the landscape resulted in similar survival of elk cows, bison cows, and bison bulls.

2. *Later postfire winter.*—During the later postfire winter, when forage quantities were enhanced in burned areas, ungulate survival generally increased with the proportion of the landscape burned (Fig. 10). Adult survival was still greater than calf survival, but the differences were less pronounced. The effect of fire pattern was most apparent at low p values (e.g., 15%), when survival was greater with the clumped fire than with the fragmented fire. For example, survival of elk cows and bulls increased from $\approx 33\%$ in a random burn to $\approx 45\%$ with a clumped burn at $p = 0.15$ (Fig. 10a). At high values of p (e.g., 60%), there generally was less difference in survival between the fire patterns, and the survival with the random pattern even exceeded the clumped pattern occasionally. There also was variability in the responses among the ungulate classes. Bison bulls had the least response to both p and spatial pattern, whereas calves of both species and elk cows showed the greatest range of response.

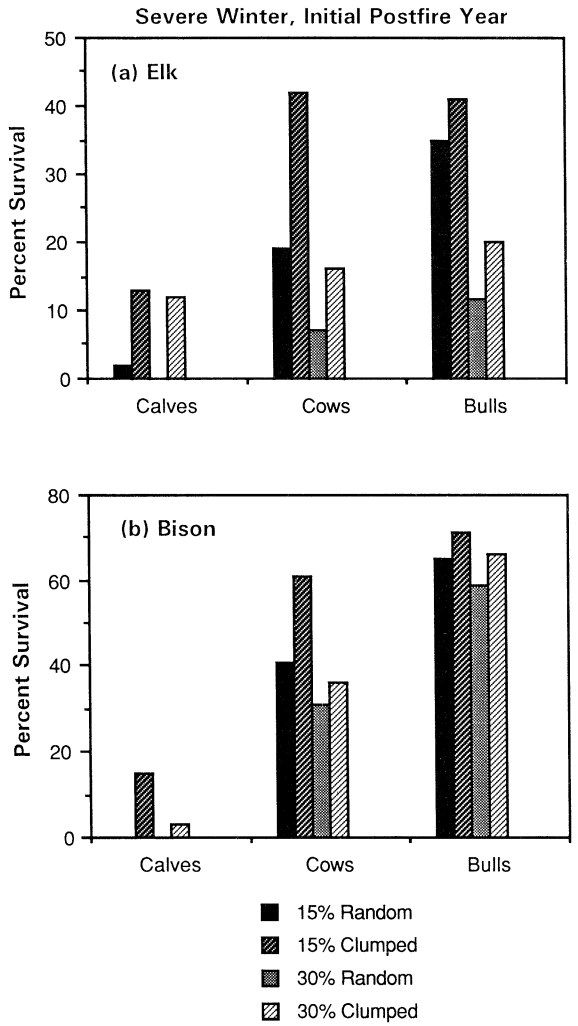

FIG. 9. Simulated survival of (a) elk and (b) bison during a postfire (i.e., no forage in burned areas) severe winter under various proportions of the landscape burned and alternative fire patterns.

ALTERNATIVE SPATIAL PATTERNS FOR THE 1988 FIRES

To further investigate the effects of alternative spatial patterns of fires with a given proportion of the landscape burned, we compared the actual 1988 fire patterns, in which 22% of the landscape was burned, with five alternative spatial arrangements that also had $p = 0.22$. These patterns again included the random and single-patch fires but also included fires distributed as 3, 6, and 12 patches (Fig. 11). We used the winter weather conditions from 1988–1989 in these simulations, i.e., initial postfire winter.

Simulation results demonstrate variability in survival in response to the spatial arrangement of burning (Fig. 12). The actual burn patterns from the 1988 fire resulted in the highest survival of elk cows and bulls and the second highest survival of calves. Among the alternative spatial arrangements, survival generally increased with increasing contagion of the burn pattern. That is, survival was lowest when the burn pattern was more fragmented and greatest when the burn was more contiguous. The single-patch burn pattern resulted in the highest survival of bison, and the actual fire patterns had the second highest survival projections. Again, the more fragmented patterns generally had lower survival.

DISCUSSION

Winter severity was the dominant influence on simulated ungulate survival (see summary of effects in Table 8). Snow accumulation and snow mass have been shown to be the most important environmental factors regulating winter survival of many ungulate species

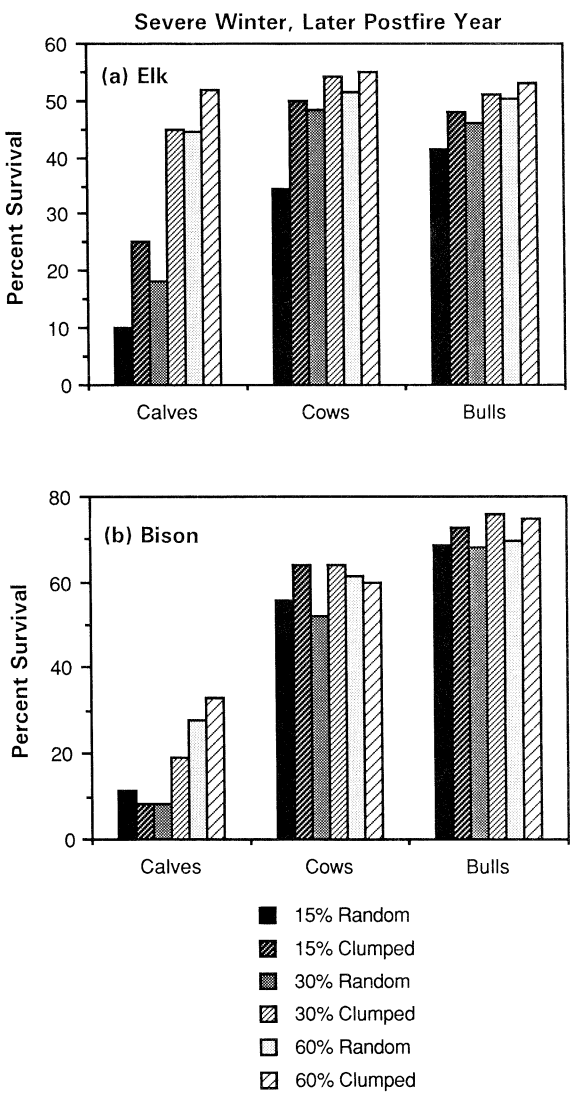

FIG. 10. Simulated survival of (a) elk and (b) bison during a second postfire (i.e., enhanced forage in some burned areas) severe winter under various proportions of the landscape burned and alternative fire patterns.

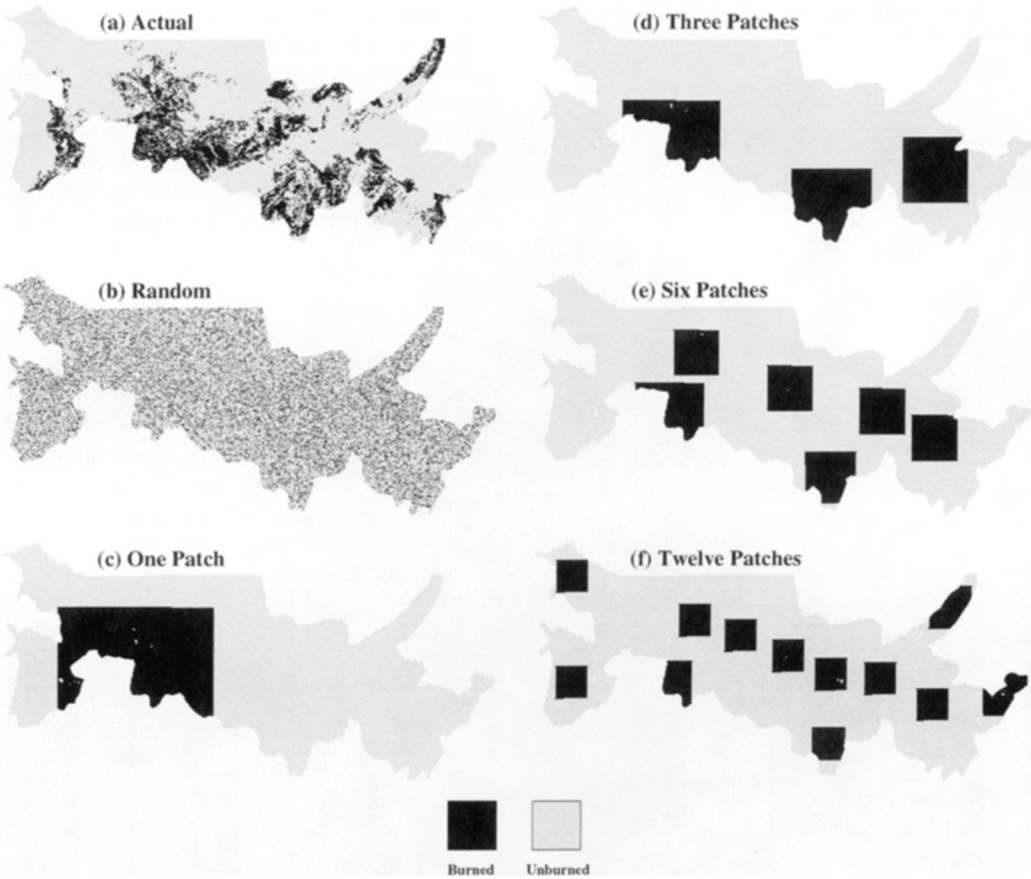

FIG. 11. Alternative fire patterns in which 22% of the landscape is considered to be burned. (a) actual, (b) random, (c) 1 patch, (d) 3 patches, (e) 6 patches, and (f) 12 patches.

(Edwards 1956, Gilbert et al. 1970, Brown and Theberge 1990). For example, Edwards (1956) has shown a negative relationship between ungulate population levels and snow depth. Although low temperatures are also an important aspect of winter severity, large ungulates possess considerable thermal inertia, aiding in thermoregulation (Hudson and Frank 1987). Thus, even though thermal factors help govern snow characteristics, it is the snow characteristics (as shown by their importance in the sensitivity and uncertainty analyses reported here) that may be of paramount importance to winter survival.

When winter conditions were severe, ungulate survival was quite low in all simulations. When winter conditions were extremely mild, even fires that affected 60% of the landscape had no effect on ungulate survival during the initial postfire winter. Thus, forage on only 40% of the northern range appeared capable of supporting a relatively large ungulate population during an extremely mild winter. In an analysis similar to ours, Hobbs (1989) found that changing input weather data in a winter simulation of mule deer resulted in a greater change in doe and fawn survival than was caused by a 10-fold change in the amount of food available to each deer at the beginning of the winter. Clearly, the reduction of forage due to fire should influence ungulate survival at some initial ungulate density, even in mild winters, but this density might be higher than would ever occur naturally. The size of the ungulate population has varied through time on the northern range, but our factorial simulation did not address the effects of population size.

The effects of fire on ungulate survival became important in our simulations when winter conditions were average to severe, and effects were apparent in both the initial and later postfire winters (Table 8). During the initial postfire winter, when no resources were available in burned areas, ungulate survival decreased with increasing fire size. During the later postfire winters, when resources were enhanced in burned areas, ungulate survival increased with increasing fire size.

In spring and summer ranges, fire during the growing season has been shown to be a strong attractor that draws ungulates into recently burned sites (Shaw and Carter 1990). Reasons frequently cited for this behavior include the high nutrient content of regrowing forage (McNaughton et al. 1988, Hobbs 1989) and the reduction of litter accumulation (Knapp and Seastedt

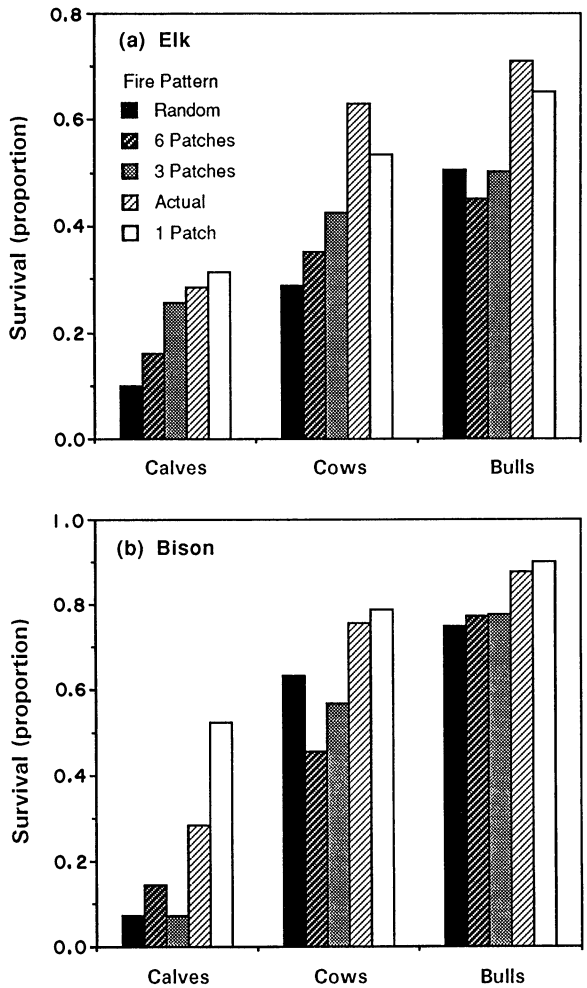

FIG. 12. Simulated survival of (a) elk and (b) bison during the postfire winter of 1988–1989 with alternative spatial arrangements of burned areas.

1986). However, as they enter dormancy most perennial species recover nutrients from leaf tissue and store them in belowground tissue (Adams and Wallace 1985), producing low-quality forage on winter range sites (Morgantini and Hudson 1989). Therefore, increases in forage quantity should be the greatest enhancement to burned winter range sites (Wallace et al., *in press*). The model simulated increased ungulate survival with burning during later postfire winters. Unlike the predictions from nutrition-based models (e.g., Hobbs and Swift 1985), this was due to the increased biomass levels in burned areas relative to similar sites that were not burned. Increased biomass has also been cited as an important reason for elk to use previously burned habitats on winter range sites in Glacier National Park (Martinka 1974).

The spatial pattern of the fire also influenced ungulate survival. Ungulate survival was greater with clumped than fragmented fire patterns during more severe winters, but only for the small to moderate fires (Table 8). During the initial postfire winter, survival could be 100% greater in the single-patch burn than in the random burn when 15% or 30% of the landscape was affected (e.g., elk in Fig. 9). When 60% of the landscape was burned, there was no ungulate survival during the severe winter (i.e., fire scale was more important than fire pattern). During the later postfire winter, survival again was enhanced most by the clumped fire pattern for the small to moderate fires (e.g., 15% and 30% in Fig. 10). When 60% of the landscape was burned, there was little difference between the two fire patterns. Other studies have shown that as the proportion of a landscape occupied by a particular habitat type increases beyond ≈ 0.6, there are few differences in landscape pattern between randomly distributed and aggregated arrangements of habitat (e.g., Gardner et al. 1987, 1991). Therefore, it is not surprising that we see few ungulate responses to spatial patterning with the large (60% of the landscape) fire size.

The interaction between fire scale and spatial pattern suggests that knowledge of fire size alone is not always sufficient to predict ungulate survival. The spatial patterning of fire will influence ungulate survival if fire covers small to moderate proportions of the landscape (e.g., 15% or 30%) and if winter snow conditions are moderate to severe. If fires affect $\geq 60\%$ of the landscape, however, it is the scale of the fire rather than the spatial pattern that is important.

When alternative fire patterns were simulated for the 1988–1989 winter, it was surprising to observe the highest elk cow and bull survival with the actual 1988 fire pattern. This result may point to the importance of the precise spatial location of a fire. The 1988 fires affected more high-elevation sites on the landscape than

TABLE 8. Summary of the simulated effects of winter severity, fire size, and fire pattern on ungulate survival in northern Yellowstone National Park during winter. Initial ungulate numbers were 18 000 elk and 600 bison in all simulations. During the initial postfire winter, forage is removed from burned areas; during the later postfire winter, forage is augmented in burned areas.

Winter severity	Fire size	Fire pattern	Ungulate survival
		Initial postfire winter	
Mild	No effect	No effect	Very high
Severe	None	···	Moderate to low
	Large	No effect	Very low
	Small to moderate	Clumped	Low
		Dispersed	Very low
		Later postfire winter	
Mild	No effect	No effect	Very high
Severe	None	···	Moderate to low
	Large	No effect	High
	Small to moderate	Clumped	Moderate to high
		Dispersed	Moderate

did our alternative spatial patterns. These locations tend to be more densely forested and are less important to the wintering ungulates and the lower elevation grassland communities. Thus, varying the position of particular fire patterns on the landscape might be worthwhile to consider in future simulations.

Our simulations did mimic known ungulate dynamics in the Yellowstone National Park landscape, and we also note that our simulations produced results similar to dynamics observed in other grazing systems subject to fire and variable winter severity. For example, our model predicted higher survival of bull bison and elk as compared to cows or calves during severe winters. Higher survival rates for bison bulls than cows have been noted in a similar environment in Canada,[7] perhaps due to their ability to move through deeper snows than the smaller females (Meagher 1973).

The sensitivity and uncertainty analyses performed on the model identified several parameters that were consistently important influences on the model projections. Of particular note were parameters associated with foraging, including the initial body masses of the ungulates, their feeding rates, and the upper threshold of snow water equivalent at which foraging ceases. The consistent importance of these parameters in explaining the variation in model output suggests the value of additional empirical study on foraging processes in snow. The sensitivity analyses suggest that energy gain is the key process influencing ungulate survival, and the unimportance of initial forage availability and maximum daily moving distances was surprising to us. However, Hobbs (1989) also observed that the processes influencing energy intake exerted a much greater impact on energy balance of mule deer during winter than processes affecting their energy expenditure.

When interpreting these simulation results, it is important to be mindful of what was not included in the model or addressed here. First, the results presented were for simulations in which the initial density of ungulates in the study area was held constant. Under varying animal densities, different results might be obtained. Second, the simulation only extends for a single winter season. Therefore, we have not included ungulate reproduction, the potential for feedbacks between the ungulates and the next season's vegetation (e.g., nutrient enhancements) or the effect of the summer precipitation on pre-winter forage availability. All of these factors are of importance in projecting the long-term dynamics of the northern Yellowstone landscape.

In conclusion, for the ungulate density simulated here, resources were not limiting to ungulates when winter conditions are mild. Hence, fire size and pattern had no appreciable effect on ungulate survival during mild winters. Resources were limiting when winter conditions were severe, however. During severe winters, fire decreased ungulate survival during the initial postfire winter but could enhance survival during later postfire winters. Both fire size and the spatial pattern of fire were important in severe winters. At some fire sizes, ungulate survival was higher with a clumped than with a fragmented fire pattern, suggesting that a single, large fire is not equivalent to a group of smaller disconnected fires.

[7] See footnote 4.

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