Landscape Ecology (2005) 20:319–333
DOI 10.1007/s10980-005-0467-1

Research article

The development of forage production and utilization gradients around livestock watering points

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Key words: Consumption, Foraging behavior, Grazing, Piosphere, Simulation model, Spatial hetereogeneity, Utilization, Eastern Washington, USA

Abstract

Large herbivores can impose spatial patterns on otherwise homogeneous vegetation, but how these patterns change through time is poorly understood. Domestic livestock pastures are model systems for studying how foraging behavior influences the development of coupled grazing and vegetation patterns. We sampled forage production and utilization by cattle along distance-from-water gradients to provide a snapshot of grazing and vegetation patterns, and then evaluated the ability of simulation models to qualitatively reproduce these patterns. In the field, forage production increased with distance from water, as expected, but utilization peaked at intermediate distances from water in two of three study areas. Likewise, simulations based on a variety of foraging strategies produced gradients in forage production and, after forage availability near water declined sufficiently, peaks in utilization at intermediate distances. Distance-from-water gradients thus represent cumulative but not necessarily present day gradients in grazing intensity. The model with a foraging strategy based on time minimization produced slightly more realistic patterns in forage abundance than a model based on energy maximization, although results were sensitive to the value of the threshold for rejecting sites of low forage biomass. However, all models produced implausible thresholds in grazing and forage distribution, suggesting that factors besides resource distribution influence herbivore distributions. Moreover, different foraging rules produced similar vegetation gradients, especially on point water source landscapes, illustrating the difficulty of inferring foraging processes from vegetation patterns.

Introduction

Large herbivores can have strong effects not only on the mean abundance of plant species and functional groups, but also on their spatial distribution (reviewed by Adler et al. 2001). Grazing mediated changes in the spatial heterogeneity of vegetation can increase or decrease habitat diversity and, in turn, the diversity of consumer species (Smith 1940; Grant et al. 1982; Bock et al. 1984; Dennis et al. 1998; Matlack et al. 2001). This influence of large herbivores on overall biodiversity in grazing ecosystems raises the possibility of using grazers as tools for conservation management (Collins et al. 1998; Fuhlendorf and Engle 2001). In order to manage habitat diversity with grazers, however, we need to understand how large herbivores influence and respond to spatial heterogeneity in resource distributions. Although we can predict grazing's effect on spatial heterogeneity at one moment in time, given information on the spatial distribution of both vegetation and grazing pressure (Adler et al. 2001), the development of these patterns over time is poorly understood (Pastor et al. 1997).

Field studies provide limited and inconsistent information on temporal change in the spatial patterns of grazing and vegetation. In the tallgrass prairie of central North America, for example, the spatial dynamics of grazing and vegetation are driven by fire.

Large herbivores preferentially graze recently burned patches (Hobbs et al. 1991; Pearson et al. 1995; Coppedge and Shaw 1998; Biondini et al. 1999), but the locations of such patches shift as new areas are burned. Burned patches are preferred for only 1–3 years, after which they are avoided (Biondini et al. 1999). In contrast, heavily grazed patches in southern African grasslands do not shift over time, leading to localized degradation (Kellner and Bosch 1992). Similarly, differences in soil characteristics between heavily grazed patches and surrounding vegetation in Tierra del Fuego grasslands indicate that the patches are stable over time (Posse et al. 2000). Rigorous quantitative description of spatiotemporal patterns of grazing and vegetation would require long-term, spatially explicit data. Satellite imagery can provide these data at coarse scales (Jano et al. 1998), but intensive field sampling would be necessary at fine scales or for response variables that are difficult to estimate remotely.

Because collecting appropriate field data is so difficult, research on the development of grazing and vegetation patterns over time often must rely on simulation models. To study the reciprocal relationship between herbivores and landscapes over time, both herbivore foraging behavior and plant growth must be modeled in a spatially explicit format. This approach has successfully explained the development of vegetation spatial patterns in boreal forest browsed by moose (Pastor et al. 1999), the breakdown of vegetation patterns in grazed arid ecosystems (van de Koppel et al. 2002), the grazing-forage quality feedbacks leading to patch grazing in grasslands (Hutchings and Gordon 2001), and the persistence of boundaries in a vegetation mosaic (Farnsworth and Anderson 2001).

These models demonstrate that predicting the effect of herbivores on spatial heterogeneity requires an understanding of their foraging behaviors (Farnsworth and Beecham 1999). Recent work on foraging behavior has emphasized two findings. First, herbivores make movement decisions based on factors operating at different spatial scales (Senft et al. 1987; Johnson et al. 2001). One of the challenges in modeling foraging behavior is assigning the proper weight to these different factors. Including optimal search efficiency at all scales, as under the marginal value strategy (Charnov 1976), can lead to a rapid and unrealistic extirpation of food resources (Moen et al. 1998). On the other hand, if foragers are too restricted in their search, and ignore resource distribution at broad scales, they will fail to utilize available resources (Farnsworth and Beecham 1999). Adding a probabilistic element to the search can solve the former problem, while allowing foragers to respond to resource gradients can solve the latter (Farnsworth and Beecham 1999). Second, because forage biomass is often inversely related to digestibility (Coppock et al. 1983; McNaughton 1984), the instantaneous rate of digestible energy gain, a function of forage quantity and quality, may be highest in areas of intermediate biomass (Hobbs and Swift 1988). If large herbivores forage to maximize energy intake, then they should choose areas of intermediate over high biomass, as many empirical and modeling studies demonstrate (Wallis de Vries and Dalebroudt 1994; Wilmshurst et al. 1995; Hutchings and Gordon 2001; Fortin et al. 2003). On the other hand, if grazers base their foraging strategy on time minimization, rather then energy maximization, they should choose areas of high biomass (Bergman et al. 2001). Time minimization and energy maximization strategies may impose different spatial patterns on the landscape, but which strategy is most common remains unknown.

A principal challenge in empirical testing of foraging models is the complexity of natural landscapes. Therefore, we should attempt to apply models in simple settings such as piospheres, defined by Andrew (1988) as the zone of ecological impact surrounding a watering point in arid and semi-arid grazing systems. Piospheres are model systems for studying pattern evolution because vegetation develops clear, well-documented gradients as a function of distance to water, a classic example of large herbivores altering the spatial heterogeneity of vegetation (Andrew 1988; Huntley 1991; Pickup et al. 1998; Turner 1998; Ludwig et al. 1999; Nash et al. 1999; Thrash 2000). Furthermore, piospheres, especially in domestic livestock systems, are bounded and easily replicated compared to more complex and open wild ungulate systems.

Despite these advantages, coupled plant-herbivore models have not been developed to study spatiotemporal patterns in piospheres. Weber et al. (1998) demonstrated that fine-scale spatial heterogeneity in grazing pressure has large consequences for vegetation in piospheres, but their model generated broad-scale heterogeneity by modeling defoliation intensity as a negative function of distance from water, making grazing distribution at this scale an input and not a response. Similarly, piosphere field studies have used distance from water as a proxy for stocking rate or grazing intensity, based on the assumption that utilization decreases monotonically with distance from water (Andrew 1988; Pickup et al. 1998; Ludwig et al. 1999; but see Pickup and Chewings 1988). This assumption may be appropriate when livestock are first introduced to a pristine pasture, but as grazing pressure alters the distribution of forage availability, we should expect that the distribution of utilization will also change. For instance, once forage availability is reduced to low levels near water, the area of most intense utilization might shift outward, producing a unimodal relationship between distance-from-water and utilization.

We used field studies and simulation models to evaluate how patterns of forage production and utilization change over time. Our field tests were conducted in piospheres of sagebrush steppe in the northwestern U.S. that have been grazed for decades and contain strong gradients in forage availability. At study areas representing a range of moisture conditions and management practices, we asked, (1) do consumption and utilization decrease monotonically with distance from water? Our primary goal was not to identify differences between the study areas, but rather to illustrate common piosphere patterns. To provide an explanation for the observed patterns, and place our snapshot field measurements in a temporal context, we constructed a series of simulation models linking herbivore foraging behavior and vegetation dynamics. We used these models to address two additional questions: (2) Under what conditions will peaks in utilization develop at intermediate distances from water? (3) Can qualitative comparisons of simulated and observed vegetation patterns provide evidence for specific livestock foraging strategies? More specifically, do time minimization or energy maximization strategies generate more realistic patterns?

Methods

Field studies

We conducted fieldwork at three study areas spanning a range of mean annual precipitation in the sagebrush steppe of eastern Washington. The 'arid' study area, located at Wanapum State Park near Vantage, WA (46.95°N, 120.01°W), receives approximately 170 mm annual precipitation, concentrated in the fall, winter, and spring, has a mean annual temperature of 12 °C, and aboveground net primary production (ANPP) can range from 35 g m^{-2} in degraded sites to 70 g m^{-2} (Adler et al. in review). The primary vegetation type is the *Agropyron spicatum-Artemisia tridentata* association (Daubenmire 1970), and is grazed every other spring by cattle. The 'semiarid' study area, located just south of Ellensburg, WA (46.86°N, 120.42°W), also falls within the *Agropyron spicatum-Artemisia tridentata* association, but receives approximately 250 mm precipitation annually, and ANPP can range from 35 to 90 g m^{-2}. Pastures at this study area are grazed every spring and summer by cattle. The 'subhumid' study area above Grand Coulee, WA (48.00°N, 119.30°W) has a cooler, wetter climate, with a mean annual precipitation of at least 300 mm, a mean annual temperature of 8°C, and ANPP ranging from 70 to 150 g m^{-2}. Vegetation at this study area belongs to the *Festuca idahoensis-Artemisia tripartita* association, and is grazed by cattle in spring-summer or summer-fall in alternate years.

We selected 3 to 4 sampling sites along 3 independent distance-from-water transects in each of these study areas. Because of the need to stratify pastures by soil type and topographic position, we located the sampling sites at variable, not fixed, distances from water. We used pastures in which stocking rate and the location of fences and water had remained relatively constant for at least 20 years. Each gradient originated from an independent water source, though sometimes two gradients were located within the same pasture. Except for one gradient at the semiarid study area originating from a stream, all water came from point sources. Whenever possible, we took advantage of long term ungrazed control sites (> 20 years ungrazed) found on road verges or in ungrazed land adjacent to the grazed pastures. The species composition on these sites was similar to that in grazed sites located far from water. At each grazed site, we constructed a 10 x 10 m cattle exclosure. We used these exclosures to measure primary production in the 1 to 2 years following their construction, assuming that composition was identical to the adjacent grazed areas. Production was estimated by direct harvest inside the exclosures at the time of peak biomass (early May at the arid study area and June at the semiarid and subhumid study areas). We used different harvesting methods for annuals and forbs, perennial grasses, and shrubs (Adler 2003; Adler et al. in review). We also harvested outside the exclosures on the same dates to measure consumption, defined as the difference between the grazed and ungrazed forage biomass (g m^{-2}) at the end of the growing season. We defined forage as all herbaceous biomass, thus excluding shrubs. Utilization was calculated as consumption divided by production. Adler et al. (in review) provides a detailed description of study areas, livestock management, site selection, and field methods.

We used mixed-effects statistical models to analyze the observed data. For analyses of forage production, which included sites with long-term protection from grazing, we transformed distance from water into a categorical variable, putting sites less than 0.5 km from water into distance class 1, sites 0.5 to approximately 1.0 km from water in class 2, sites greater than 1.0 km from water in class 3, and ungrazed sites in class 4 (Adler et al. in review). We then analyzed the production of all perennial grass species, or just the dominant perennial grass in each study area, as a function of distance-from-water class and precipitation (arid, semiarid, or subhumid), treating transect as a random factor nested within precipitation. For analyses of consumption and utilization, we could ignore long-term ungrazed sites and model the response variables as a function of absolute distance from water, a continuous variable. In this case, we ran a separate analysis for each study area, again treating transect as a random effect. All analyses were performed in R (version 1.8.1, 2003).

Model development

We linked a vegetation submodel with an individual-based herbivore foraging model. We ran simulations on a circular landscape with a point water source, and assumed that vegetation at time zero was homogeneous. We further assumed that subsequent changes in vegetation caused by grazing were identical along any radius extending from the watering point. This simplifying assumption allowed us to model these two dimensional landscapes in one dimension. The area represented by each position along this distance-from-water transect increases as the animal moves out from the watering point. If each position x is separated by a distance of one, the areas represented by positions $1,2,3\ldots x$ are 3.14, 9.42, $15.71\ldots\pi x^2$- $\pi(x\text{-}1)^2$.

We also ran simulations on a rectangular landscape with a linear water source to determine the importance of geometric effects. On this landscape, each position on the distance-from-water transect represents exactly the same area, a strip parallel to the water source with area determined by the width of the pasture and the distance between each position on the distance-from-water gradient.

The vegetation model was composed of two functional types: grass, the dominant competitor and the source of forage; and shrubs, which are not consumed. Shrubs increase in biomass on sites where grazing decreases grass biomass. We describe the dynamics of these functional types using a discrete time version of a Lotka-Voltera competition model:

$$\frac{dG_x}{dt} = \frac{R_G G_x(K_G - G_x - \alpha_S S_x)}{K_G} + m - c \qquad (1)$$

$$\frac{dS_x}{dt} = \frac{R_S S_x(K_S - S_x - \alpha_G G_x)}{K_S} + m - T \qquad (2)$$

where G_x is biomass of grass at position x, S_x is shrub biomass at position x, R_G and R_S are the instantaneous growth rates of grasses and shrubs, K_G and K_S are the grass and shrub carrying capacities, α_S is the effect of shrubs on grasses and α_G is the effect of grasses on shrubs. Consumption, c, is a function of herbivore density and forage availability at position x, and trampling damage to shrubs, T, is also a function of herbivore density at x. The small immigration rate m, identical for both functional types, prevents local extinction. Grass biomass at each position is updated with respect to losses to consumption as they occur, but changes in grass and shrub biomass due to growth and trampling are calculated only at the end of each day.

The key characteristic of the foraging submodel is that every animal begins each day at the water source (position = 1) and then forages independently until it meets its daily intake requirement. As forage availability near water decreases, the number of foraging bouts necessary for an animal to reach its requirement will increase (since evaluating animal performance was not one of our objectives, we do not report these results). At each position, the animal has to decide whether or not to take a bite of vegetation, based on a 'start-eating rule.' After removing one bite, the animal must decide which direction to move, based on a movement rule. In this respect our models differ from those in which an animal reduces the food resource in a patch to a certain level before moving. In fact, our model represents one extreme of the partial consumption spectrum. However, Farnsworth and Beecham (1999) showed that leaving a patch before it was depleted had few effects on model results, and Moen et al. (1997) found that animal fitness was higher when forage was only partially depleted in a cell.

We explored a series of models representing variations on the rules for making these decisions, and for determining the biomass removed with each bite. In the first model, animals attempt to maximize forage intake, a time minimization strategy. The second model represents a null foraging strategy in which animals always move away from water. In the third, we incorporate a trade-off between forage quality and quantity that represents an energy maximization strategy. We explain implementation of the first model in detail and then, briefly, the variations introduced for the next two models.

The first model, and the one we used to explore model sensitivity to key parameters, is the time minimization model (TMin). Grazers in this model attempt to maximize their instantaneous rate of biomass intake. Since the time period (t) of every one-bite foraging bout equals one, intake rate (g t^{-1}) and available intake per bite (g) are equivalent. In this discussion we refer to the latter quantity. The start-eating rule is based on a comparison between available intake at the animal's current position and mean intake for the entire gradient. This rule assumes that animals have knowledge of resource conditions across the whole gradient, a good assumption for all but the first days after their introduction to the landscape. If available intake at the animal's current position is greater than a specified fraction of mean intake, the animal eats. If available intake falls below this threshold, the animal continues to move. Movement in this TMin model is also based on available intake. The animal compares the mean available intake within a specified perception distance in either direction, and then takes one step in the direction of greater mean intake with a probability p (the probability of making the correct decision). Using movement distances greater than one, and adding variability in movement distances, did not change our modeling conclusions.

We calculated available intake at each position as a function of biomass density:

$$c_x = a(1 - e^{-bG_x}) \cdot t \tag{3}$$

where c_x is the forage consumed by the herbivore in one bite at position x, G is grass biomass, a and b are constants, and time, t, equals one. We interpret a as the maximum bite size, while b determines the slope of the function (Figure 1A). Available intake increases with biomass when forage is scarce, but then saturates at high levels of forage biomass. This function is a phenomenological form of Gross et al.'s (1993) mechanistic model for herbivore functional response. The model updates available intake every time a bite is taken.

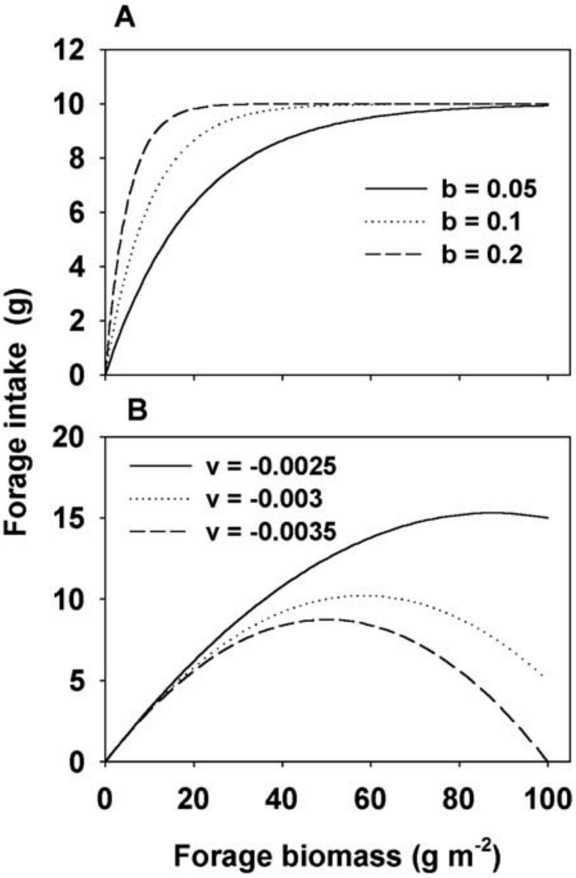

Figure 1. The relationship between forage biomass and forage intake per bite in A) models based on total forage intake (Equation 3, a=10) and B) digestible dry matter intake (Equation 4, u=0.35) for various values of the parameters controlling the shape of the functional responses.

Model output variables are grass biomass, shrub biomass, consumption, and utilization at each position along the distance-from-water gradient. The values of these variables are saved at specified time steps. Consumption and utilization are calculated over a specified time period: consumption, which we calculate from the plant's perspective, is the sum of all intake at each position over this time period, while utilization is consumption divided by the sum of grass biomass at the start of the time period and all growth that occurred during the time period.

The second model, called the maximum distance model (MaxDist), uses the same start eating rule as

Table 1. Parameter values used in simulations comparing different foraging behaviors on different landscapes.

Parameter	Description	Value
Landscape structure		
L	Length of distance from water gradient (m)	3000
W	Width of linear water source pastures (m)	200
d	Distance between each position on the gradient (size of cells) (m)	1
Vegetation		
K_G	Grass carrying capacity (g)	100
K_S	Shrub carrying capacity (g)	100
R_G	Grass maximum growth rate (g g^{-1})	0.02
R_S	Shrub maximum growth rate (g g^{-1})	0.01
α_G	Grass competition coefficient (g g^{-1})	0.8
α_S	Shrub competition coefficient (g g^{-1})	0.2
m	Immigration (g)	0.001
T	Trampling damage (g)	0.001
Herbivores and foraging		
N	Number of herbivores in point / linear water sources landscapes	50 / 10
DR	Daily required intake (g)	10,000
ET	Start-eating threshold (fraction of mean intake)	0.2
p	Probability of correct movement decision	0.9
PD	Perception distance (m)	1
a	Maximum bite size (g)	10
b	Shape of functional response in TMin and MaxDist models	0.1
u	First parameter for functional response in EMax model	0.35
v	Second parameter for functional response in EMax model	−0.003

the TMin model, but instead of making movement decisions based on available intake rates, animals always move away from the water source with the probability p.

The third model, called the energy maximization quality model (EMax) takes into account a trade-off between biomass quantity and quality. We incorporated the trade-off phenomenologically, by making available intake a quadratic function of biomass

$$c_x = (uG_x + vG_x^2) \cdot t \tag{4}$$

where c_x is available intake, now interpreted as available digestible energy, and u and v are constants (Fig 1B). Both the start-eating rule and the movement rule are based on this measure of digestible intake, rather than available intake as in the previous models.

Model simulations

We first ran a series of simulations to test the influence of various model parameters on the simulated patterns. We ran these simulations with the TMin model on both point and linear water sources landscapes and compared output at day 300, calculating consumption and utilization for periods of 50 days. We emphasize that these 'days' represent a somewhat arbitrary time step; our objective was not to accurately model the rate of vegetation change, but to explore how patterns may theoretically change over undefined time. To compare patterns generated by the different models, we ran each of the models on each landscape using constant parameter values (Table 1). The landscapes were large enough so that animals never reached the end of the distance from water gradients. We selected vegetation parameters to reflect a dominant forage grass, and a less competitive unpalatable shrub. We chose the herbivores' maximum bite size and daily intake to approximate cattle, with values of 10 g (Gross et al. 1993) and 10,000 g (Morrison 1961) dry matter, respectively. We arbitrarily set the probability of a correct move at 0.9 and the perception distance at 1 after determining that their values had relatively little influence on the qualitative form of the simulated patterns. We set the start-eating threshold below 1 in order to generate gradients in forage biomass (see Results).

The number of herbivores had to be smaller in the linear water source landscapes because their effective size was small compared to the point source

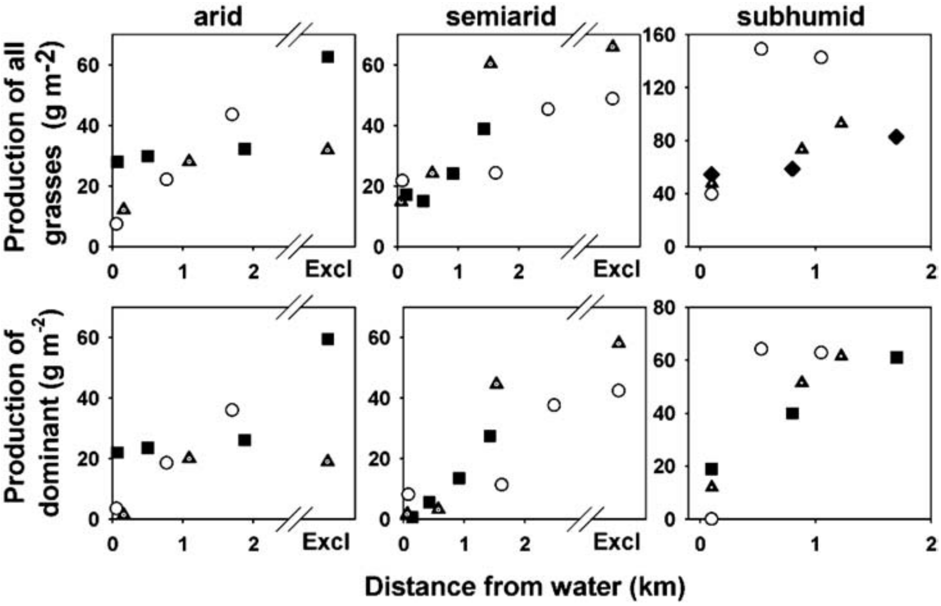

Figure 2. Total production of all grass species (top row of panels) and the production of the dominant grass species (bottom row) along distance-from-water gradients in arid, semiarid, and subhumid study areas in sagebrush steppe of central and eastern Washington state. Symbols denote different transects within each study area. 'Excl' refers to long-term, ungrazed exclosure sites.

landscapes in which total area per position increased with distance from water. We ran each of these simulations to 500 days, outputting results every 50 days, except for the MaxDist model on the linear water source landscape, which we ran to 1000 days since gradients were slow to develop in this situation. Because the patterns resulting from replicate simulations were indistinguishable, all results shown represent a single model realization.

Results

Field observations

Production of grasses, the dominant component of forage in sagebrush steppe, increased along distance-from-water transects in the arid, semiarid, and subhumid study areas (df = 3, 12; F = 4.79; $p = 0.02$) (Figure 2). The qualitative form of the increase, however, was variable. On some gradients, production increased rapidly at distances close to water, but slowly further from water, while on other gradients production increased only at locations furthest from water or in ungrazed exclosures. When only the dominant forage species was considered (*A. spicatum* at the arid and semiarid study areas, and *F. idahoensis* at the subhumid study area), decreases in production near water were more dramatic (df = 3, 12; F = 13.02; $p < 0.001$) (Figure 2). On at least one gradient in each study area, production of the dominant was close to zero at the location closest to water. Shrub production decreased with distance to water, although the higher shrub production near water did not completely offset the decreased grass production (Adler et al. in review).

Consumption was not influenced by distance from water at the arid study area (df = 1, 4; F = 2.08; $p = 0.22$), but had a negative quadratic relationship (concave down) with distance from water at the semiarid (df = 1, 5; F = 6.78; $p = 0.048$) and subhumid study areas (df = 1, 2; F = 13.51; $p = 0.067$) (Figure 3). Utilization, the proportion of available forage production consumed, decreased linearly with distance from water at the arid study area (df = 1, 4; F = 20.31; $p = 0.012$), but peaked at intermediate distances (quadratic relationship) along gradients at the semiarid (df = 1, 5; F = 8.17; $p = 0.035$) and subhumid study areas (df = 1, 2; F = 106.06; $p = 0.009$) (Figure 3).

Influence of model parameters on simulated patterns

The parameter with the strongest effect on resulting piosphere patterns was the start-eating threshold, the

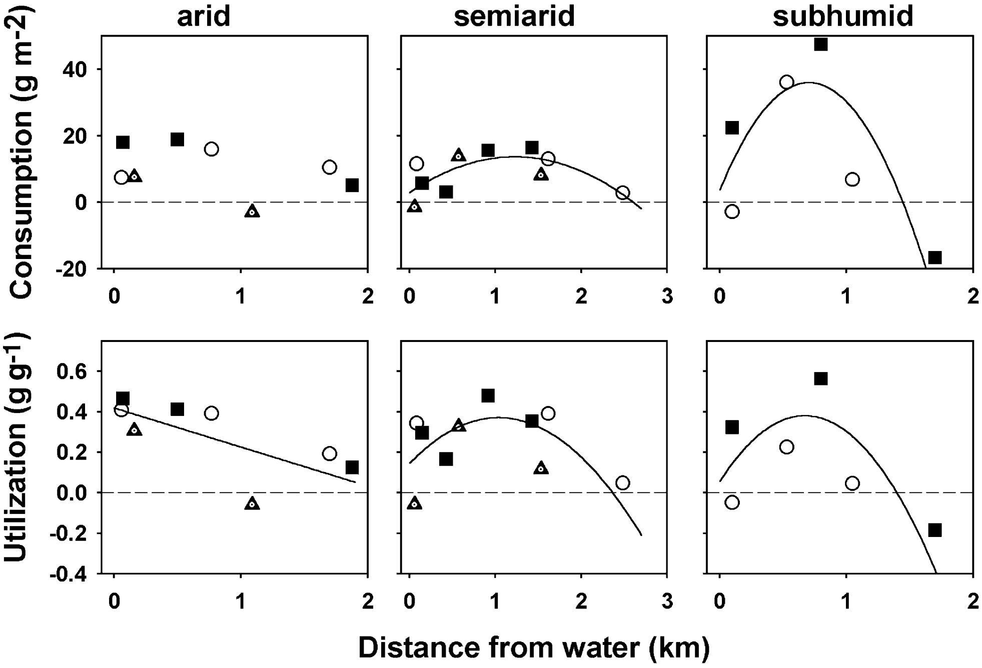

Figure 3. Consumption and utilization along distance-from-water gradients in arid, semiarid, and subhumid sagebrush steppe of central and eastern Washington. Symbols denote different transects within each study area. Points falling below the dashed lines (consumption or utilization equal to zero) occur when biomass in the ungrazed temporary exclosures is higher than biomass in the grazed area due to spatial heterogeneity. The solid regression lines shown are based on significant ($p < 0.05$) distance-from-water parameters estimated by a mixed effects model, and represent the mean response averaged across transects.

fraction of average intake at which the grazer chooses to eat. With the threshold set at 1, as predicted by the marginal value theorem (Charnov 1976), decreases in forage biomass occurred evenly across the landscape, preventing strong gradients from forming (Figure 4A). In contrast, with the threshold set at 0.99, a strong gradient in forage abundance developed. Grass biomass was depleted down to the start-eating threshold at locations closest to water. At the outer edge of this degraded zone, grass biomass increased very rapidly, but the increase slowed as distance from water increased further. The tail of this curve gradually approached grass carrying capacity, which was maintained at distances from water never reached by the grazers. Lowering the start-eating threshold further decreased the level of grass biomass within the degraded zone near water, but had little effect on the pattern on the rest of the gradient (Figure 4A). In the EMax model, however, gradients developed even with the start-eating threshold set at 1. Because we were interested in the response of grazers to the development of gradients in forage production under all the foraging behavior models, in the following simulations we set the start-eating threshold below 1.

Increasing the number of animals increased the size of the severely degraded zone, and also increased the portion of the gradient affected by grazing, since animals had to walk farther to meet their daily requirement (Figure 4B). Increasing the daily intake requirement had little effect on the size of the degraded zone, but increased the length of gradient affected by grazing, because a higher requirement led to longer distances walked (Figure 4C). Changes in the perception distance used to make movement decisions had virtually no effect on the pattern of grass biomass (Figure 4D). When the probability of correct movement decisions was high, the size of the degraded zone was small and the length of gradient visited by grazers long relative to simulations with lower probability of correct decisions in which animals were more likely to return to graze an already degraded location (Figure 4E). Smaller maximum bite sizes forced animals to travel further, decreasing the size of the severely degraded zone and increasing the length of gradient affected

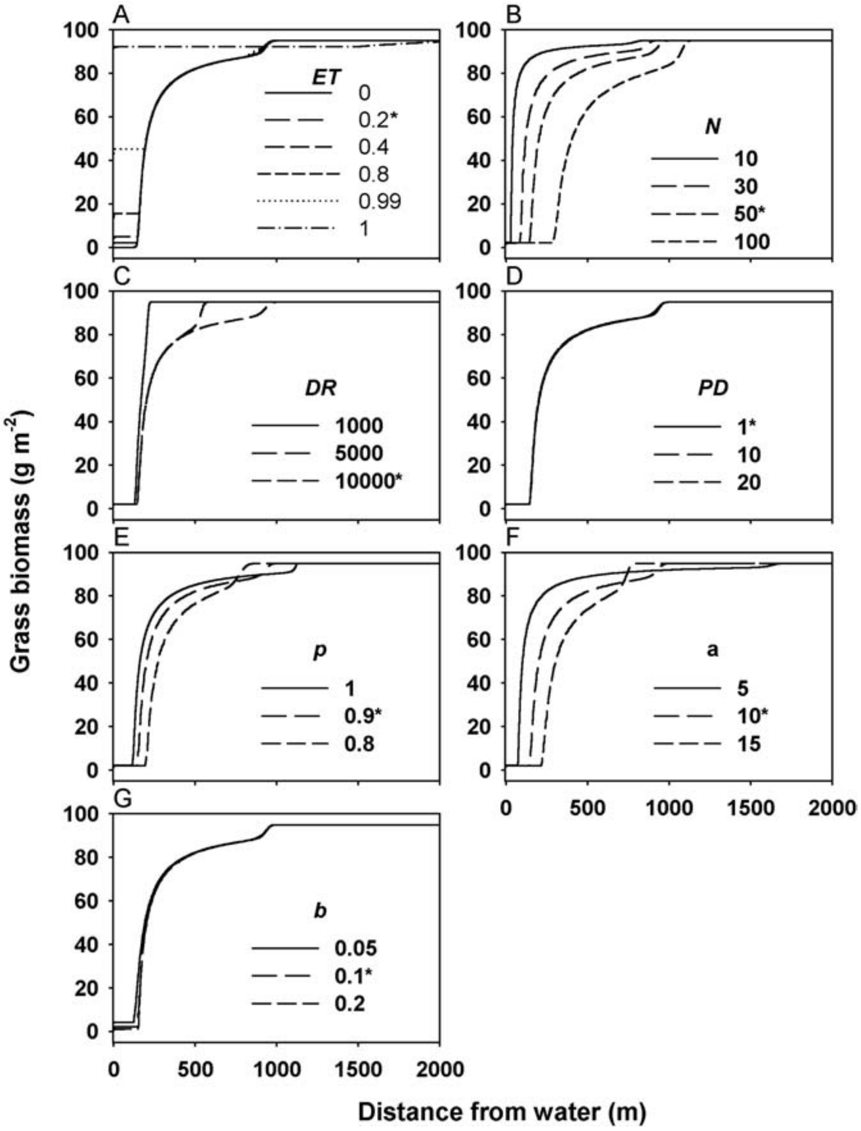

Figure 4. The influence of model parameters on simulated grass abundance across a distance-from-water gradient, using the time minimization (TMin) model on a landscape with a point water source. For each simulation, grass biomass is shown at day 300. The *'s indicate parameter values used in simulations comparing different models. Parameters are defined in Table 1.

by grazing (Figure 4F). Altering the parameter *b* that determines the slope of the functional response had only small effects on the pattern of grass biomass (Figure 4G).

Running the TMin model on a rectangular landscape with a linear water source also produced steep increases in grass biomass with distance from water. Model parameters had effects similar to those on the point water source landscape.

The instantaneous growth rate of grass, R_G, had strong effects on the development of patterns in grass biomass and utilization. At low growth rates, decreases in grass biomass near water occurred rapidly and, in turn, utilization shifted away from water, producing a peak at an intermediate distance in both point and linear water source landscapes (Figure 5). At high growth rates, severe decreases in grass biomass close to water took more time to develop, as did shifts in utilization away from water. Under high growth rates on the linear water source landscape, the intermediate distance peak in utilization never developed (Figure 5).

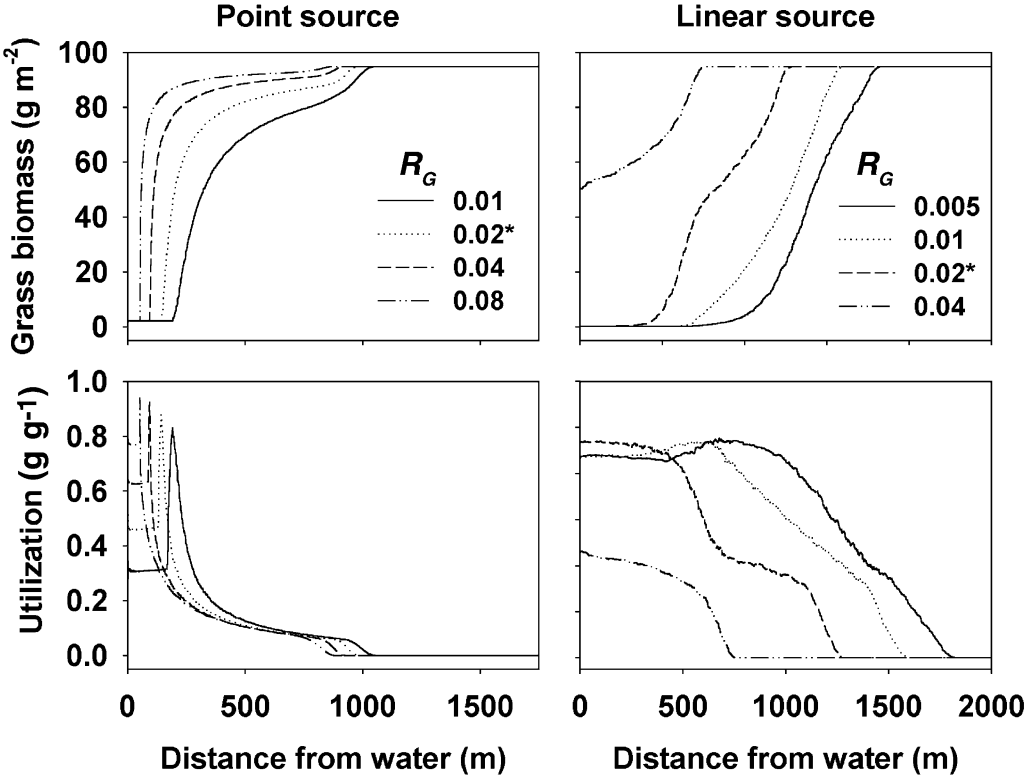

Figure 5. The effect of changes in grass instantaneous growth rate (R_G) on patterns in grass biomass and utilization at day 300. Panels on the left show results from the TMin model on a landscape with a point water source, while panels on the right show results from a linear water source. The *'s show the value of the parameter used to compare different models.

Temporal development of patterns generated by different foraging models

On landscapes with a point water source, the TMin model generated a gradient in grass biomass that increased in extent with time: both the size of the severely degraded zone near water, and the portion of the landscape affected by grazing grew over time (Figure 6). Shrub biomass followed the opposite pattern, increasing with time, except for locations closest to water where trampling was severe; further from water, grass competition kept shrub biomass low. Consumption was initially highest close to water, but this peak shifted away from water over time. Similarly, utilization initially decreased with distance from water, but then developed a narrow peak at an intermediate distance that shifted away from water over time. The MaxDist model produced virtually identical results to the TMin model. The EMax model, however, produced distinct patterns. As in the previous models, grass biomass was degraded down to the start-eating threshold close to water, but the growth of this zone over time was more rapid and the increase to carrying capacity at the outer margin of this zone much more abrupt. Shrub biomass, correspondingly, increased more rapidly and over a larger area. The peak in consumption shifted outward relative to the TMin and MaxDist models, and utilization developed a bimodal distribution that shifted away from water with time (Figure 6).

Comparing the different models run on the linear water source landscape produced results similar to those from point water source landscapes, with two important exceptions. First, while the TMin and MaxDist models generated similar patterns on the point water source landscape, on the linear water source landscape they generated very distinct patterns, with gradients in production and utilization taking more time to develop under the MaxDist model on the linear water source landscape (Figure 7). Second, whereas the EMax model led to a bimodal pattern of utilization on the point water source landscape, on the landscape with a linear water source the peak in utilization was unimodal and

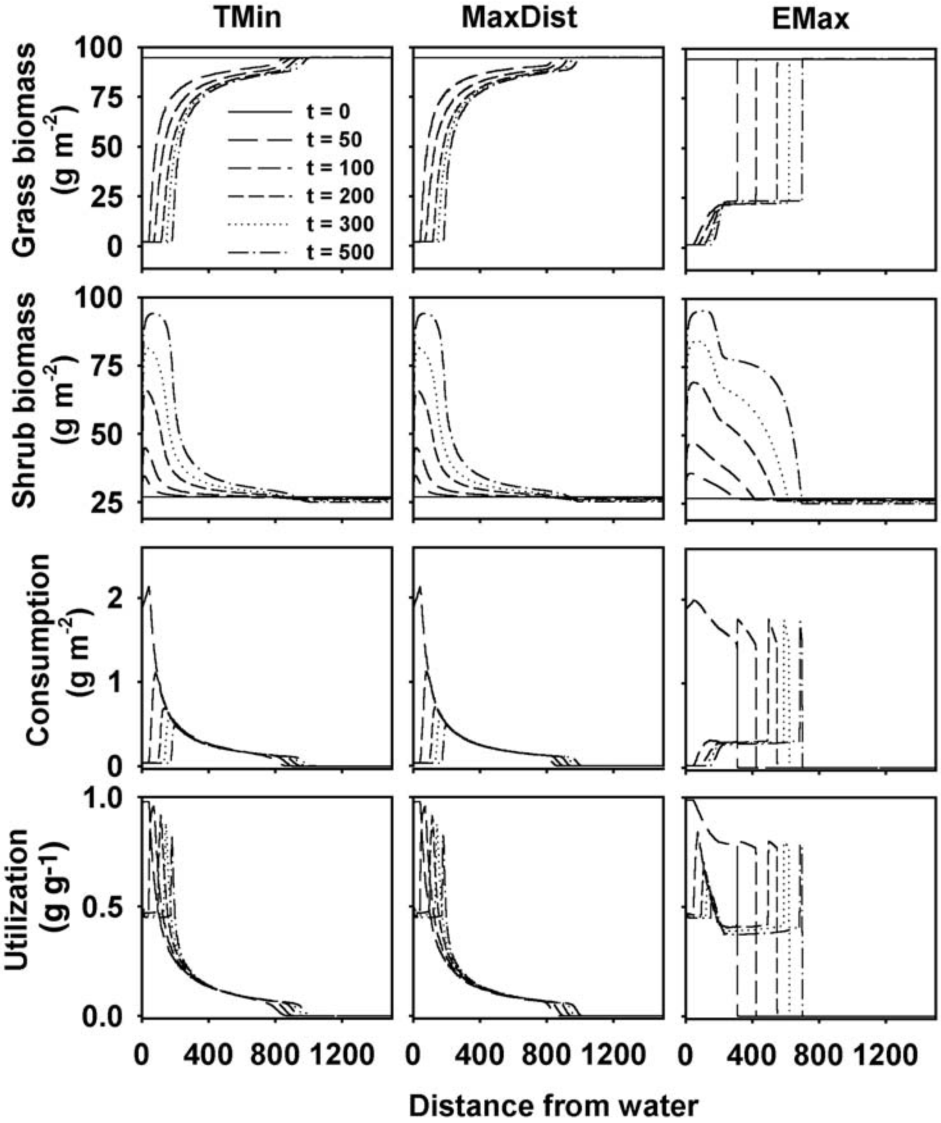

Figure 6. Simulated temporal changes in patterns of grass and shrub biomass, consumption, and utilization under different foraging models run on a landscape with a point water source. Lines correspond to patterns at different days (t = 0, 50...500) during the simulation. Consumption and utilization were calculated for the 50 day period preceding each output time.

occurred at the outermost edge of the zone experiencing grazing (Figure 7).

Discussion

Changes in the distribution of grazing over time

The development of peaks in consumption at intermediate distances from water should be expected: as forage availability is dramatically reduced near water, absolute consumption must decline as well. But piosphere studies typically have assumed that *utilization*, not just consumption, would remain high near water. In other words, even though forage availability declines, the high density of grazers near water still would lead to a large *proportion* of forage being consumed. In contrast, our field observations showed that at two of our three study areas, utilization was significantly higher at intermediate distances from water than at the sites closest to water. This result means that grazers removed a smaller proportion of

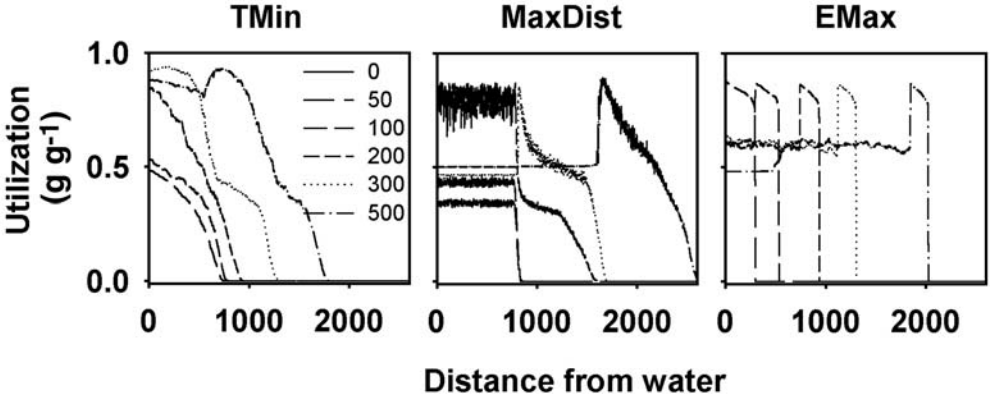

Figure 7. Simulated temporal changes in utilization under different foraging models run on a landscape with a linear water source. For the TMin and EMax models, lines correspond to patterns at days 0, 50...500 of the simulation. For the MaxDist model, patterns took more time to develop, and lines correspond to days 0,100...1000. Utilization was calculated for the 50 day period preceding each output time.

forage in degraded areas near water than in areas farther from water with more abundant forage. Even at the arid study area, where utilization decreased monotonically with distance from water, differences in utilization between sites adjacent to water and those hundreds of meters away were quite small. The different pattern at this study area may be due to more conservative management requiring pastures to be rested in alternate years, while grazing occurs every year at the semiarid and subhumid study areas. Our direct measurements of utilization across distance-from-water gradients are unique, to our knowledge, but published data on livestock densities across such gradients do provide indirect evidence for intermediate peaks in utilization. Pickup and Chewings (1988) showed that observed and modeled cattle densities peaked at intermediates distances in semi-arid Australian piospheres. Turner and Hiernaux (2002) estimated livestock density around villages in sub-Saharan Africa and also found that densities were highest at intermediate distances.

Our models also generated patterns of utilization that peaked at intermediates distances from water under a wide variety of parameters and foraging behaviors. The simulations demonstrated that the intermediate peak in utilization does not develop until forage abundance is decreased to very low levels close to water. Except for the EMax model, this degree of degradation did not occur unless the start-eating threshold was set at least slighlty below 1, raising questions about the stability of solutions based on the marginal value theorem. The value of this threshold is critical near 1 because of the shape of the herbivore functional response: accepting a site with a marginally lower level of available intake means accepting a site with a substantially lower standing biomass. Altering additional variables that influence the rate of degradation, such as stocking rate, maximum bite size, and the growth rate of grasses, can slow down or prevent the development of the intermediate peaks in utilization. Because forage availability near water decreases more rapidly on point than linear water source landscapes, the intermediate peak in utilization develops sooner, and because the ultimate extent of the degraded area is larger on the linear source landscapes where animal density is less diluted with distance, the peak in utilization shifts further from water.

Both the field and model results suggest that when grazers are first introduced to a new pasture with uniform forage abundance, or in pastures where grazers never cause dramatic changes in forage abundance, we should expect utilization to decrease monotonically with distance from water, as piosphere field studies often assume. Once forage abundance has been reduced to very low levels near water, however, we should expect peaks in utilization at intermediate distances. Distance-from-water thus represents a gradient in historical or cumulative grazing intensity, but not necessarily a gradient in current utilization.

Simulations over longer time scales showed that the intermediate peak in utilization persisted, but continued to shift away from water and gradually decreased in magnitude. However, our models cannot be expected to provide reliable results on long time scales for two reasons. First, we did not model herbivore energetics, so changes in forage abundance have no feedback on the grazer population in our models. In reality, as forage availability declines with time, the grazers must walk ever further to satisfy their daily requirements. At a certain point, this increase in energy expenditure will have consequences for individual and population growth. In domestic livestock pastures, this typically translates into a decreased stocking rate or decreased reproductive rates (Paruelo and Sala 1992; Golluscio et al. 1998), which would limit or slow the expansion of the degraded area near water. The second reason our models should not be used to simulate long-term patterns has to do with our use of the standard Lotka-Volterra equations for vegetation growth and competition. Plant growth in most grazing systems is seasonal, and while the Lotka-Volterra approach may approximate vegetation dynamics during the growing season, how defoliation affects growth the following season is more complex. For example, field studies show that a plant's ability to recover the season following a severe defoliation event depends on the timing of defoliation (Blaisdell and Pechanec 1949; Ganskopp et al. 1988). Modeling patterns of forage production over the long-term would require a better understanding of these inter-annual dynamics and an effort to define model time steps in a way that represents accurate rates of vegetation change.

Time minimization or energy maximization?

All models run on the point water source landscape with the start-eating threshold set below 1 produced patterns with extremely abrupt thresholds in plant biomass, consumption, and utilization. Adding area-restricted search (Stern 1998; Fortin et al. 2003), which allows animals to move quickly through areas of low forage availability and more slowly through areas of high forage abundance, had little effect on patterns generated by the TMin model (not shown). Although our simulated grass biomass patterns are quite similar to the logistic model proposed by Graetz and Ludwig (1978), the steepness of the ascending portion of the curves seems unrealistic. While some of the piospheres surveyed by Graetz and Ludwig do demonstrate steep transitions, most field data, including ours, show gradual changes in plant or forage biomass with distance from water (Graetz and Ludwig 1978; Pickup and Chewings 1988; Pickup et al. 1994). Patterns simulated by the EMax model produced even steeper thresholds than the TMin model, which could be interpreted as evidence that energy maximization may be less common in natural systems than time minimization strategies, consistent with a recent field study (Bergman et al. 2001).

The implausible transitions our simulations produced indicate that other factors not included in the models have important influences on animal movement. In our models, animal distribution is controlled exclusively by the location of water and forage availability. As a result, when the simulated grazers are introduced to a pristine, homogeneous, landscape, they will graze close to water until they deplete forage biomass and are then forced to disperse. We expected the MaxDist model, in which animals always move away from water, to produce less concentrated grazing and thus smoother gradients in vegetation. The fact that this model also generated unrealistically steep thresholds in forage biomass, at least on the point source landscape, suggests that factors causing the animals to disperse must be quite strong and may need to operate independently of forage availability.

Field studies have identified influences on animal movements that our models ignored. Armstrong and Robertson (2000) found that the need for shelter from harsh winter weather had a strong effect on sheep distributions. Similarly, deer selected habitat based on proximity to forested shelter (Mysterud et al. 1999). Social dynamics, inevitably an important factor in herds, can constrain patch choice and, in one modeling study, influence intake rates and resource variability (Beecham and Farnsworth 1998). Allowing foragers to gather and retain information about resource distributions, and not simply respond to conditions at their current local position, can also influence movement (Beecham and Farnsworth 1998). If these factors compel animals to explore distant areas of the pasture, even when forage is available closer to water, then models including them might generate smoother, more realistic patterns of vegetation and grazing.

Inferring process from pattern

Our simulations demonstrate an interaction between landscape geometry and animal behavior. Commonly observed piosphere patterns do not result automatically from the concentration of animals near water, but depend on foraging rules. Conversely, different foraging rules can produce similar patterns. In point water source landscapes, the TMin model and the MaxDist model, in which animals always move away from water, produced virtually identical spatiotemporal patterns of grass and shrub biomass, consumption, and utilization. The concentration of animals around water was so intense, and the development of steep gradients in forage availability so rapid in time, that maximizing intake, the search strategy in the TMin model, required rapid movement away from water. In contrast, the geometric constraint was relaxed on the linear water source landscape, allowing different behaviors to produce more distinct patterns.

That different foraging strategies can produce similar patterns underscores the difficulty of inferring process from pattern. Data on animal movements, patterns of plant biomass, or grazing pressure may not be sufficient to allow clear determination of the factors influencing animal movement. By gathering such data on a variety of different landscapes, however, we may improve our ability to identify the true underlying mechanisms.

Acknowledgements

We thank Bill Lauenroth, Tom Hobbs, Dave Swift, Andrew Illius, and J.M. Morales for valuable comments and suggestions. We thank Iain Gordon, Dean Anderson, and an anonymous reviewer for suggestions that greatly improved the manuscript. P.B.A. was supported by a NSF Graduate Fellowship and a NSF Dissertation Improvement award.

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