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A landscape simulation model of winter foraging by large ungulates

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ABSTRACT

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Ungulate winter grazing was simulated on simple random and actual landscape patterns using an individual-based modeling approach to explore the effect of landscape heterogeneity on foraging dynamics. The landscape was represented as a 100×100 grid with each cell considered to be either a resource or nonresource site. Random maps were generated by specifying the proportion, p, of the landscape occupied by resource sites. Actual landscape maps were obtained from the spatial arrangement of sagebrush–grassland habitats in subsections of northern Yellowstone National Park, Wyoming. Each resource site was assigned an initial forage abundance, and a specified number of ungulates were distributed randomly across the landscape on resource sites. Three alternative search-and-movement rules, which incorporated different movement scales and assumptions about ungulates' knowledge of the landscape, were compared. Grazing was simulated as a recipient-determined, donor-controlled flow with a nonlinear feedback. Daily energy balances were computed for each ungulate by subtracting energy cost from energy gain, and ungulates were assumed to die when they reached 70% of their lean body weight.

Simulation results suggested that when resources were abundant across the landscape (i.e., high p), the search-and-movement rule selected to simulate foraging was not important. That is, a variety of strategies should suffice under high-resource conditions, and there was no benefit to having a more efficient rule. However, when resources were scarce (e.g., low p or high ungulate densities), then the ability to discern resource abundances and to move over greater distances resulted in lower mortality. For a given p, the difference between a fragmented (i.e., random) and aggregated (i.e., real) arrangement of resource

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sites was only pronounced when the ability of the animals to move was very limited. In these situations, survival was always greater in the real landscapes. Individual-based spatial models developed for specific landscapes and species could be quite valuable in enhancing our understanding of landscape dynamics and large herbivores.

INTRODUCTION

The response of populations to patchy environments has long been of interest to ecologists (see Wiens, 1976). Patch size and connectivity influence the abundance, movement patterns, and persistence of populations within a landscape (e.g., Den Boer, 1981; Fahrig and Merriam, 1985; Fahrig and Paloheimo, 1988; Milne et al., 1989; Foster and Gaines, 1991). The abundance and distribution of resource patches may be of particular importance (O'Neill et al., 1988). For instance, the spatial arrangement and density of plants influences the success of herbivores in finding food (Kareiva, 1983; Risch et al., 1983; Stanton, 1983; Cain, 1985). If resource patches differ in quality across a landscape, individuals should exhibit some degree of selection among patches or habitats (Wiens, 1976; Stephens and Krebs, 1986; Senft et al., 1987).

Theoretical considerations of optimal foraging and diet selection (Westoby, 1974; Wiens, 1976; Owen-Smith and Novellie, 1982; Senft et al., 1987) suggest that large generalist herbivores will respond differently to fragmented vs. contiguous spatial arrangements of resources. For example, winter habitat sites that were isolated from other suitable patches were not used by white-tailed deer in New England (Milne et al., 1989). Theoretical studies suggest that organisms must operate at larger spatial scales (i.e., search a larger area) as resources become scarce and clumped across a landscape (O'Neill et al., 1988). In addition, the effectiveness of different foraging tactics may vary with the spatial distribution of resources. Results from a stochastic model of the relationships between various herbivore searching strategies and the density and arrangement of food plants demonstrated that the effectiveness of a strategy depended on whether resources were patchy or clumped (Cain, 1985).

The expression of individual habitat preferences also should be affected by population density. For example, at low total population sizes, only the highest quality sites should be occupied. As density increases, optimal patches are degraded and other habitat types have equal potential quality. At this point, patch use should expand, assuming perfect choice capabilities of the organisms (Wiens, 1976, p. 92). Thus, there is a wide range of population responses to spatial heterogeneity.

In this paper, we present a spatial simulation model developed to elucidate interactions between wintering ungulates and the abundance and

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distribution of forage. The development of simulation models that explicitly incorporate organismal responses to spatial heterogeneity has been challenging (Turner and Gardner, 1991). Models have been developed to simulate animal movement patterns (e.g., Siniff and Jesson, 1969; Yano, 1978; DeAngelis and Yeh, 1984; Swingland and Greenwood, 1984) and optimal foraging strategies (e.g., Owen-Smith and Novellie, 1982; Stephens and Krebs, 1986), but explicit spatial patterns generally have not been included. Spatially explicit models to explore organism responses to heterogeneous landscapes are relatively new (e.g., Milne et al., 1989; Saarenmaa et al., 1988; Fahrig, 1991; Hyman et al., 1991; Roese et al., 1991; Pulliam et al., 1992).

Ungulates foraging in a heterogeneous landscape provide an interaction between spatial patterns and ecological dynamics that is of interest to both ecologists and land managers. Ungulates make distinct choices among potential feeding areas and respond to spatial and temporal heterogeneity at a variety of scales (Senft et al., 1987), and there is extensive literature on the interactions between grazers and grasslands (e.g., Crawley, 1983; McNaughton et al., 1988; and many others). We focus on winter foraging because winter range conditions are the primary determinant of large ungulate survival and reproduction in many areas (e.g., Houston, 1982; Parker et al., 1984; Wickstrom et al., 1984).

To explore the effect of landscape-level resource patterns, grazing dynamics were simulated using an individual-based modeling approach (Huston et al., 1988; Roese et al., 1991) on random and actual landscape patterns. Simple random maps serve as a neutral model for the effects of spatial pattern (Gardner et al., 1987; Gardner and O'Neill, 1991). Our model simulates a general large ungulate but could be parameterized easily for particular species. A general model is useful because it can provide insights into the ecological processes of interest and generate testable hypotheses. We use the model to explore the influence of resource abundance, resource heterogeneity, ungulate density, and alternative search-and-movement rules on ungulate foraging dynamics and survival. We are particularly interested in the effect of landscape heterogeneity on the winter foraging dynamics of large ungulates, and the conditions under which landscape heterogeneity is important.

A LANDSCAPE MODEL OF UNGULATE WINTER FORAGING

Consider an ungulate moving through a winter landscape, searching for resources, and grazing. The ungulate has an initial location on the landscape and, if forage is available, the animal is likely to remain there and feed. The amount of forage on the site declines as the animal feeds;

because it is winter, forage is not replenished. Grazing continues until resources are depleted and/or it is no longer energetically profitable to remain there, at which time the animal moves to another site. The animal will continue to move until it locates another patch of resources. The landscape perceived by the animal is dynamic because forage availability changes through the winter. Grazing depletes resources, and snow conditions may make some areas inaccessible. The survival of the ungulate depends on its ability to locate enough forage to maintain a viable body weight.

The landscape

The landscape is represented as a grid with each grid cell assigned to a resource category. The grid-cell structure is useful because (1) it is compatable with remotely sensed imagery and GIS 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 gridded landscape data (e.g., Turner and Gardner, 1991). Resource categories are binary (i.e., grid cells are classified as either resource or nonresource) on a 100×100 grid with each grid cell assumed to represent one hectare. The landscape is characterized by (1) the proportion, p, of the landscape occupied by resource sites, (2) the spatial arrangement of resource paches, and (3) the total amount of resource available across the landscape.

Landscape patterns used in the simulations included randomly generated maps and actual maps (Fig. 1). To generate random maps, the proportion, p, of the landscape occupied by resource sites was first specified. Each grid cell was then assigned to be either a resource or nonresource site by generating a random number between 0 and 1 and comparing the value to p. If the random number was $\leqslant p$, the grid cell became a

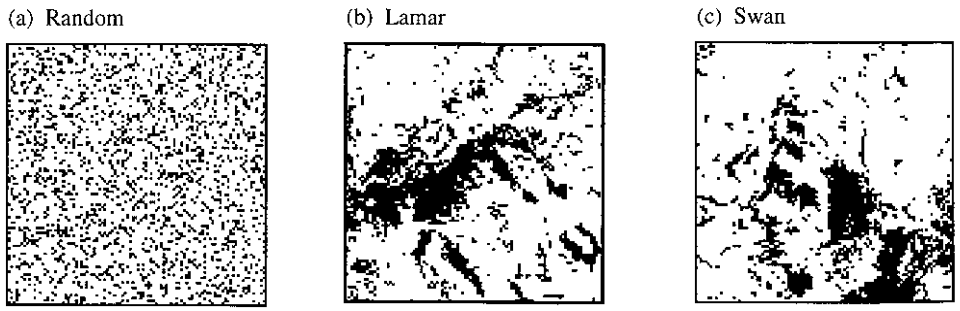

Fig. 1. Illustration of landscape maps used in these simulations including a random map in (a) and two real maps showing sagebrush grassland habitats in northeastern (Lamar, (b)) and northwestern (Swan Lake Flat, (c)) Yellowstone National Park, Wyoming. Grid cells shown in black are resource sites and in white are non-resource sites. In all three maps, the proportion, p, of the landscape occupied by resource sites is 0.22.

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resource site. The characteristics of randomly generated maps have been described elsewhere (see Gardner et al., 1987; Gardner and O'Neill, 1991). For a given value of p, patches in random maps are smaller, more numerous, and more dispersed across the landscape when compared to real landscape patterns, and differences between random and actual maps are greater when p is relatively low (i.e., $p < 0.6$) (Gardner et al., 1987, 1991, 1992). Resource patterns derived from real landscape maps were obtained from vegetation data stored in the geographical information system (GIS) for Yellowstone National Park. We subsampled the GIS data and selected two nonoverlapping 100×100 grid-cell sections of the northern portion of the Park. The maps were converted to binary resource categories by considering sagebrush–grassland areas to be resource sites and all other habitats to be nonresource sites. In fact, Yellowstone's ungulates also forage in forests and other vegetation types, but grassland areas are especially important feeding sites in winter (Houston, 1982). The proportion of both landscape maps occupied by resource sites was 0.22.

Each resource site within a landscape was assigned an initial quantity of available forage. Data collected across the northern sagebrush–grassland area of Yellowstone National Park in January 1990 (Table 1) were used to provide reasonable estimates of winter forage availability. Two alternative methods of initializing forage abundance were explored. First, we used a 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 field data. In both cases, the total forage available in the landscape at the beginning of the simulation was the same for a given value of p.

Ungulate distribution

The initial number of ungulates present on the landscape was specified, then animals were assigned to groups of k identical individuals and distributed randomly on resource sites. The use of ungulate groups is reasonable biologically (Meagher, 1973; Franklin and Lub, 1979; Tefler and Cairns, 1979; Geist, 1982) and would be appropriate for the 1-ha spatial resolution of the model. In the simulations presented here, we varied the initial number of ungulates but maintained a group size of six ungulates. Only one group could occupy a grid cell at any one time.

Search and movement rules

Each ungulate group was located at the beginning of each time step, set at one day in these simulations. If the group was located on a resource site, it grazed as described in the next section. If it was located on a nonre-

TABLE 1

Parameters and variables used in the simulations

Parameter	Value	Source
Initial biomass (B)		
mean	1400 kg/ha	unpublished data, Jan. 1990
standard deviation	600 kg/ha	unpublished data, Jan. 1990
Upper threshold (α)	1000 kg/ha	unpublished data, Jan. 1990
Refuge biomass (r)	600 kg/ha	unpublished data, Jan. 1990
Maximum feeding rate (τ)	0.05	estimated
Initial body weight per ungulate (BW_i)	200 kg	Cassirer and Able (1990)
Ungulate group size	6 ungulates/group	literature (see text) and observation
Search radius	10 grid cells	estimated
Maximum moving distance	10 grid cells/day	estimated
Variable	**Levels stimulated (see text for explanation)**	
Initial forage distribution	even, heterogeneous	
Initial ungulate density	198, 594, 1188 animals	
Search-and-movement rules	one-grid-cell, closest-resource-site, best-direction	
Proportion of the landscape occupied by resource sites	0.1, 0.3, 0.5, 0.7, 0.9	
Landscape pattern	random, actual (Swan and Lamar)	

source site or a site on which resources had been reduced, the group moved. There are a variety of means by which the directional movement of ungulates can be represented in a model. We compared three alternative movement rules: (1) the one-grid-cell rule; (2) the closest-resource-site rule; and (3) the best-direction rule. Common to all three rules is a search radius within which an ungulate can perceive resources in the landscape from its present location. In the one-grid-cell rule, an animal moves to an unoccupied adjacent grid cell at random among resource sites in the patch. The animal can move only one grid cell per time step. An animal that is located on a nonresource site will search the landscape and move toward the most promising resource area. The search entails comparing the number of resource sites 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 sites within the search radius. Thus, movement patterns are essentially represented at two scales: random movement within resource patches and directional movement across the heterogeneous landscape. However, the one-grid-cell rule limits movement

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Grazing

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to one grid cell per time step. One additional constraint is placed on movement such that the animal cannot return immediately to the site it just left. This simple self-avoidance rule precludes an artificial back-and-forth movement.

The next two rules permit movements up to a maximum distance during each time step. In both rules, an ungulate can move among sites until it either obtains the maximum forage intake or reaches the maximum movement distance permitted for a day. In the closest-resource-site rule, an animal that is ready to move will examine the landscape within the search radius and identify the resource site that is closest to its present location. The animal then moves to the closest unoccupied resource site and grazes. If there is more than one closest-resource site, a choice between the closest sites is made at random. If there are no resource sites within the search radius, both the movement distance and direction are selected at random. The closest-grid-cell rule ignores the overall abundance of resource sites in different directions. In the best-direction rule, an ungulate is given knowledge about resources on the landscape. The animal compares the number of resource sites present in each of four different wedge-shaped areas (north, south, east, or west) within a set radius. The animal then moves to the nearest unoccupied resource site in the direction that has the greatest number of resource sites. 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 site in another direction is closer.

Grazing

Forage intake, I, is assumed to be a function of (1) the maximum rate of ingestion, τ, (2) the initial body weight, BW_i, of the ungulate, and (3) a negative feedback, $f(B)$, based on the amount of resource, B, available on a particular site:

$$I = \tau \times BW_i \times f(B). \tag{1}$$

We held BW_i constant at 200 kg and τ at 0.05, resulting in a maximum daily intake of 10 kg per day for each ungulate. The negative feedback term assumes that the grazer achieves its maximum foraging rate if forage is available at or above a threshold, α. As resources fall below this threshold, forage intake will decline linearly until it reaches zero, which occurs when available resources fall below some refuge level, r, below which they are unavailable to the grazer (Wiegert, 1979; Turner, 1988). The mathematical form of this negative feedback is

$$f(B) = \begin{cases} 1, & B \geqslant \alpha \\ 1 - [(\alpha - B)/(\alpha - r)], & r < B < \alpha \\ 0, & B \leqslant r \end{cases}. \quad (2)$$

The function ranges from 0 to 1 as B increases from r to α. For $B \leqslant r$, $f(B)$ is assumed to be equal to 0 (no forage intake), and for $B \geqslant \alpha$, $f(B)$ is assumed to be equal to 1 (maximum forage intake). Between α and r, $f(B)$ generates a linear 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 changes the number and size of resource patches (i.e., contiguous resource sites) throughout the simulation.

As resources on the site decline, the animal also is assumed to have an increased likelihood of moving to a new feeding site. In the model, this is implemented probabilistically as a function of the amount of resource on a site. As resource declines below α, the probability of moving increases until it reaches 1.0 at the refuge level of forage.

Ungulate energetics

Our purpose in developing this model was to explore alternative model formulations. Therefore, we implemented reasonable but simple energetic rules derived from the literature to simulate weight loss rather than including a detailed energetics model specific to a particular species (e.g., Hobbs, 1989). 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)). We then assumed a general relationship of 2000 kcal/kg of animal body mass, equivalent to an initial energy content of 400 000 kcal per ungulate. Energetic costs were assumed to be a basal cost plus a travel cost. To estimate a basal daily energy cost in winter for a 200-kg ungulate, we assumed the animal would spend 12 h standing and 12 h lying down. Energy expenditure at rest is approximately 0.005 kcal $\cdot$ kg^{-1} $\cdot$ min^{-1} for ungulates in the winter (Parker et al., 1984), and energy expenditure while standing and feeding is approximately 0.08 kcal $\cdot$ kg^{-1} $\cdot$ min^{-1} (Cassirer and Able, 1990, p. 89). Therefore, basal metabolic costs (BMC) were estimated as follows:

$$\begin{aligned} BMC_{\text{daily}} &= BMC_{\text{resting}} + BMC_{\text{standing/grazing}} \\ &= (720 + 11\,520)\ \text{kcal/day} \\ &\sim 12\,000\ \text{kcal/day} \end{aligned} \quad (5)$$

If the same 200-kg ungulate spends 12 h lying down and 12 h walking, its winter energetic cost will increase. Assuming that maximum sustainable

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metabolic rate is approximately 1.5 times the basal rate (Morehouse and Miller, 1976, p. 136; Lamb, 1978, p. 62; the additional expenditure allowed for travel in a day is 6000 kcal/day, or a total expenditure of 18 000 kcal/day. We fixed the maximum daily movement distance in the model at 10 grid cells (1 km), and then divided the 6000 kcal/day by this maximum distance to determine the energy cost of moving to be 600 kcal/grid cell. Assuming that a 200-kg ungulate is moving, this travel movement cost (TMC) can also be represented as 3 kcal · grid cell^{-1} · ungulate kg^{-1}. 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), so the actual cost of movement for each animal is calculated based upon its current body mass. Thus, daily energy cost in the model is calculated by:

$$EC = BMC_{\text{daily}} + (BW \times TMC \times s) \tag{6}$$

where EC = total energy cost per day, BMC_{daily} = basal metabolic cost per day, BW = body mass of the ungulate, TMC = travel movement cost per grid cell per kg of ungulate body mass, s = distance traveled, in grid-cell units.

We assume that the ungulates die at 70% of their lean bodyweight (e.g., 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 had 20% of its bodyweight in fat going into the winter. Therefore, given an initial body mass of 200 kg, the ungulate had 40 kg in fat, giving a lean body weight of 160 kg. The simulated ungulates died when their body weight reached 70% of 160 kg, or 112 kg.

Energy balance was calculated each day for each ungulate as the difference between energy gained and total energy costs. Energy available in forage was assumed to be 1133 kcal/kg dry weight, a reasonable estimate for herbaceous forage (National Research Council, 1984), and we assumed no differences in forage quality. The parameter values used in these simulations result in animals reaching their lean body weight (160 kg) at the end of a 120-day simulation under basal metabolism only (i.e., no movement). Thus, the ungulates will always lose energy during the winter, but will lose more when moving.

Landscape pattern analysis

The spatial pattern of resources on the landscape was analyzed during the simulations by using a modified version of the spatial analysis program (SPAN) developed by Turner (1990a,b). Patches were defined as groups of contiguous resource sites that shared an edge in common; diagonal neighbors were not considered to be part of the same patch. The proportion of

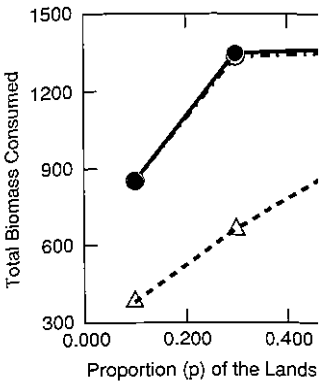
the landscape occupied by resource sites, the number of resource patches, and the size of the largest patch were calculated at each time step.

SIMULATIONS

The simulations presented here were run for 120 days. Because the model is stochastic, simulations were replicated ($n = 10$) in a Monte Carlo fashion and the results summarized statistically. There is an almost infinite number of simulations that could be run to explore the questions posed in the objectives and the interactions among the parameters. We have selected a set that we think will be instructive: (1) examining the three movement rules when the initial number of ungulates is fixed, but the proportion of the landscape occupied by randomly distributed resources varies; (2) examining the three movement rules when the proportion of the landscape occupied by resources is fixed, but the initial number of ungulates varies; (3) varying both initial ungulate numbers and the proportion of the landscape occupied by resources; and (4) comparing real and random maps in which the proportion of the landscape occupied by resource sites is the same.

Fixed initial ungulate number, variable p

Initial simulations were conducted using the three alternative movement rules with a fixed number of ungulates (198 simulated as 33 groups) on random landscape maps in which p was varied between 0.1 and 0.9. Results demonstrated differences among movement rules in the total forage consumed per ungulate (averaged over all 198 ungulates) during the simulation (Fig. 2). The most forage was obtained with the best-direction and closest-resource-site rules and the least with the one-grid-cell rule. There was less benefit to having more efficient search rules when resources were abundant (i.e., high p). No difference in total biomass consumed per ungulate was observed between the two methods of initializing the forage. However, when the daily forage consumption patterns were compared, cyclical oscillations were observed when the same initial biomass value was assigned to each resource site but not when biomass was assigned from a statistical distribution (Fig. 3). The cycle corresponded to the time required to deplete resources on a grid cell. As resources decreased, the probability of the ungulates moving increased, and these grazing and movement dynamics were artificially synchronized by assuming that all resource sites initially contained the average resource value. To eliminate this artifact, all subsequent simulations were conducted with the initial forage values assigned from a normal distribution.



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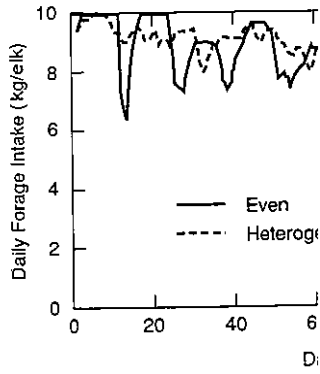

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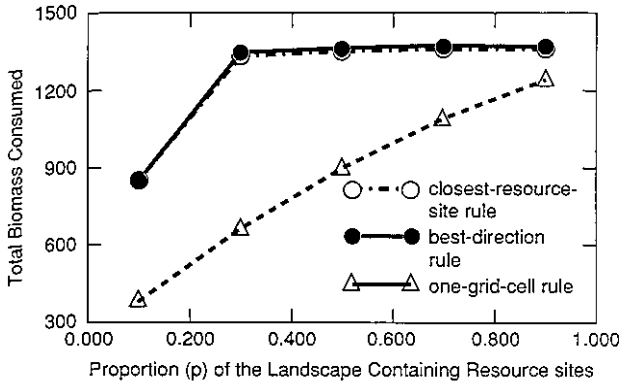

Fig. 2. Total forage obtained per ungulate during a 120-day simulation with three alternative movement rules (see text for description) when resource sites are distributed at random on a 100×100 landscape. The proportion, p, of the landscape occupied by resource sites was varied.

Variable initial ungulate number, fixed p

The next set of simulations fixed the proportion of the landscape occupied by resource sites at 0.1, in the range of resource availability where the movement rules showed the greatest difference, and varied ungulate density. Group size remained constant, so different ungulate densities were simulated by varying the number of groups. Total forage consumption per ungulate decreased with increasing ungulate density, as expected (Fig. 4). Among movement rules, the one-grid-cell rule always resulted in the lowest resources obtained per day and showed the least response to ungulate

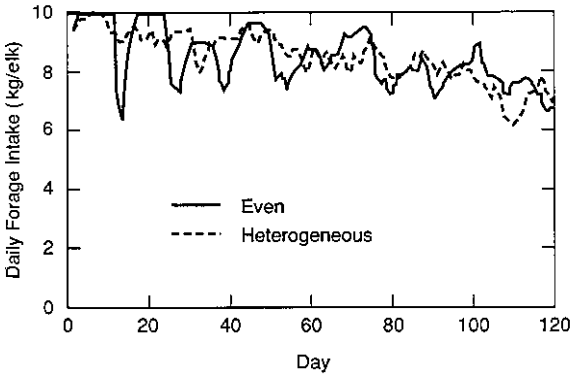

Fig. 3. Daily forage consumption per ungulate during a 120-day simulation with the best direction rule when resource sites are distributed at random and occupy 0.1 of a 100×100 landscape. Total biomass on the landscape was the same but was distributed spatially by assigning the mean biomass value to each resource site (even distribution) or by using a statistical distribution such that the total biomass on the landscape is the same but forage varies on a per-grid-cell basis (heterogenous distribution).

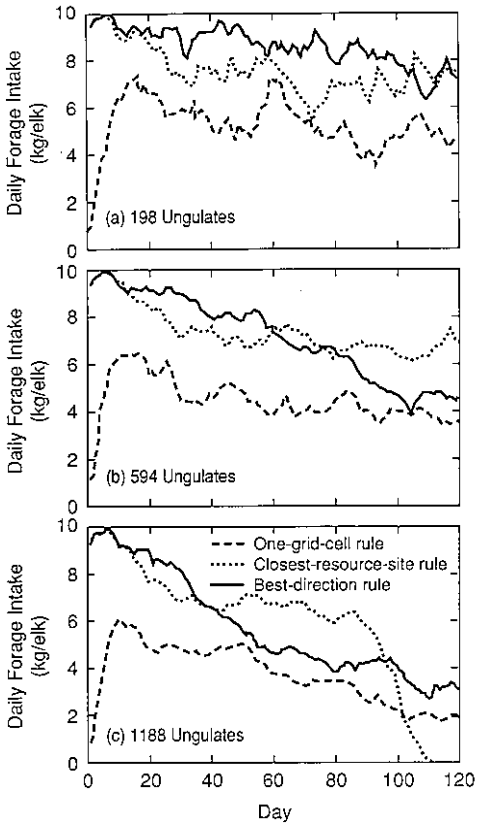

Fig. 4. Daily forage consumption per ungulate during a 120-day simulation with three alternative movement rules when resource sites are distributed at random and occupy 0.1 of a 100×100 landscape. Initial ungulate abundance is varied as follows: (a) 198, (b) 594, and (c) 1188.

density (Fig. 4). With the one-grid-cell rule, ungulates at low or moderate densities maintained fairly steady average daily forage consumption throughout the 120-day simulation, but average consumption per ungulate began to drop dramatically near day 90 at high ungulate densities. With the best-direction and closest-resource-site rules, ungulates consumed forage near the maximum possible rate during the first 30 days of the simulation. Although it declined through time, at least some consumption was maintained throughout the simulation at all ungulate densities with the best-direction rule.

When the mean daily energy balance per live ungulate was examined, there was little difference between the closest-resource-site and best-direction rules (Fig. 5). When initial ungulate density was relatively low (198 ungulates), the one-grid-cell rule resulted in lower energy balance values than the best-direction or closest-resource-site rules (Fig. 5a). This differ-

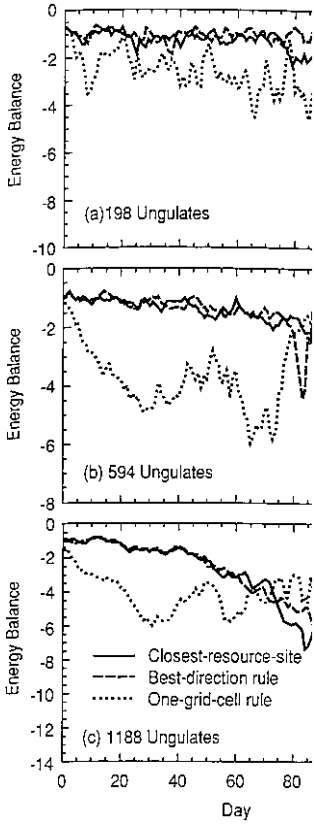

Fig. 5. Mean daily energy bala
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Ungulate survival foll
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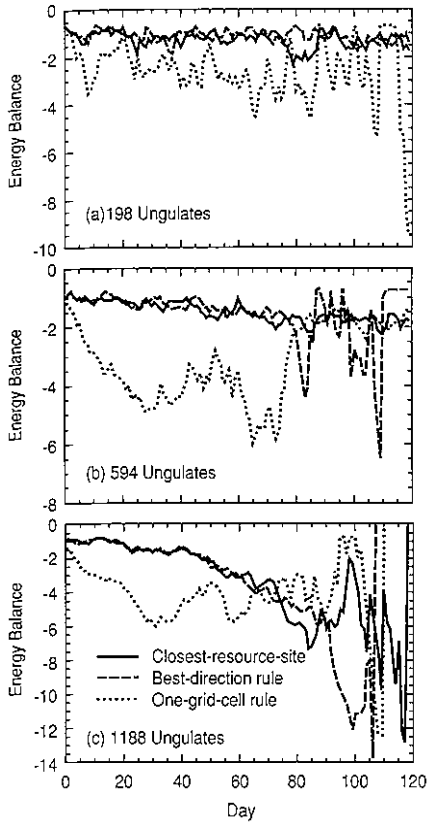

Fig. 5. Mean daily energy balance per ungulate with three alternative movement rules when resource sites are distributed at random and occupy 0.1 of a 100×100 landscape. Initial ungulate abundance is varied as follows: (a) 198, (b) 594, and (c) 1188.

ence was more pronounced when 594 ungulates were simulated (Fig. 5b), when the one-grid-cell rule showed a rapid decline followed by wide fluctuations beginning near day 80. When initial ungulate number was increased to 1188 animals (Fig. 5c), wide fluctuations in energy balance were apparent with all three movement rules, with the closest-resource-site rule having fluctuations with the lowest magnitude.

Ungulate survival followed a pattern similar to that of energy balance (Fig. 6). There were few differences between the closest-resource-site and best-direction rules, and survival was always lowest with the one-grid-cell rule. Ungulate numbers were maintained longer into the simulation when initial densities were lower, declining further and earlier when initial densities were high. For example, with the closest-resource-site rule, mortality began around day 105 for an initial density of 198 animals (Fig. 6a), at day 65 for 594 animals (Fig. 6b), and at day 50 for 1188 animals (Fig. 6c).

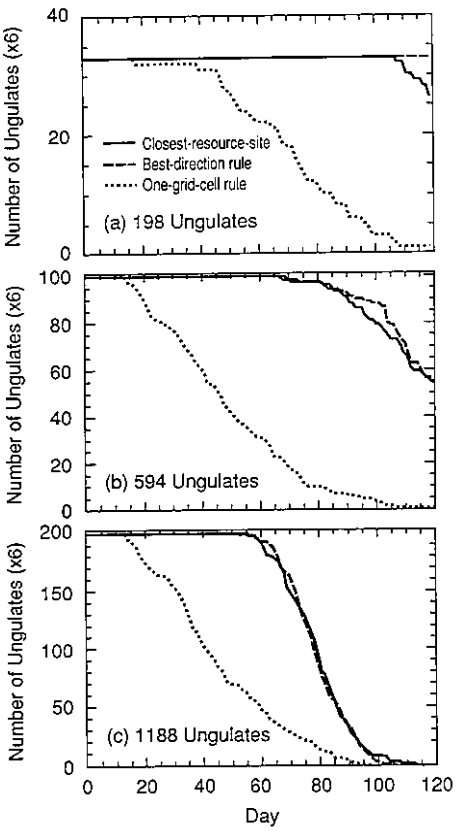

Fig. 6. Number of surviving ungulates with three alternative movement rules when resource sites are distributed at random and occupy 0.1 of a 100×100 landscape. Initial ungulate abundance is varied as follows: (a) 198, (b) 594, and (c) 1188.

Variable initial ungulate number, variable p

If we examine ungulate survival over simulations with a range of ungulate densities and resource abundances (Table 2), we again see little difference between the closest-resource-site and best-direction rules and much lower ungulate survival with the one-grid-cell rule. However, the interaction between resource abundance and ungulate density is apparent even with the closest-resource-site and best-direction rules. When 33 groups were simulated, most animals survived even under low resource conditions (i.e., $p = 0.1$). When 99 groups were simulated, survival was only about 55% at $p = 0.1$. When ungulate density was increased to 198 groups, survival declined to $\sim 83\%$ when $p = 0.3$ and dropped dramatically to nearly 0 at $p = 0.1$.

Real vs. random landscape patterns

Following these initial simulations, the model was run on the real landscape patterns derived from Yellowstone National Park and the results

TABLE 2

Ungulate group survival in ran
proportion, p, of the landsca
ungulates are varied. Number
below in parentheses

Movement rule	Prop
	0.1
Initial ungulates = 33 groups	
Closest resource site	26
	(24–
Best direction	28
	(25–
One grid cell	1
	(0–3
Initial ungulates = 99 groups	
Closest resource site	54
	(48–
Best direction	52
	(42–
One grid cell	1
	(0–
Initial ungulates = 198 groups	
Closest resource site	1
	(0–
Best direction	1
	(0–
One grid cell	1
	(0–

compared with simulatio
p. Differences in ungu
landscapes were most p
small (e.g., the one-gric
(Table 3). Survival with
the other two rules. Surv
rule than with the bes
Random landscape pat
ungulate densities for th
that permitted longer m

A very simple means
introduced by assuming
the winter. This was imp
each site by 6.0 kg/da

TABLE 2

Ungulate group survival in random landscapes with alternative movement rules when the proportion, p, of the landscape occupied by resource sites and the initial number of ungulates are varied. Numbers are means over 10 replicate simulations; range is shown below in parentheses

Movement rule	Proportion of the landscape occupied by resoucre sites				
	0.1	0.3	0.5	0.7	0.9
Initial ungulates = 33 groups					
Closest resource site	26 (24–29)	29 (23–33)	32 (30–33)	32 (31–33)	32 (31–33)
Best direction	28 (25–33)	32 (31–33)	32 (30–33)	32 (31–33)	32 (31–33)
One grid cell	1 (0–3)	10 (7–12)	17 (14–22)	21 (19–26)	24 (22–27)
Initial ungulates = 99 groups					
Closest resource site	54 (48–60)	87 (78–93)	92 (87–95)	95 (91–98)	96 (94–98)
Best direction	52 (42–61)	92 (87–95)	95 (91–98)	96 (93–98)	97 (95–98)
One grid cell	1 (0–1)	12 (6–16)	30 (26–37)	47 (37–61)	69 (62–74)
Initial ungulates = 198 groups					
Closest resource site	1 (0–1)	164 (156–174)	180 (175–186)	184 (181–187)	190 (185–194)
Best direction	1 (0–1)	167 (156–179)	184 (179–190)	190 (184–194)	192 (188–195)
One grid cell	1 (0–2)	11 (7–16)	47 (39–53)	84 (74–98)	119 (106–131)

compared with simulations on random landscapes having the same value of p. Differences in ungulate survival in simulations on real and random landscapes were most pronounced when ungulate moving distances were small (e.g., the one-grid-cell rule) or when ungulate densities were high (Table 3). Survival with the one-grid-cell rule was always lower than with the other two rules. Survival was slightly higher with the closest-resource-site rule than with the best-direction rule when ungulate density was high. Random landscape patterns resulted in lower ungulate survival at all ungulate densities for the one-grid-cell rule, but not for the other two rules that permitted longer movement distances.

A very simple means of including a potential effect of snow was then introduced by assuming a continuous decline in available forage through the winter. This was implemented by decrementing the forage available on each site by 6.0 kg/day beginning at the end of the first simulated day.

TABLE 3

Ungulate group survival in random and real landscapes with alternative movement rules when the initial number of ungulates is varied. Numbers are means over 10 replicate simulations; range is shown below in parentheses

Movement rule	Landscape pattern ($p = 0.22$)		
	Lamar	Swan	Random
Initial ungulates = 33 groups			
Closest resource site	32 (31–33)	31 (29–32)	30 (28–32)
Best direction	32 (30–33)	32 (30–33)	31 (29–32)
One grid cell	14 (9–18)	12 (8–19)	3 (1–5)
Initial ungulates = 99 groups			
Closest resource site	94 (91–96)	88 (83–92)	81 (76–90)
Best direction	95 (91–98)	82 (78–86)	84 (78–88)
One grid cell	33 (24–41)	23 (18–27)	5 (2–8)
Initial ungulates = 198 groups			
Closest resource site	173 (162–181)	147 (134–155)	128 (110–148)
Best direction	172 (164–181)	126 (120–134)	133 (122–145)
One grid cell	41 (34–47)	18 (12–22)	4 (2–7)

Increased energy costs associated with travel through snow were not simulated. The trends in survival patterns remained the same when snow effects were simulated in the real and random landscape (Table 4). Snow reduced forage availability and hence decreased ungulate survival in all simulations. Again, there were no differences between the closest-resource-site and best-direction rules. The one-grid-cell rule always resulted in lower survival and was sensitive to the pattern of resources on the landscape (i.e., random vs. real).

The heterogeneity of the landscape (i.e., the abundance and spatial distribution of resources) changed during the simulations (e.g., Fig. 7). As the animals deplete resources, the proportion of the landscape containing resources declines. However, the number of resource patches and size of the largest resource patch also change. For example, in a simulation conducted with 600 ungulates on a real landscape map (Swan Lake Flats), the number of resource patches increased and the size of the largest patch

TABLE 4

Ungulate group survival in si
forage by 6 kg/day. The in
landscape, and three alternati
replicate simulations; range is

Movement rule
Initial ungulates = 33 groups
Closest resource site
Best direction
One grid cell
Initial ungulates = 99 groups
Closest resource site
Best direction
One grid cell
Initial ungulates = 198 groups
Closest resource site
Best direction
One grid cell

decreased as resources v
indicates that resources
the simulation progresse

DISCUSSION

The simple model pr
large ungulate foraging
abundant across the land
and movement is not ve
suffice under high-resou
more-efficient rule. Opt
(e.g., Stephens and Kreb
low p or high ungulate d
movement (e.g., incorpo
over greater distances) r

ernative movement rules
means over 10 replicate

Random
30
(28–32)
31
(29–32)
3
(1–5)
81
(76–90)
84
(78–88)
5
(2–8)
128
(110–148)
133
(122–145)
4
(2–7)

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patches and size of
ıle, in a simulation
ɔ (Swan Lake Flats),
of the largest patch

TABLE 4

Ungulate group survival in simulations with snow, which was assumed to decrease available forage by 6 kg/day. The initial number of ungulates is varied on a random and real landscape, and three alternative movement rules are compared. Numbers are means over 10 replicate simulations; range is shown below in parentheses

Movement rule	Landscape pattern ($p = 0.2$)	
	Swan	Random
Initial ungulates = 33 groups		
Closest resource site	32	33
	(32–33)	(32–33)
Best direction	33	32
	(32–33)	(31–33)
One grid cell	7	1
	(4–12)	(0–3)
Initial ungulates = 99 groups		
Closest resource site	94	93
	(90–97)	(89–98)
Best direction	92	96
	(86–96)	(93–98)
One grid cell	13	2
	(10–16)	(0–4)
Initial ungulates = 198 groups		
Closest resource site	20	38
	(14–29)	(23–58)
Best direction	18	27
	(7–28)	(12–49)
One grid cell	10	2
	(4–18)	(1–4)

decreased as resources were consumed during the simulation (Fig. 7). This indicates that resources became more fragmented across the landscape as the simulation progressed.

DISCUSSION

The simple model presented here offers some interesting insights into large ungulate foraging. The results suggest that when resources are abundant across the landscape (e.g., high p), the choice of a rule for search and movement is not very important. That is, a variety of strategies will suffice under high-resource conditions, and there is no benefit to having a more-efficient rule. Optimal foraging theory makes the same prediction (e.g., Stephens and Krebs, 1986). However, when resources are scarce (e.g., low p or high ungulate densities), then a more-efficient rule for search and movement (e.g., incorporating the ability to discern resources and move over greater distances) resulted in lower mortality.

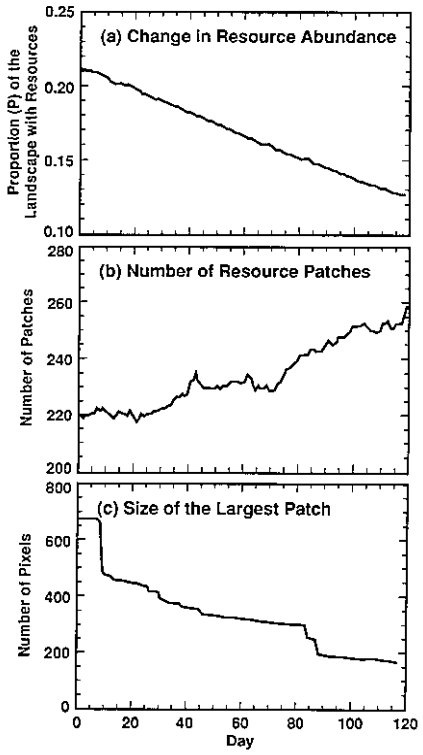

Fig. 7. Changes in measures of landscape pattern during a 120-day simulation of 100 ungulates that used a real landscape map (Swan Lake Flats) and the closest-resource-site rule for movement. A resource patch was defined as a group of cells containing forage that were contiguous in the vertical or horizontal directions.

For a given proportion of the landscape occupied by resource sites, the difference between a fragmented (i.e., random map) and aggregated (i.e., real map) arrangement of resources sites was only pronounced when the ability of the animals to move was very limited, as in the one-grid-cell rule. However, the other two rules used a daily moving distance of one tenth the linear dimension of the landscape map. Thus, it remains plausible that pattern differences could have a greater influence on a landscape with a greater spatial extent. Other theoretical studies of organism movement on landscapes in which the spatial arrangement of resources or suitable habitat was varied have demonstrated that landscape connectivity is affected by both the landscape pattern and the scale at which an organism moves (O'Neill et al., 1988; Gardner et al., 1989, 1993; Wiens and Milne, 1989; Pearson et al., 1993). Our simulations support these results. When animals could only move one grid cell per time step, a fragmented landscape pattern resulted in greater mortality than an aggregated landscape pattern. When animals could move multiple grid cells per time step (i.e.,

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ACKNOWLEDGEMENTS

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the closest-resource-site and best-direction rules), there was no effect of spatial arrangement in these simulations.

We did not explore the interaction between a range of proportions of the landscape occupied by resources and the spatial dispersion of those resources. Using a similar stochastic modeling approach, Cain (1985) found that the effect of spatial heterogeneity on the success of an insect herbivore was dependent on p. When resources were scarce, resources dispersed in a uniform pattern were more difficult to find than if they were clumped. When resources were abundant, resources dispersed in a clumped pattern were more difficult to find than if they were uniformly dispersed. These results suggest the value of future simulations with the ungulate model in which a range of p values combined with spatial dispersion patterns is explored.

The simulation results suggest that, of the three movement rules compared, the closest-resource-site rule would be the best choice for simulating winter ungulate foraging. Although there were few differences between the closest-resource-site and best-direction rules, the closest-resource-site rule is the more conservative of the two. In a moose foraging model in which alternative search strategies were compared, Saarenmaa et al. (1988) found no difference in nutrition balance between global and local search strategies. The best-direction rule assumes ungulates have perfect knowledge of an area within a given radius from their current position, which would be difficult to test. The one-grid-cell rule is essentially a neutral model for movement, and daily movement distance is limited unrealistically. Our results imply that animal movement will generally be complex and cannot be approximated by simple diffusion. Finally, the closest-resource-site rule also is computationally simpler than the best-direction rule.

Individual-based spatial models are rich in behavior. In examining these simulations, we focused solely on foraging success (e.g., total and daily forage consumed), ungulate energetics, and ungulate survival to illustrate the interactions among parameters. However, a spatially explicit model such as this offers a vast array of other outputs that could be examined and compared with data. For example, the number of animals moving each day, mean distances traveled, trajectories of movement for individual animals, and the identification of areas of high and low feeding activity all could be explored. Models developed for specific landscapes and species could be quite valuable in enhancing our understanding of the interactions between landscape dynamics and large herbivores.

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ABSTRACT

Waelbroeck, C., 1993. Climate-
modelling approach. *Ecol. M*

A physical model of the soil
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