

Landscape Simulation of Foraging by Elk, Mule Deer and Cattle on Summer Range

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Introduction

Cattle, mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) share more area of spring, summer and fall range than any other combination of wild and domestic ungulates in western North America (Wisdom and Thomas 1996). Not surprisingly, conflicts over perceived competition for forage have a long history, yet knowledge about actual competition is limited (Van Dyne et al. 1984b, Hobbs et al. 1996, Johnson et al. 1996). One of the first studies of the Starkey Project was designed to address the issue of whether mule deer and elk compete with cattle for available forage on summer range. A component of this study was to build a forage allocation model that could be used to analyze forage allocation problems on summer range in the Blue Mountains. This model would use data on animal spatial distributions, resource selection patterns, behavioral interactions and diet selection of cattle, elk and mule deer that was collected as

part of the Starkey Project at the Starkey Experimental Forest and Range (Starkey) (Johnson et al. 2000; Coe et al. 2001, 2004; Findholt et al. 2004).

Modeling the forage removal and animal performance for multiple species of ungulates across large landscapes is a complex problem (Weisberg et al. 2002). The high degree of temporal and spatial variability in ungulate distributions, forage production and nutritional value of forage contribute to the problem (Wisdom and Thomas 1996). Several early forage allocation models built for western rangelands were never widely used, owing to insufficient data, model complexity and institutional barriers (Van Dyne et al. 1984a, McInnis et al. 1990). A prototype forage allocation model built from Starkey data (Johnson et al. 1996) suffered from similar problems but did provide a framework for further discussions and model development (Vavra et al. 2004). This model used linear programming with a weighted objective function that contained terms for forage production, forage energy content and resource selection coefficients. Animal foraging behavior could be optimized with respect to each of these three variables or some weighted combination. The Johnson et al. (1996) model generated reasonable predictions of species distributions and forage consumption patterns at monthly time steps. However, the linear programming framework was cumbersome and had limited capability to analyze the temporal dynamics of ungulate foraging behavior.

Using many of the parameters from the earlier work, we built a more detailed, spatially explicit, individual animal foraging model, called the Starkey foraging model (SFM). Initial testing of this model was described in Vavra et al. (2004). In this paper, we describe additional developments and testing, and we demonstrate the model's capability to predict forage removal and animal performance at Starkey. Ultimately, the model or subsequent outgrowths are intended for use in allotment management planning on summer ranges shared by cattle, mule deer and elk.

Methods

The SFM uses empirical data on habitat preferences, forage production, forage quality and energy dynamics of cattle, mule deer and elk. These data are coupled with information on foraging behavior to simulate forage consumption by the three ungulates on the Starkey landscape. The SFM was developed in Object Pascal, using the Delphi 6 (Borland Inc.) integrated development environment.

Data sources used for the SFM are described in detail by Vavra et al. (2004) and are summarized here.

Habitat preferences for each species were incorporated using resource selection functions developed at Starkey (Johnson et al. 2000, Coe et al. 2001). These resource selection functions (RSFs) were estimated from Starkey telemetry data, collected between 1993 and 1996, and were estimated for monthly time steps, from April through October (Tables 1, 2). The RSF's represent the probability of an animal visiting a particular pixel over the monthly interval, as described by Johnson et al. (1996, 2000).

Forage production was estimated using several empirical models built from Starkey data (clipped plots from 1993–2000) and other sources (Vavra et al. 2004). We built functions to predict herbage production as a function of calendar day for grasslands, ponderosa pine (*Pinus ponderosa*) and riparian ecotypes. The equations for these ecotypes were extrapolated to the seven plant-association groups in the model (moist meadows, dry meadows, bunchgrass and shrub lands, warm dry forests with grass understory, warm dry forests with shrub understory, cool moist forest with grass understory, cool moist forests with shrub understory). The forage production was partitioned into forbs, grass and shrubs, using scaling factors developed by Hall (1973) and Johnson and Hall (1990). The growth functions were also adjusted for canopy closure on a pixel basis, using relationships developed at four grazing exclosures at Starkey and the data of Pyke and Zamora (1982). Forage growth was represented in the model on a daily time step, and we used the same growth functions for forage regrowth as those used for initial forage growth.

Forage quality, as measured by in vitro digestible energy (IVDDM) of forage, was obtained from the literature (Holechek et al. 1981, Svejcar and Vavra 1985, Sheehy 1987, Westenskow 1991) and data from Starkey. Digestible energy (DE) was calculated from IVDDM using methods of McGinnis et al. (1990), with estimates made on a monthly time step.

The spatial dynamics of animal foraging were modeled as a multiscale process that involved the selection of foraging patches and the subsequent selection of forage within the patch. We used concepts and data from a variety of sources for the foraging component of the model (Spalinger and Hobbs 1992; Gross et al. 1993, 1995; Shipley and Spalinger 1995) as well as observations on elk and mule deer movements at Starkey (Ager et al. 2003). Foraging patches were defined at the same scale as the Starkey spatial database, that is, each 30-

Table 1. Coefficients of resource selection functions for mule deer and elk during six monthly time steps in Main Study Area 1993 to 1996, Starkey Experimental Forest, northeastern Oregon. Seasons 1 to 6 correspond to May 16 to June 15, June 16 to July 15, July 16 to August 15, August 16 to September 15, September 16 to October 15, and October 16 to November 15. Coefficients are standardized (top) and nonstandardized (bottom). Coefficients for elk when cattle were not present were estimated in Smith-Bally pasture (seasons 2 and 5) and Bear pasture (seasons 3 and 4).

Season	Intercept	Distance to edge of patch	Forage produced	Shape of patch	Distance to traffic zero	Distance to traffic low	Distance to traffic medium	Distance to traffic high	Percent slope	Aspect east west	Aspect north south	Topographic convex	Soil depth	Distance to cover	Percent can. cover	Distance to cattle fence	Elk distance to water
Deer 1	-3.4588						-0.4284	-0.3431	0.2505	0.2159		0.2346					
	-25.2478						-0.0005	-0.0003	0.0200	0.2951		0.0449					
2	-3.8910							-0.5615	0.2326	0.1344		0.1250					
	-15.4409							-0.0003	0.0186	0.1830		0.0239					
3	-4.4878							-0.5473	0.3817	0.1723	0.2151	0.0818					
	-12.1049							-0.0006	0.0305	0.2353	0.3210	0.0156					
4	-3.7869							-0.4496	0.2767	0.1254		0.0936		-0.2073			
	-12.3734							-0.0007	0.0221	0.1703		0.0179		-0.0016			
5	-3.9353						-0.3948	-0.5563	0.2355			0.1174					
	-14.3405						-0.0003	-0.0006	0.0188			0.0224					
6	-3.9259									0.0811		0.1466		-0.1514			
	-17.8403									0.1097		0.0280		-0.0012			
Elk 1	-2.4546						0.1191		-0.1119			0.1181	0.1470		0.0552		
	-14.0412						0.0001		-0.0089			0.0226	0.0121		0.0025		
2	-2.8329	-0.0378	-0.0568	-0.0455		-0.2775	0.0741		0.1075	-0.0442	0.1034	0.1944	0.1384				
	-21.2643	-0.0008	-0.0003	-0.2897		-0.0004	0.0001		0.0086	-0.0607	0.1543	0.0371	0.0114				
No cattle	-2.9761			-0.1288		-0.2905			-0.2912	-0.1899		0.2856	0.1601	-0.2750	0.2510	0.2891	
	-26.8541			-0.7677		-0.0004			-0.0223	-0.2701		0.0477	0.0126	-0.0021	0.0015	0.0007	
3	-3.6208	0.1038	0.0377	-0.0681			0.1237	0.2306	0.1190		0.2491	0.1617	0.1851	-0.1919	0.1776		
	-20.3917	0.0022	0.0002	-0.4333			0.0002	0.0002	0.0095		0.3722	0.0309	0.0153	-0.0015	0.0081		
No cattle	-3.3056			-0.1649		0.3010	0.3256	0.5570	-0.1375	-0.1520	0.1803	0.3226	0.3783	-0.4220			0.1815
	-32.3572			-0.9822		0.0004	0.0003	0.0008	-0.010	-0.2119	0.2587	0.0534	0.0300	-0.0032			0.0011
4	-3.0575	0.0992			0.1182	0.0984		0.1946			0.1946	0.1706	0.1527	-0.1558	0.1709		
	-20.4503	0.0021			0.0005	0.0002		0.0003			0.2900	0.0326	0.0126	-0.0012	0.0078		
No cattle	-2.6522		-0.1112								0.1301	0.1945	0.1697		0.2209		0.1823
	-19.5567		-0.0005								0.1867	0.0323	0.0134		0.0098		0.0011

Table 1 (continued). Coefficients of resource selection functions for mule deer and elk during six monthly time steps in Main Study Area 1993 to 1996, Starkey Experimental Forest, northeastern Oregon. Seasons 1 to 6 correspond to May 16 to June 15, June 16 to July 15, July 16 to August 15, August 16 to September 15, September 16 to October 15, and October 16 to November 15. Coefficients are standardized (top) and nonstandardized (bottom). Coefficients for elk when cattle were not present were estimated in Smith-Bally pasture (seasons 2 and 5) and Bear pasture (seasons 3 and 4).

	Season	Intercept	Distance to edge of patch	Forage produced	Shape of patch	Distance to traffic zero	Distance to traffic low	Distance to traffic medium	Distance to traffic high	Percent slope	Aspect east west	Aspect north south	Topographic convex	Soil depth	Distance to cover	Percent can. cover	Distance to cattle fence	Elk distance to water
Elk	5	-3.1617	0.0463				0.0822											
		-19.0188	0.0010				0.0001					0.2379	0.1598	0.1212	-0.1813	0.1874		
No cattle	6	-2.2976		-0.2736	-0.1136							0.3556	0.0305	0.0100	-0.0014	0.0085		
		-9.4488		-0.0012	-0.6781							0.2324	0.0907		-0.3904			0.2638
	6	-3.2960								0.0978		0.3325	0.0151		-0.0030			0.0016
		-20.4223								0.0078		0.1396	0.1757	0.0915	-0.1612	0.0580		
												0.2073	0.0336	0.0075	-0.0012	0.0026		

Table 2. Coefficients of resource selection functions for cattle during four monthly time steps in cattle pastures 1993 to 1996 at Starkey Experimental Forest, northeastern Oregon. Seasons 2 to 5 correspond to June 16 to July 15, July 16 to August 15, August 16 to September 15, and September 16 to October 15. Coefficients are standardized (top) and nonstandardized (bottom).

	Season	Intercept	Distance to edge	Forage produced	Distance to road	Distance to fence	Percent slope	Aspect east west	Topographic convex	Soil depth	Distance to cover	Percent can. cover	Distance to water
Cattle	2	-2.4895	-0.0613		-0.1756	0.3043	-0.4726	-0.1063	-0.0526		-0.2089	-0.2743	0.1252
		2.8039	-0.0014		0.0008	0.0008	-0.0365	-0.1489	-0.0088		-0.0016	-0.0123	0.0008
	3	-3.0240	-0.1597	0.0452	-0.9849		-0.1370	-0.0917	-0.0660	0.0943		0.0563	-0.1300
		4.0840	-0.0033	0.0005	-0.0007		-0.0120	-0.1217	-0.0139	0.0078		0.0028	-0.0007
	4	-2.8177	-0.1728	0.0747			0.0747	-0.0584					-0.7470
		-2.4244	-0.0036	0.0007			0.0007	-0.0754					-0.0009
	5	-2.7450	-0.2228	0.0864		0.1516							
		0.9900	-0.1710	0.0004		0.0004			-0.4536	0.0711		-0.1650	
									-0.0075	0.0056		-0.0013	

by-30 meter pixel. Selection of foraging patches was modeled by using a neighborhood search algorithm that searched a 10 by 10 pixel neighborhood and that subsequently chose the pixel that maximized an index of preference according to:

$$\text{PREF}_p = (\text{RSF}_{\text{spm}} * W_{\text{rsf}}) + (\text{DE}_{\text{pm}} * W_{\text{qual}}) + (\text{F}_{\text{pm}} * W_{\text{mass}}) \quad (1)$$

where PREF_p equals pixel preference score for pixel p ; RSF_{spm} equals resource selection function score ($0 < \text{RSF} < 1$) for pixel p , species s , and month m ; DE_{pm} equals digestible energy in megacalories per kilogram forage for pixel p and month m ; and F_{pm} equals forage (in kilograms per hectare) present on pixel p and month m .

Here, W_{rsf} , W_{qual} and W_{mass} are weighting coefficients that control the relative importance of habitat selection, forage quality (DE) and standing forage biomass in the foraging process, respectively. The formulation recognized that both resource selection functions and forage characteristics need to be considered in the selection of foraging areas. Initially, we used a product of RSF_{spm} , DE_{pm} and F_{pm} to calculate the preference score and included the weighted coefficients W_{qual} , W_{rsf} and W_{mass} as exponents. This method created some scaling issues that led to the current formulation. Although the weighted coefficients could be species-specific, we used the same values for each species in the present simulations. Pixels were selected for foraging by randomly sampling the pixels and respective preference scores in each 10 by 10 pixel neighborhood 90 times (90 percent of the total number of pixels) to reflect the fact that animals have a less than perfect knowledge of the surrounding forage conditions. The pixel with the highest preference score was selected, and foraging was initiated. A range of values was used for the weighting coefficients in equation (1) as well as the spatial search parameters as part of the model building process. Values used in the simulations for equation (1) are described later. To prevent animals from foraging on high RSF pixels with very low or nonexistent forage biomass, we added a constraint that required a selected pixel to contain 80 percent of the forage biomass of the previously selected pixel. Although foraging areas still could be selected based primarily on their RSFs, this constraint also had the effect of moderating the rate of forage depletion of the pixels with the highest RSF scores and allowed the simulation of RSF-driven foraging without resulting in infinite pixel searches.

To allow for selection of foraging areas outside the animal's sensory detection range, we nested the neighborhood search within a low-frequency metaneighborhood search that allowed simulated animals to move (i. e. Levy flight, Marell et al. 2002) to another neighborhood if larger values for equation (1)

were found. We experimented with a range of values for the search neighborhood size, the metaneighborhood size, and the “jump” frequency and distance. In the current simulations, we set values for the metaneighborhood at 100 by 100 pixels, the jump frequency at 0.1 and the jump distance at 3,281 feet (1,000 meters).

Once a foraging pixel was selected, consumption of forage (grass, forbs and shrubs) was modeled with simulated individual bites. Bite size was estimated using data from foraging trials conducted at Starkey (Findholt et al. 2004) and elsewhere (J. Cook, personal communication), and it was 0.04 ounces (1.1 g) for cows, 0.007 ounces (0.20 g) for mule deer and 0.02 ounces (0.55 g) for elk. It should be noted that we did not constrain intake rate by bite size or other bite-dependent variable (Gross et al. 1993); hence, the bite process served primarily as a mechanism to sample the three types of vegetation data in the pixel over successive bites. Bite selection in the pool of simulated forage at each pixel was modeled as a Monte Carlo process that simulated successive bites that removed forage types in proportion to the sum of total forage available multiplied by simulated forage DE at the pixel, quantified as:

$$P_{ts} = \frac{(F_{pdt} * WB_{mass}) + (DE_{pmt} * WB_{qual})}{\sum_i [(F_{pdt} * WB_{mass}) + (DE_{pmt} * WB_{qual})]} \quad (2)$$

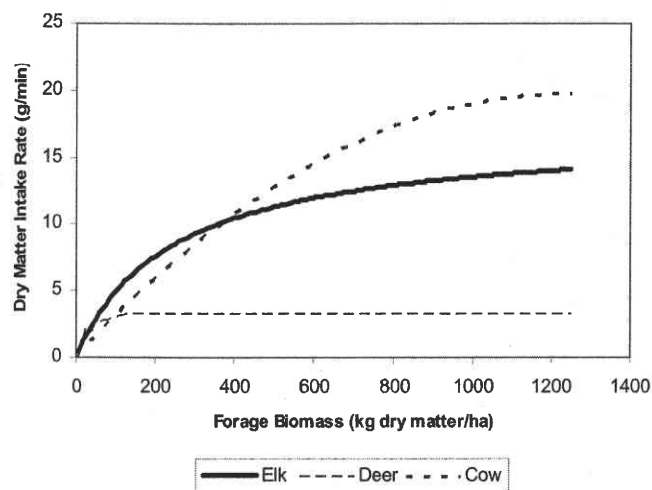
where P_{ts} equals probability of removing forage type t for species s ($0 < P_{ts} < 1$); F_{pdt} equals forage (in kilograms per hectare) of type t on pixel p at day d ; DE_{pmt} equals digestible energy (in megacalories per kilogram) for forage type t , pixel p , and month m ; WB_{mass} equals weighting factor for forage biomass; and WB_{qual} equals weighting factor for forage quality.

This foraging process simulated removal of vegetation in proportion to biomass and energy content, or some weighted combination. It also recognized that, while animals can focus their foraging on specific forage types, other nonpreferred types are also depleted at a lesser rate. Initially, we used WB_{mass} of 1.0 and WB_{qual} equal to metabolic body weight (body weight^{-0.75}), with the idea that mule deer would select for high forage DE, and cattle would select for forage bulk (Findholt et al. 2004). Elk, with their intermediate body weight, were simulated as having a foraging behavior intermediate to that of mule deer and cattle (Findholt et al. 2004). Initial simulations showed that stronger weighting of

the energy component was needed to significantly influence the forage composition.

Using the foraging rules described above, simulated animals were allowed to forage until they consumed 4.8 ounces (135 g) of forage dry weight per kilogram of metabolic body weight (Cook et al. 2004) or until the total foraging time per day exceeded 12 hours (Cook 2002), whichever condition came first. The foraging time was calculated using relationships between standing biomass and intake rate from Wickstrom et al. (1984:1,291) for elk and for mule deer, and from data from Starkey for cattle (Figure 1). For elk, we used the relationship for mixed forest conditions presented by Wickstrom et al. (1984) and combined the grass and mixed-forest data to develop a relationship for mule deer. Intake rates could also have been predicted using relationships between bite size and plant size (Spallinger and Hobbs 1992), but the latter data were not available for conditions at Starkey.

Figure 1. Relationship between standing forage biomass and dry matter intake rate for elk, mule deer and cattle. Functions for elk and deer were developed from data in Wickstrom et al. (1984). The elk relationship was developed from the Wickstrom et al. (1984) mixed-forest type relationship. The function for cattle was developed from grazing trials on Starkey and the bison data in Spallinger and Hobbs (1992).



Energy balance and weight change was updated daily using prorated monthly energy requirements (Table 3) obtained from a number of sources (Hudson and White 1985a, b; Cook 2002). Daily energy generated by consumed forage was calculated, using the energy conversion equation as:

$$Me = 1000 \times (F \times (0.038 \times \%DE + 0.18)/1.22) \quad (3)$$

where DE equals digestible energy (megacalories per kilogram of forage) and F equals forage biomass (dry matter in kilograms per hectare) consumed on a given day of forage.

Negative energy balances were translated into a weight loss by using a conversion rate of 6 megacalories per kilogram. Positive daily energy balances

Table 3. Daily energy demands of adult female mule deer, cow and elk, in millicalories per day, by month. Data from Hudson and White (1985a, b), Sheehy (1987) and Cook (2002).

Species	Month						
	Apr.	May	June	July	Aug.	Sept.	Oct.
Cattle	23.0	23.0	23.0	22.0	21.0	19.0	18.0
Elk	10.0	10.5	16.0	15.9	13.2	12.0	11.0
Deer	3.0	3.0	6.3	4.3	4.3	3.6	3.1

were translated into a weight gain by using the conversion rate of 12 megacalories per kilogram.

Most simulations used herd sizes of 500 cows, 450 elk and 250 mule deer under a summer deferred-rotation grazing system (April 15 to November 15, 210 days). These are the approximate stocking rates and the summer range foraging season at Starkey. In other simulations, the stocking rates varied, depending on the objective of the simulation. On each day, cattle foraging was simulated first, followed by elk and then mule deer, which gave cattle preference over elk and mule deer and which gave elk preference over mule deer for the available forage (Coe et al. 2004). Initial weights were set at 992 pounds (450 kg), 507 pounds (230 kg) and 132 pounds (60 kg) per animal for cows, elk and mule deer, respectively, based on data from Starkey. Typical execution time for the model was about one minute. We first ran simulations to examine the effects of different weights in the pixel preference equation on animal performance, foraging patterns and movements. This involved 125 simulations where each weight was varied by a factor of 10 between 1 and 100,000. We selected a set of weights where the model outputs appeared to be not overly influenced by the values and replicated observed animal performance at Starkey. The effects of different weights in equation (2) were then tested in a similar process in an additional 25 simulations. We then ran additional simulations to test how incremental changes in the number of cattle, mule deer and elk (2–2,500) and in forage production (10–100 percent of normal) affected animal performance. The latter simulations were intended to represent varying drought intensities. Reductions in forage quality from drought (Vavra and Phillips 1980, Weisberg et al. 2002) were not modeled due to limited data.

Results

Simulations using a range of values (1–100,000) for the W_{rsf} , W_{mass} and W_{qual} coefficients in equation (1) produced reasonable weight gains for cattle, elk

Figure 2. Simulated weight change in cattle for a range of values for W_{rsf} and W_{mass} in equation (1). X axis contains values for the W_{mass} (forage biomass) weights for the first equation. Legend entries are the values for W_{rsf} in equation (1). Animal populations were 500 cattle, 450 elk and 250 mule deer.

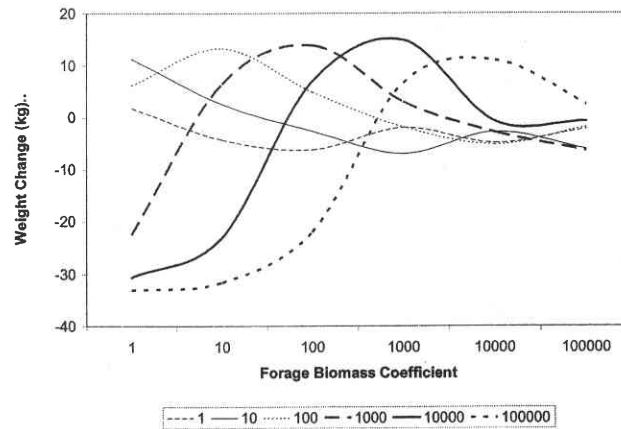


Figure 3. Simulated weight change in mule deer for a range of values for W_{rsf} and W_{mass} in equation (1). X axis contains values for the W_{mass} . Legend entries are the values for the W_{rsf} . Animal populations were 500 cattle, 450 elk and 250 mule deer.

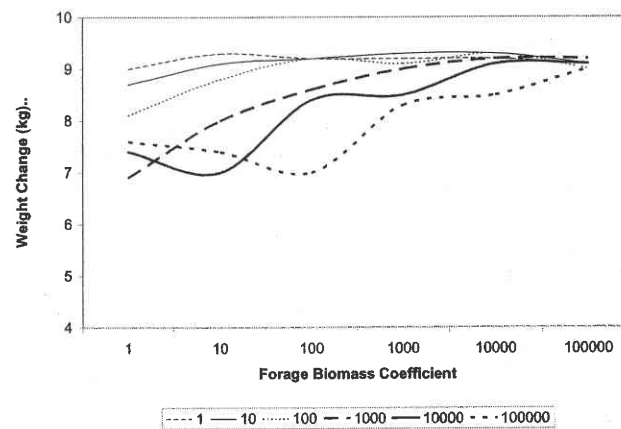
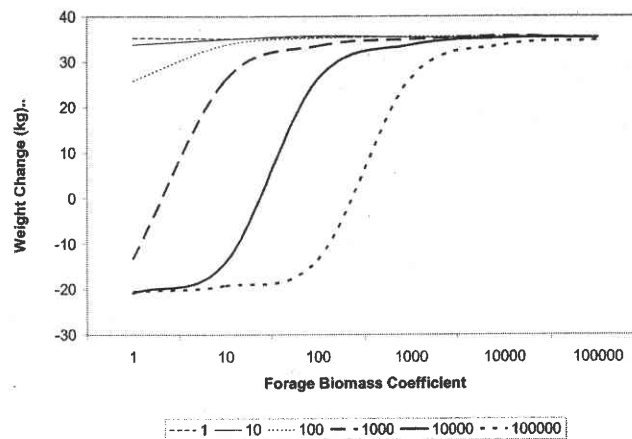
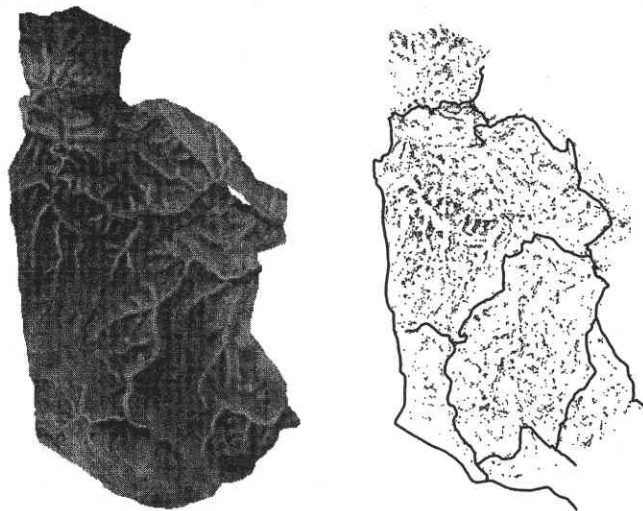


Figure 4. Simulated weight change in elk for a range of values for W_{rsf} and W_{mass} in equation (1). X axis contains values for the W_{mass} weights for equation (1). Legend entries are the values for the W_{rsf} weights in equation (1). Animal populations were 500 cattle, 450 elk and 250 mule deer.



and mule deer (Figures 2–4). For instance, mule deer, which generally gain around 11 to 22 pounds (5–10 kg) per animal at Starkey, showed simulated weight gains of 15.4 to 19.8 pounds (7–9 kg) for the range of coefficients tested. Cattle and elk showed more pronounced changes in animal weights (Figures 2, 4); although, a wide range of coefficients replicated the weight changes observed for cattle 0 to 22 pounds (0–10 kg) and elk 22 to 44 pounds (10–20 kg) at Starkey. For all species, increasing W_{rsf} relative to W_{mass} , forced simulated animals to forage in areas of high RSF values (Figure 5) and generally resulted in decreased animal weights. The effect of increasing W_{rsf} on weight reductions was dampened as the F_{mass} coefficient was increased to values above 1000.

Figure 5. (A) Plot of resource selection functions for elk developed for Starkey data (Coe 2004). Values plotted were the sum of the monthly RSF scores, described in Coe (2004), and range from near 0.15 (white) to 1.5 (black). (B) Results of simulation showing relative forage removal by elk within the Starkey area using W_{rsf} of 10,000 and W_{mass} of 1,000. Dark areas correspond to areas of highest forage removal.



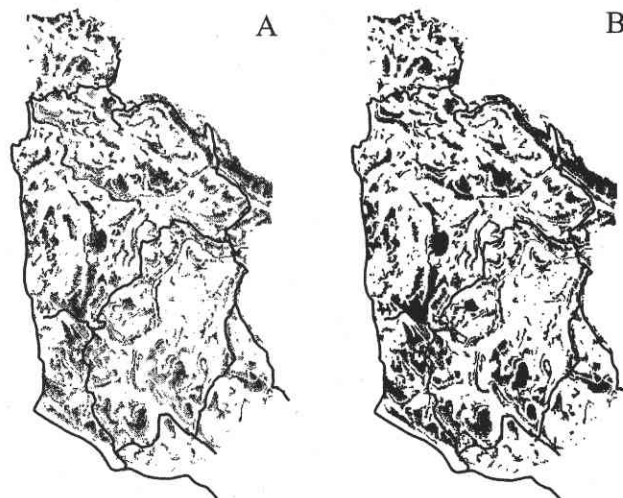
Changes in average cattle weights ranged from -72.6 to 26.4 pounds (-33 to 12 kg) (Figure 2), the negative weight changes being associated with a high values of W_{rsf} and low values of W_{mass} . Cattle showed an intermediate optimal weight gain of 22 pounds (10 kg) when the W_{rsf} was increased by a factor of 10 over the W_{mass} . This trend was not found for elk or mule deer (Figures 3, 4). The most plausible explanation for this is that a higher forage quality is realized at this combination of W_{mass} and W_{rsf} ; although, this was not tested.

Results of simulations for elk showed weight changes between -44 pounds (-20 kg) and 77 pounds (35 kg), with weight gains over a wide range of W_{rsf} and W_{mass} . However, when the W_{rsf} became 1,000 times the W_{mass} , negative weight changes were observed. Unlike cattle, weight changes with different

combinations of W_{rsf} and W_{mass} were asymptotic with the maximum values at about 77 pounds (35 kg). Compared to the W_{mass} and W_{rsf} coefficients, changing the forage quality (W_{qual}) coefficient had a very minor effect, producing weight differences less than 2.2 pounds (1 kg) over the entire range (1–10,000) of values simulated.

Simulated animal distributions were compared with the maps of the RSF scores to examine how well the model replicated observed animal distributions at Starkey (Figure 5). For space reasons, we limit the comparison to elk and note that the findings for elk are typical for the cattle and mule deer. The comparison is made difficult by the fact that the RSF maps represent a long-run probability of animal use during presumed periods of peak foraging based on 6 years of telemetry data; whereas, the outputs from a simulation run represent animal use for one season and represent only foraging activities. We did not perform statistical testing of the differences in simulated versus observed distributions; although, this would have provided more definitive comparison. The maps show that simulations with high values of W_{rsf} generated animal distributions that were compatible with the RSF maps (Figure 5). In contrast, simulations with a relatively high weighting for W_{mass} generated markedly different animal distributions that reflected high levels of foraging on productive grassland meadows (Figure 6a).

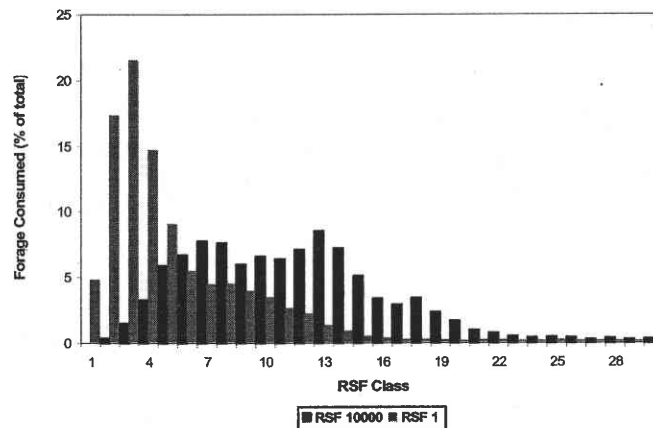
Figure 6. Results of simulation showing relative forage removal by elk within the Starkey area using weights of W_{rsf} of 1,000 and W_{mass} of 10,000. Dark areas correspond to areas of highest forage removal. (B) Same as (A), with forage production reduced to 10 percent of normal.



The effect of changing W_{rsf} and W_{mass} weights on the relative use of pixels with different RSF scores was examined by assigning the RSF probabilities

to integer classes from 1 to 40 and then measuring the forage removal for each class. The integer classes were generated by rescaling the RSF scores by 100 times. Values above 0.4 were assigned the integer class 40. Simulations were run with W_{rsf} of 10,000 and W_{mass} of 1, and W_{rsf} and W_{mass} both equal 1. The results (Figure 7) showed that a significant amount of forage was removed from higher RSF class pixels when W_{rsf} was weighted at 10,000 versus 1. The difference is somewhat magnified, however, by the overall higher total forage removal in the simulations, where both the W_{rsf} and W_{mass} coefficients are set at one.

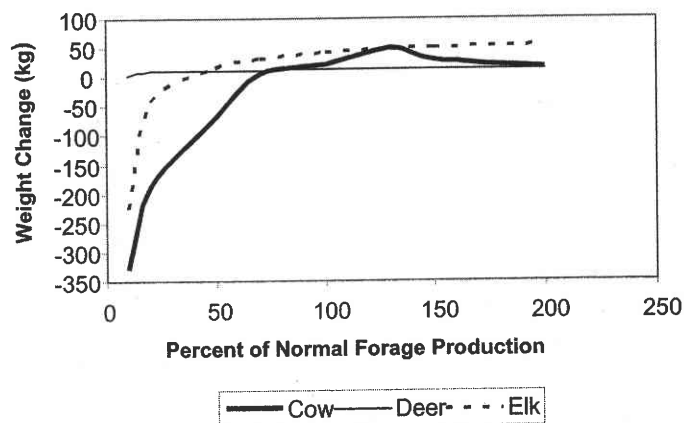
Figure 7. Forage consumption by two simulated elk using W_{rsf} weights of 1 and 10,000 and W_{mass} of 1. Data plotted are the percent of total forage consumed in each RSF class. RSF classes were calculated as RSF times 100. The figure shows that increasing the RSF weight for selecting foraging pixels results in a larger percentage of forage removal from the higher RSF pixels.



To choose a set of coefficients for further simulations we looked for values that resulted in weight changes that approximated those observed at Starkey using the highest possible values of W_{rsf} . In this way we could simulate the approximate animal performance at Starkey while replicating animal distributions to the extent possible. We also were interested in finding coefficients where the simulated weight gains did not change sharply with small changes in the coefficients. Using these criteria we selected a W_{mass} of 1,000 and W_{rsf} of 10,000, with W_{qual} of 1. Then, we simulated a range of values for the WB_{mass} and WB_{qual} coefficients in equation (2). These simulations were to examine how selecting for forage biomass versus energy within a pixel would affect animal performance. The results of this simulation showed that a wide range of coefficients generated the same results for all three species, when the WB_{qual} coefficient was reduced to less than 10. In the latter case, weights dropped by a maximum of 22 pounds (10 kg) for elk and lesser amounts for the other species. Accordingly, we set both WB_{qual} and WB_{mass} at 10 for the remaining simulations.

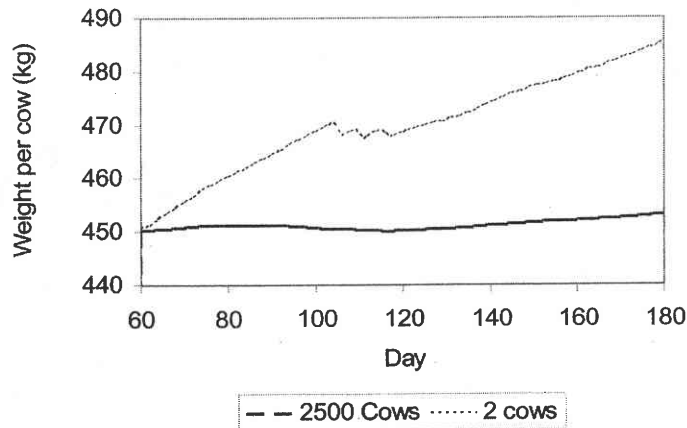
In a subsequent set of simulations, the forage production was varied from 10 to 100 percent of normal, using the model coefficients selected above. These simulations examined the effect of disturbances, like drought, on animal performance. The results showed that, as forage production was decreased, weights for cattle and elk were markedly reduced, while mule deer were not affected (Figure 8). The effect of reduced forage production on weight change was nonlinear and started when forage production was about 60 percent of normal for cattle and 50 percent for elk (Figure 8). For all species, the response resembled the intake rate functions incorporated into the model (Figure 1). Most likely, the weight reductions resulted from lower intake rates associated with reduced standing forage biomass. Some slight differences were noted in the simulated animal distributions for between normal and 10 percent forage production, the latter showing more area foraged (Figure 6a,b).

Figure 8. Results of simulations to examine the effect of reductions in forage production on average animal weight change for cattle, elk and mule deer. Simulations used 500 cows, 60 mule deer and 450 elk. Forage production was reduced by a constant percentage of the normal growth rate throughout the growing season.



Simulations to examine how animal performance varied under different population levels showed intraspecific effects for all three species. Simulations where the cattle herd was varied between 2 and 2,500 animals did not result in changes in elk or mule deer weights. However, average weight change per cow was reduced from 76.8 to 7 pounds (34.9 to 3.2 kg) when the herd size was increased (Figure 9). Likewise, when the mule deer population was increased from 2 to 2,500 animals, mule deer weights decreased from 17 to 4 pounds (7.8–1.7 kg) per animal. Elk population increases from 2 to 2,500 animals resulted in elk weights decreasing from 74 to 15 pounds (33.7–6.8 kg) per animal. Interspecific effects on animal weights were negligible, except in the elk

Figure 9. Changes in average animal weight for cattle over the grazing season for a cattle population of 2 and 2,500.



simulations where cattle weights declined from 44 to 35.9 pounds (20.0–16.3 kg) per animal when elk were increased from 2 to 2,500 animals. Elk weight decreased by only a fraction (73.7 versus 73.3 pounds [33.5 vs. 33.3 kg]) per animal and mule deer weights were unchanged when the cattle population was increased from 2 to 2,500.

Discussion

Foraging behavior by free ranging ungulates on large landscapes over time is a complex process that can only be approximated with models (Turner and Wu 1994, Moen et al. 1997, Weisberg et al. 2002). The current work illustrates the inherent complexity of the problem for summer range conditions in the Blue Mountains. While our model does not consider many of compensatory mechanisms in the foraging process, it can replicate animal weight dynamics observed at Starkey as well as provide reasonable predictions of animal distributions. The model demonstrated that both forage biomass and RSF scores need to be included in a simulation model to replicate observed animal distributions and weight changes and that some balance between the two best summarizes actual foraging behavior at the landscape scale. We found that modeling forage site selection based on RSF scores resulted in significant weight loss for cattle and elk and, to a lesser extent, mule deer. Forage depletion on high RSF pixels probably reduced forage intake rates and led to the lower weight gains. In addition, RSF scores for elk and mule deer did not always reflect selection of the most productive foraging areas, due to other habitat considerations, like distance to open roads. When forage site selection was based primarily on standing

biomass, the simulated animal distributions were not representative of Starkey telemetry data. Simulations showed that, by weighting the RSF about 100 times less than forage biomass to calculate pixel preference scores, the model would produce reasonable animal weights and select high RSF pixels as well.

Comparing empirical animal distribution with the simulations was difficult because the former developed from six grazing seasons of data and showed more diffuse spatial patterns of animal use, compared to the latter. Although the RSF values used for the model were estimated for peak foraging periods, they likely include observations when animals were not foraging as well. Thus without consideration of these other activities in the model there will always be some discrepancy between RSF values and simulated animal foraging patterns. The two data sources could be made more comparable if the animal distributions generated by the forage model were compared with the same number of animal locations simulated directly from the RSF probabilities.

When we measured forage removal, with respect to RSF probabilities on the Starkey landscape, and changed the RSF weights in the pixel preference equation, we found that the model did indeed lead simulated animals to spend more time foraging in areas with higher RSF scores. Using these methods, additional simulations could be performed to measure the loss of foraging opportunities as a result of selecting foraging pixels on the basis of distance to roads or other human influences. In this way, the effect of human disturbance on animal performance could be examined.

We were also able to quantify changes in animal performance, resulting from a reduction in forage production at the landscape scale. Reductions in forage production might result from drought or natural disturbance. Changes in animal weight with decreasing forage production closely resembled the functional response of intake rate to decreasing forage biomass for the three species (Figure 1) and shows the importance of forage intake dynamics in the context of modeling animal performance (Gross et al. 1993). Simulating animal performance under a range of forage production values should also consider increased movements (Wickstrom et al. 1984) and, in the case of drought-limited forage production, a reduction in forage quality (Vavra and Phillips 1980, Weisberg et al. 2002). The latter relationship could easily be incorporated into the SFM; although, there is little data from which to develop a quantitative relationship. Vavra and Phillips (1980) observed a 20- to 30-percent reduction in digestible dry matter during a drought year when precipitation was 39 percent of normal. Reductions in forage

quality of this magnitude would have a significant impact on simulated animal weights.

We observed negligible interspecific effects on animal weight when population levels of each species were varied between 2 and 2,500 animals. However intraspecific effects were observed for all three species, manifested in reduced weight gain, compared to simulations where population levels replicated those at Starkey. Weisberg et al. (2002) also found stronger intraspecific than interspecific competition for forage when they modeled cattle and elk on shared range. Hobbs et al. (1996) in their study of elk and cattle competition found significant reductions in calf weights while cow weights were not significantly unchanged. Competitive effects among the species might be better studied with our model by examining changes in forage intake rates over the season instead of animal weights. Adding calves to the model might also provide a means to study the competition question in more detail. In any event, additional model refinements and a battery of simulations are needed to carefully examine questions of competition among the three species.

The major challenge to refine the current model is to determine what mechanisms in the foraging process are the most important determinants of landscape scale foraging behavior and animal performance. Environmental heterogeneity (Shipley and Spalinger 1995, Etzenhouser et al. 1998, WallisDeVries et al. 1999, Johnson et al. 2002), movement rules (Gross et al. 1995) and cognitive abilities all influence the foraging behavior of ungulates on large landscapes. For the purposes of analyzing stocking on summer range in the Blue Mountains, some of the finer details of the foraging process may not be needed in the current model. One important gap in the model is the lack of local data on the functional response of intake rate for cattle, elk and mule deer for conditions at Starkey. Development of these relationships should be a high priority since these functions are strong determinants of animal performance for scenarios where forage biomass is limited, due to high stocking rates or low forage production. Modeling intake rate at the bite level, rather than using standing biomass, may provide different results than obtained here since intake rate is poorly correlated with standing biomass for highly selective foragers, like mule deer (Spallinger and Hobbs 1992).

Considerable detail could be added to the energetic component of our model by building on previous work (Wickstrom et al. 1984; Hudson and White 1985a,b). For instance, we did not change energy budgets to reflect increased

daily movements at lower levels of standing forage biomass. We also did not consider the energy requirements as a function of animal age. Another important addition would be the growth and development of calves for all three species.

Our ultimate goal is to use the SFM to evaluate different grazing management strategies on summer range landscapes, in areas like the forest types of the interior western United States, and to test various hypotheses about the effects of alternative stocking rates for ungulates. In this regard, the objective might be to identify the existence of key stocking thresholds that correspond to changes in animal performance at the species level (Hobbs et al. 1996). Such a tool is currently not available for use in allotment management planning on lands administered by the U. S. Department of Agriculture, Forest Service and the U. S. Department of Interior, Bureau of Land Management, the two largest federal land managers in the United States. Moreover, the mechanistic structure of our model, based on individual foraging behavior, could help managers and public interests improve their understanding of how ungulates use the landscape to meet their foraging needs.

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