LANDSCAPE-LEVEL INTERACTIONS AMONG UNGULATES, VEGETATION, AND LARGE-SCALE FIRES IN NORTHERN YELLOWSTONE NATIONAL PARK

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INTRODUCTION

The scale of the 1988 fires in Yellowstone National Park (YNP) raised numerous questions for the management of natural areas subject to large, infrequent disturbances. An important management issue in YNP involves the interaction of large-scale fire with the large assemblage of native ungulates and vegetation dynamics in the landscape. In this 2-year research project, we are using landscape modeling and field studies to address basic questions about the effects of fire scale and heterogeneity on (1) resource utilization and survival of free-ranging elk (Cervus elaphus) and bison (Bison bison) and (2) the production and regeneration of preferred forage grasses and aspen in northern YNP. We are testing a series of eight hypotheses within the framework of two basic questions. First, we ask whether there are thresholds in fire size that interact with winter severity and ungulate density to determine ungulate resource use and survival on the winter range in northern YNP. This question focuses on the effects of fire size, regardless of the spatial pattern of burning. Second we ask, if large fires occur, does the spatial distribution of burned areas (and hence of higher quality forage) influence ungulate resource use during winters subsequent to the first post-fire year. In this question, we are addressing the effects of spatial pattern on herbivory.

We focus on elk and bison because these are by far the most numerous ungulates in the area (Houston 1982), and we have chosen to examine winter grazing and browsing 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 ways that we represent as hypotheses described later. In addition, the activities of animals can be readily monitored in the winter, and the exact locations of feeding and bedding sites can be determined. Travel routes are easily monitored, and the ability to sight animals is high; therefore, group locations and sizes can be readily determined.

This research complements ongoing studies in YNP by expanding the spatial scale at which

plant-herbivore dynamics are considered and by explicitly addressing the effects of spatial heterogeneity. Our research will produce a spatially explicit simulation model of the 78,000 ha winter range that predicts plant and ungulate dynamics under varying fire sizes, fire patterns, winter weather scenarios, and ungulate densities. The model and field studies will allow quantitative comparisons of the effects of large and small fires on ungulate survival and will thereby permit the simulation of the effects of alternative fire management scenarios.

STUDY AREA

The northern winter range comprises some 78,000 ha in YNP, although its effective areal extent varies from year to year and during the course of a single winter in relation to snow conditions (Houston vegetation is predominantly 1982). The sagebrush-grassland, interspersed with coniferous aspen groves, and riparian willow forests, communities (Despain 1991). Tree-ring evidence suggests that eight to ten extensive fires occurred in the area during the last 300-400 years, but no large fires have occurred previously in this century During the 1988 fires, (Houston 1973). approximately 34% of the winter range burned, including 10% of the grasslands (Preliminary Burn Survey 1988).

♦ FIELD STUDIES

ASPEN SAMPLING

It has been hypothesized that the extensive fires in the past periodically stimulated abundant browse and forage production across a large portion of the landscape, thereby permitting some aspen sprouts to escape browsing long enough to regenerate tree-sized stands. We tested this hypothesis following the 1988 fires by sampling sprout density and browsing intensity in six burned aspen stands, in six unburned stands located close to the fires, and in six "remote" unburned stands located 2 to 4 km from the fires.

METHODS

Aspen sampling was initiated in May 1990. A total of 18 aspen stands were selected for study,

including three stands at each of six sites: two burned areas, two unburned areas located near an extensive burn, and two unburned sites remote from an extensive burn. The locations of these stands were digitized, and distances to burned areas determined by using the GIS (Table 1). A permanent transect was extended through the middle of the longitudinal axis of each stand. From this central transect, all browsed and unbrowsed aspen sprouts were counted in five 1 m belt transects that extended from the central transect to the edge of the stand. Belt transects alternated between the left and right sides of the central transect and were spaced equidistantly. Aspen sprouts were classified as "new" sprouts of the year or "old" sprouts that were greater than one year in age. In addition, sprouts were categorized by height in 10 cm increments.

The 18 aspen stands were resampled in September 1990 to estimate summer browsing intensity and the abundance of sprouts available for winter browsing. Following discussions with park biologist Don Despain, a new category was added. Aspen sprouts were classified by growth form (juvenile or adult) because the juvenile growth form is the only type that can potentially reach tree size. Because our hypotheses address the potential of some individuals to escape herbivory and reach tree size, this additional category is useful. Sampling was repeated during May and September 1991.

During September and October 1990, increment cores were obtained from aspen trees in stands adjacent to the 18 study stands for determination of stand age structure. Data regarding the establishment periods of mature aspen stands in the Park will enhance our interpretation of the implications of fire and ungulate browsing for the potential establishment of new stands following the 1988 fires. During October and November 1990, the aspen stands were revisited to obtain samples for biomass abundance and forage quality analysis. Five sprouts > 50 cm in height and five sprouts < 50 cm in height were collected from the stands but outside the permanent belt transects. These samples were dried to constant mass, weighed, then ground for chemical analysis.

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RESULTS AND DISCUSSION

Most of the extant tree-sized aspen on the

Category	Study Area Name	Distance to Burned Areas (m)
Unburned, 'remote'	McMinn Bench	3171
	Crevice Creek	1792 to nearest small burn patch
		5150 to main burned area
Unburned, 'near'	Blacktail	426
	Lamar	340
Burned	Blacktail	0
	Upper Lamar	0

Table 1. Distances of aspen study areas from areas burned during the 1988 fires in Yellowstone National Park.Three aspen stands were sampled in each study area.

winter range became established in the late 1800's. Aspen clones are persisting through root sprouting, but few tree-sized stems have regenerated during the 20th century, in part because of heavy winter browsing of sprouts by elk.

Sprout densities in the spring and fall of 1990 and 1991 were significantly greater in the burned stands than in the unburned stands (Table 2). Protein analysis of aspen sprouts sampled in the autumn of 1990 indicate that sprouts from burned stands contain slightly more protein $(\sim 7\%)$ than sprouts from unburned stands ($\sim 6\%$). However, there were no significant differences in browsing intensity; all stands were heavily browsed in both winters and lightly browsed in the summers. We conclude that the fires of 1988 probably will not lead to substantial regneration of tree-sized aspen stands on the northern range. The episode of tree regeneration in the late 1800's apparently resulted not just from extensive fires, but also possibly from altered elk foraging behavior in the presence of wolves, and cooler, wetter climatic conditions.

GRASSLAND SAMPLING

The grassland sampling serves several purposes. First, a set of pre-winter biomass samples obtained in autumn 1990 provides estimates of the available winter forage in different vegetation classes. These values are being used to initialize the simulation model. Second, biomass samples obtained from six 30 m by 30 m gridded plots were used to estimate the finer scale spatial heterogeneity of forage availability and provide greater insight into the foraging decisions made by ungulates within resource patches. Third, biweekly observations of fixed viewing areas will provide time-series data on habitat utilization by ungulates on the northern range throughout the winter. These data will be used to determine actual habitat use and test the ability of the simulation model to make reasonable projections of patterns of ungulate habitat use. Fourth, biomass samples obtained from grazed and ungrazed sites throughout the winter will be used to estimate grazing intensity as a function of site-specific variables such as snow depth, snow density, slope, and aspect. These data also will be used in testing the model.

METHODS

Extensive analyses initially were conducted on the YNP GIS to locate sampling sites for all the grassland studies. The northern range study area was demarcated following Houston (1982) then stratified into the following vegetation classes based upon burning status and gross primary productivity: (1) burned mesic grassland; (2) burned moist grassland; (3) burned wet grassland; (4) unburned dry grassland; (5) unburned mesic grassland; (6) unburned moist grassland; (7) unburned wet grassland; (8) burned canopy burned forest; and (9) unburned canopy forest. For the pre-winter forage biomass estimates,

Category	D	Density of aspen sprouts (ha ⁻¹)				
	Adult	Juvenile	Total			
	Fall	1990	A Branch Marine			
and a second	(7.40)		155.050			
Burned	67,619	89,740	157,359			
	(113,582)	(123,708)	(216,667)			
Unburned, 'near'	28,870	34,312	63,182			
	(31,785)	(36,218)	(64,378)			
Unburned, 'remote'	48,399	24,053	72,453			
	(59,228)	(31,963)	(72,879)			
a wa glash	Fall	1991				
Rumed	82,420	41,140	123,561			
and the second	(120,266)	(49,664)	(159,616)			
Unburned, 'near'	28,790	21,389	50,180			
	(26,162)	(26,214)	(49,416)			
Unburned, 'remote'	26,999	10,948	37.948			
Editoria - Lasterio franceses	(37,453)	(15,049)	(44,505)			

a minimum of three sampling sites were located within each of these classes, spanning the geographic extent of the northern range. However, it was possible to sample additional sites within these categories for a final total of 43 (Table 3). The location of each site is stored in the GIS. At each site, two 100 m transects were established such that the transects are perpendicular and intersect at their mid points. Ten biomass samples were obtained from 20 cm x 20 cm plots along each transect, for a total of 20 samples per site. Samples were dried to constant mass and the mass recorded. Subsamples of the biomass collected from each site were then ground and prepared for forage quality analysis. The pre-winter biomass sampling was begun during the first week of October and completed by mid-November of 1990.

Sampling was completed in November of 1990

on six 30 m x 30 m plots for analysis of the spatial variability in available forage at a relatively fine scale. A burned and unburned site were sampled for mesic, moist, and wet grasslands (Lamar Valley, Hellroaring, and Blacktail areas, respectively). At each site, a uniform grid was established such that grid points were placed at 2 m intervals. At each grid point, aboveground biomass in a 10 cm x 10 cm plot was clipped to ground level, dried to constant mass, and the mass recorded. Thus, these data provide 225 spatially explicit estimates of aboveground forage biomass at each of six sites. These data allow us to explore fine-scale spatial variability in forage distribution and the implications of alternative ungulate foraging strategies given this spatial variability.

Ungulate viewing areas were located by using the vegetation classification generated with YNP GIS

Burn Category	Moisture Class	Site Name
Burned	Mesic grassland	Lamar
		Pleasant Valley
		Rescue Creek
		Blacktail
Burned	Moist grassland	Crystal Bench
		Lamar
		Pleasant Valley
		Rescue Creek
		Lamar Canyon
		Hellroaring
		Swan Lake
Burned	Wet grassland	Lamar
	C C	Pleasant Valley
		Rescue Creek/Blacktail
		Lamar Canyon
		Swan Lake
Burned	Canopy forest	Lamar
		Petrified Tree
		Undine Falls
Unburned	Dry grassland	Slough Creek
		Phantom Lake
		MacMinn Bench
[2] 25의 가격 20년 - 1997년 [2] 1997년 - 199		Rainbow Lake
Unburned	Mesic grassland	Lamar
		Little America
		Gardiner Mud Flat
		Blacktail
		Rainbow Lake
Unburned	Moist grassland	Lamar
		Peanut Pond
		Lower Slough
		Mammoth
		Lamar Canyon
		Geode Creek
		Hellroaring

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Table 3 (continued)	au ay an a malant apart will any d	n in mente mana la site
Burn Category	Moisture Class	Site Name
Unburned	Wet grassland	Lamar Round Prairie Lower Slough Turkey Pen Creek Lamar Canyon
Unburned	Canopy forest	Lamar Elk Creek Undine Falls

and by considering accessibility in winter. Twelve viewing areas, each of which provides a view of several square kilometers of the northern range, were established. The boundaries of each viewing area were digitized and stored in the GIS. Each viewing area was visited at a two-week interval beginning in January 1991. The location and sizes of ungulate feeding areas, the percent area affected by feeding craters (in 20% intervals), and the number and locations of elk and bison present at the time of viewing were recorded on 7 1/2' topographic maps. If light, sun angle or weather conditions reduced visibility, the area for which data could not be obtained for that time period was also mapped. These time-series data were digitized in the GIS. Snow conditions through the winter were estimated by recording snow depth and water content at 20 locations along two perpendicular 0.5 km transects at the viewing sites. In addition, snow conditions along a range of slopes and aspects were sampled periodically through the winter along transects.

The field sampling to estimate grazing intensity throughout the winter was modified from our original proposal because of logistic constraints. Both the number of vegetation types sampled and the sampling frequencies were reduced. Burned and unburned moist and wet grasslands were sampled in early winter and late winter to estimate grazing intensity. Biomass was clipped in fifteen grazed and ungrazed paired plots at two or three sites within each habitat type. These data will be used to check model projections periodically during the winter simulations and to relate grazing intensity to local snow conditions. Sampling was completed at the end of the winter season (but before "green up"), when the procedures used to estimate pre-winter forage availability were repeated to determine the amount of biomass remaining on the winter range.

RESULTS AND DISCUSSION

Analysis of the pre-winter forage availability in autumn of 1990 indicates an increase in biomass with increasing moisture and, in general, greater biomass in burned than unburned areas within a given moisture class (Table 4). Burned mesic and moist grasslands had approximately 50 to 100% more forage than equivalent unburned sites. However, burned and unburned wet grasslands have similar biomass values. Forage quality did not differ among sites (Table 4).

Grazing intensity (i.e., the proportion of available forage lost to grazing) in late January did not vary between burned and unburned areas or between wet and moist grasslands (Table 5). However, because the amount of biomass available differed among sites, ungulates obtained differential amounts of forage. Burned sites yielded more forage than unburned sites, and wet sites yielded more forage than moist sites.

Biomass distributions within the 30 m x 30 m grids were analyzed by using geostatistics. No

Burn Class	Moisture Class	Quantity (g/m ⁻²)	Protein (%)	ADF (%)	NDF (%)
Burned	Mesic grassland	170.5 [⊾]	5.46°	60.99ª	38.85°
	Moist grassland	150.3 ^b	5.06ª	61.45°	38.85ª
	Wet grassland	232.0ª	5.42ª	59.43ª	37.43°
	Canopy forest	76.5 ^{c,d}	5.54ª	50.67ª	38.87*
Unburned	Dry grassland	34.0 ^d	5.45°	63.55°	37.90ª
	Mesic grassland	63.3°	6.04ª	51.00ª	33.60ª
	Moist grassland	122.3 ^b	6.99ª	60.57°	39.03°
	Wet grassland	225.8ª	5.02ª	63.23ª	37.50°
	Canopy forest	32.3 ^d	6.43ª	58.00ª	40.20°

Table 5.Mean ungrazed biomass, grazed biomass, and grazing intensity as measured during early winter.Samples were collected during late January and early February 1991.

Burn Category	n	Ungrazed (g/m ²)	Grazed (g/m ²)	Grazing Intensity (%) (g/m ²)	Forage Obtained
	*		Moist Grasslands		
Burned	23	73.2	24.0	64.6	49.2
Unburned	16	59.6	16.8	68.3	42.8
			Wet Grasslands		
Burned	16	168.4	39.6	49.3	128.9
Unburned	16	47.2	21.6	47.4	25.6

significant autocorrelation was found in the biomass distribution in any of the sampling grids. The spatial distribution of the 30 highest biomass points was not significantly different from the Poisson distribution, suggesting that even high biomass is distributed randomly at this spatial scale. However, there were some interesting comparisons in biomass availability among sites (Table 6). At both the moist and mesic sites, more biomass was available in the burned than in the unburned grid, whereas at the wet site, more biomass was found within the unburned grid. Average biomass differed among sites, with the greatest amount in the wet site followed by moist then mesic.

In addition, the amount of biomass that an ungulate might obtain from each grid by using alternative foraging strategies was simulated. In each grid, the amount of biomass that could be obtained from 30 points was simulated in three ways: (1) by selecting random points within the grid; (2) by using actual distributions of feeding craters mapped in similar 30-m x 30-m areas during the winter of 1988-89; and (3) by selecting the grid points with the highest biomass values. The third sampling pattern represents a "smart" feeding pattern of an ungulate with perfect knowledge of biomass distribution within a feeding patch. The "smart" sampling protocol yielded significantly more biomass than the others, but there was no difference in the forage obtained by using the random or actual patterns. This suggests that ungulates may be grazing at random within a feeding patch and that the selection of feeding areas occurs at a broader spatial scale. Because forage quality did not vary among habitats, site selection is likely to be based on the quantity of available forage.

Data analyses for the remaining field studies are in progress. Conclusions will be reported when the study has been completed.

MODEL DEVELOPMENT

THE INITIAL MODEL

The model we developed initially simulated the winter foraging dynamics of large ungulates when the distribution of preferred forage across the landscape is spatially heterogeneous. This initial model permitted us (1) to develop the necessary algorithms for the simulations on the actual Yellowstone landscape, and (2) to explore the interaction of initial conditions and alternative algorithms using known conditions and with lesser computational intensity than required for the northern range. Resource categories were binary (i.e., grid cells are classified as either resource or nonresource) and a 100 x 100 gridded landscape was used in the simulations. Resource sites were distributed across the landscape such that they occupied some proportion, p, of the landscape and had a particular spatial arrangement (e.g., random, patchy, or aggregated). Each resource site was then assigned an initial quantity of forage available at the beginning of the winter season. Two alternative methods of initializing forage abundance were explored. First, we used a

Table 6.	Mean biomass within the 30 m x 30 m
	grids (n = 225 per grid). Means
	followed by the same letter are not
	different from one another (p \leq 0.05,
	Duncan's Multiple Range test).

Site	Burn Category	Quantity (g/m ⁻²)
Blacktail	Burned	90.8°
(mesic)	Unburned	53.0 ^d
Hellroaring	Burned	129.5 ^b
(moist)	Unburned	103.0°
Lamar	Burned	118.8 ^b
(wet)	Unburned	203.0ª

homogeneous distribution in which the mean forage abundance was assigned to each resource site. Second, we used a heterogeneous distribution of forage abundances in which the forage assigned to a particular cell was obtained from a normal distribution based on the mean and variance of the field data. In both cases, the total forage available in the landscape is the same for a given value of p, the proportion of the landscape occupied by resource sites. We assumed each grid cell to represent 1 ha and initially used preliminary data collected across the northern range in January 1990 to provide reasonable estimates of forage availability.

The number of ungulates initially present on the landscape was specified at the beginning of the simulation, and groups of individuals were distributed randomly within resource patches. The use of ungulate groups is reasonable biologically and would be appropriate for the 1 ha spatial resolution of the model. We also specified in the initial model that only one individual or group can occupy a single grid cell at one time.

Forage intake, I, was assumed to be a function of the maximum rate of ingestion, t; the amount of resource available on a particular site, B; and a negative feedback, f(B), based on resource limitation:

$$\mathbf{I} = \mathbf{t} \ \mathbf{x} \ \mathbf{B} \ \mathbf{x} \ \mathbf{f}(\mathbf{B}) \ . \tag{1}$$

The ungulate was assumed to have some maximum foraging rate which can be maintained above a certain threshold, a, of forage availability. As resources fall below this threshold, forage intake will decline until it reaches zero, which can occur when available resources are either completely consumed or fall below some refuge level, r, below which they are unavailable to the grazer (Wiegert 1979, Turner 1988). The mathematical form of the negative feedback is:

$$f(B) = \{1 - [(a - B)/(a - r)]\}.$$
 (2)

The function ranges from 0 to 1 such that when B < r then f(B) = 0 and forage intake (eq. 1) will also go to zero. When $B \ge a$, then f(B) = 1 and forage intake will be at a maximum. Between a and r, f(B) is linear and generates an asymptotic decline in the rate of forage intake. When resources on a particular grid cell fall to the refuge level, that cell is no longer considered to be a resource site. Thus, resource depletion generates changes in the number and size of resource patches on the landscape throughout the simulation.

As resources on the site decline, the animal was also assumed to have an increased likelihood of moving to a new feeding site. This was implemented probabilistically as a function of the amount of resource on a site. As a resource declines in quantity, the probability of moving increases until it reaches 1.0 at the refuge level of forage.

Three alternative simple movement rules were developed: (1) the one-pixel rule; (2) the closest resource pixel rule; and (3) the best direction rule. Common to all three rules is a search distance defining the radius (from its present location) within which an ungulate can perceive resources in the landscape. With the one-pixel rule, an animal that is located within a patch of high resources will forage on a grid cell then, as forage declines on that cell, the animal can move to an adjacent pixel at random among resource sites in the patch. The animal can move only one pixel per time step. An animal that is located on a nonresource site away from a resource patch searches the landscape then moves directionally toward the most promising resource area. The search entails comparing the number of resource pixels present in each of four different wedge-shaped areas

(north, south, east, or west) within a set radius, which can be varied to represent the resource utilization scales of different animal species. The actual movement is then limited to one adjacent cell in the direction that contains the greatest number of resource pixels. One additional constraint was placed on movement such that the animal cannot return immediately to the grid cell it just left. This simple self-avoidance rule precludes an artifical back-and-forth movement.

The next two rules permit movements up to some maximum distance during each time step. In both rules, an ungulate can move sequentially among grid cells until it either obtains the maximum daily forage intake or reaches the maximum movement distance. In the closest resource pixel rule, an animal that is ready to move will examine the landscape within the search radius and identify the resource pixel that is closest to its present location. The animal then moves to the closest unoccupied resource pixel and grazes. If there are more than one closest resource pixel, a choice between the closest sites is made at random. The closest pixel rule ignores the overall abundance of resource sites in different directions. In the best direction rule, an ungulate compares the number of resource pixels present in each of four different wedge-shaped areas (north, south, east, or west) within a set radius, as in the one pixel rule. The animal then moves to the nearest unoccupied resource site in the direction that has the greatest number of resource sites within the wedge. Thus, by using the best direction rule, an individual should be moving toward the region that contains the greatest concentration of resource sites, even if a single resource cell in another direction is closer.

For initial model development, simple energetic rules for a generic winter foraging ungulate were estimated from the literature. The initial body weight for each ungulate was set at 200 kg (e.g., in Yellowstone National Park, female adult elk average ~245 kg going into the winter and calves average ~109 kg [Cassirer and Able 1990]). Assuming a general relationship of 2,000 Kcal/kg of animal body mass, this is equivalent to an initial energy content of 400,000 Kcal per ungulate. Next, basal energetic costs in the absence of movement had to be estimated. We assume that the basal cost in winter for a 200 kg ungulate is 12,000 Kcal/day, assuming that it spends 12 hr standing and 12 hr lying down. Energy expenditure at rest is approximately 0.005

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kcal/kg-min for ungulates in the winter (Parker et al. 1984:477), and energy expenditure while standing and feeding is approximately 0.08 Kcal/kg-min (Cassirer and Able 1990:89). Therefore, basal metabolic costs (BMC) are estimated as follows:

Resting BMC = 0.005 Kcal/kg-min * 200 kg * 12 hr * 60 min/hr = 720 Kcal/day. (3)

Standing and Grazing BMC = 0.08Kcal/kg-min * 200 * 12 * 60 = 11,520 Kcal/day. (4)

Daily BMC = 720 Kcal/day + 11,520 Kcal/day = 12240 kcal/day ~ 12000 kcal/day. (5)

If the same 200 kg ungulate spends 12 hr lying down and 12 hours walking, it's winter energetic cost will increase. Assume that maximum sustainable metabolic rate is 1.5 times the basal rate. Then, the additional expenditure for maximum travel distance is

12,000 Kcal/day * 1.5 = 18,000 Kcal/day. (6)

which represents an additional 6,000 Kcal/day over the daily BMC. The energetic cost per unit of distance moved can then be calculated. In the initial model, the maximum daily movement distance is set at 10 grid cells. Therefore, the cost of moving per grid cell is determined by

6000 Kcal/day =	= 600 Kcal/grid cell	
max 10 grid	in a character a shown in	
cells daily		
movement		
distance	(7	7)

Assuming that it is a 200 kg ungulate that is moving, the cost can also be represented as 600 Kcal/grid cell / 200 kg = 3 Kcal/grid cell-ungulate kg. Because the total cost of moving decreases as body weight goes down (it takes less energy for a light animal to move than a heavy one), the actual cost of movement for each animal is calculated based upon its body mass. Thus, energy cost in the model is calculated by:

EC = BMC + (BM * TMC * s)

(8)

where

EC = total energy cost per day,

BMC = basal metabolic cost,

BM = body mass of the ungulate,

- TMC = travel movement cost per grid cell per kg of ungulate body mass,
- s = distance travelled, in grid cell units.

We assumed that the ungulates die at 70% of their lean bodyweight (body weight at death for mule deer is 30% loss: Wallmo et al. 1977). Going into the winter, a moose has 23% of its body mass in fat, and a mule deer 10%. We assumed that our generic ungulate has 20% of its bodyweight in fat going into the winter. Therefore, given an initial body mass of 200 kg, the ungulate has 40 kg in fat, giving a lean body weight of 160 kg. The simulated ungulates will die when their body weight reaches 70% of 160 kg, or 112 kg.

Energy balance is calculated each day for each ungulate as the difference between energy gained and total energy costs. The maximum feeding rate is set in the model at 10 kg dry forage per ungulate per day. The daily energy intake is set such that under basal metabolism only and maximum forage intake, the animals will end the simulation (120 days) at their lean body weight (160 kg). Thus, the ungulates will alway lose energy during the winter, but will lose more when moving. Assuming a maximum forage intake rate of 10 kg/elk/day, the energy available in the forage must be 1133 Kcal/kg dry weight, a reasonable estimate for herbaceous forage. This will generate 160 kg animals at the end of a 120-day simulation assuming basal metabolism only and maximum forage intake.

To provide an initial estimate of the effects of increasing snow depth and density throughout the winter, we incrementally reduced the availability of forage on the simulated landscape on a daily basis. Each day, the available forage was reduced by 6 kg/ha, resulting in forage being at the refuge value when the simulation was concluded at day 120.

RESULTS OF THE INITIAL MODEL

We completed an extensive series of simulations with this initial model. Along with the three alternative movement rules, two methods of distributing initial forage biomass values, and simulated snow and no-snow conditions, we systematically varied a variety of model parameters. Ungulate foraging was simulated with random resource distribution patterns and with two 10 km x 10 km sections of grassland habitats within the Northern Range. In random maps, resources were simulated as occupying 10, 30, 50 70, and 90% of the landscape. A variety of ungulate densities were also simulated.

Simulation results suggest that ungulate foraging may be most efficient when resources are aggregated and least efficient when resources are randomly distributed. When resources become limiting (e.g., snow conditions make forage unaccessible), the differences in spatial patterns appeared to be less important. Differences in spatial patterns also appear less important as animals becomes increasingly more mobile (i.e., have relatively large maximum daily movement distances). The one-pixel rule always results in the least forage obtained by ungulates during the simulation, and generally results in a more variable daily energy balance and the lowest ungulate survival. Few differences were observed between the closest pixel and best direction rules, although the closest pixel rule generated slightly better ungulate survival under conditions of low resources.

THE NORTHERN YELLOWSTONE PARK MODEL

The Northern Yellowstone Park Model is a spatially explicit simulator of elk and bison dynamics in the 78,000 ha northern range. Because of the irregular shape of the northern range, the landscape is represented as a 592 x 290 grid in which 78,000 pixels are included in the study area. The spatial resolution is one hectare. The model incorporates twelve vegetation classes, including burned and unburned of six categories: dry grasslands, mesic grasslands, moist grasslands, wet grasslands, aspen stands, and forest. The forage in each grid cell at the beginning of a simulation is assigned statistically from our pre-winter estimates of biomass in each Thus, each vegetation type is vegetation class. characterized by its mean biomass, but individual grid cells contain values within a 95% confidence interval from the mean. The spatially explicit information on topography (elevation, slope and aspect), vegetation types, burning patterns, and precipitation zones used in the model were obtained from the YNP GIS. We created a series of maps and digital data files for the model in which data were aggregated into a limited number of categories within each data layer. For example, aspect categories were aggregated to represent mesic (north, northeast, and northwest), xeric (south, southeast, and southwest) and intermediate (east and west) sites.

Six ungulate classes are included in the model: cow, calf and bull groups of both elk and bison. Each ungulate class is assigned a characteristic maximum ingestion rate and initial body weight. Ungulates are simulated in groups of four. At the beginning of the simulation, elk are distributed randomly on resource sites across the northern range. Bison are distributed randomly within sections of the range such that 90% of the bison occurring in the upper range and 10% in the lower range. The total number of elk and bison is specified by the user at the beginning of the simulation.

To simulate search and movement, we use the closest-resource-pixel rule developed in the initial model. This rule contains the fewest implicit assumptions about ungulate knowledge of resources and seems reasonable biologically. Ungulates move to the nearest grid cell that contains available resources within a radius that represents the maximum daily moving distance. If there are more than one resource grid cells at the same distance, the cell with the greater resource is selected. The resource status of grid cells is described by a biomass preference index that incorporates the amount of biomass present, its energy content, and its availability as influenced by snow.

Snow conditions are changed every 15 days in the model. We are in the process of developing empirically-based relationships for snow accumulation from YNP data and snow measurements we made during the 1990-91 winter. Snow is distributed across the landscape based on the elevation, slope, and aspect of each grid cell. Snow has two major effects in the model. First, the depth and density of snow influences forage by reducing the amount of biomass available to the ungulates. Second, snow can reduce the distance that ungulates can travel in a

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day and increase the energetic cost of movement.

Foraging is represented by a differential equation with a nonlinear feedback term, as described in the initial model, but available biomass (a function of snow) is substituted for total biomass in eqs. 1 and 2. As in the initial model, animals can move and forage from cell to cell each day until they have ingested their maximum possible forage or moved the maximum daily moving distance. The probability of an ungulate leaving a grid cell is a function of its available biomass. As available biomass declines, the probability of moving increases. Energy balances are calculated daily for each ungulate. As described earlier, ungulates are assumed to die when the reach 70% of their lean body weight.

The model is generally run for 180 days, approximating a winter season, but the duration can be specified by the user. Because the model is stochastic, replicate simulations of the same set of initial conditions can be run and the results summarized statistically. Analyses of landscape pattern and some summary statistics are computed within the model itself. Other statistical analyses can be done on output files by using SAS.

The simulation model is written in standard FORTRAN, contains 14 subroutines and the main program, and runs in a workstation environment (e.g., Sun Sparc II and DEC 5000 workstations). In addition, a procedure written in the C language provides a bridge for passing the output matrix to **PV-WAVE** (Precision Visuals' Workstation Visualization Environment), which provides real-time display of landscape changes, ungulate movement, and snow and resource distributions. Model visualization serves two primary purposes: (1) our interpretations of the simulation results are enhanced; and (2) communication of our results to YNP managers and other scientists will be greatly improved. Eventually, model runs will be recorded on videotape. The visualization includes both maps and graphs, and the user can specify which output to display for any given simulation. For example, the following data can be displayed for each of the six ungulate categories: (1) mean forage consumed per ungulate; (2) mean daily energy gain, cost and balance; (3) number of animals surviving; (4) number of ungulates moving daily; and (5) mean daily moving distance. In addition, one can view graphs of landscape characteristics such as the number of resource patches, average patch size, largest patch size, and total available forage for elk and bison.

We are presently completing the parameterization of the model and testing its predictions against empirical data. A sensitivity analysis will then be conducted to evaluate the relative influence of different parameters in the model on simulation results. During the last phase of the research, we will conduct a factorial set of simulations in which we vary the fire pattern on the landscape, the number of ungulates, and the severity of the winter.

CONCLUSION

The combination of landscape modeling and field studies that we are conducting will permit the quantitative testing of hypotheses about the effects of fire scale and heterogeneity on native ungulates and plants on the northern range in YNP. Data collection, data analysis, and model development are continuing during the second year of our study. In the coming six months, we will complete our data analyses, test the model and perform a sensitivity analysis, then project plant and ungulate dynamics with different scenarios of fire size and pattern, winter weather conditions, and ungulate densities.

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