Assessing Management Alternatives for Ungulates in the Greater Teton Ecosystem using Simulation Modeling

6 February 2003
Final Report

N. T. Hobbs[1], G. Wockner[1], F. J. Singer[1,2]

Collaborators: G. Wang[1], L. Zeigenfuss[2], P. Farnes[3], M. Coughenour[1], and S. Delgrosso[1]

1. Natural Resource Ecology Lab, Colorado State University, Fort Collins, CO
2. US Geological Survey, BRD, Fort Collins, CO
3. Dept. of Earth Sciences, Montana State University, Bozeman, MT

Executive Summary

Introduction to the Modeling Approach

Managers of ungulate populations in the Greater Teton Ecosystem and the National Elk Refuge, a segment of the Greater Teton Ecosystem, have raised three questions regarding interactions between populations of native ungulates, notably elk and bison, and the winter habitats that support those populations. We have addressed these questions using simulation modeling.

The first question focuses on the balance between forage supplies on the winter range and the size of ungulate populations. In short, managers seek an understanding of the number of animals that can be supported by natural forage supplies under a range of weather conditions. To address this need, we created the Forage Accounting Model (Part I of this report). The Forage Accounting Model simulates forage intake by ungulates across a range of elk population sizes and during a range of climatic conditions for the growing season and for winter. In addition, we simulated varied bison populations for the Greater Teton ecosystem. This model predicts the proportion of forage supplies consumed across the landscape (forage utilization) and also calculates 'forage deficits' resulting from a variety of population sizes in the system. Forage deficits represent the difference between the total supply of forage and the total forage required by ungulates. We exercised the Forage Accounting Model using assumptions from four of the Alternatives developed for the ongoing Environmental Impact Statement (EIS) for ungulate management. The EIS assumptions manipulate three variables: numbers of bison, willow availability, and irrigation.

The Forage Accounting Model predicts forage utilization by ungulates, but does not provide insight into the consequences of different levels of utilization. Thus, the second question we addressed focuses on the impacts of different levels of utilization of winter forage on ecosystem processes, primarily net primary production and nutrient cycling. To address this question, we used the CENTURY Ecosystem Model (Part II of this report). The CENTURY model simulates biogeochemical changes in vegetation and soil due to grazing. We simulated intense grazing effects on two vegetation types prevalent on the Teton winter range -- wet meadow and sagebrush. We examined the effects of two levels of utilization (50% and 80%) on soil carbon, mineralized nitrogen, and net annual production over a 150-year time-span. Ongoing fieldwork by F. Singer will later be compared with these simulations.

The third question focuses on the consequences of forage deficits on population performance. Specifically, we asked "What are the effects of food shortages on elk mortality?" To address this question, we employed the Over-Winter Mortality Model (Part III of this report). The Over-Winter Mortality Model was used to estimate the energy balance through simulation of energy intake and expenditure of individual elk in four age/sex classes. We estimated starvation mortality using the same scenarios for animal abundance, available forage, and snow conditions as we employed in the Forage Accounting Model.

These three models complement each other in important ways. The Forage Accounting Model, developed for this project, predicts forage supply, deficits, and utilization. The CENTURY Ecosystem Model, developed for other projects at the Natural Resource Ecology Lab at Colorado State University and then adapted to our present needs, incorporates the utilization predictions from the Forage Accounting Model in addressing the impacts of winter forage utilization on the ecosystem. The Over-Winter Mortality Model, first developed for mule deer in Colorado, was adapted for elk to meet the needs of this project. It uses the forage supply, utilization, and deficits predicted by the Forage Accounting Model in simulating the effects of forage supply on elk mortality. We brought these three models together to provide reasonable answers to the questions raised by the ungulate managers.

In this report we describe each model and the insights we gained from its use, as well as conclusions that can be drawn from the combined knowledge. The first three sections focus on each of the three models and the corresponding results. In a final, concluding section, we aggregate results across the models and draw general conclusions relevant to managing ungulates in the Greater Teton Ecosystem.

Key Findings

The Forage Accounting Model

We describe a simple accounting model that predicts imbalances between forage supply and animal forage requirements on winter ranges used by native ungulates (elk, moose, and bison) in the Greater Teton Ecosystem and the National Elk Refuge (NER). The model predicts *forage utilization* and *forage deficits.* We depict forage utilization in a map of the study area where cells are coded to represent the percentage of pre-winter forage supplies consumed by native ungulates during winter. Forage deficits are defined as the amount of forage required by ungulates that exceeds the amount available during any week of the winter, summed over all weeks. The model uses data on forage standing crops at the beginning of winter, snow distribution during winter, pre-winter precipitation conditions, and offtake rates of ungulate populations.

We exercised the Forage Accounting Model in the Greater Teton Ecosystem for different levels of elk (0-18,000 animals) and bison (250 - 2000) abundance, while holding moose populations constant (890). In addition to simulations for the ecosystem as a whole, we also exercised the model solely on the National Elk Refuge with elk populations of 0 -10,000, bison populations of 250 -2000, and 20 moose. The number of elk at which forage deficits begin to occur during a specific winter under specified assumptions represents an “equilibrium point” on the landscape at which forage supply and demand are in balance. Table 1 provides a quick synthesis of these equilibrium points for each scenario proposed in the Environmental Impact Statement (EIS) for the broader Teton study area and NER.

Although the numbers in Table 1 represent clearly demarcated points of equilibrium, each is associated with a margin of error, a series of underlying assumptions, and an accompanying graph in the body of this report. All these factors should be evaluated together. Additionally, the equilibrium points in Table 1 only represent the points at which deficits begin to occur; elk are known to rely on stored energy reserves to survive winters, and, therefore can likely incur small forage deficits without dying of malnutrition.

Table 1. Numbers of elk at which forage supply and demand are in equilibrium under various management scenarios based on a Forage Accounting Model for the Greater Teton Ecosystem, Wyoming. Modeling was done for a range of snow severity types and pre-winter precipitation scenarios, because these factors influence forage availability and supply. Alternative #1 represents the status quo, that is, the assumption that management actions will be the same in the future as in the past.

	Pre-Winter Precipitation Scenario					
	Drought			Mean		
	Snow Severity Type			Snow Severity Type		
	Severe	Above-Average	Average	Severe	Above-Average	Average
Alternative #1 (500 bison, flood irrigation, willow available on NER)						
Greater Teton Ecosystem	0	1,800	5,500	1,000	6,000	16,000
NER only	0	0	2,000	0	0	5,000
Alternative #2 (500 bison, no flood-irrigation, willow available on NER)						
Greater Teton Ecosystem	0	1,600	5,300	900	5,900	15,800
NER only	0	0	1,700	0	0	4,500
Alternative #3 (1,000 bison, flood-irrigation, no willow available on NER)						
Greater Teton Ecosystem	0	0	3,000	0	5,000	14,000
NER only	0	0	0	0	0	3,300
Alternative #4 (350 bison, center-pivot irrigation, no willow available on NER)						
Greater Teton Ecosystem	0	1,600	5,700	1,500	7,200	17,000
NER only	0	0	2,000	0	0	5,500

In addition to the above analysis, we also ran experiments with the Forage Accounting Model on the Greater Teton Ecosystem to examine effects of: (1) removing all domestic grazing from public lands in the Teton ecosystem, and (2) removing effects of agriculture and residential development on forage supplies in and around the town of Jackson. Our simulations indicated that removing all domestic grazing would have negligible effects on forage deficits in all winter severity types, because most domestic grazing does not occur on the critical ungulate winter range. Providing forage to elk populations equivalent to the pre-settlement vegetation now subsumed by development in and around Jackson also had negligible effects on forage deficits during severe winters. During average winters, adding this forage substantially reduced deficits by allowing elk to graze on the additional forage available. However, addition of these forage supplies did not *eliminate* forage deficits for the current population size of elk, suggesting that current elk numbers may exceed what could have been supported in the Greater Teton Ecosystem under pristine conditions.

The CENTURY Ecosystem Model

The CENTURY Ecosystem Model simulates exchanges of carbon (C) and nitrogen (N) among atmosphere, soil, and vegetation. Required inputs used to drive the model include monthly maximum/minimum temperature and precipitation data, soil properties, vegetation type, and current and historical land use. Disturbances and management practices such as grazing, fire, cultivation, and fertilizer additions can be simulated. We simulated the response of two vegetation types (wet meadow and sagebrush) to two levels of forage utilization by elk (50% and 80%). Other required inputs were estimated based on CENTURY modeling in similar systems.

Current and ongoing Teton field sampling work by F. Singer and R. Stottlemyer on nitrogen pools and vegetation will later be used to corroborate these preliminary findings.

CENTURY predicted that ungulate grazing would not harm plant production on the winter range at either level of grazing intensity, because elk are consuming standing dead forage of low nutritional content during winter. Furthermore, higher grazing levels may actually *increase* future plant production, because ungulates return more nitrogen to the soil than they consume, thereby accelerating nutrient cycling. Results from CENTURY suggest that heavy winter-season grazing in this system, as predicted by the Forage Accounting Model, is sustainable, and that soil C and nutrient levels are not depleted and may increase. As long as elk are concentrated at high densities on the winter range, the CENTURY model will predict positive feedbacks on production due to higher net N inputs versus N offtake from grazing.

The Over-Winter Mortality Model
Forage deficits predicted by the Forage Accounting Model will likely cause elevated mortality in over-wintering elk populations. We adapted the energy balance model of Hobbs (1989) to estimate starvation mortality by simulating energy intake and expenditure by elk in four age/sex classes (calves, yearling males, adult females, bulls) during average, above average and severe winters with average pre-winter precipitation conditions. This energy balance model allocates elk populations to map cells based on snow water equivalents, allows elk to consume available herbaceous and shrubby forage, and predicts mortality based on forage shortfalls and animal nutritional needs.

Simulated mortality of calves ranged from a low of 4% during an average winter at a total population size of 6,000 to a high of 42% during a severe winter at a population of 18,000. Increasing population density was associated with roughly proportionate increases in estimated mortality. Starvation mortality for adult cows was predicted to be 1% for a population of 6,000 animals in an average winter rising to a high of 25% for a population of 18,000 during a severe winter.

Table of Contents

Executive Summary: Introduction to the Modeling Approach……………………………………i
Key Findings……………………………………………………………..ii
Acknowledgments……………………………………………………………………...vi

Part I. The Forage Accounting Model……………………………………………………1
Introduction…………………………………………………………………………1
Modeling Approach…………………………………………………………………...1
Model Description………………………………………………………………………2
Model Results on the Greater Teton Ecosystem for EIS Alternative #1………………10
Model Results on the NER for Alternative #1……………………………………………19
Discussion for Alternative #1………………………………………………………23
Forage Accounting Model Results for all EIS Alternatives…………………………..25
Graphical Model Results for the EIS Alternatives #2 - #4…………………………….27
Discussion for Alternatives #2 - #4……………………………………………………..33

Part II. Provisional CENTURY Ecosystem Modeling………………………………...............34
Introduction…………………………………………………………………………34
The Century Model……………………………………………………………………34
Model Input Parameters……………………………………………………………..35
Modeling Assumptions……………………………………………………………..37
Results…………………………………………………………………………………37

Part III. The Over-Winter Mortality Model…………………………………...............…41
Introduction…………………………………………………………………………41
Methods……………………………………………………………………………41
Results………………………………………………………………………………42

Conclusions…………………………………………………………………………44

References……………………………………………………………………………..46

Appendix A. Vegetation Production Methods……………………………………………...49

Appendix B. Snow Model Methods……………………………………………...............51

Appendix C: Tables………………………………………………………………………57

Acknowledgements

Funding was provided by the Natural Resources Preservation Program (NRPP) allocation for work in national parks – U. S. Geological Survey – Biological Resources Division, and from Grand Teton National Park. We acknowledge Robert Schiller of Grand Teton National Park for project organization and administration as well as Bruce Smith of the National Elk Refuge. We also thank Phil Farnes of Snowcap Hydrology and Montana State University for the snow model algorithms and snow measurements, and for assistance with refining the snow model; and Michael Coughenour of the Natural Resource Ecology Lab (Colorado State University) for developing the snow model computer code.

Part I.
The Forage Accounting Model

Introduction

We constructed a forage accounting model to examine the consequences of management actions in balancing forage supplies with the forage demands of populations of native ungulates in the Greater Teton Ecosystem and the National Elk Refuge (a portion of the Greater Teton Ecosystem). We first describe our modeling approach and explain two predictions made by the model; forage utilization and forage deficits. We then describe how the model works. We subsequently use the model to examine relationships among elk population density, bison populations, precipitation-based forage production, and winter severity. The model was run on two study areas: the Greater Teton Ecosystem, and the National Elk Refuge (NER), and was used to predict forage deficits for each Alternative in the EIS on both study areas.

Modeling Approach

Our modeling philosophy favors simple models over complex ones. This is because simple models are easier to explain, understand, and defend than models that include high levels of detail. Our approach is to begin with a simple "base model," and add detail incrementally as it is needed to address questions unresolved by the simpler model.

We built a simple accounting model that tracks the impacts of a variety of densities of ungulates on forage supplies as winter progresses. The model includes annual variation in forage production, effects of snow on forage availability, and effects of grazing and browsing on the forage supply. We call it an accounting model because it is analogous to a model of cash reserves and flows in a business. In essence, it answers questions on the bottom line – does forage availability match forage requirements of ungulates or is there a deficit or surplus at the end of winter? The accounting approach was motivated by a major justification for supplemental feeding -- animals are fed during winter to compensate for deficits in forage supply. Thus, a logical starting point for our efforts was to quantify the magnitude of these deficits under different conditions.

The Concept of Forage Deficits and Forage Utilization
There are two concepts that are important in understanding the accounting model. The first concept is *forage deficits*. Forage deficits represent the difference between the total supply of forage available during the winter and the total forage required by a given population of ungulates, which include bison, moose, and elk in this study. Thus, forage deficits are affected by population size, which affects forage demand, as well as snow accumulation (measured as snow water equivalents, SWE), which affects access to forage, and forage production, which affects forage supply. We calculated forage deficits by estimating the daily intake of populations of a given size, subtracting that intake from the daily forage supply, and summing negative values over all time-steps of the winter.

The second important concept is a common measure of habitat use called *forage utilization.* Forage utilization is simply the percent of the total available forage removed by the ungulates from a given location in the study area. We depict this on a map where map-cells are coded with the utilization percent. Forage utilization gives us a measure of ungulate impact on habitat. Part

II of this report, which discusses the CENTURY Ecosystem Model, will analyze and quantify the effect of forage utilization on net primary production and nutrient cycling.

Model Description

Study Areas

Two study areas were delineated (Fig. 1). The first, larger area, the Greater Teton Ecosystem, corresponds to the boundary depicted in the Steele et al. (1999) report on Jackson Valley vegetation. The southern boundary reaches to the southern edge of the Town of Jackson, the northern edge is at the north end of Jackson Lake, the western edge is about halfway between the crest of the Tetons and the Idaho border, and the eastern edge runs roughly to Togwotee Pass. This boundary roughly encompasses the current boundary of the Jackson elk herd as defined by Wyoming Game and Fish Department. In addition, it contains all of the supplemental snow measurement sites reported by Farnes et al. (1999). The second area is the boundary of the National Elk Refuge, which is a subset of the larger study area.

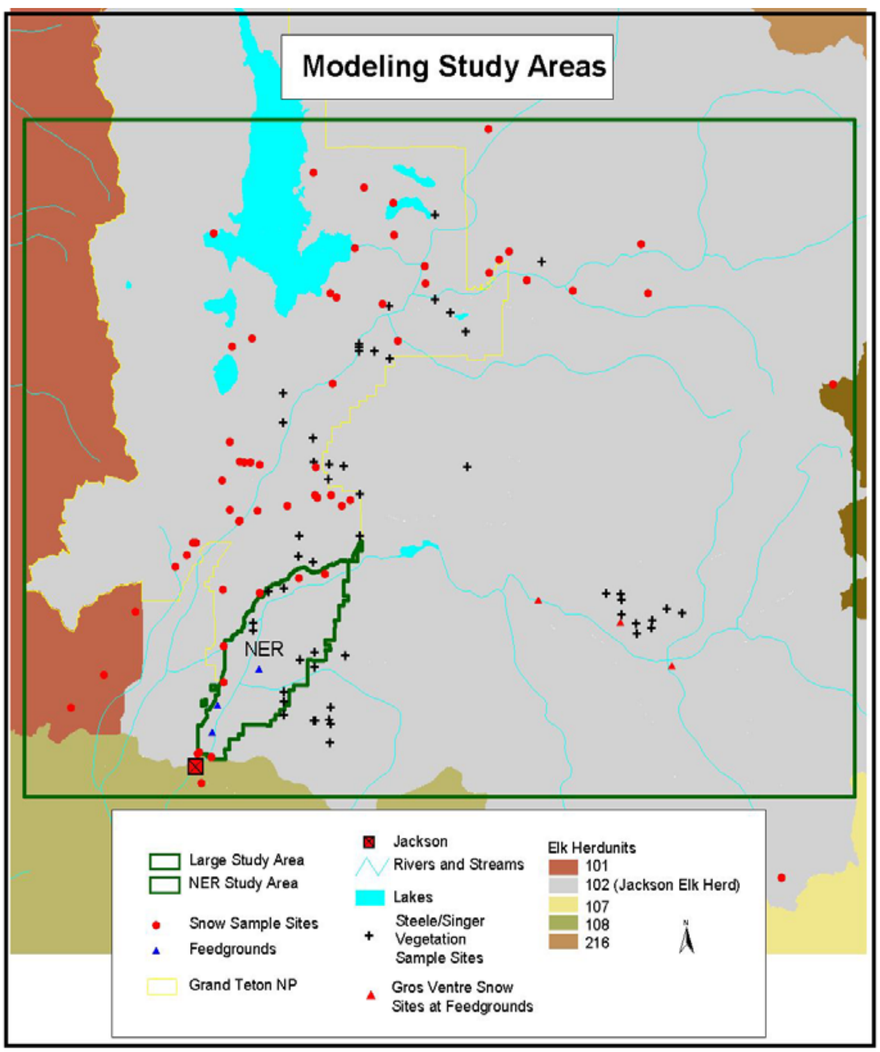

Figure 1. Study area and sample site locations used to develop and run the forage accounting model for ungulates in the Greater Teton Ecosystem, Wyoming.

Algorithm
The model (Fig. 2) operates at a weekly time step. For each week of the winter, the model calculates snow water equivalents (SWE) on each 30 x 30 meter cell in the study area and sums the amount of forage that is available at each 1-inch SWE increment. Snow water equivalent is the average amount of water existing as snow. Although snow features such as crusting density and depth hoar can influence ungulates, Farnes has argued that SWE is the single best measure that incorporates most other snow pack features and can be used to predict ungulate responses (Farnes et al. 1999). Grazing/browsing pressure by populations of bison, elk, and moose is first allocated to the forage available in completely open areas (i.e., cells with 0 inches SWE). If additional demand exists, it is allocated to cells with 1 inch of SWE. Any additional demand is allocated to progressively greater snow depths, with a linear reduction in forage availability occurring in relation to SWE greater than 2 inches (Table 2). This approach has been used successfully to model effects of snow on forage availability in other studies (Hobbs 1989, Turner et al. 1994).

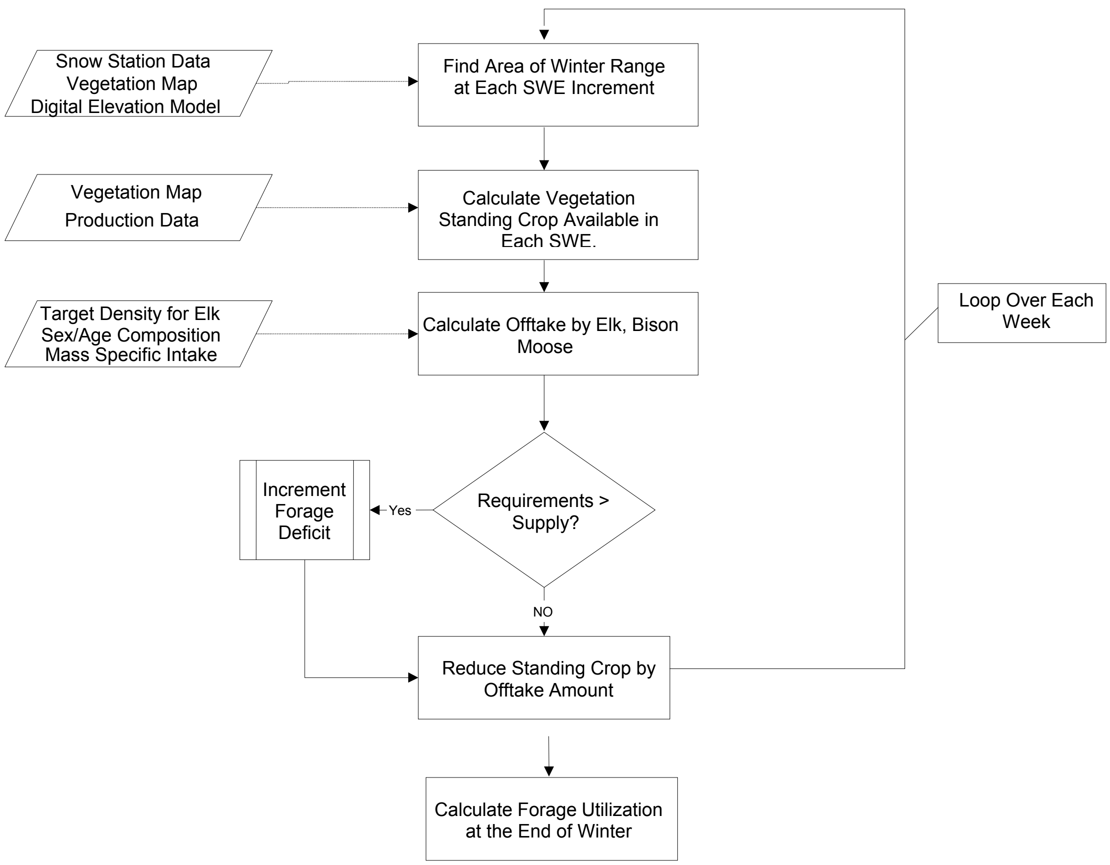

Figure 2. Flow chart of data and processes in the forage accounting model. The model cycles through these calculations at weekly intervals.

If there is forage demand in excess of the supply in all of the cells during any week, then this excess is accumulated in the *forage deficit.* At the end of the winter, we calculate *forage utilization* for each cell in the vegetation map by dividing the total amount of forage removed from each cell by the pre-winter standing crop of that cell.

The model is driven by data on the standing crop at the beginning of winter, snow distribution during winter, and offtake rates of ungulate populations (Fig. 2).

Table 2. Percent of forage considered available to ungulates in the Greater Teton Ecosystem, Wyoming as snow water equivalents increase.

Snow Water Equivalents (inches)	Available Forage (%)
0	100
1	100
2	100
3	75
4	50
5	25
6+	0

Vegetation Data

The accounting model requires spatially explicit data on production of vegetation available at the beginning of winter. We developed these data from maps of vegetation communities and field data on production in each community.

We obtained a complete vegetation coverage from Utah State University (Homer 1995) that was created in 1996 for all of U.S. Forest Service Region 4 using remote sensing interpretation techniques. Vegetation coverages were also obtained from Grand Teton National Park (GTNP) and the National Elk Refuge (Fig. 3). GTNP data were developed from aerial photography while NER data were developed from a combination of aerial photography and ground-based mapping. Discussions with other coverage users suggested that the NER coverage was the most accurate, followed by the GTNP coverage, followed by the Utah State University coverage. Thus, we merged these coverages to use the most accurate data wherever it was available, using the Utah State University coverage only to fill in gaps not covered by the GTNP or NER data.

Each coverage had different vegetation coding schemes, consequently, we developed a crosswalk table to convert the vegetation codes into a single, more standardized, scheme (Appendix C: Table C-1). The Utah State University coverage had 68 separate vegetation types, GTNP had 60, and NER had 32. The essential data in the vegetation table were the name of the vegetation type and the annual production of herb/shrub. Our model consolidates these categories into 15 vegetation types (Fig. 4). These categories were chosen because they provided usefully different vegetation types for which we could obtain production information in the nearby environment. Using the descriptions provided in the metadata for the Utah State University coverage, descriptions for non-forested (Mattson and Despain 1985) and forested (Steele 1983) habitat used to create the GTNP coverage, and the vegetation categories of the NER coverage, vegetation categories from each coverage were matched up as accurately as possible.

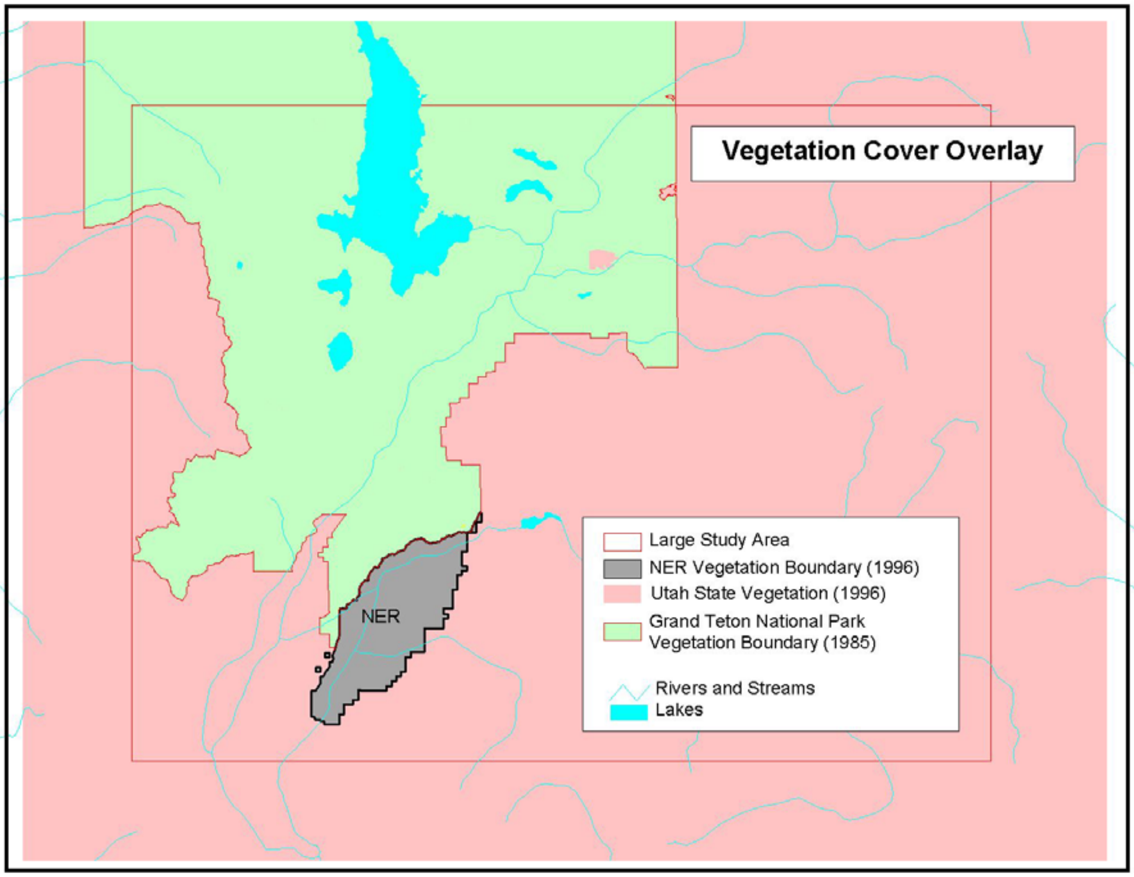

Figure 3. Extent of coverages used to assemble unified vegetation map for use in Forage Accounting Model for ungulates in the Greater Teton Ecosystem, Wyoming.

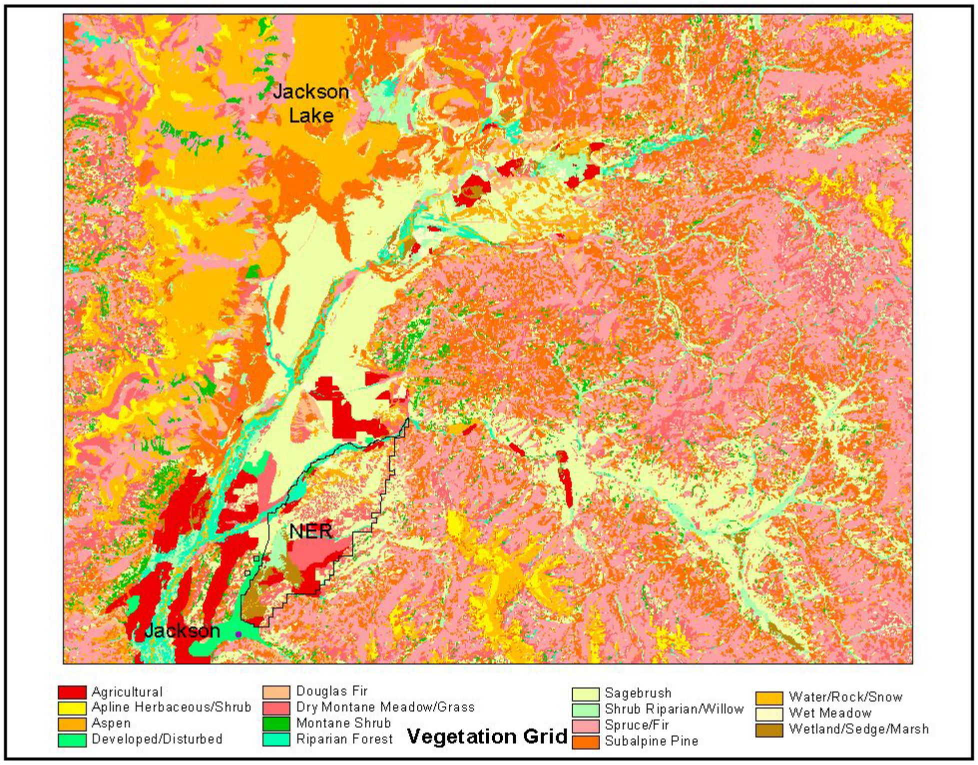

Figure 4. Vegetation map used in the Forage Accounting Model for the Greater Teton Ecosystem, Wyoming. This map was created by using a cross-walk of vegetation categories to combine data from three coverages to produce a single map representing 15 vegetation categories.

Data on annual production for each vegetation type were obtained from studies conducted by Biological Resources Division (BRD)--USGS, National Elk Refuge (NER)--USFWS, and Bridger-Teton National Forest --U.S. Forest Service. Each data set was collected in a different manner, therefore it was necessary to standardize the data so that they could be combined to make full use of all available data for estimating average production values. Mean year, wet year, and dry year production values were estimated (Table 3). Wet year production equals 150% of the mean year; dry year equals 45% of the mean year. A detailed description of the methods used to derive these estimates is given in Appendix A.

Spatial Heterogeneity of Forage and Initial Forage Availability
Managers raised a question about the spatial heterogeneity of production due to varying rainfall over the study area. For example, sagebrush on the NER may produce differently than sagebrush in the upper Gros Ventre River drainage. We attempted to create a spatially explicit production map based on actual production measurements across the study area. However, these estimations did not yield significant spatial differences in production for each vegetation type. While we recognize that rainfall may vary across the area, and the production may vary with it, field data could not support these distinctions.

Although the production estimates in Table 3 represent total production on the landscape, a question was raised at a meeting of managers and modelers in Jackson in February 2002 about forage availability to ungulates. It was suggested that a significant amount of measured forage is totally unavailable to ungulates because it is unpalatable or is obstructed by inedible plant tissue.

Based on past experiences of measured offtake, meeting participants estimated this unavailability between 50% and 25%. Using elk offtake data gathered from the study area (Steele et al. 1999) and other offtake data from similar systems (Hobbs et al. 1996, Singer et al. 2002), we estimate this percentage to be 35%. Our model uses this estimation by initially decrementing the production values by 35% at the beginning of winter.

Table 3. Average annual production (pounds/acre) of vegetation produced in average, wet, and dry years in the Greater Teton Ecosystem, Wyoming. Values were derived from data collected by the National Elk Refuge, U.S. Geological Survey—Biological Resources Division, and Bridger-Teton National Forest.

Code	# of Cells	Vegetation Name	Mean Production (pounds/acre)	Wet Year Production (pounds/acre)	Dry Year Production (pounds/acre)
1	1,158,538	Spruce/Fir	1,162	1,743	523
2	147,739	Douglas Fir	705	1,058	317
3	834,291	Subalpine Pine	1,167	1,751	525
4	148,500	Aspen	1,712	2,568	770
5	68,064	Riparian Forest	2,524	3,786	1,136
6	690,177	Sagebrush	1,190	1,785	536
7	147,658	Shrub Riparian/Willow	2,125	3,188	956
8	91,805	Montane Shrub	1,708	2,562	769
9	105,584	Alpine Herbaceous/Shrub	1,693	2,540	762
10	440,890	Dry Montane Meadow/Grass	895	1,343	403
11	27,067	Wet Meadow	2,385	3,578	1,073
12	34,630	Wetland/Sedge/Marsh	4,760	7,140	2,142
13	457,338	Water/Rock/Snow	0	0	0
14	117,513	Agricultural	2,498	3,747	1,124
15	18,881	Developed/Disturbed	4,334	6,501	1,950

Snow Distribution
We predicted temporal and spatial variation in snow water equivalents (SWE) using a model developed by Michael Coughenour and Phil Farnes in the 1990s for Grand Teton National Park. The model uses input data from snow stations and interpolates among them to produce a surface of predictions. It was written as a broader precipitation model with the capabilities of predicting precipitation level, snow depth, and SWE, depending on various input and model switches. For the current modeling effort, we used SWE because it is the primary determining factor for ungulate migratory behavior. A detailed description of implementation of the snow model and corrections developed for the Gros Ventre River Valley snow shadow are presented in Appendix B.

Ungulate Offtake
The model requires estimates of the total amount of forage consumed by elk, bison, and moose on the study area. We calculated offtake assuming that each animal consumes dry matter equal to 2% of its body mass each day (Cordova et al. 1978, Baker and Hansen 1985, Baker and Hobbs 1987). We estimated an average body mass for each ungulate species weighted by the sex and age

composition of their current populations. Animal age/sex counts were obtained from participating state and federal wildlife agencies. Average weights for each species and for each age/sex class were gathered from literature (Meagher 1973, Houston 1982). A sample of the spreadsheet calculations used to estimate these weighted averages appears in Appendix C: Table C-3.

Model Overlays

The model overlays a SWE grid on the vegetation grid during each time step. For example, when snow accumulation is relatively light, the model allows foraging over large areas of the winter range (Fig. 5). However, when snow accumulation is heavy, there are very few areas that are available for foraging (Fig. 6).

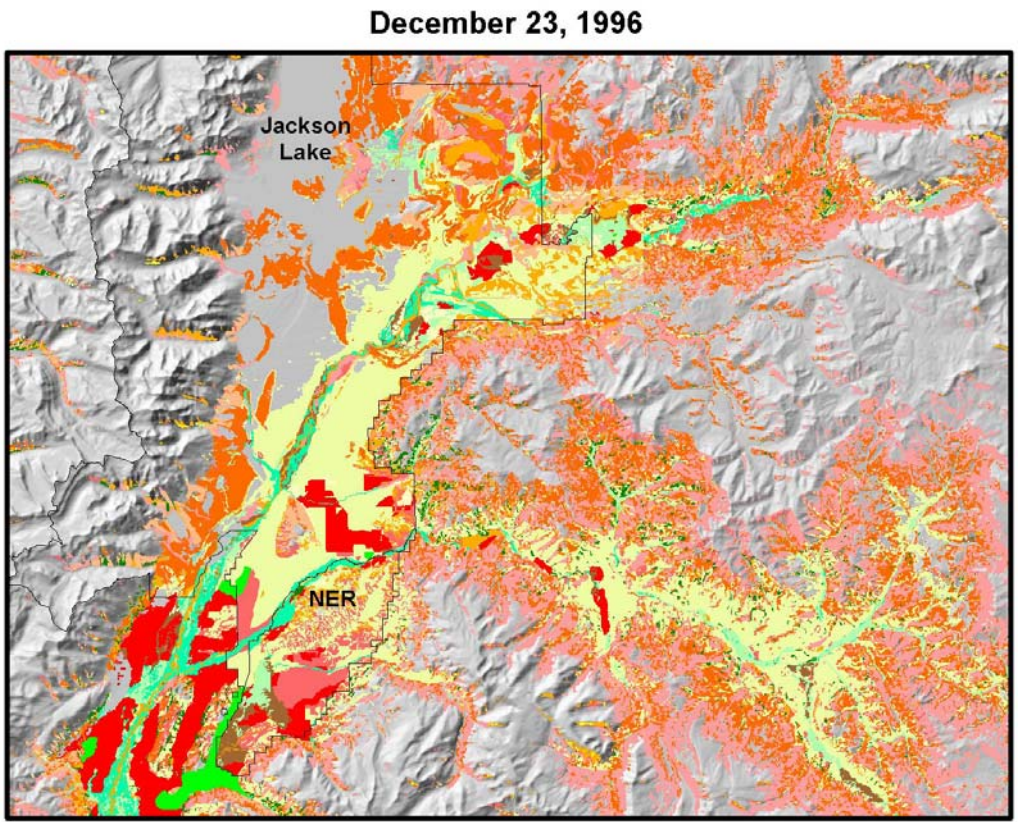

Figure 5. Overlay of snow accumulation ≥ 6 inches snow water equivalents (SWE) on the Greater Teton Ecosystem, Wyoming vegetation map for December 23, 1996. Grey shading indicated areas of the landscape with ≥ 6 inches SWE. (Map adjusted for Gros Ventre River Valley snow correction.)

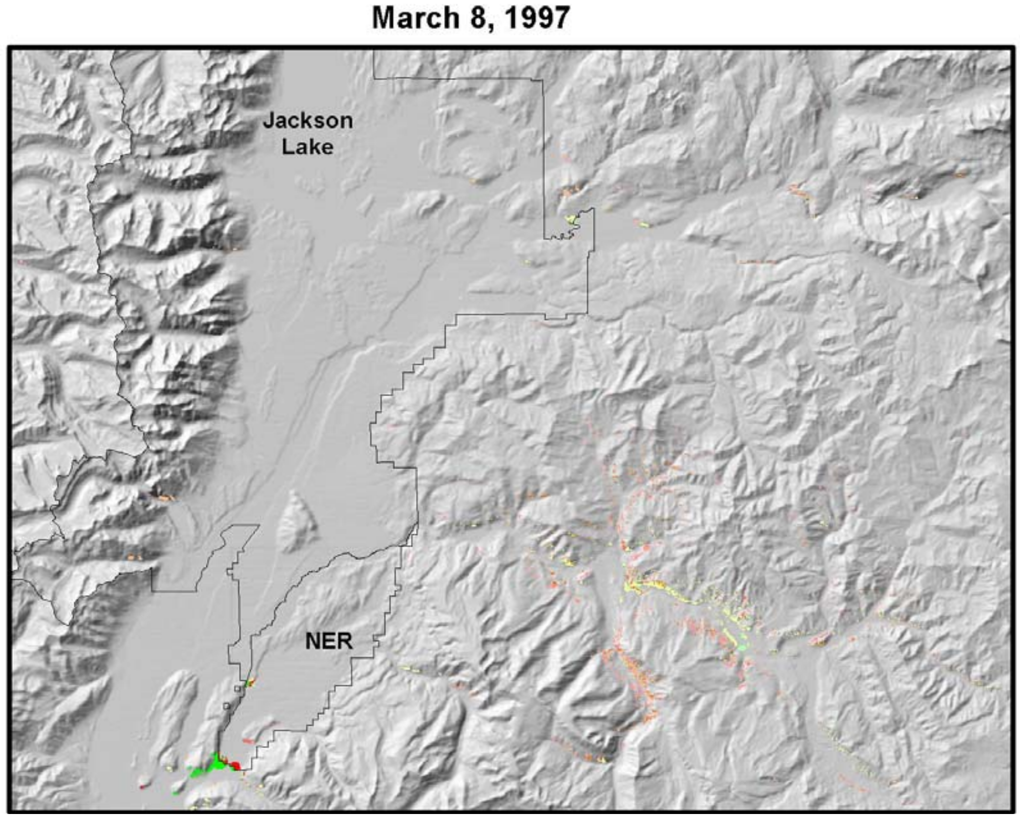

Figure 6. Overlay of snow accumulation ≥ 6 inches snow water equivalents (SWE) on the vegetation map for Greater Teton Ecosystem, Wyoming for March 8, 1997. Grey shading indicates areas of the landscape with ≥ 6 inches SWE. (Map adjusted for Gros Ventre River Valley snow correction.)

Modeling Scenarios
We exercised the model on both study areas -- the Greater Teton Ecosystem, and the NER (Fig. 1). Within each study area we ran a series of simulations accounting for (1) varying populations of elk -- between 0 and 18,000, (2) varying SWE winters -- average, above average, and severe, (3) varying pre-winter precipitation conditions -- drought, mean, and wet, and (4) varying populations of bison as specified by the EIS Alternatives' assumptions. On the Greater Teton Ecosystem, the model projections include offtake for 890 moose. On the NER, the model projections include offtake for 20 moose. On the Greater Teton Ecosystem, we varied elk populations between 0 and 18,000 animals, and ran enough simulations to get the shape of a trend line following the data points. On the NER, we varied elk populations between 0 and 10,000. Wintering bison populations have been growing very quickly in the valley. In 1999 there were roughly 500 bison in the study area whereas in 2002 the number was 650.

We varied winter severity using three types of winter snow conditions: average, above average, and severe. We chose 1996 as an example of an average winter, 1982 as a moderately severe, or above average, winter, and 1997 as a severe winter. These choices were justified by consulting Farnes et al. (1999), which presents a table of estimated mean SWE for the 50-year recording period in the Hunter-Talbot hayfields. Using Farnes' table, we ranked snow severity using the SWE measurement on the hayfields. 1996 came in as the mean ranking while 1982 was above average.   Although four winters prior to 1980 were more severe than 1997, portions of our snow data set only went back to 1980. Thus we used 1997 as the "most severe on record." We also consulted with Farnes, who concurred with these choices of representative years.   In addition to this ranking, we also calculated average area available to ungulates per day based on snow water equivalents during the six snowiest weeks of each winter (Table 4).

Table 4. Average acres available to large ungulates per day based on snow water equivalents in the six snowiest weeks of each winter. Estimates are given for winters that are of average severity, above average, and severe.

	Acres available to ungulates (< 6" of snow water equivalents)		
	1996 – Average Winter Severity	1982 – Above Average Winter Severity	1997 – Severe Winter Severity
Whole Study Area	50,947	19,649	12,003
NER only	8,531	2,560	690

Model Results on the Greater Teton Ecosystem for EIS Alternative #1 (status quo)

We estimate the margin of error for the results in the Greater Teton Ecosystem to be ± 20%. We cannot firmly quantify this error, but believe, based on our expertise derived from similar systems, that ± 20% is a reasonable approximation.

These results should not be used as the sole factor in determining the appropriate numbers of elk and bison on the Teton ecosystem or the NER. Instead, these results should be used as a starting point for management decisions, and used along with other pertinent factors such as long-term local knowledge, the results of other research, and management objectives not factored into this modeling effort. We do not interpret these results as the "carrying capacity" of the landscape, nor do we support an interpretation that assumes specific levels of mortality based on forage deficits. "Carrying capacity" is a complicated ecological concept that is not directly addressed by this model, and mortality estimates are provided in Part III of this report.

Throughout this report, we refer to graphs of forage deficits as a function of elk population size. These graphs show how forage deficits change and elk numbers increase given a range of assumptions about weather and the abundance of bison. In evaluating the forage deficit graphs, we refer to the point where each line intersects the x-axis as the point where forage offtake balances forage supplies. As populations increase above this level, that is, to the right of this intersection point, forage requirements exceed supplies, resulting in forage deficits. Although forage deficits and an imbalance may occur, we do not suggest that mortality always follows. Elk are known to rely on stored energy reserves to survive winters and therefore can likely incur small forage deficits without dying of malnutrition.

Forage Deficits

Assumptions in Alternative #1 are "status quo," i.e., that management actions will be the same in the future as in the past. Flood irrigation will continue on the cultivated fields of the NER, elk will be able to browse the willow stands on the NER, and bison numbers will grow unregulated.

We modeled forage deficits for Alternative # 1 under three pre-winter precipitation conditions--drought (Fig. 7), mean precipitation conditions (Fig. 8), and wet precipitation conditions (Fig. 9). Each figure has three sets of colored lines: the black set represents the average winter, the green set represents the above average winter, and the red set represents the severe winter. Each set of winter severity lines contains model projections for three levels of bison: the solid lines are the model projections for 500 bison, the dashed lines are for 1000 bison, and the dotted lines are for 2000 bison.

We predict forage deficits will begin to occur as elk populations reach 5,500 and higher during an average winter with pre-winter drought conditions and a population of 500 bison (Fig. 7, solid black line). Similarly, in an average winter preceded by drought conditions and a population of 1,000 bison (Fig. 7, dashed black line), forage deficits begin at approximately 3,800 elk in the Greater Teton ecosystem. In an above-average winter with 500 bison (Fig. 7, solid green line), forage deficits begin to occur at about 1,800 elk. As winter severity and bison numbers increase, deficits occur with smaller and smaller numbers of elk. The drought scenario utilizes 45% of the forage available in the mean precipitation scenario.

In a severe winter with a population of 500 bison and a pre-winter drought, deficits will begin to occur even when there are zero elk (Fig. 7, solid red line). These deficits occur because the 500 bison and the 890 moose are consuming all the available forage. This situation occurs in several of the modeled scenarios for the severe winter with low bison numbers, and in milder winters when bison numbers are high.

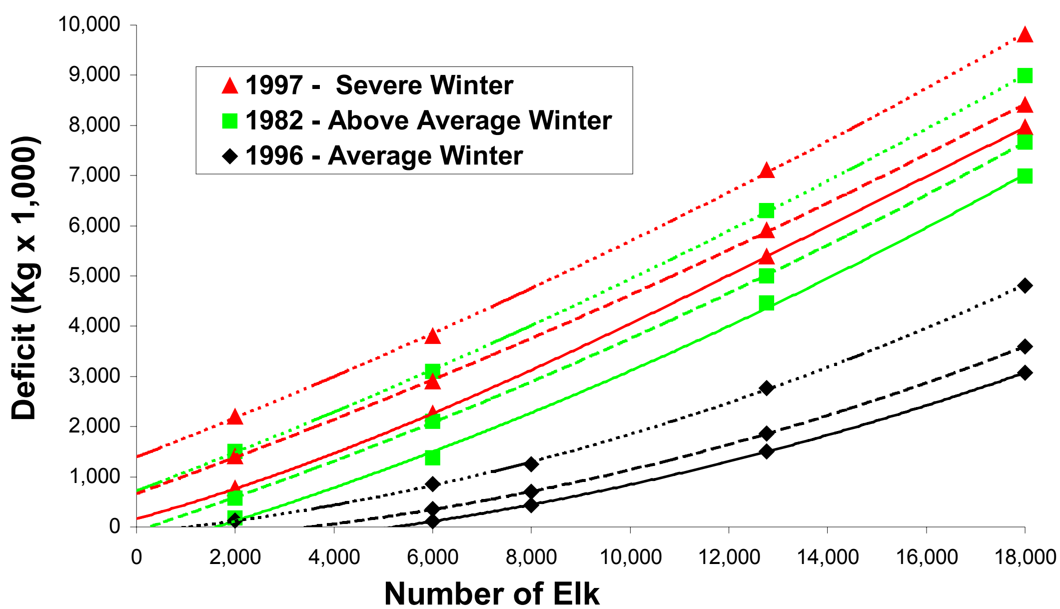

Figure 7. Forage deficits at varying numbers of elk predicted by the forage accounting model under three winter severity types with a pre-winter drought scenario for the Greater Teton Ecosystem, Wyoming. Projections were made under the conditions of EIS Alternative #1 (status quo) with a population of 500 bison (solid lines), 1000 bison (dashed lines), and 2000 bison (dotted lines).

Under mean pre-winter precipitation conditions, the increase in precipitation causes significantly higher forage production across the landscape, which translates into significantly more forage available to ungulates. Thus, compared to the drought scenarios, forage deficits occur at much higher numbers of elk across all model scenarios. In the average winter, with 500 bison (Fig. 8, solid black line), forage deficits occur at about 16,000 elk. In the above average winter with 500 bison (Fig. 8, solid green line), forage deficits occur at about 6,000 elk. The severe winter causes deficits to occur at much lower numbers of elk, about 1,000 with 500 bison. As in drought conditions, severe winters and high bison numbers result in deficits even at zero elk.

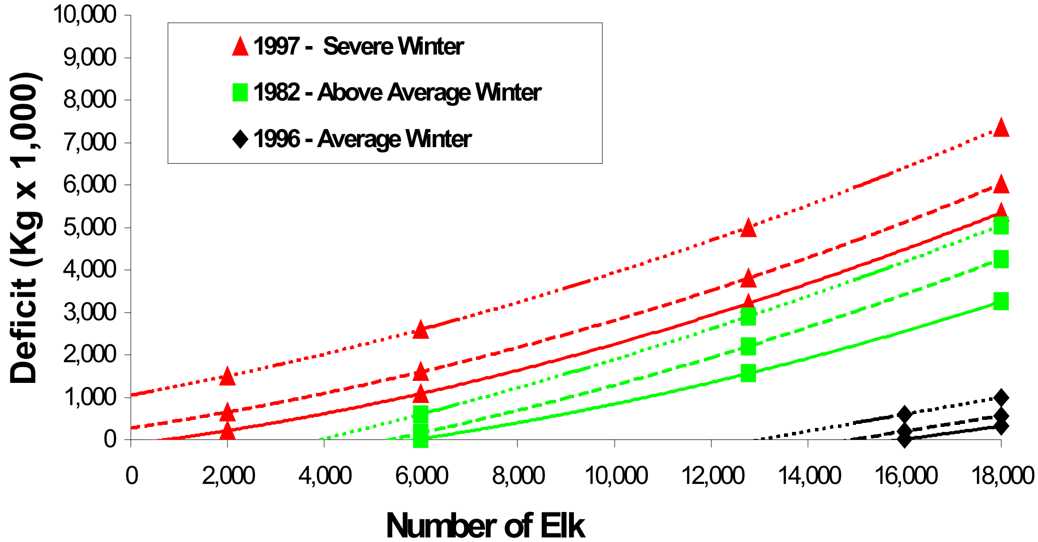

Figure 8. Forage deficits at varying numbers of elk predicted by the Forage Accounting Model under three winter severity types with mean pre-winter precipitation scenario for the Greater Teton Ecosystem, Wyoming. Projections were made under the conditions of EIS Alternative #1 (status quo) with a population of 500 bison (solid lines), 1000 bison (dashed lines), and 2000 bison (dotted lines).

Wet precipitation conditions (Fig. 9) increase forage availability, consequently decreasing forage deficits. In the wet precipitation scenarios, no deficits occur for any modeled population size of elk and bison in the average winter. In the above average winter with 500 bison, deficits occurred at 12,000 elk. In the severe winter with 500 bison, deficits started with 3,000 elk.

Forage Utilization

Forage utilization is simply the percent of forage removed by the ungulates from a given location in the study area as predicted by the Forage Accounting Model. Managers are often concerned about forage utilization because high utilization can be construed as a measurement of habitat degradation. Here, we briefly describe utilization results, while leaving a quantified analysis of utilization effects for Part II of this report, "The CENTURY Ecosystem Model."

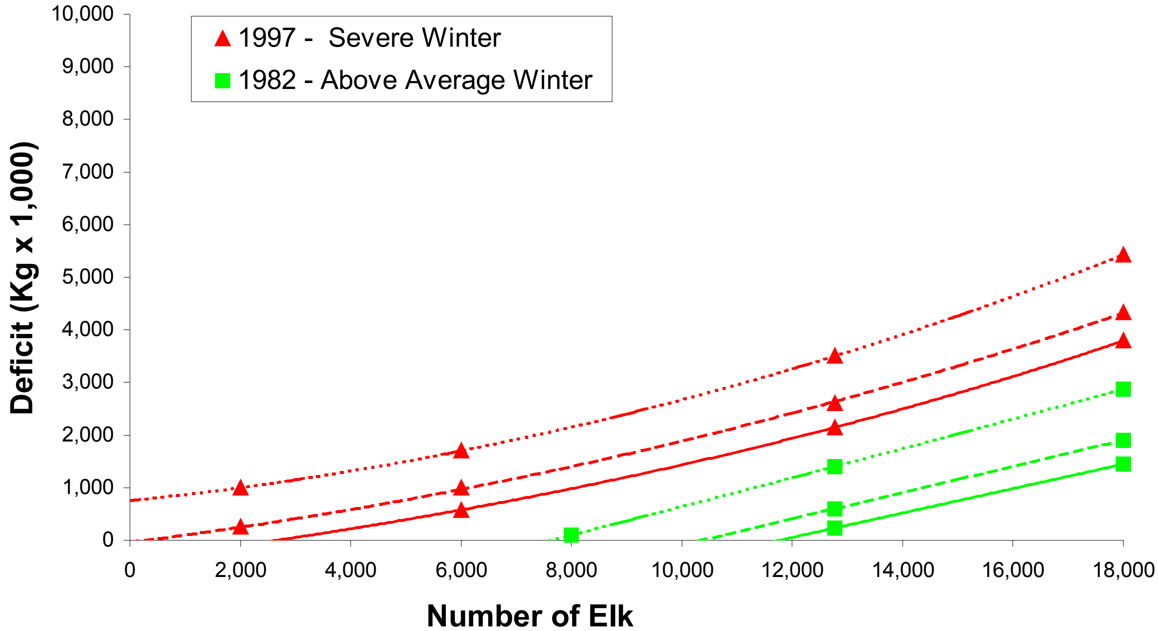

Figure 9. Forage deficits at varying numbers of elk predicted by the Forage Accounting Model under two winter severity types with a wet pre-winter precipitation scenario for the Greater Teton Ecosystem, Wyoming. Projections were made under the conditions of EIS Alternative #1 (status quo) with a population of 500 bison (solid lines), 1000 bison (dashed lines), and 2000 bison (dotted lines).

For the utilization results, we held precipitation and bison variables constant, and varied the number of elk and winter severity. We estimate that between 42 and 155 km^2 of winter range will be used in excess of 50% in an average winter with 500 bison and with elk populations of 6,000 to 18,000 (Fig. 10). Utilization area increases in the average winter because rising numbers of elk push out and onto low-SWE areas of the range. During above average and severe winters, we estimate between 61 and 105 sq km of winter range will be subject to utilization of ≥50%. In above average and severe winters, utilization area approaches an asymptote at higher elk population sizes. This effect occurs because snow is blanketing the landscape and prohibiting elk from moving onto outlying areas. As long as elk populations are >14,000 animals, more severe winters will protect forage from being highly utilized. It should be understood however, that this reduction in utilization would lead to increased deficits and probably lead to a sharp increase in starvation mortality.

Figure 11 maps forage utilization for the Greater Teton Ecosystem under a scenario of 12,771 elk, 500 bison, and mean pre-winter precipitation in an average SWE winter. Although maps for other sets of conditions (winter severity and elk numbers) would differ slightly, this map is indicative of the general layout of utilization across the Greater Teton ecosystem. The black areas represent utilization of 50% or greater on the landscape which corresponds with areas that receive the least snow coverage.

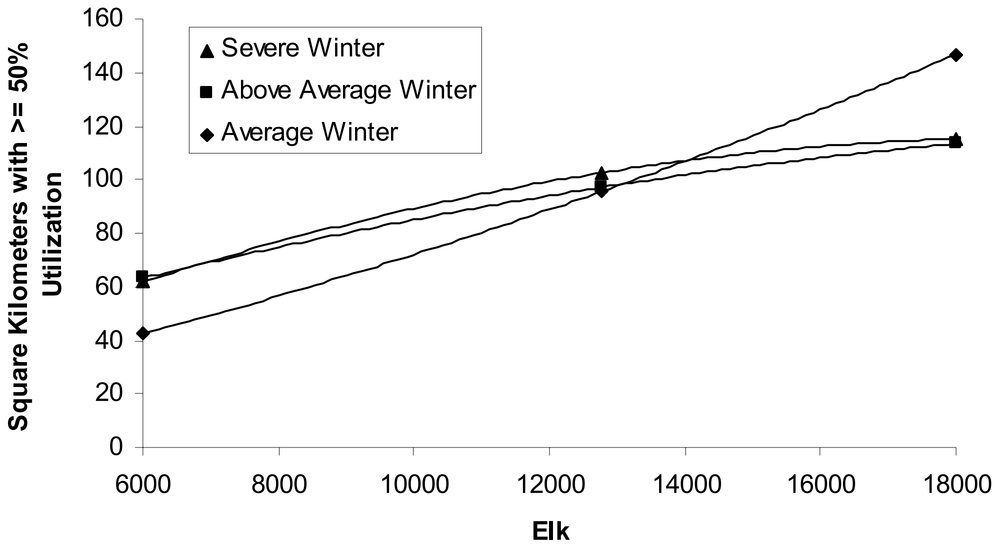

Figure 10. Area (km^2) of winter range with predicted utilization levels $\geq$ 50% as a function of elk population size during three winter severity types with mean pre-winter precipitation and 500 bison.

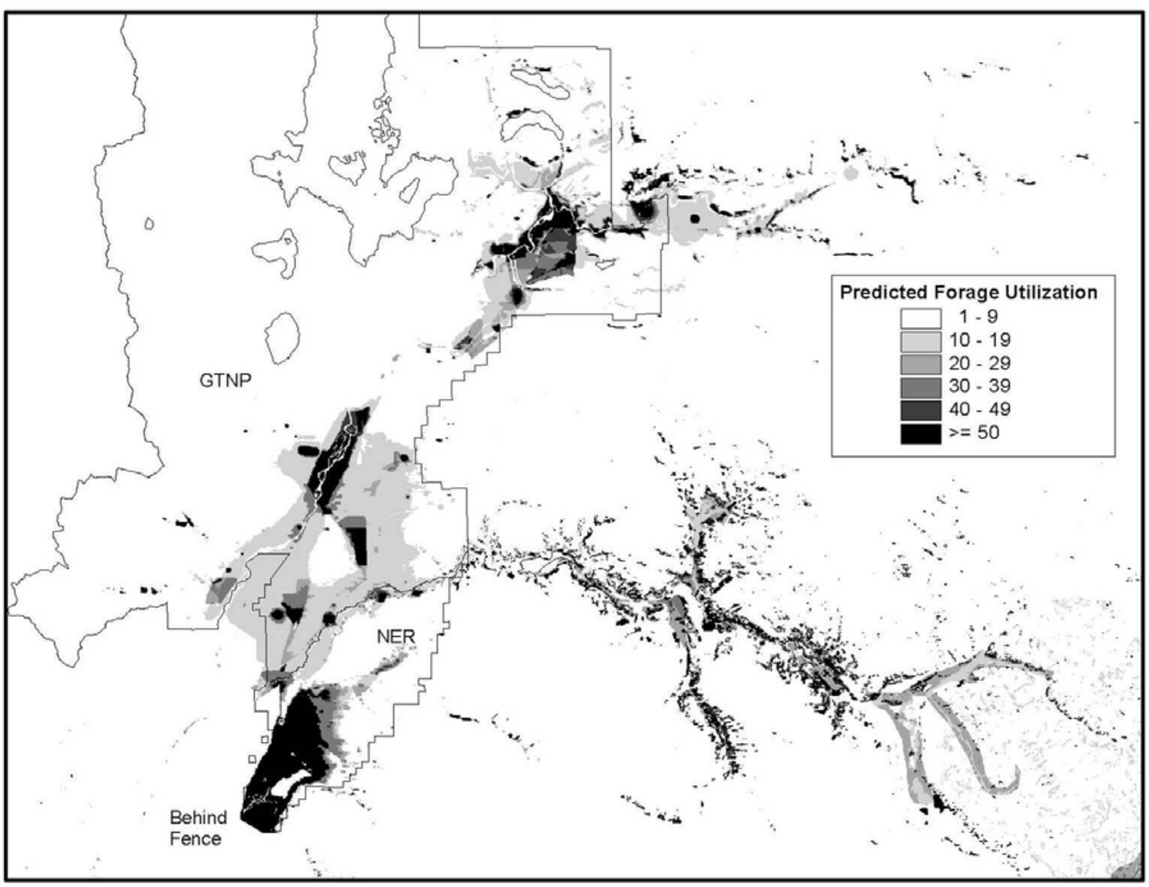

Figure 11. Predicted forage utilization (%) in the Greater Teton Ecosystem, Wyoming, for 12,771 elk in an average winter with average pre-winter precipitation and 500 bison.

Effects of Development in the Town of Jackson
One justification for supplemental feeding of elk is that it compensates for forage that would be available to native ungulates if their winter range had not been developed by human settlement in the town of Jackson. Although this justification is widely offered, it is based on a largely untested assumption of parity in the amount of forage fed and the amount lost to development. We analyzed this assumption as follows: If the development in the town of Jackson were exactly compensated by supplemental feeding, then adding the amount of forage lost to development in the town of Jackson to the natural forage currently available should theoretically *remove* the forage deficit. If supplemental feeding overcompensates for the development of the Jackson area, then forage deficits should remain despite "adding" the Jackson town forage base back into current supplies. If supplemental feeding undercompensates, then a forage surplus should result by adding the town of Jackson forage base back into the forage available to ungulates.

We examined this assumption by simulating two scenarios that represent conditions with reduced or eliminated effects of human developments. We refer to the first scenario as "without fence." This scenario assumed that elk would no longer be restricted to habitat north of the ungulate fence on the National Elk Refuge and would be allowed to use agricultural lands and native pastures in and around Jackson.

The ungulate fence near Jackson was built in the 1950s to keep elk from feeding on farmland during the winter. It follows the boundary of the NER along the south side of the refuge where the refuge adjoins the town of Jackson, and along the west side of the NER where it is bounded by US Highway 26/89/191. The fence partially obstructs natural migration paths down the Valley especially in severe winters when elk historically migrated to lower elevations down the Snake River through and beyond the town of Jackson. However, the NER is not fenced along its north and east borders. The fence has one-way crossovers to allow animals to move into the NER from the side bordering the highway, but they are only able to leave by traveling out the north and east sides. While the fence inhibits the movements of large ungulates, other wildlife are able to cross through or under the fence. To implement the "without fence" scenario, we simply added the forage in these areas to the forage supplies in the base model. The area added is the white area in Figure 11 -- "Behind Fence."

We refer to the second scenario as "presettlement." In this scenario, we modified the current vegetation to reflect patterns that were more likely before agricultural development of the Jackson Valley (irrigation, seeding, fertilization, etc.) As an approximation of these conditions, we assumed that vegetation south of the NER ungulate fence was composed of roughly equal parts of wet meadow and sagebrush-grassland.

Model results (Fig. 12) suggest that at 2,000 elk in the severe winter, forage deficits are reduced by 51% (from 217,000 kg to 110,000 kg) when forage south of the fence is added. However, at 18,000 elk, this deficit reduction shrinks to 13%. Similarly for the presettlement scenario, at 2,000 elk in the severe winter, deficits are reduced by 26%, but shrink to 6.2% at 18,000 elk. Forage deficits are completely offset in the average winter, even at 18,000 elk. However, the "with fence" deficits were small in the average winter, so the offset is less meaningful. Given the current elk population of 12,000 – 14,000, it is safe to say that even if elk moved to the area south of the NER fence, moving even to the southern boundary of the study area, forage deficits in a severe winter would be reduced, but not eliminated. For high populations of elk to avoid deficits in severe winters, they would need to migrate further south along the Snake River drainage. Forage deficits are completely offset in the average winter, even at 18,000 elk. However, the "with fence" deficits were small in the average winter, so the offset is less meaningful.

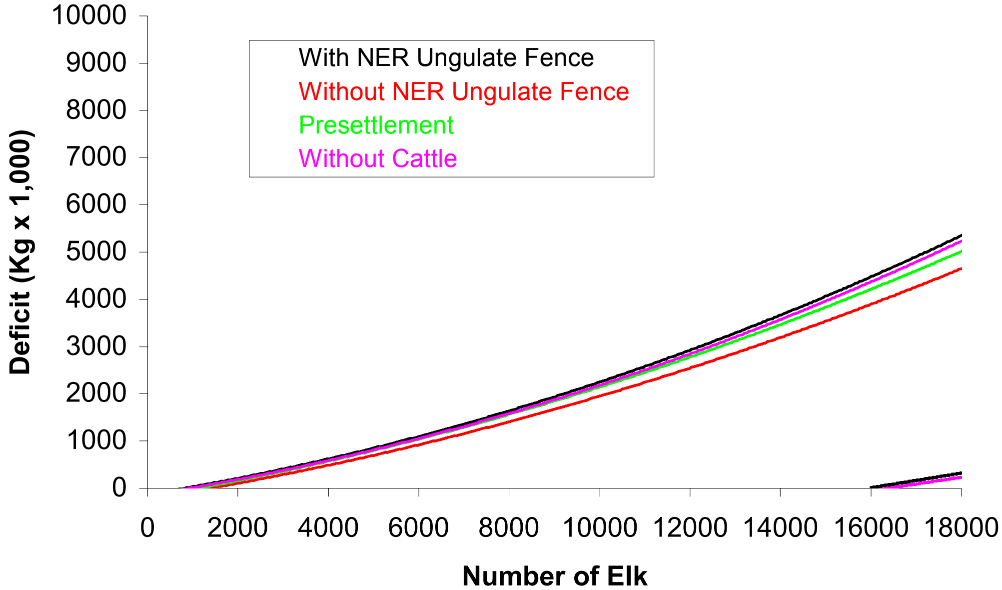

Figure 12. Forage deficits predicted under different assumptions about effects of the town of Jackson and cattle offtake. The model was run on severe and average winters with mean pre-winter precipitation and 500 bison. Severe winters are depicted by upper set of four lines; average winters are depicted by the lower set of two lines. The "with fence" scenario assumes no forage use by native ungulates south of the NER ungulate fence. The "without fence" scenario assumes that native ungulates are able to use vegetation south of the ungulate fence as currently mapped. The "presettlement" scenario assumes that native ungulates are able to use vegetation south of the ungulate fence and that this vegetation is composed of 50% sagebrush and 50% wet meadow. The "without cattle" scenario assumes no cattle grazing on the Greater Teton Ecosystem, Wyoming.

Removal of the NER Ungulate Fence

A model run that accurately portrays the spatial effects of removing the NER ungulate fence is not feasible with current data and understanding. If the fence were removed and feeding were discontinued, the Jackson elk herd would probably migrate south of the town of Jackson and intermingle with other herds from which they have been separated for many years. We are able to offer two general scenarios that shed light on the effects of removing the NER ungulate fence and cessation of feeding. First, under the "without fence" scenario, utilizations ≥50% are predicted throughout the town of Jackson, and would be constrained only by the elevation gradient that exists around the town (Fig. 13).

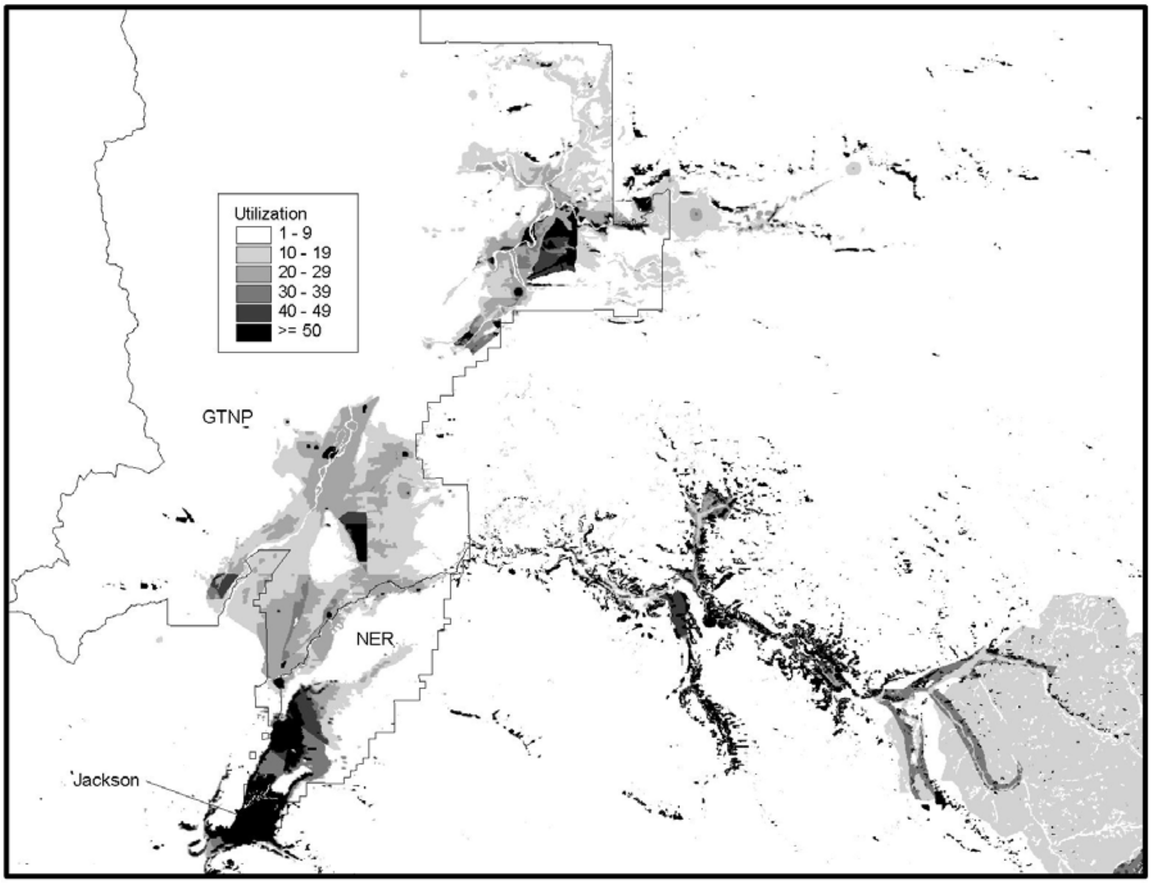

Figure 13. Predicted forage utilization under a model scenario of an average winter with average pre-winter precipitation and 12,771 elk without the NER ungulate fence. Very high utilization would likely continue south of the NER into the town of Jackson, Wyoming, due to more shallow snow depths in that area.

Second, we ran the snow model on a larger area and corrected it for the Gros Ventre River Valley snow shadow (Fig. 14). The snow shadow is an effect caused by the process of precipitation being removed from the air as it rises over the mountains from the west and descends the leeward (eastern) side, leaving less available to be deposited on the leeward side. The Tetons cause a "shadow" where there is decreasing snowfall accumulation to the east of the range (i.e. the Gros Ventre River Valley). The original snow model did not account for this effect, and overestimated snowfall in the Gros Ventre River drainage. Therefore, a correction had to be made to the snow model to adjust for this overestimation (Appendix B). The black cells on the map depict areas with 6 inches or less of SWE on March 8, 1997, the snowiest day available in the database. Results indicate that elk could winter in the Gros Ventre River Valley or south of Jackson in the Snake River Canyon as it winds towards Alpine, and lower areas of Hoback Canyon.

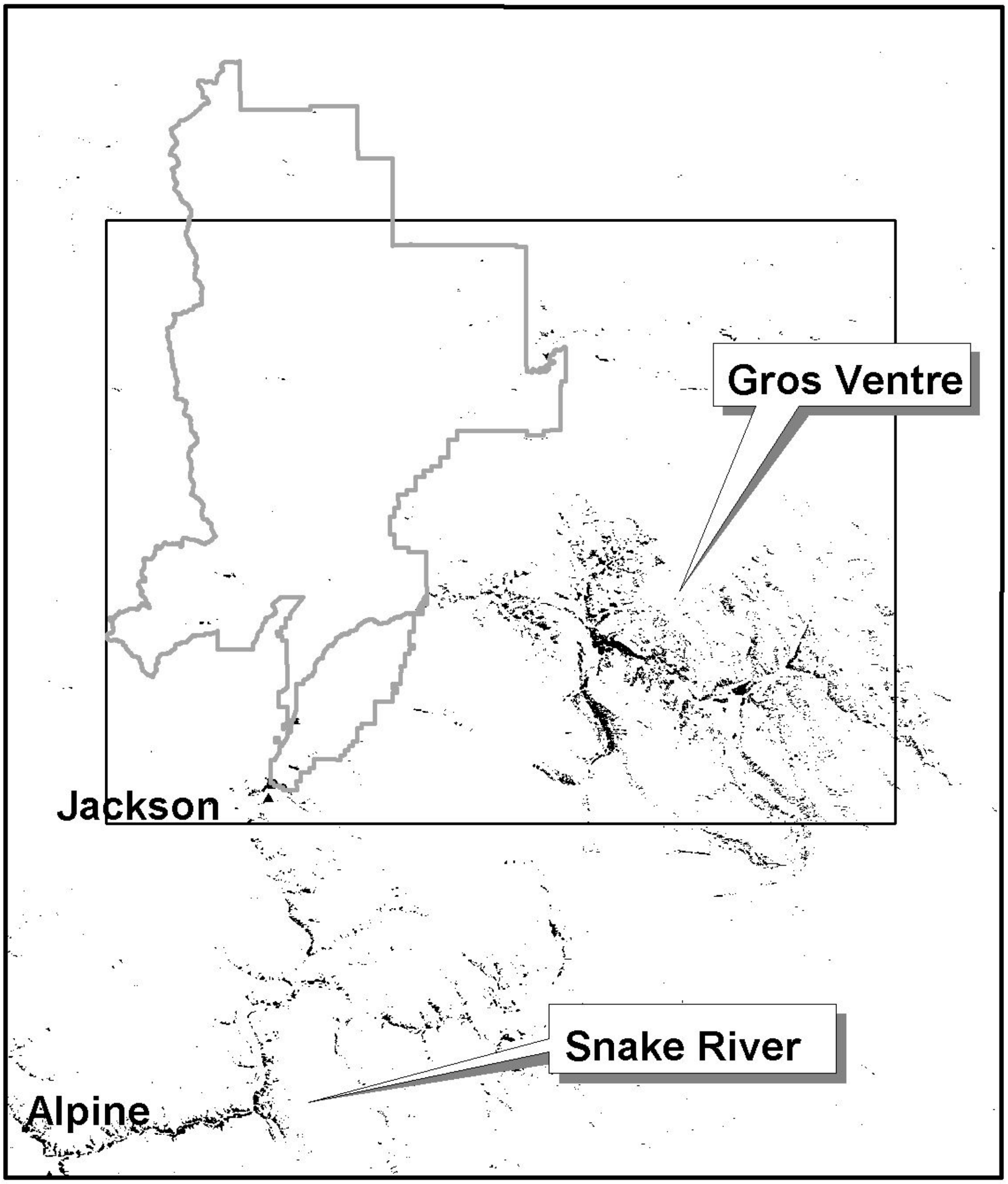

Figure 14. Black cells indicate likely migration routes and wintering areas in severe winters. The Gros Ventre River Valley and the lower Snake River Valley are predicted to receive the highest elk numbers and utilization should the NER ungulate fence be removed, due to lesser snowpack in those areas.

Effects of Cattle Grazing

To examine the effects of cattle grazing on forage deficits we estimated the biomass consumed by cattle during summer and subtracted that from the pre-winter standing crop. We did this by overlaying coverages of grazing allotments on the vegetation map, estimating the total forage removed as a function of the stocking rate, and subtracting that estimate from the pre-winter forage supply. In addition, Steve Kilpatrick (Wyoming Game and Fish Department) reviewed and offered small changes to the cattle offtake map.

The model projections (the purple lines on Fig. 12) revealed negligible effects of cattle grazing on forage deficits for wild ungulates. Although the total amount of forage consumed by livestock was substantial -- about 0.5% of the total production on the Teton ecosystem -- most of this consumption occurred on areas that were not critical elk winter range. As elk numbers increased, deficit differences with and without cattle became quantifiable (the difference between the black line and the purple line in Fig. 12). At 18,000 elk, "with fence" deficits were 5,346,000 kilograms whereas "without cattle" deficits were 5,229,000 kilograms, a difference of 117,000 kilograms or 2.2%.

Model Results on the National Elk Refuge for Alternative #1

Adapting the Forage Accounting Model to the NER

The Forage Accounting Model was initially written to run on the Greater Teton Ecosystem utilizing the weekly SWE maps created by the snow model. These weekly snow maps are the factor that drives elk migration throughout the study area. To adapt the model to run only on the NER, we continued to use the snow maps as the migratory switch but we only allowed elk to consume forage on the NER rather than on any area beyond the NER's borders. This forced all elk onto the NER's forage as soon as snow began (roughly on Nov. 1st) and kept them there until the end of the period of snow cover (roughly June 1st). At the beginning of the snow season, the animals were allowed to spread out over the entire NER, but as snow accumulated, they were restricted to low SWE areas. As snow melted, they were allowed to spread out over the low-SWE areas on the NER.

Real migratory movements are likely to be different. On the study sites, elk slowly move onto the NER as snow accumulates, and slowly move off as snow melts. Because our model cannot mimic these real movements, our numeric estimates of forage deficits are overly high, i.e., real deficits may be lower than those depicted in the following figures, and higher numbers of elk may be supported before deficits occur. For example, if deficits start at 6,000 elk, this can be interpreted as "at least" 6,000 elk are needed to incur deficits. While the actual number may be 7,000 or 8,000, it is definitely not 5,000. Thus, the margin of error for the NER should be construed differently than for the Greater Teton Ecosystem. On the NER, deficit predictions represent the lowest limit in the margin of error. We roughly estimate the upper limit as the lower limit plus 50%. Again, we cannot firmly quantify this error but believe it is a reasonable approximation.

Modeled Scenarios

For Alternative #1, we exercised the Forage Accounting Model on the National Elk Refuge and ran simulations for (1) varying populations of elk -- between 0 and 10,000, (2) varying winter severity -- average, above average, and severe, (3) varying pre-winter precipitation conditions -- drought, mean, and wet, and (4) three populations of bison -- 500, 1000, and 2000. These model projections include offtake by 20 moose. We also ran a scenario that simulated center-pivot irrigation of 1,170 acres of the cultivated fields on the NER, which are currently flood-irrigated.

In an average winter following severe pre-winter drought conditions with 500 bison, as elk populations reach 2,000 and higher, we predict forage deficits will begin to occur on the NER (Fig. 15, solid black line). Note in Figure 15 that all of the other lines do not touch the x-axis, i.e., deficits occur even when elk numbers are zero animals. These deficits occur because in any week, the 500 bison and 20 moose are consuming all forage.

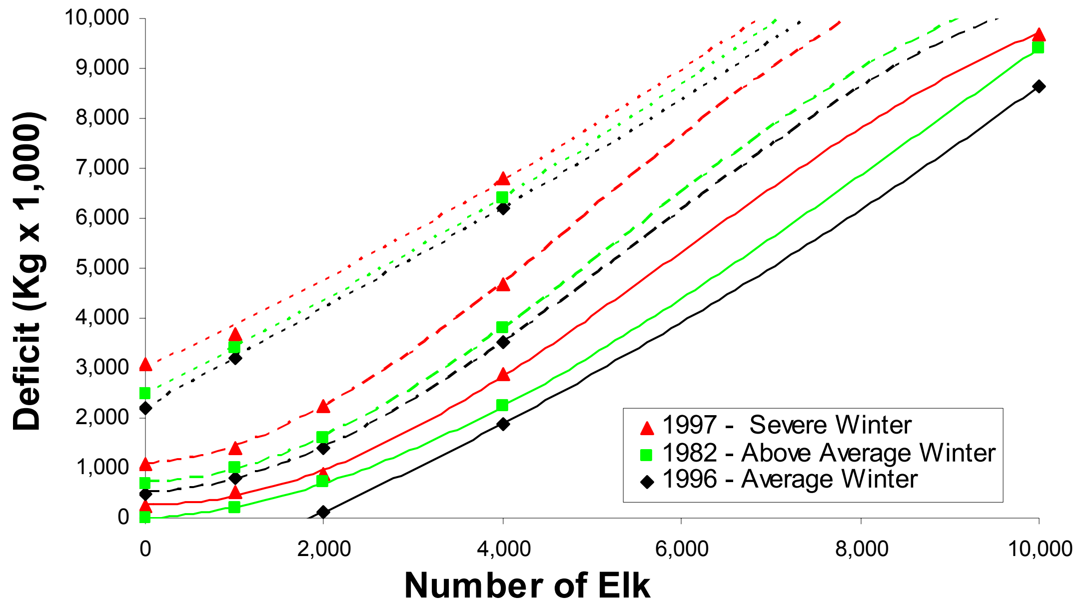

Figure 15. Forage deficits at varying numbers of elk predicted by the Forage Accounting Model under three winter severity types with a pre-winter drought scenario for the National Elk Refuge, Wyoming. Projections were made under the conditions of EIS Alternative #1 (status quo) with populations of 500 bison (solid lines), 1000 bison (dashed lines), and 2000 bison (dotted lines).

Mean precipitation conditions create significantly more forage for ungulates and cause deficits to occur at much higher numbers of elk in average winters (Fig. 16). With 500 bison in the average winter (the solid black line), forage deficits occur at about 5,000 elk. With 1,000 bison, deficits occur at about 4,000 elk, and with 2,000 bison, at about 2,000 elk. Though mean precipitation increases forage production, there is still sufficient snow in above average and severe winters to incur deficits at zero elk across all bison numbers.

Wet precipitation conditions (Fig. 17) increase forage availability, which similarly decreases forage deficits. In the wet precipitation scenarios, deficits occur at roughly 9,200 elk in the average winter and at 800 elk in the above average winter with 500 bison. Severe winters still cause deficits to begin at zero elk due to the extreme snow cover on the landscape.

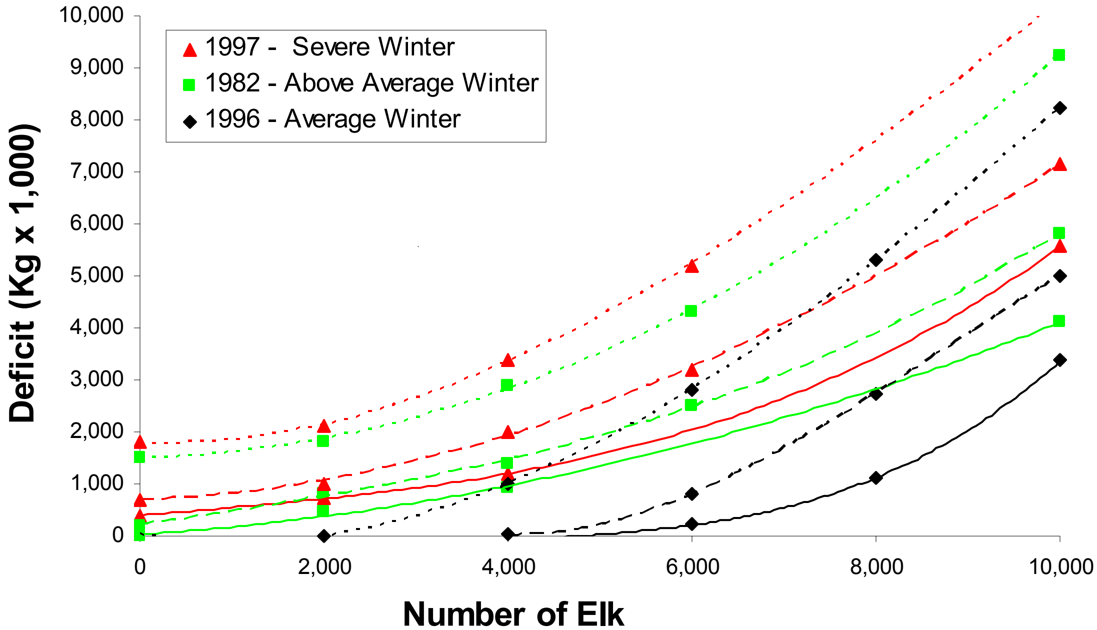

Figure 16. Forage deficits at varying numbers of elk predicted by the Forage Accounting Model under three winter severity types with mean pre-winter precipitation for the National Elk Refuge, Wyoming. Projections were made under the conditions of EIS Alternative #1 (status quo) with populations of 500 bison (solid lines), 1000 bison (dashed lines), and 2000 bison (dotted lines).

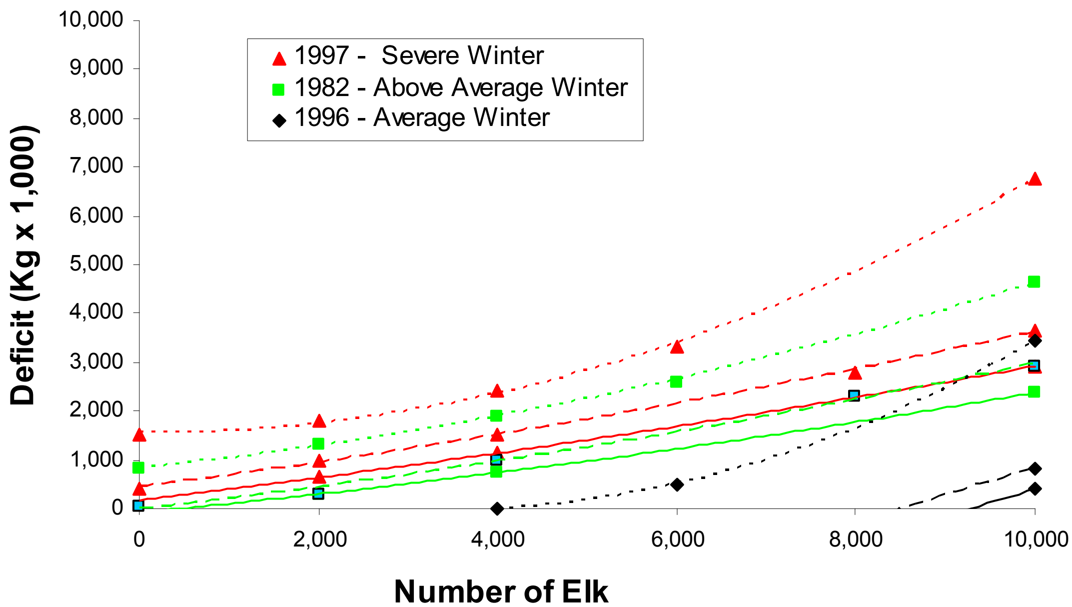

Figure 17. Forage deficits at varying numbers of elk predicted by the Forage Accounting Model under three winter severity types with wet pre-winter precipitation conditions for the National Elk Refuge, Wyoming. Projections were made under the conditions of EIS Alternative #1 (status quo) with populations of 500 bison (solid lines), 1000 bison (dashed lines), and 2000 bison (dotted lines).

Irrigation Experiment
We created an additional model experiment to address questions on the value of irrigation on the NER. Managers may want to center-pivot irrigate ~1,170 acres of the NER to raise production, thereby increasing the biomass of forage available to wintering elk. As per the description in the document "Irrigation System Rehabilitation Plan Environmental Assessment" (U.S. Fish and Wildlife Service, National Elk Refuge, October 1998), we created a model scenario in which production values on the following NER project areas were increased to reflect center-pivot irrigation: McBride, Chambers, Nowlin, Ben Goe, and Headquarters (Fig. 18). Currently these areas are flood-irrigated resulting in about 2,500 lbs/acre of production whereas center-pivot irrigation will result in about 5,000 lbs/acre. For this experiment, we varied only the irrigation acreage, holding precipitation and bison constant (average precipitation and 500 bison).

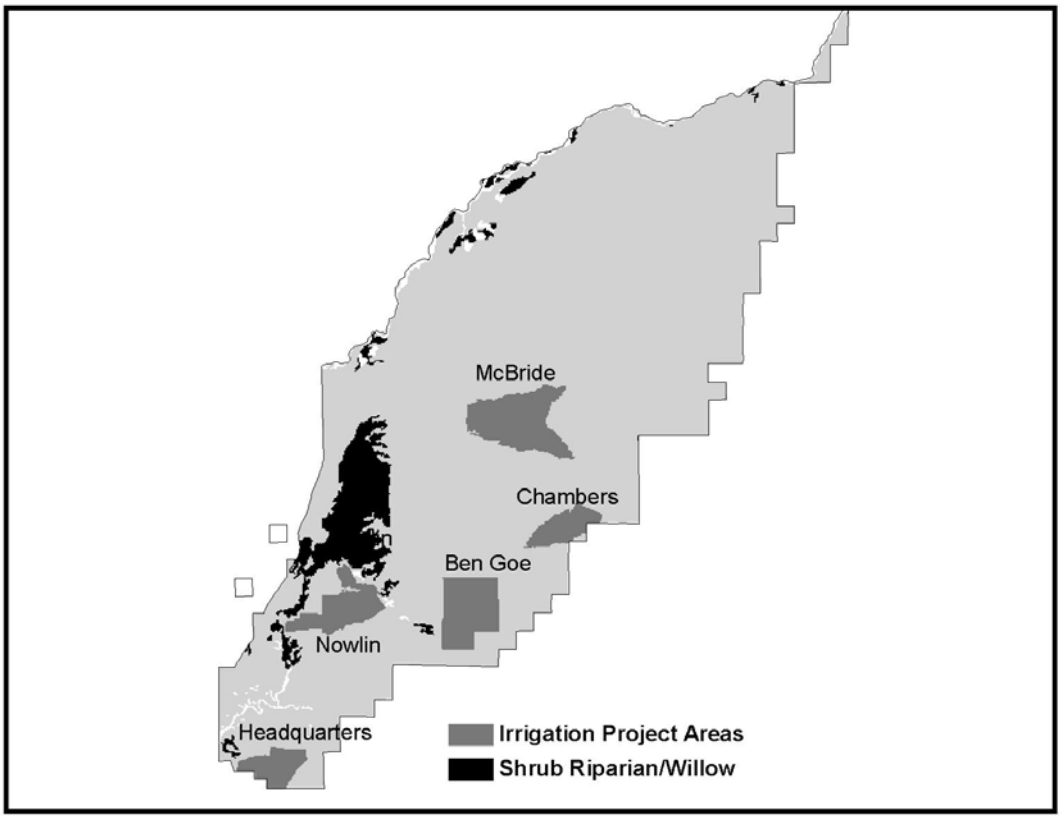

Figure 18. Irrigation project areas and location of willow patches on the National Elk Refuge, Wyoming.

Center-pivot irrigation of the four NER project areas had a significant positive impact by decreasing forage deficits in an average winter under average precipitation with 500 bison (Fig. 19, solid lines). For the flood-irrigated scenario in the average winter, deficits begin at about 5,000 elk and are 3,371,000 kilograms at 10,000 elk. For the center-pivot irrigated scenario, deficits begin at about 6,000 elk and are 2,207,000 kilograms at 10,000 elk. In a severe and above-average winter, the change in deficits is less pronounced. Both severe and above-average winters have deficits beginning right at zero elk. As the number of elk increases, a slight difference exists between the two scenarios, culminating in a deficit of 5,560,000 kilograms at 10,000 elk for the flood-irrigated scenario, and a lesser deficit of only 4,711,000 kilograms for the center-pivot irrigated scenario (a 15% reduction in forage deficit). With center-pivot irrigation, the average winter results in a greater reduction of the forage deficit because more of the range is available to ungulates for foraging based on snow water equivalents. In the severe and above-average winter, the upper NER irrigated project areas are covered in too much snow at critical weeks during the winter to substantially influence forage deficits.

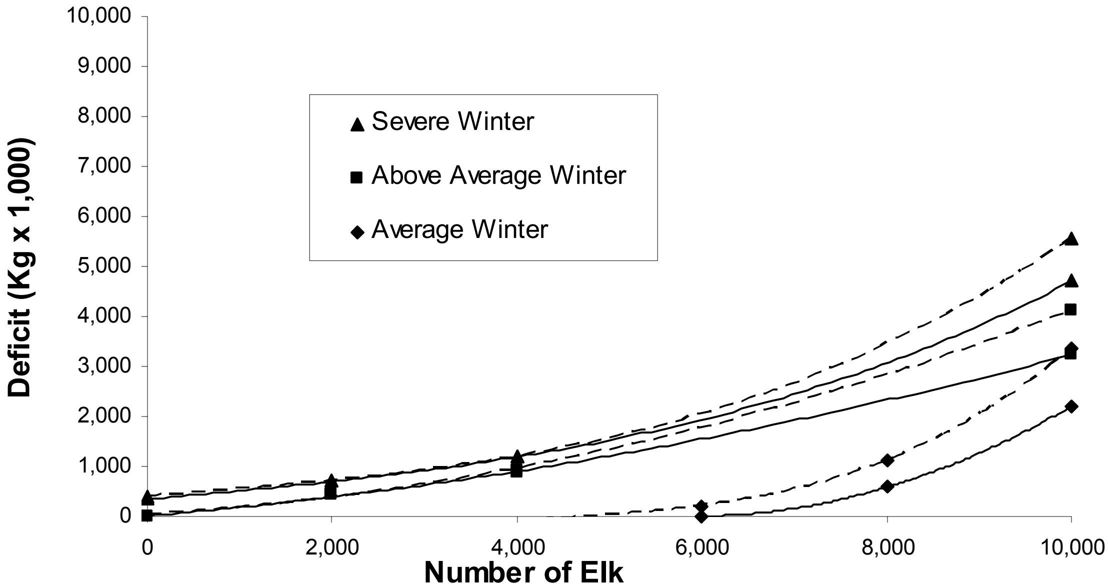

Figure 19. Predicted forage deficits for the Irrigation Model Experiment on the National Elk Refuge, Wyoming. Solid lines represent center-pivot irrigation; dotted lines represent flood (status quo) irrigation.

Discussion for Alternative #1

Our model revealed that the balance between the forage supply and the forage requirements of wintering ungulates is tightly linked to winter severity and growing season precipitation. Although both of these weather conditions can determine the number of animals that can be supported by native forage, snow accumulation exerts the strongest effects. During average winters with average precipitation conditions and 500 bison present, the number of elk that can be sustained on the entire landscape approaches 16,000. But as winter severity or drought are encountered, this number drops dramatically.

Currently, elk and bison are supplementally fed on the NER to alleviate food shortages caused by snow severity as well as drought conditions. Additionally, it is argued that supplemental feeding is needed to compensate for forage supplies lost to the area behind the NER's ungulate fence. Our model experiments suggest that the ungulate fence plays an important role by inhibiting migration and foraging for native ungulates, and that removing the fence would increase forage availability especially during average winters. However, our model predicts that significant forage deficits would still occur during more severe winters even if the ungulate fence were removed and native ungulates were allowed to graze in and around the town of Jackson as well as on nearby agricultural lands. This suggests that historic elk populations: (1) may have been smaller than current ones, and/or (2) may have suffered high levels of mortality during severe winters, and/or (3) likely used lower elevation ranges south of our Jackson study area, such as the lower Snake River, the Gros Ventre River drainage, and possibly even the Red Desert area. Historic observations indeed verify large groups of elk moved up the Gros Ventre River drainage to spend winter in the Red Desert, and moved to winter in the lower Snake River drainage (Cromely 2000).

The influence of grazing by livestock on forage supplies for native ungulates has emerged as a controversial question for managers in the Greater Teton Ecosystem. Our model experiments suggest that cattle grazing does not play an important role in determining availability of forage for native ungulates during winter. This is the case because the preponderance of livestock grazing occurs on areas of the landscape that accumulate deep snow during the winter. As a result, increasing forage on these areas by removing livestock grazing may increase forage biomass but it does not increase forage available to wintering ungulates. Removing cattle from the system had negligible impacts on predicted forage deficits. If cattle have any influence, it would be on the distribution and forage available to elk and bison during the summer months. The empirical portion of this study verified that both elk and bison will make some use of cattle grazed lands during the summer months, but there was active avoidance of cattle herds (Zeigenfuss et al. 2001, Singer et al. 2003). Unfortunately, we did not study summer forage needs of the ungulates and we do not know if summer range or summer forage was in any way limiting to either elk or bison.

We predict that approximately 100 km^2 of winter range will be utilized at a 50% rate or higher given current numbers of elk and bison, and varying climatic conditions. Part of this high level of use is caused by the NER ungulate fence because it inhibits natural foraging patterns and migration. However, we emphasize that as long as animals select areas that are relatively snow free in preference to areas where snows are deep, we should anticipate locally high levels of forage utilization on some sites. Although reducing population density can reduce the area of the landscape that falls into the "high-use" category, we project that some "hot spots," or areas of very high grazing offtake, will occur at any reasonable population. The effect of these forage utilization rates and hot spots will be analyzed in the next section of this report -- Part II, The CENTURY Ecosystem Model.

Bison numbers play an important role in forage deficits. Given the number of bison recorded at the start of this project (~500), approximately 16,000 elk can forage on the whole Valley system without incurring deficits in an average winter with average pre-winter precipitation conditions. When bison numbers double to 1,000, average elk numbers that incur no deficits under average conditions drop to 15,000; when bison numbers quadruple to 2,000, the desirable elk numbers drop to 13,000. Doubling bison numbers to 1,000 also substantially increases forage deficits in more severe winters, and quadrupling bison numbers to 2,000 causes severe stress on the system during most climatic conditions.

The results for the NER should be evaluated differently than those for the Greater Teton Ecosystem. Instead of a mean estimation with a surrounding margin of error, the NER's results should be construed as the "lowest possible number of elk" which corresponds to the deficit measurement. On the NER study area, this number represents the lowest limit in the margin of error. We roughly estimate the upper limit as equal to the lower limit plus 50%.

Given this stipulation, we estimate that the NER can support at least 5,000 elk in average winters with mean pre-winter precipitation and 500 bison. In above-average and severe winters, deficits occur at all levels of elk except in the wet pre-winter precipitation scenario. In our irrigation experiment, we found that 1,000 additional elk could forage on the NER before deficits would occur in average winters with average pre-winter precipitation and 500 bison. Forage deficits would be reduced in severe winters especially with high numbers of elk.

Forage Accounting Model Results for all EIS Alternatives

We were asked to run the model and provide results for Alternatives #1 - #4 in the EIS and also provide a summary table of where deficits begin for each Alternative given its underlying assumptions as follows:

Alternative #1 (status quo): Flood irrigation of the NER's cultivated fields; All of the NER's willow is available to ungulates; Three levels of bison -- 500, 1,000, 2,000.

Alternative #2: No irrigation of the NER's cultivated fields; All of the NER's willow is available to ungulates; Two levels of bison -- 250, 500.

Alternative #3: Flood irrigation of the NER's cultivated fields; Bison = 1,000; Two amounts of the NER's willow are available to ungulates -- none and one-half.

Alternative #4: Center-pivot irrigation of the NER's cultivated fields; Bison = 350; Two amounts of the NER's willow are available to ungulates -- none and one-half.

For all of the alternatives, the Forage Accounting Model was run on both the Greater Teton Ecosystem and the NER study area. The cautions for interpretation discussed for Alternative #1 in the previous sections also apply to the results for Alternative #2 - #4. In addition to these stipulations, please note that the model is not sufficiently sensitive to discriminate between some of the Alternatives and their underlying assumptions. For example, the difference between the forage offtake from 350 bison and 500 bison is so small that the difference between the deficit results from those scenarios is subsumed by the model's margin of error. Similarly, the difference between types of irrigation, and the question of willow exclusion, also offered results that were subsumed by the model's margin of error.

We report these results with both a summary table and deficit graphs. First, Table 5 reports the number of elk at which forage deficits begin to occur. The number in each cell represents the "equilibrium point" on the landscape at which the estimated forage supply exactly offsets demand by the elk population. This number is the point at which the deficit curve hits the x-axis. Higher numbers of elk will cause forage deficits to occur. When interpreting these numbers, keep in mind that it is almost assured that wintering elk can sustain small levels of forage deficits by using stored energy reserves (fat and lean body mass) to survive. Because of this, we suggest interpreting the numbers in the table together with the curves in the graphs that follow. If the deficit curve remains low (near the x-axis), i.e., < 500,000 kg, then wintering elk may be able to utilize stored energy reserves to survive rather than incur starvation mortality. In other words, small forage deficits can occur without causing high levels of mortality from starvation, but at larger forage deficits, extensive mortality of elk would occur.

Table 5. Summary table for number of elk at which forage equilibrium occurs for all proposed elk management EIS alternatives on the National Elk Refuge and Greater Teton Ecosystem, Wyoming.

	Pre-winter Precipitation Scenario								
	Drought			**Mean**			**Wet**		
	Snow Severity Type			**Snow Severity Type**			**Snow Severity Type**		
	Severe	**Above**	**Average**	**Severe**	**Above**	**Average**	**Severe**	**Above**	**Average**
Alternative #1 (status quo)									
With 500 Bison									
Greater Teton Ecosystem	0	1,800	5,500	1,000	6,000	16,000	3,000	12,000	>18,000
NER only	0	0	2,000	0	0	5,000	0	800	9,200
- with center-pivot irrigation				0	0	6,000			
With 1,000 Bison									
Greater Teton Ecosystem	0	200	3,800	0	5,800	15,000	200	10,200	>18,000
NER only	0	0	0	0	0	4,000	0	500	8,500
With 2,000 Bison									
Greater Teton Ecosystem	0	0	1,500	0	4,000	13,000	0	7,800	>18,000
NER only	0	0	0	0	0	2,000	0	0	4,000
Alternative #2 (no irrigation of cultivated fields on NER)									
With 250 Bison									
Greater Teton Ecosystem	700	1,800	6,000	1,800	7,500	16,400			
NER only	0	0	2,000	0	0	5,700			
With 500 Bison									
Greater Teton Ecosystem	0	1,600	5,300	900	5,900	15,800			
NER only	0	0	1,700	0	0	4,500			
Alternative #3 (with 1,000 bison and flood-irrigation of NER's cultivated fields)									
No Willow on NER Available									
Greater Teton Ecosystem	0	0	3,000	0	5,000	14,000			
NER only	0	0	0	0	0	3,300			
One-half of Willow on NER Available									
Greater Teton Ecosystem	0	0	3,200	0	5,500	14,200			
NER only	0	0	0	0	0	3,500			
Alternative #4 (with 350 bison and center-pivot irrigation of NER's cultivated fields)									
No Willow on NER Available									
Greater Teton Ecosystem	0	1,600	5,700	1,500	7,200	17,000			
NER only	0	0	2,000	0	0	5,500			
One-half of Willow on NER Available									
Greater Teton Ecosystem	0	1,800	6,000	1,800	7,400	17,100			
NER only	0	0	2,500	0	200	6,000			

Graphical Model Results for the EIS Alternatives #2 - #4

Model Results for Alternative #2

Alternative #2 assumptions: (1) 250 and 500 bison, (2) no irrigation of the cultivated fields on the NER, and (3) all willow is available.

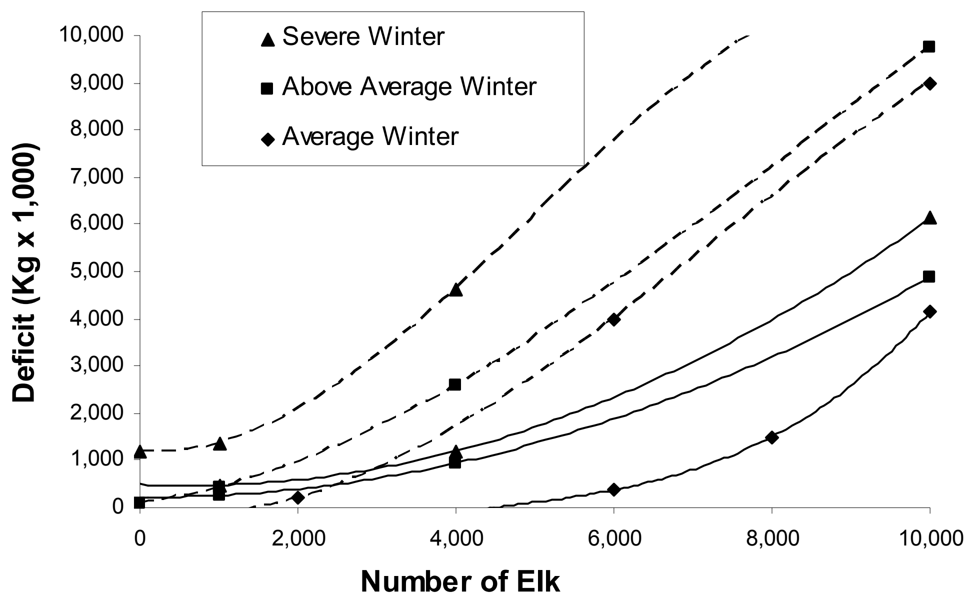

Figure 20. Predicted forage deficits for the National Elk Refuge using EIS Alternative #2 with 500 bison. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions (as occurred in 2001).

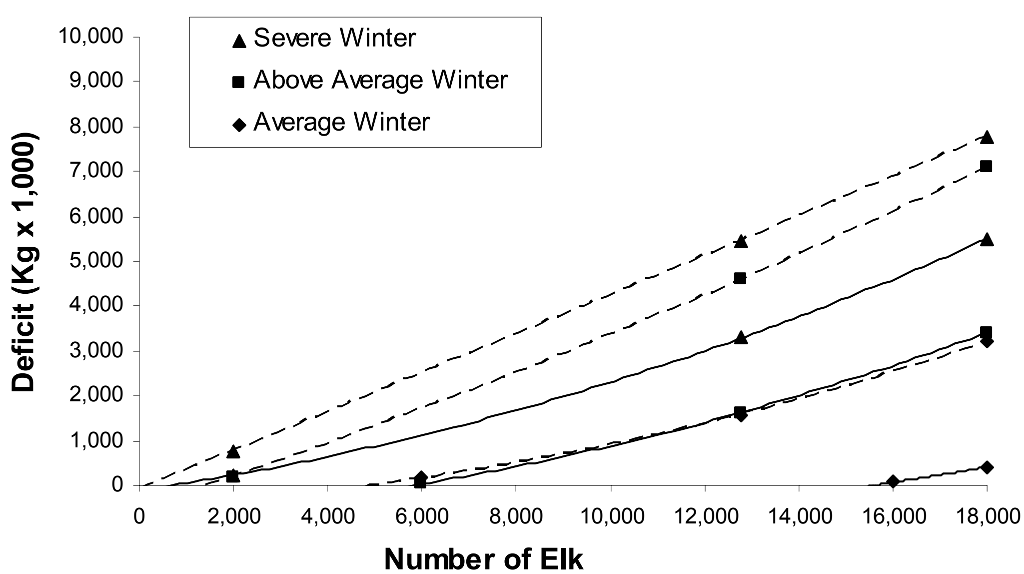

Figure 21. Predicted forage deficits on the Greater Teton Ecosystem using EIS Alternative #2 with 500 bison. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent these winter severities under drought pre-winter precipitation conditions (as occurred in 2001).

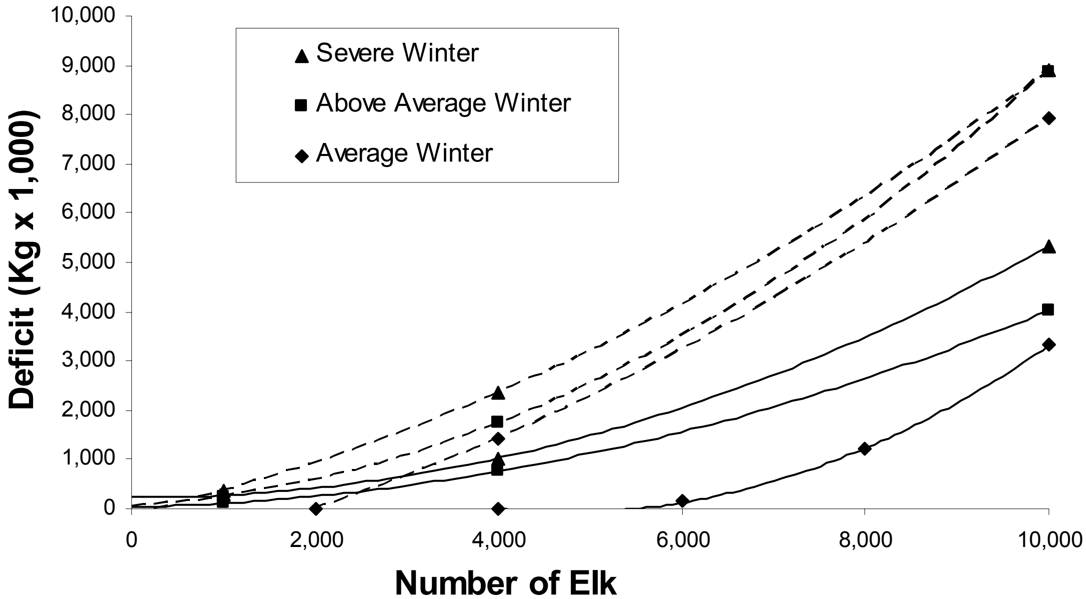

Figure 22. Predicted forage deficits for the National Elk Refuge using EIS Alternative #2 with 250 bison. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions (as occurred in 2001).

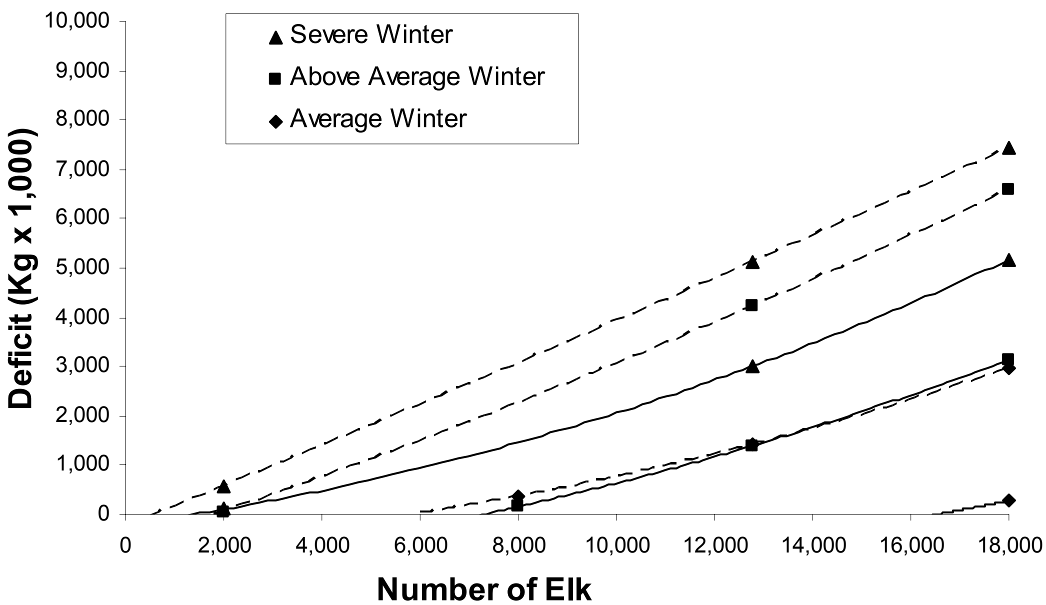

Figure 23. Predicted forage deficits for the Greater Teton Ecosystem using EIS Alternative #2 with 250 bison. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions (as occurred in 2001).

Model Results for Alternative #3
Alternative #3 assumptions: (1) 1000 bison, (2) cultivated fields on the NER are flood-irrigated (status quo), and (3) willow on the NER is all fenced off or half-fenced off.

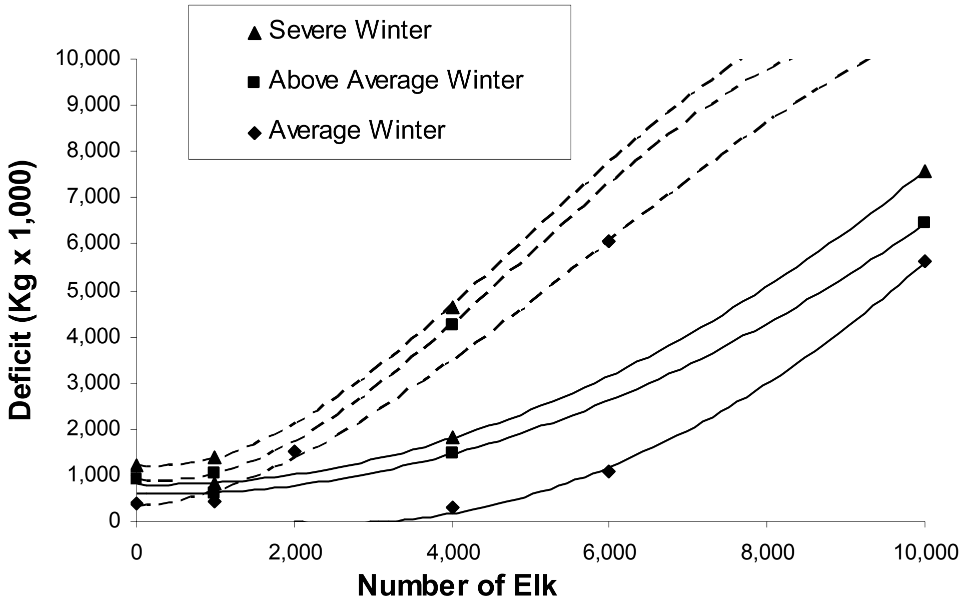

Figure 24. Predicted forage deficits for the National Elk Refuge using EIS Alternative #3 with no forage available in vegetation coded "shrub riparian/willow." The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions (as occurred in 2001).

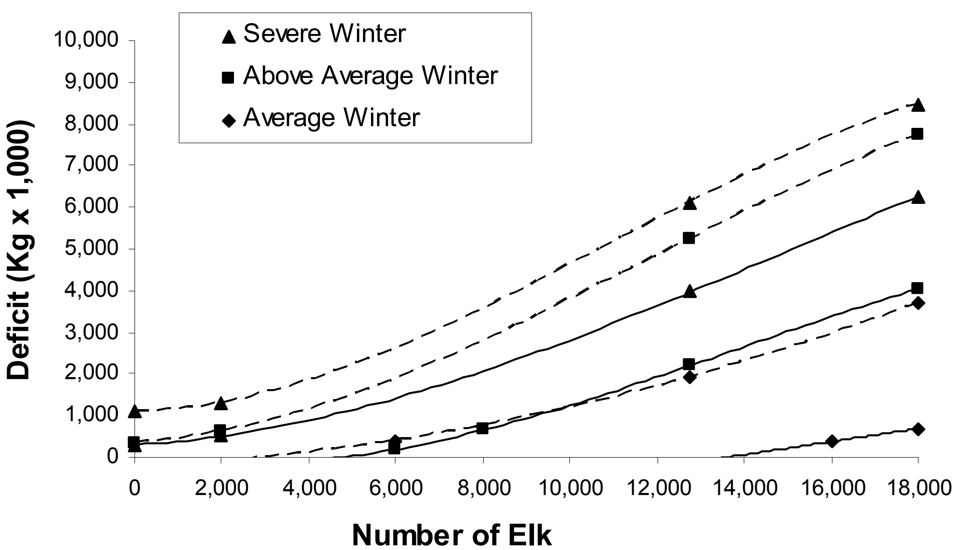

Figure 25. Predicted forage deficits for the Greater Teton Ecosystem using EIS Alternative #3 with no forage available in vegetation coded "shrub riparian/willow" on the National Elk Refuge. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions (as occurred in 2001).

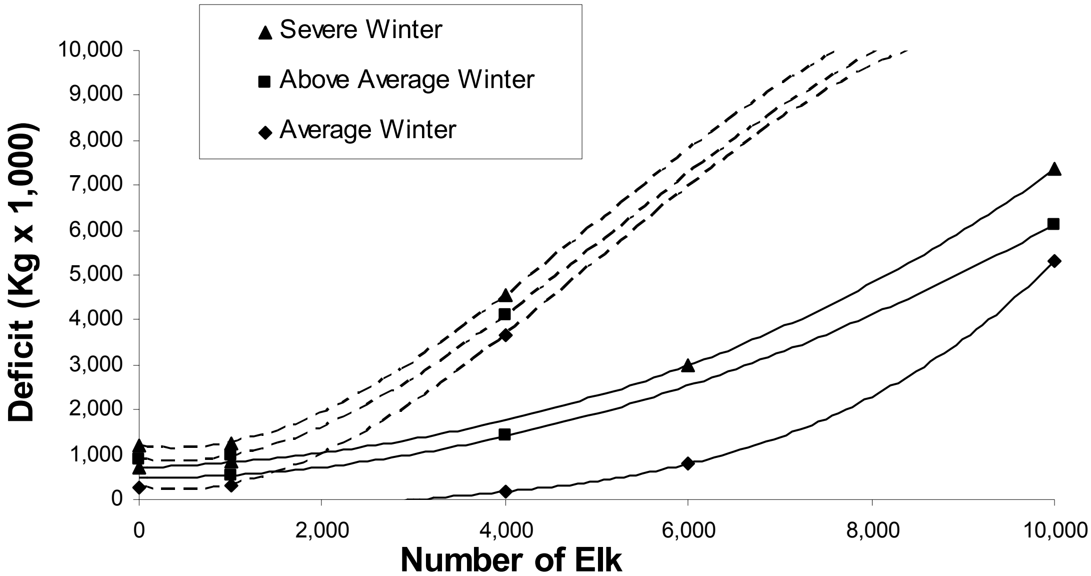

Figure 26. Predicted forage deficits for the National Elk Refuge using EIS Alternative #3 with one-half of the forage available in vegetation coded "shrub riparian/willow." The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions (as occurred in 2001).

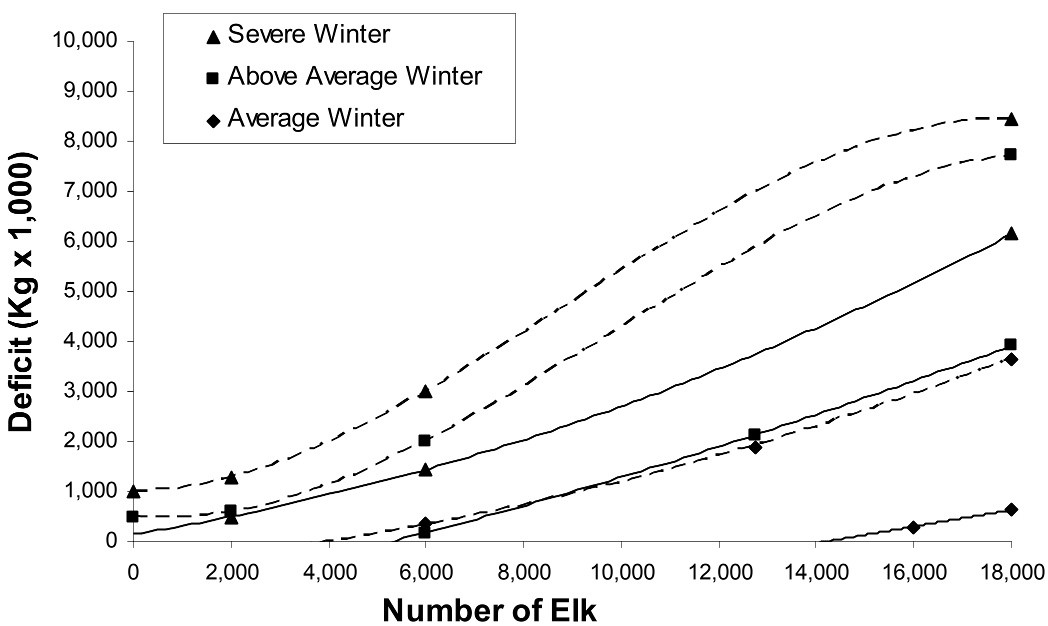

Figure 27. Predicted forage deficits for the Greater Teton Ecosystem using EIS Alternative #3 with one-half of the forage available in vegetation coded "shrub riparian/willow" on the National Elk Refuge. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions.

Model Results for Alternative #4
Alternative #4 assumptions: (1) 350 bison, (2) cultivated fields on the NER are center-pivot irrigated, and (3) willow on the NER is all fenced off or half-fenced off.

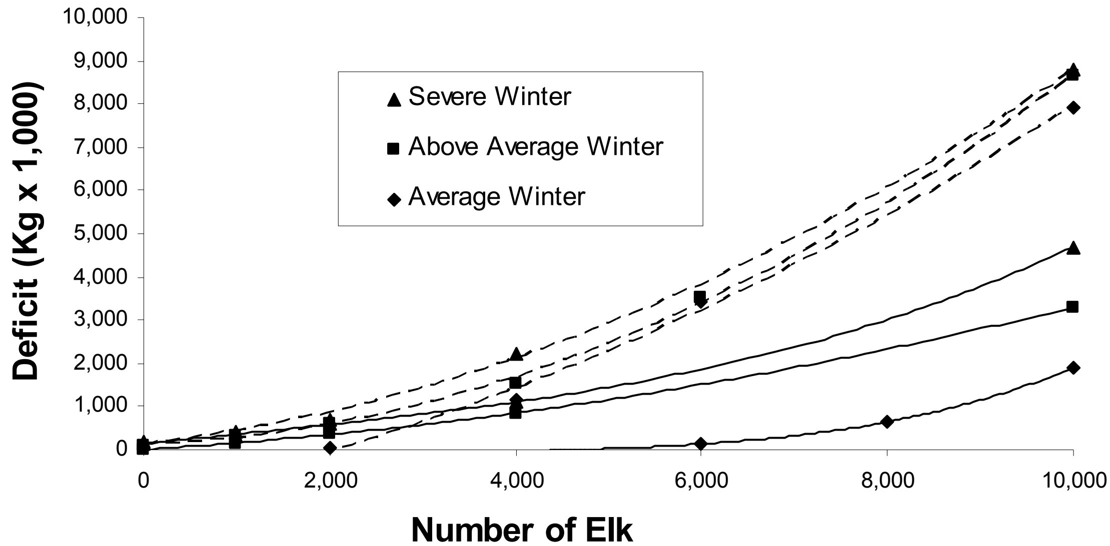

Figure 28. Predicted forage deficits for the National Elk Refuge using EIS Alternative #4 with no forage available in vegetation coded "shrub riparian/willow." The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions.

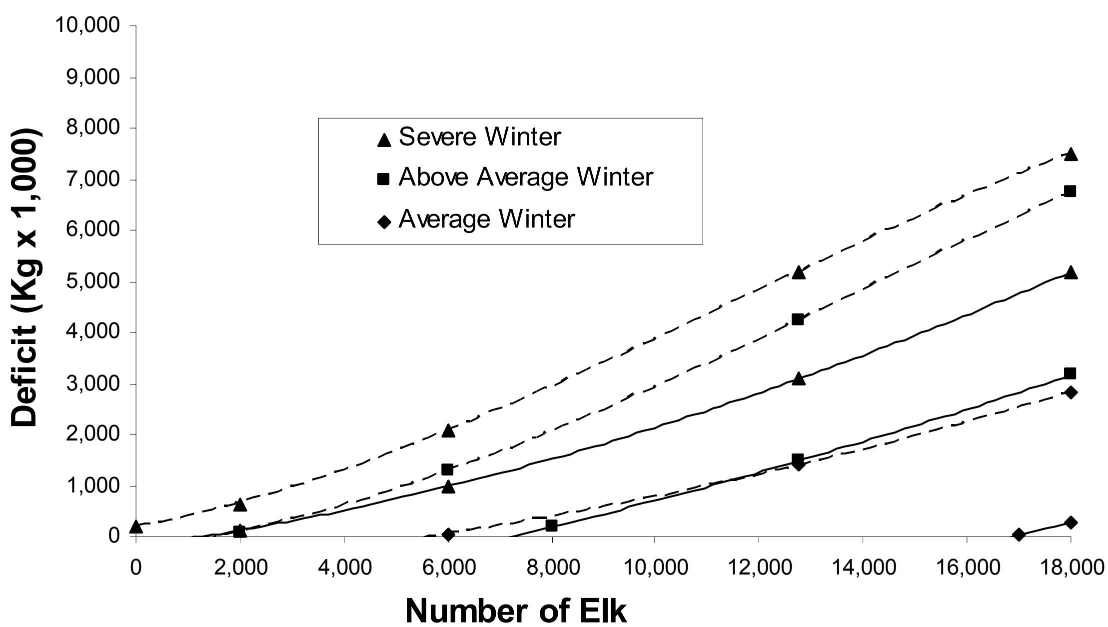

Figure 29. Predicted forage deficits for the Greater Teton Ecosystem using EIS Alternative #4 with no forage available in vegetation coded "shrub riparian/willow" on the National Elk Refuge. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions.

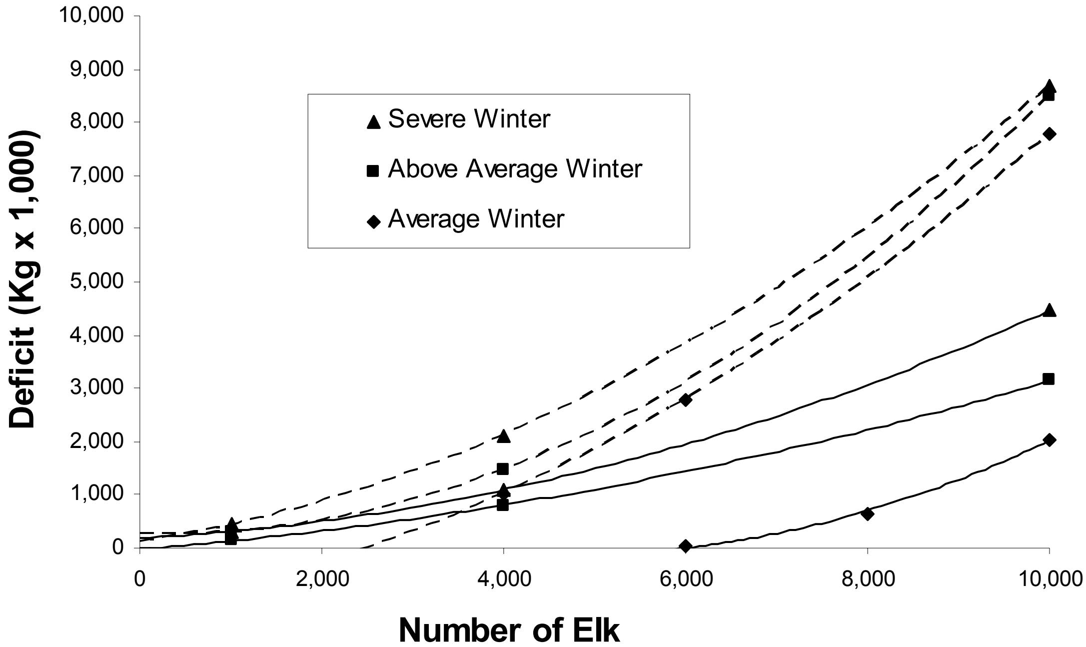

Figure 30. Predicted forage deficits for the National Elk Refuge using EIS Alternative #4 with one-half of the forage available in vegetation coded "shrub riparian/willow." The solid lines represent mean pre-winter precipitation conditions, and dashed lines represent drought pre-winter precipitation conditions.

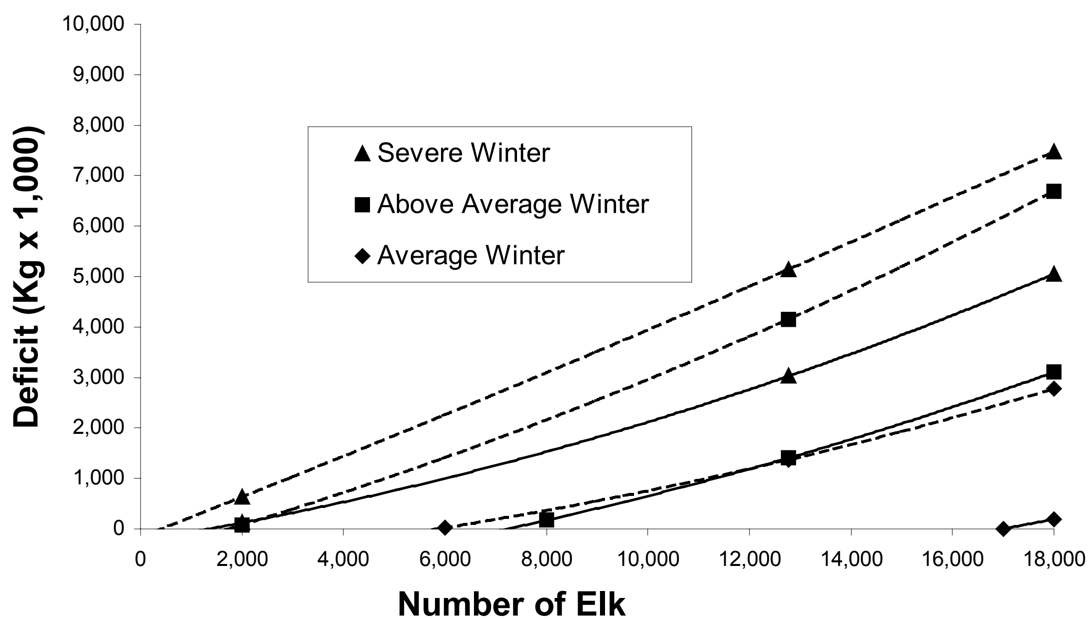

Figure 31. Predicted forage deficits for the Greater Teton Ecosystem with one-half of the forage available in vegetation coded "shrub riparian/willow" on the National Elk Refuge. The solid lines represent mean pre-winter precipitation conditions, and the dashed lines represent drought pre-winter precipitation conditions.

Discussion for Alternatives #2 - #4

The EIS Alternatives attempt to consider effects of manipulating three variables: bison numbers, willow availability on the NER, and irrigation of the NER's cultivated fields. The net effects of these three variables on forage deficits will be the following:

1. Increasing bison numbers will increase overall forage deficits.
2. Fencing off willow on the NER will increase deficits.
3. Irrigating the cultivated fields on the NER will decrease deficits -- center-pivot more so, flood irrigation less so.

Because the vegetation manipulations (willow, irrigation) would occur on the lower portion of the NER, the effects will be less pronounced when the model is run on the Greater Teton Ecosystem than the NER. Additionally, because above average and severe winters have some weeks where snow blankets the landscape, the effects of vegetation manipulations are less pronounced than in average winters.

Alternative #2 is designed to mimic "more natural vegetation conditions" by allowing willow use and not irrigating the cultivated fields. This alternative also manipulates bison numbers, setting them at either 250 or 500. The net effect of "more natural conditions" is slightly higher overall deficits than Alternative #1, and slightly fewer elk before deficits occur. In the average winter with average precipitation and 500 bison, deficits begin at 5,000 elk in Alternative #1 but begin at 4,500 in Alternative #2. If bison numbers are kept at 250, deficits begin at 5,700 elk in Alternative #2.

Alternative #3 lets bison numbers increase naturally to 1,000, and one-half or all of the willow stands on the NER are fenced. This Alternative restricts forage for elk more than any other Alternative because both increased bison numbers and willow fencing cause higher forage deficits. In an average winter with average precipitation and no willow availability (i.e., 100% fenced), deficits begin at 3,300 elk. With one-half willow availability, deficits begin at 3,500 elk.

Alternative #4 holds bison numbers to 350 while center-pivot irrigating the cultivated fields and fencing off willows. Viewed in stages, lower bison numbers (350) will decrease deficits, center-pivot irrigation will decrease deficits, and willow fencing will increase deficits. The net effect of these three manipulations is slightly lower deficits than Alternative #1, which allows slightly more elk to find forage before deficits occur. In an average winter with average precipitation conditions and 350 bison, deficits begin at 5,500 elk when all the willow is fenced off and 6,000 elk when one-half of the willow is fenced off.

In total, the manipulations in the three EIS Alternatives have fairly mild effects on forage deficits and elk numbers. Only Alternative #3, which allows 1,000 bison and fences willow, has a significant restricting effect on elk forages. The net effects of Alternatives #2 and #4 vary little from status quo management. Both the potential willow habitat and the irrigated fields on the NER comprise roughly 1,000 acres, and are relatively minor portions of the Greater Teton Ecosystem. If managers want to have a significant impact on the deficits for the entire Jackson elk herd, vegetation manipulations will have to occur on a much larger scale. And, as stated earlier, because snow blankets much of the valley landscape in some weeks of above average and severe winters, vegetation manipulations have significantly less effect in severe than in average winters.

Part II.
Provisional CENTURY Ecosystem Modeling

Introduction

Results from simulations using the Forage Accounting Model in Part I of this report suggest that substantial areas of the winter range will experience forage utilization exceeding 50% under all management alternatives. High levels of use will occur for some areas at virtually all population levels of elk during all winters. This heavy utilization on the winter range is intensified by the existence of the NER ungulate fence that inhibits natural migration to lower, snow-free elevations. Additionally, field measurements (Steele et al. 1999, Zeigenfuss et al. 2001) depict heavy utilization (as high as 60-70%) throughout the winter range in the lower portion of the NER and the lower elevations of the Gros Ventre River Valley. In this section, we report results from the CENTURY simulation model that portray biogeochemical changes in vegetation and soil resulting from grazing by elk and bison in the Greater Teton Ecosystem. The central question we address here is whether or not high levels of grazing will harm long-term productivity of vegetation communities.

This modeling effort is based on estimated inputs of soil and vegetation chemistry, because field data were not yet available. Current and ongoing field sampling work by F. Singer on nitrogen pools and vegetation will later be used to verify these projections. A final, revised run of CENTURY may be made at that time, but only if the empirical verifications do not agree with projections reported here. Variations from the projections presented here, however, are considered unlikely since we used well-established variables from the literature for ecosystems that are very similar to the grazing systems in the Greater Teton Ecosystem.

The CENTURY Model

The CENTURY ecosystem model (Metherell et al. 1993) simulates exchanges of carbon (C) and nitrogen (N) among the atmosphere, soil, and vegetation. Required inputs used to drive the model include monthly maximum/minimum temperature and precipitation data, soil properties, vegetation type, and current and historical land use. Disturbances and management practices such as grazing, fire, cultivation, and fertilizer additions can be simulated. CENTURY includes submodels for plant productivity, decomposition of dead plant material and soil organic matter (SOM), and soil water and temperature dynamics. Flows of C and N are controlled by the amount of C in the various pools (e.g. SOM, plant biomass), the N and lignin concentrations of the pools, abiotic temperature/soil water factors, and soil physical properties related to texture. SOM is divided into three pools based on decomposition rates (Parton et al. 1993, 1994). Decomposition of SOM and external nutrient additions supply the nutrient pool that is available for plant growth. Plant growth is controlled by a plant-specific maximum growth parameter, nutrient availability, and 0-1 multipliers that reflect shading, water, and temperature stress. Net Primary Productivity (NPP) is allocated among leafy, woody, and root compartments as a function of plant type, season, soil water content, and nutrient availability.

CENTURY has been used to successfully simulate soil C and NPP levels in various natural and managed systems including grasslands (Parton et al. 1993) and agricultural systems (Parton and Rasmussen 1994). For this project, the grazing subroutine was used to model the effect of migrating elk on the native grasslands and shrublands on the NER and the Gros Ventre River

Valley. Although dozens of output variables are available, this modeling effort focused on soil C, soil N, and annual NPP because these variables are of most interest to range managers. A flowchart representing the CENTURY model is shown in Figure 32.

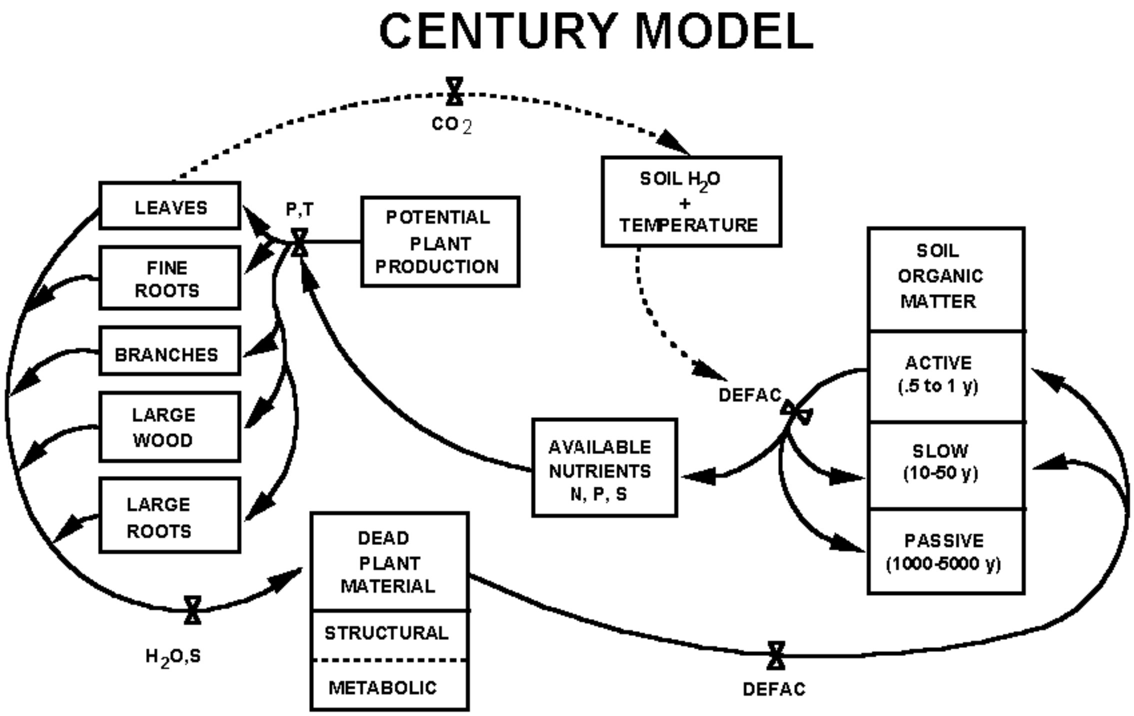

Figure 32. Flowchart of the variables and processes simulated in the CENTURY Model.

Model Parameters

Vegetation Types

Two vegetation types were simulated -- wet meadow and sagebrush. We assumed that wet meadow was 100% herbaceous (graminoids and forbs) with annual production values of ~200 gC/m^2; and that sagebrush was a 50/50 herbaceous/sagebrush mix with annual production values ~120 gC/m^2. These production values were also used in the Forage Accounting Model, and were derived from field measurements (Zeigenfuss et al. 2001).

These vegetation types were chosen for two reasons. First, they are the same vegetation types being sampled in 2001 and 2002 by F. Singer for verification of these projections. Second, they also correspond with the major vegetation types that receive significant offtake in the Forage Accounting Model, and comprise much of the NER and the winter range in the Gros Ventre River drainage. The Forage Accounting Model was used to predict areas where utilization was 50% or greater in an average winter preceded by average pre-winter precipitation with 500 bison present (Fig. 33).

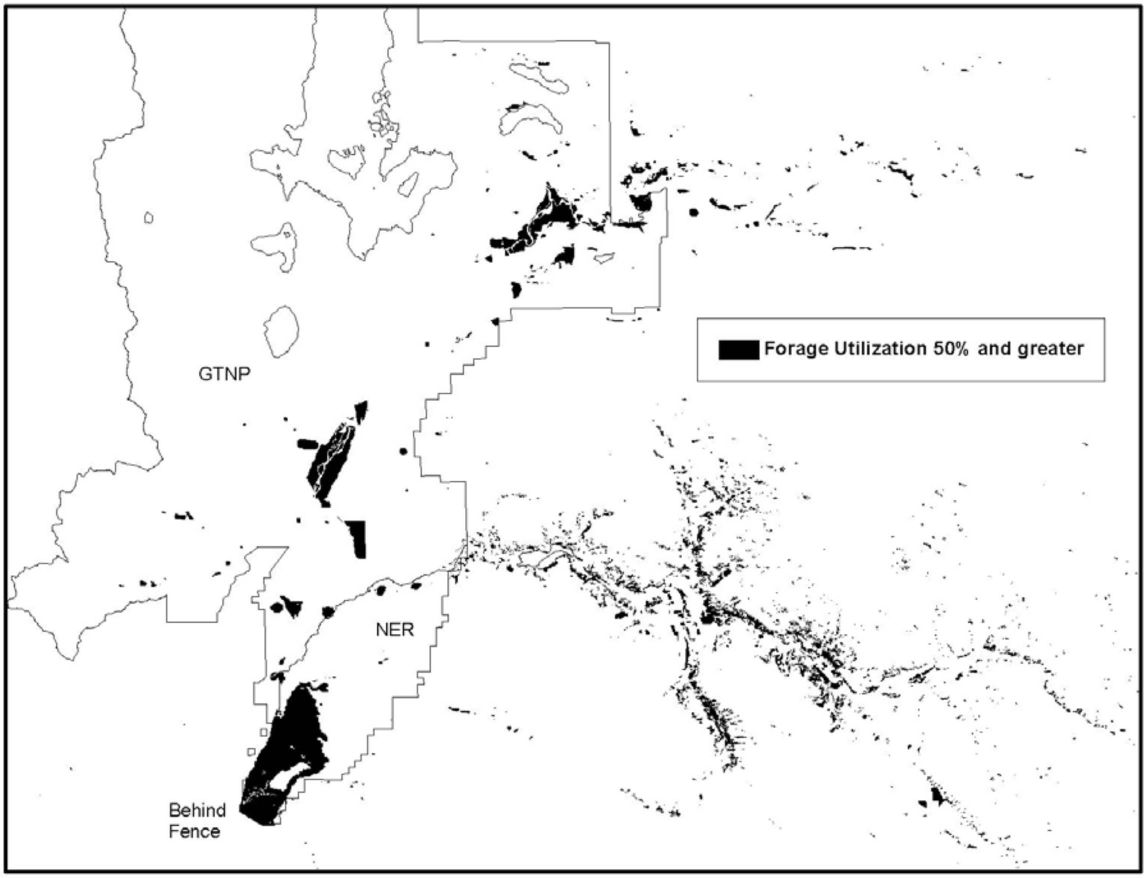

Figure 33. Areas of the Greater Teton Ecosystem where forage utilization was predicted to be 50% or greater during an average winter with average pre-winter precipitation and 500 bison.

Weather

Weather is a primary driver of the CENTURY model. Monthly weather data were obtained from the permanent weather station at Moose, Wyoming. Although stations at Jackson and Moran were also available, the station at Moose provided temperature and precipitation measurements intermediate between the extremes of Jackson and Moran, and thus provided a reasonable compromise that could be used for the entire low-lying winter range in the Valley.

Other Input Parameters

Other primary input parameters include soil type and texture, C/N ratios, life span and other parameters for the vegetation types, and annual N inputs from wet and dry deposition. Soil and vegetation parameters were based on values used in CENTURY simulations of a similar system in Rocky Mountain National Park (Schoenecker et al. 2002). Annual N inputs were tuned so that simulated NPP values agreed with observed NPP for the sagebrush and meadow communities (Singer et al. 2003). Required N inputs were higher for the meadow than the sagebrush/grass system. This is reasonable because low-lying meadows are depositional zones and they receive nutrient inputs from surface runoff and other sources.

Modeling Assumptions

Three modeling assumptions guided this process. The NER ungulate fence near Jackson was built in the 1950s to keep elk from feeding on farmland during the winter. The fence partially obstructs natural migration paths down the Valley, especially in severe winters when elk usually migrated to lower elevations down the Snake River through and beyond the town of Jackson. Thus, for simplification, we assumed that no grazing occurred on the winter range prior to the construction of the fence. Using annual Net Primary Production values measured from field data (Singer et al. 2003), we let the model reach equilibrium over a 2,900-year time-span during this no-grazing period. This assumption is reasonable because the production values were derived from elk-free enclosures on the winter range, and therefore, mimics grazed-free pre-fence production on native vegetation types.

Our second major assumption was that the ungulate fence caused artificial concentrations of elk on the winter range, and, consequently unnatural grazing levels on the grass and shrubland. This is the same assumption that applied in the Forage Accounting Model. We modeled two grazing intensities, 50% and 80%, of standing dead grass and shrub. All grazing on the most intensely grazed portions of the winter range occurs during the months of January through April, and, because the forage is dead and the ground frozen, this causes no negative impact on the next year's production.

Third, standing dead grass is poor quality forage for elk and has significantly less nitrogen content than summer grasses. One of the critical input parameters for CENTURY in a grazed system is the ratio of nitrogen excreted by the animal to nitrogen consumed. When elk consume standing dead forage, this ratio is typically $\geq$1.0. This occurs because the endogenous nitrogen lost from the animal in urine and feces exceeds the nitrogen consumed in forage. Hobbs (1996) and Mould and Robbins (1981) have calculated nitrogen levels in elk excrement in relation to forage quality. These calculations yielded 1.09 gN/day of output-to-intake for poor-quality, standing-dead forage when elk have a stable bodyweight. Additionally, when elk are eating poor quality forage in the depth of winter, they often lose weight. Thus, we also modeled a scenario where elk lost 15% of their body weight over the four-month grazing period. Weight loss causes additional nitrogen excretion from the animal's lean body mass through the urine, thereby increasing the nitrogen output/intake ratio (Hobbs 1989; D.M. Swift, Natural Resources Ecology Lab, Colorado State University, pers. comm.). When elk lose weight, we used a ratio of 1.25 gN/day of output-to-intake.

Results

In wet meadow communities, the first 50 years of the model depict the pre-grazing equilibrium scenario (Fig. 34). Beginning in year 51, when the fence was built, we simulated two levels of grazing intensity, 50% and 80%. Both grazing levels accelerated nutrient cycling and caused increases in soil carbon and net annual production (Fig. 34). The magnitude of this acceleration is proportional to grazing intensity, with greater effects occurring at 80% grazing intensity. When elk are losing weight, higher N inputs accelerate the system to an even greater extent and increased plant production leads to higher soil carbon levels.

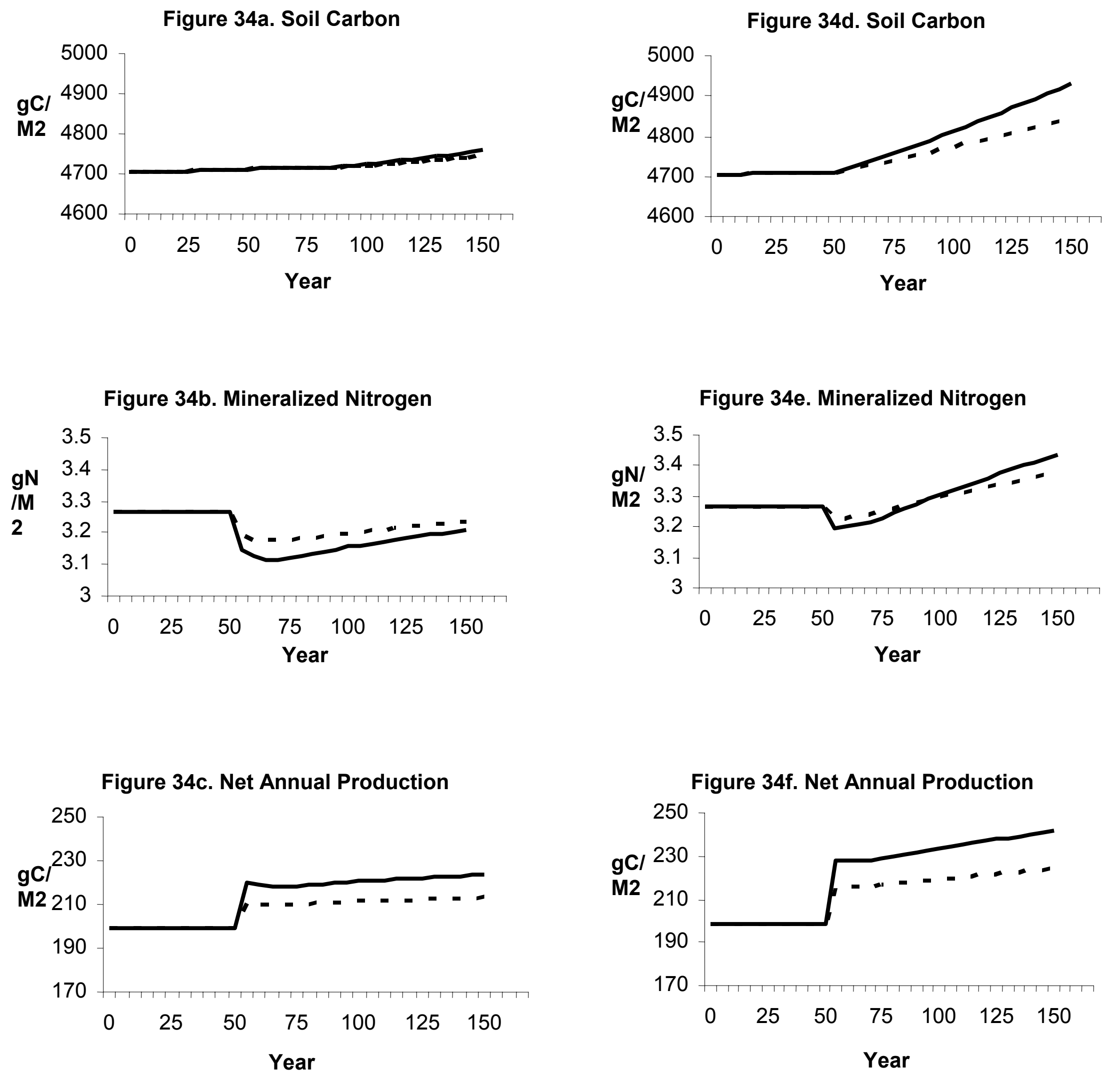

Figure 34. Carbon and nitrogen levels in wet meadow communities, predicted by the CENTURY Model for two grazing levels in the Greater Teton Ecosystem, Wyoming. The solid black line depicts 80% removal of forage and the dotted line depicts 50% removal. Figures 34a – 34c depict the "elk not losing weight" scenario. Figures 34d – 34f present the "elk losing weight" scenario.

Similarly, in sagebrush communities, the first 50 years of the model depict the pre-grazing equilibrium scenario (Fig. 35). Beginning in year 51, when the fence was built, we simulated two levels of grazing intensity, 50% and 80%. When elk were not losing weight (Fig. 35 – left), soil carbon and mineralized nitrogen remained stable or slowly declined. Net annual production initially jumped to a higher level and then stabilized over the 100-year model run. The higher level of grazing caused slightly increased production; the lower level caused stabilized production. When elk were losing weight (Fig. 35 – right), all values increased. Net annual production increased faster with the higher grazing level and when elk were losing weight. Both of these can be explained by N inputs. Because the dead forage is of such poor quality, the animals excrete more N than they extract from the system, thereby shifting carbon-nitrogen ratios in soil toward levels favoring N-mineralization. As grazing intensity increases, net N inputs to the system also increase, and when elk are losing weight the ratio of N outputs to inputs is even higher. Higher N inputs lead to enhanced mineralization, which releases more N from soil organic matter. This feedback causes increased plant growth and stable or increasing soil C levels.

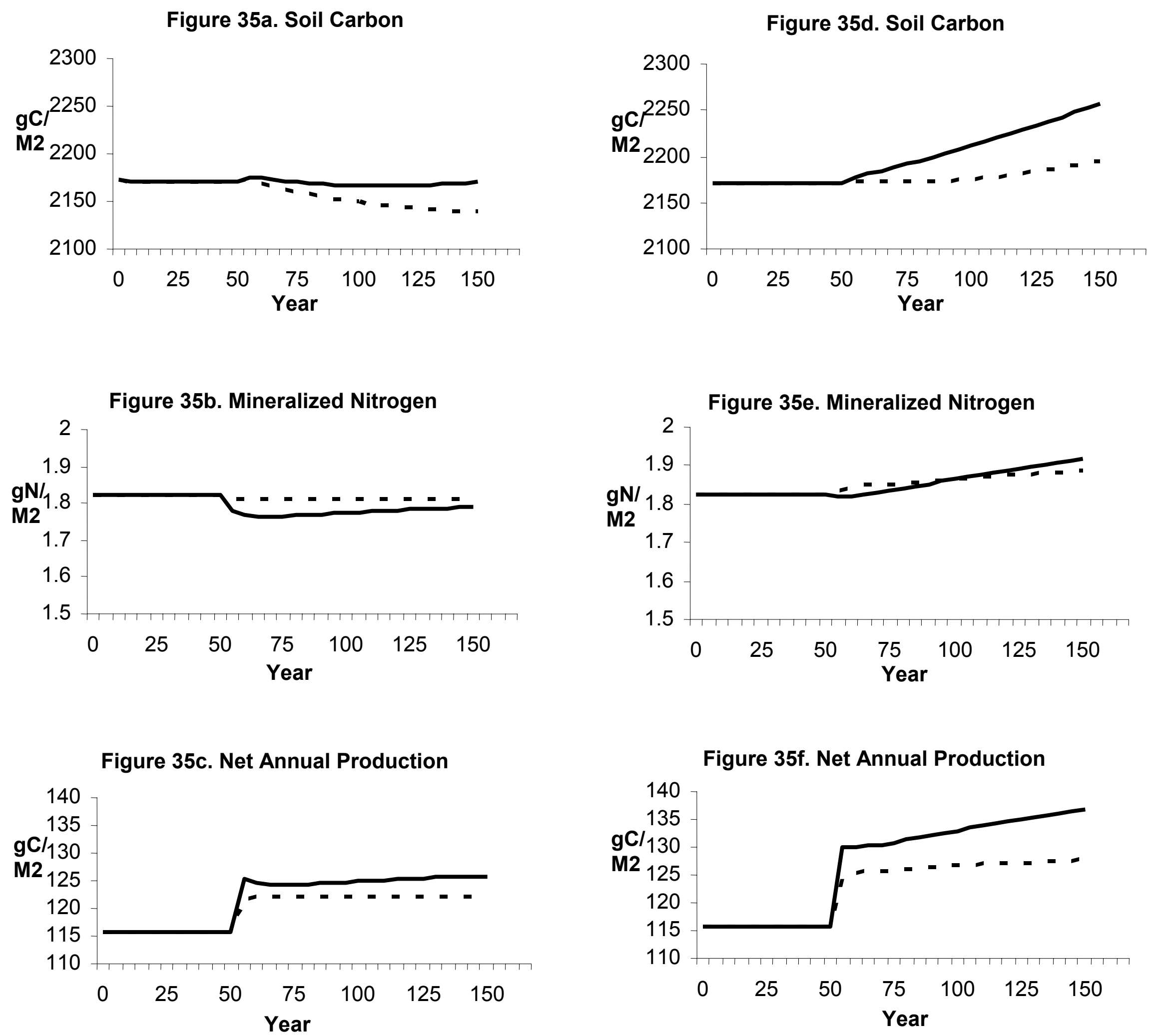

Figure 35. Carbon and nitrogen levels in sagebrush communities predicted by the CENTURY Model for two grazing levels in the Greater Teton Ecosystem, Wyoming. The solid black line depicts 80% removal of forage and the dotted line depicts 50% removal. Figures 35a – 35c depict the "elk not losing weight" scenario. Figures 35d – 35f depict the "elk losing weight" scenario.

Overall, the results in both vegetation types were similar. There is no negative effect on plant production because elk are consuming standing dead forage in the depth of winter. Furthermore, higher grazing levels will cause higher future production levels, because elk accelerate nutrient cycling by returning more nitrogen to the soil than they consume. As long as elk are concentrated at high densities on the winter range, the CENTURY model will predict positive feedbacks on production due to higher net N inputs related to grazing. The feedback is exacerbated due to low

N volatilization because of weather conditions. We presume that cold weather and snow cover keep N from volatizing into the atmosphere during winter.

These CENTURY results suggest that heavy winter-season grazing in this system, as predicted by the Forage Accounting Model, is sustainable and that soil C and nutrient levels are not significantly depleted and may increase. Nitrogen ‘hotspots’ and higher production will occur corresponding to animal density. If elk stay on the winter range longer with low-grade forage resulting in weight loss, increased nitrogen hotspots and increased future production will result. Figure 33 could also been seen as a ‘nitrogen deposition map’ wherein animals deposit nitrogen gathered throughout the entire summer range onto this limited winter area. Ongoing fieldwork by F. Singer will help corroborate these findings.

Part III.
The Over-Winter Mortality Model

Introduction

Forage deficits, predicted by the Forage Accounting Model (described in Part I), will likely cause elevated mortality in over-wintering elk populations. For this analysis, we adapted the energy balance model of Hobbs (1989) to estimate starvation mortality by simulating energy intake and expenditure by elk in four age/sex classes (calves, yearling males, adult females, bulls) during winter. The predictions of mortality provided by this model are, perhaps, more easily interpreted than the predictions of forage deficits and overuse provided by the Forage Accounting Model. However, while these interpretations may be easier to understand, they are also subject to a far greater potential for error. This is simply because the Over-Winter Mortality Model has approximately 10 times as many parameters as the Forage Accounting Model, and each of these parameters is estimated with some uncertainty. Therefore, we suggest that quantitative results of the energy balance model should be viewed with caution. However, we are confident that the qualitative trends we have observed are reasonable.

Methods

Elk populations were allocated to map cells based on snow water equivalents (SWE) under the assumption that elk use the areas of the landscape with shallow SWE in preference to areas with deep SWE, and that they will not use areas with > 6" SWE. So, during each week of the winter, we distributed the total population to map cells with SWE < 6" in order of increasing SWE (categories = 0", 1", 2"…). The number of animals assigned to a cell was determined by the available biomass of forage within that cell estimated by the Forage Accounting Model (Part I). We calculated the weekly requirements of individuals and assigned no more animals than could be supported for one week by the available biomass. We assumed that a group of elk, or sub-herd, in any given cell, had the same age/sex composition as the entire herd (proportion of calves: 0.15; yearling males: 0.05; bulls: 0.15; cows: 0.65). If a SWE-depth category of cells could support <5 elk, then only bulls were assigned to these cells. We calculated daily intake based on the average body mass of sex and age classes and their proportions in the population, assuming the body mass of a calf (age = 6 months) was 200 pounds, yearling 350 pounds, bull 675 pounds, and cow 500 pounds.

Foods were categorized into two categories; herbaceous and shrubs. We assumed that when SWE was >30 cm, shrubs comprised 100% of elk diet. If the SWE depth was in the range of 20-30 cm, the proportion of herbs in the diet increased in direct proportion to decreasing SWE. When SWE was <20 cm, the diet consisted of 100% herbs. Available foods of the cells of each SWE-depth category were updated daily by removing the amount of biomass consumed by elk.

The percentage of each elk age class that died was based on assumed average fatness and the standard deviation in fat reserves at the beginning of the winter. We assumed that 67% of pre-winter energy reserves came from fat and 33% from lean body and that the size of these reserves was a normally distributed random variable. Based on that assumption, we used the standard normal probability density function to calculate the proportion of the population that had energy reserves less than the magnitude of the energy deficits incurred during winter. We assumed that this was the proportion of each age class that starved (Hobbs 1989).

We ran simulations with initial conditions for populations set at 6,000, 12,771 and 18,000 animals for an average winter (1996), above average winter (1982), and severe winter (1997).

Results

Simulated mortality of calves ranged from a low of 4% during an average winter at a total population size of 6,000 to a high of 42% during a severe winter and a population of 18,000 (Figs. 36-38). Increasing population density was associated with increases in estimated mortality. Starvation mortality for adult cows was predicted to be 1% for a population of 6,000 animals in an average winter rising to a high of 25% for a population of 18,000 during a severe winter.

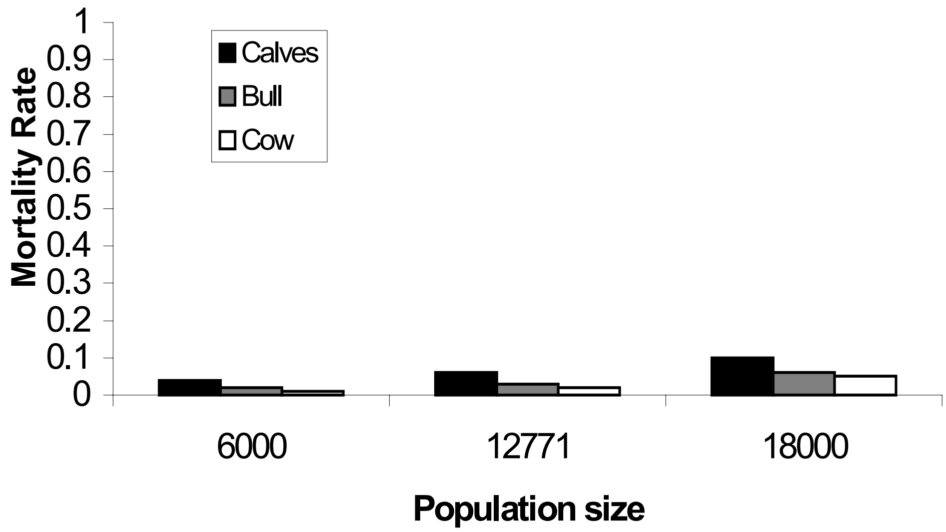

Figure 36. Predicted elk winter mortalities for the Jackson Elk Herd under different population densities assuming conditions for an average winter, such as occurred in 1996.

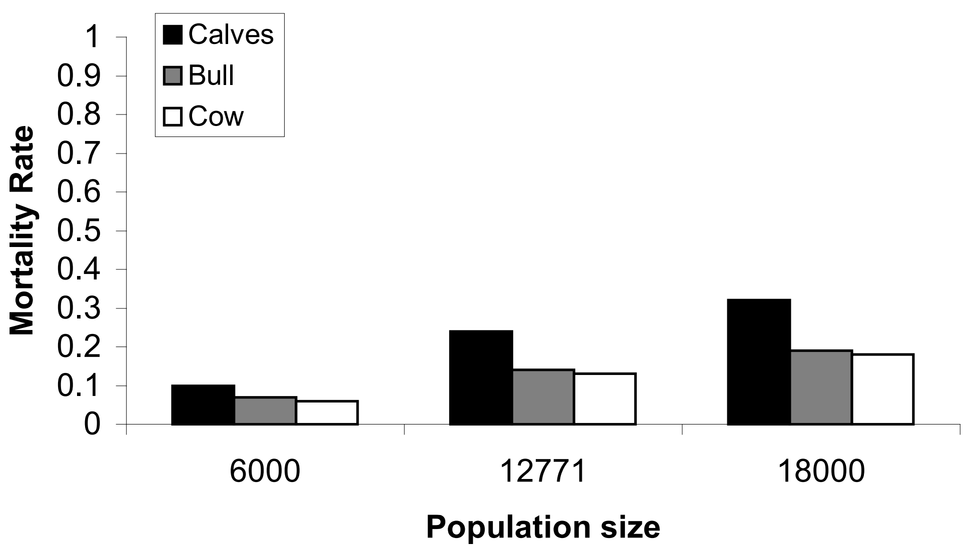

Figure 37. Predicted elk winter mortalities for the Jackson Elk Herd under different population densities in a winter of typical above-average severity, such as occurred in 1982.

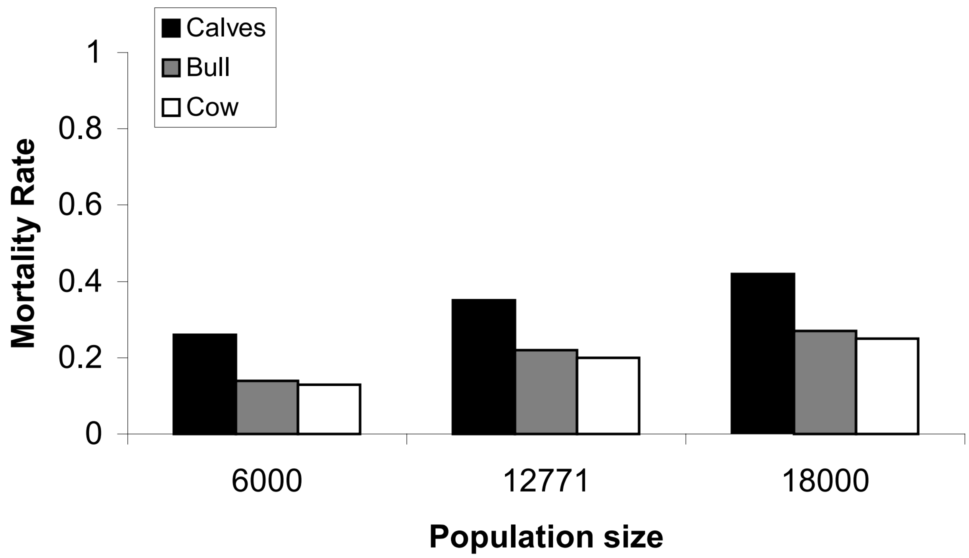

Figure 38. Predicted elk winter mortalities for the Jackson Elk Herd under different population densities under typical conditions for a severe winter, such as occurred in 1997.

Conclusions

The main implications of these three overlapping models are:

1. Forage utilization rates ≥50% will occur on the winter range at all elk population levels and during all winter severities. The area of winter range used ≥50% will increase with the elk population and winter severity. However, these high utilization rates may not negatively effect, and may even enhance, future soil fertility and plant production.

2. In average SWE winters with average pre-winter precipitation and 500 bison, roughly 16,000 elk can find forage on the Greater Teton Ecosystem without incurring forage deficits and roughly 5,000 elk can find forage on the NER without incurring deficits.

3. Winter snow has a deleterious effect on forage availability and causes critical imbalances in forage supply/demand at most elk population levels during above average and severe winters.

4. Severe drought, as occurred in 2001, reduces forage production to 45% of the mean and increases forage deficits for all winter conditions and at all elk population levels. When drought during the growing season precedes severe winters, forage deficits are extreme. In the absence of artificial feeding, high mortality of elk may be expected during these winters, possibly resembling what occurred during the winter of 1988-89 in Yellowstone National Park following both a drought and a severe winter.

5. Increasing the number of bison present has a mild effect on forage deficits on the Greater Teton Ecosystem during average winters with average pre-winter precipitation conditions, but has a more substantial effect when climatic conditions worsen. On the NER, increasing bison numbers will greatly exacerbate forage deficits and the ability of elk to find adequate forage.

6. Cattle grazing has a negligible effect on forage deficits, because most of it does not occur in areas where forage is available to native ungulates during winter.

7. Supplemental feeding overcompensates for the forage made unavailable by the NER ungulate fence. Historic elk populations: (1) were either smaller than current ones, and/or (2) may have suffered high levels of mortality during severe winters, and/or (3) likely migrated long distances to winter in lower elevation ranges along the Snake River south of Jackson and likely migrated up the Gros Ventre River drainage to winter in the Red Desert.

8. Starvation of adult animals is expected to occur at relatively low levels (about 5%) at all levels of population and winter severity, but starvation may increase to as high as 30% during severe winters when elk population levels are high (18,000).

9. Only EIS Alternative #3 has a substantial effect of restricting forage availability for elk and increasing forage deficits. Alternatives #2 and #4 have only mild effects. The EIS Alternatives manipulate three variables: bison numbers, willow availability on the NER, and irrigation of the NER's cultivated fields. The net effect on forage deficits of these three variables will be the following:

   a. Increasing bison numbers will increase forage deficits.
   b. Fencing off willow on the NER will increase forage deficits.

c. Irrigating the cultivated fields on the NER will decrease forage deficits -- center-pivot more so, flood irrigation less so.

References

Baker, D. L., and D. R. Hansen. 1985. Comparative digestion of grass in mule deer and elk. Journal of Wildlife Management 49:77-79.

Baker, D. L., and N. T. Hobbs. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Canadian Journal of Zoology 654:1978-1984.

Cordova, F. H., J. O. Wallace, and R. D. Pieper. 1978. Forage intake by grazing livestock: a review. Journal of Range Management 31:430-438.

Coughenour, M. B. 1992. Spatial modeling and landscape characterization of an African pastoral ecosystem: a prototype model and its potential use for monitoring drought. Pp. 787-810 *in* D.H. McKenzie, D.E. Hyatt and V.J. McDonald (eds.). Ecological Indicators, Vol. I. Elsevier Applied Science, London and New York.

Coughenour, M. B. 1993. The SAVANNA landscape model – Documentation and Users Guide. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.

Coughenour, M.B. 1994. Elk carrying capacity on Yellowstone's northern elk winter range - Preliminary modeling to integrate climate, landscape, and elk nutritional requirements. Pp. 97-112 *in* D. Despain (ed.). Plants and Their Environments: Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem, Mammoth Hot Springs, Sept. 1991. Technical Report NPS/NRYELL.NRTR-93/XX. USDI/NPS. Denver, CO.

Coughenour, M. B., and F. J. Singer. 1996. Yellowstone elk population responses to fire - a comparison of landscape carrying capacity and spatial-dynamic ecosystem modeling approaches. Pp. 169-180 *in* J. Greenlee (ed.). The Ecological Implications of Fire in Greater Yellowstone. International Association of Wildland Fire, Fairfield, WA.

Cromely, C. M. 2000. Historic elk migrations around Jackson Hole, Wyoming. Yale Forestry and Environmental Bulletin Series 104.

Farnes, P. E., and W. H. Romme. 1993. Estimating localized SWE on the Yellowstone Northern Range. Presented at the Joint Eastern-Western Snow Conference, Quebec City, Quebec.

Farnes, P., C. Heydon and K. Hansen. 1999. Snowpack in Grand Teton National Park and Snake River Drainage above Jackson, Wyoming. Department of Earth Sciences, Montana State University.

Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101.

Hobbs, N. T. 1996. Modification of Ecosystems by Ungulates. Journal of Wildlife Management. 60(4):695-713.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. Ecological Applications 6:200-217.

Homer, C. G. 1995. Intermountain Region: Land Cover Characterization. Metadata on CD from Utah State University.

Houston, D. B. 1982. The Northern Yellowstone elk: ecology and management. Macmillan Publishing Company, New York, New York.

Mattson, D., and D. Despain. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem. YNP document.

Meagher, M. 1973. The Bison of Yellowstone National Park. National Park Service, Scientific Monograph Series, Number One.

Metherell, A. K., L. S. Harding, C. V. Cole, and W. J. Parton. 1993. CENTURY soil organic matter model environment, Technical documentation, Agroecosystem version 4.0. Great Plains System Research Unit Technical Report No. 4. USDA-ARS, Fort Collins, Colorado.

Mould, E. D., and C. T. Robbins. 1981. Nitrogen metabolism in elk. Journal of Wildlife Management 45(2):323-334.

Parton, W. J., and P. E. Rasmussen. 1994. Long-term effects of crop management in wheat/fallow: II. CENTURY model simulations. Soil Science Society of America Journal 58:530-536.

Parton, W. J., J. M. O. Scurlock, D. S. Ojima, T. G. Gilmanov, R. J. Scholes, D. S. Schimel, T. Kirchner, J. C. Menaut, T. Seastedt, E. Garcia Moya, A. Kamnalrut, and J. L. Kinyamario. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochemical Cycles 7:785-809.

Parton, W. J., D. S. Ojima, C. V. Cole, and D. S. Schimel. 1994. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. Pp. 147-167 *in* Quantitative Modeling of Soil Forming Processes. Soil Science Society of America, Special Pub. 39, Madison, WI**.**

Schoenecker, K. A., F. J. Singer, R. S. C. Menezes, L. C. Zeigenfuss, and D. Binkley. 2002. Sustainability of vegetation communities grazed by elk in Rocky Mountain National Park. Pp. 187-204 *in* F. J. Singer and L. C. Zeigenfuss (compilers). Ecological Evaluation of the Abundance and Effects of Elk Herbivory in Rocky Mountain National Park, Colorado, 1994-1999. Final report to the National Park Service, Rocky Mountain National Park on Cooperative Agreement No. 1445-0009-94-1074 (USGS) Subagreement 2 between the National Park Service, Biological Resources Discipline of U.S. Geological Survey, and Natural Resources Ecology Lab, Colorado State University. Open File Report 02-208. 268 pp.

Singer, F. J., L.C. Zeigenfuss, B. Lubow, and M.J. Rock. 2002. Ecological evaluation of potential overabundance of ungulates in U.S. national parks: a case study. Pp. 205-248 *in* F. J. Singer and L. C. Zeigenfuss (compilers). Ecological Evaluation of the Abundance and Effects of Elk Herbivory in Rocky Mountain National Park, Colorado, 1994-1999. Final report to the National Park Service, Rocky Mountain National Park on Cooperative Agreement No. 1445-0009-94-1074 (USGS) Subagreement 2 between the National Park Service, Biological Resources Discipline of U.S. Geological Survey, and Natural Resources Ecology Lab, Colorado State University. Open File Report 02-208. 268 pp.

Singer, F. J., L. C. Zeigenfuss, M. Rock, and M. Tobler. 2003. A synthesis of data, model-based analyses, and refinements of possible management scenarios for bison and elk in the Jackson

Valley: Final report on the empirical data collection. USGS-BRD, Fort Collins Science Center, Fort Collins, Colorado. Unpublished report (in press).

Steele, R. 1983. Forest habitat types of eastern Idaho-western Wyoming. USFS Report INT-144.

Steele, V., F. J. Singer, and M. Coughenour. 1999. Percent Utilization of Vegetation in Grand Teton National Park, the National Elk Refuge and the Gros Ventre Area of Bridger Teton National Forest: Mid-Season Progress Report, USGS-BRD, Fort Collins, Colorado. Unpublished report.

Turner, M. G., L. Wallace, W. H. Romme, and A. Brenkert. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecological Applications 4(3):472-496.

U.S. Fish and Wildlife Service, National Elk Refuge. 1998. Irrigation System Rehabilitation Plan Environmental Assessment. Jackson, WY.

Zeigenfuss, L. C., F. J. Singer, M. Rock, and M. Tobler. 2001. A synthesis of data, model-based analyses, and refinements of possible management scenarios for bison and elk in the Jackson Valley. USGS-BRD, Annual Report, Fort Collins, Colorado.

Appendix A: Vegetation Production Methods

Data on annual production for each vegetation type used in the Forage Accounting Model (Table 3) were obtained from studies conducted by Biological Resources Division (BRD) – USGS, National Elk Refuge (NER) – USFWS, and Bridger-Teton National Forest – U. S. Forest Service. Each data set was collected in a different manner, therefore it was necessary to standardize the data so that they could be combined for estimating average production values.

The Bridger-Teton National Forest data were collected from 1994-1999. Sample points were randomly generated in areas of highest priority for forest management activities. As a result, less information was available on vegetation types that do not encompass areas of high management priority. Data on plant production was visually estimated in weight classes. For the purpose of estimating average production, the midpoint of the class was assigned to the sample point (Appendix C: Table C-2).

Data on dominant and codominant tree, shrub, and herbaceous species were assessed to determine the appropriate Utah State University vegetation categories for each sample. Because no data were available on forest canopy closure at the sample points, all points in forested types of a species (or species grouping) were combined. Total production was calculated by summing the midpoints for shrub, grass, and forb production.

Data from portions of the NER were collected from 1987-1999; however, data for the entire refuge existed in electronic format for 1999 only. The remainder of the 1987-1999 data was from the south end of the refuge, and as a result, some vegetation types that only occur in the north end of the refuge were only represented in 1999. Production was estimated using the Soil Conservation Service double sampling method, whereby visual estimates are made for all points on a transect in a particular vegetation type, and a sub-sample of these points is clipped and weighed to calibrate the visual estimates.

Plant productivity estimates for the BRD study were collected from 1996-1998 and were obtained by clipping, drying, and weighing vegetation in several 0.25 m^2 quadrats at several sites for each vegetation type.

Mean production values were calculated for each vegetation category in each of the data sets. Vegetation was grouped in broad categories based on dominant tree, shrub, or herb species and tested for differences between all the individual categories within these broad groups using Fisher's least significant difference test for multiple comparisons of means. Based on the results of these tests, 15 new vegetation categories were developed. The final mean production values for the new vegetation categories were calculated using all data from the three data sets. No data existed in the available data sets for three of the new categories: alpine herbaceous, alpine shrub, and disturbed/developed. Production values for the alpine categories were approximated based on work done by Marilyn Walker at the Niwot Ridge Long Term Experimental Range near Nederland, Colorado. These data were found on the Niwot LTER web site (http://culter.colorado.edu). Values for disturbed/developed areas, where irrigated and fertilized lawns are maintained, were expected to be similar to values for sub-irrigated bluegrass found in the NER and BRD data. The values estimated using these data were similar to those measured in disturbed sites in the town of Estes Park, Colorado in another study (Singer et al. 2002) and such values were therefore considered adequate.

Estimating production in wet and dry years was approached two ways. First, using annual precipitation and 30-year average precipitation values available on the web from the University of Nebraska's High Plains Climate Center (http://www.hprcc.unl.edu), several years with greater than average (1996 and 1997) and lower than average (2001, 1994, 1992, 1988) precipitation at the Jackson, Moose, and Moran weather stations were chosen. Average production values were calculated for the wet years and dry years for each vegetation category and each data set separately. Because reliable data for wet, dry, and average years were not available for all vegetation types, the percentage of mean annual production, for those types that were best represented, was calculated for each data set for both wet and dry years. These best data were then averaged to get a mean percentage of production to be applied across all vegetation types.

Dry year production ranged from 45-91% of mean annual production across the data sets with a mean of 85%. Wet year production ranged from 129-180% of mean annual production across all data sets with a mean of 150%. We chose to use 150% of average as the wet year production and 45% of average as the dry year production. We chose 45% because managers wanted a severe drought scenario based on recent 2001 precipitation.

Managers raised a question about the spatial heterogeneity of production due to varying rainfall over the study area. For example, vegetation biomass production in the sagebrush type on the NER may be different than in the sagebrush type in the Gros Ventre River Valley. We attempted to create a spatially explicit production map based on actual production measurements across the study area. However, these estimations did not yield significant spatial differences in production for each vegetation type. While we recognize that rainfall may vary across this area, and that production may vary with it, field data could not support these distinctions.

Appendix B: Snow Model Methods

The model is based on an algorithm to spatially interpolate point data, while correcting for effects of elevation. Coughenour (1992, 1993) first developed this algorithm as part of a spatially explicit ecosystem model called SAVANNA. The same algorithm was used in a landscape carrying capacity model for elk on Yellowstone's northern elk winter range (Coughenour 1994, Coughenour and Singer 1996). The first application of the model to Yellowstone was at a research conference held in Yellowstone in 1991 (Coughenour 1994). In this application, GIS maps for elevation and vegetation (developed using Grass GIS software) were read into a model to calculate snow depth, available forage for elk, and elk carrying capacity on a biweekly basis throughout the winter. The model produced output files that were read into the GRASS GIS, to produce maps of snow depth and elk carrying capacity. These output maps were presented at the 1991 conference.

At about the same time, Phil Farnes was conducting studies of snow distributions on the Yellowstone northern elk winter range (Farnes and Romme 1993). He quantified the ways that slope, aspect, and tree cover affect snow pack, as compared to measurements made on a standard, level, treeless sample site. He also developed ways to integrate data from numerous snow water sample sites into a unified database, and ways to use snow water equivalent to calculate an index of winter severity that combines stress effects of cold temperature and heavy snow on elk (Farnes et al. 1999).

The idea of combining the Coughenour model with the Farnes data into a stand-alone data model was the outcome of initial research on bison and elk carrying capacity by the two researchers in Grand Teton National Park (GTNP). Robert Schiller and Francis Singer conceived the idea for that project. Coughenour conducted preliminary SAVANNA modeling studies and Farnes collected snow data in GTNP. To create the stand-alone model, Coughenour combined his earlier elevation-based model with the slope/aspect/tree cover relationships of Farnes, to convert the snow data assembled by Farnes into maps of snow water equivalents in GTNP. Coughenour and Farnes delivered the snow data model to GTNP in 1999, at the same time Farnes delivered his unique data set (Farnes et al. 1999). Subsequently, N. T. Hobbs, F. J. Singer, G. Wockner, and L. Zeigenfuss initiated a new phase of GTNP carrying capacity research and revised the snow model for use in the Forage Accounting Model for the Jackson elk herd.

The snow model is driven by three primary sources of data; a digital elevation model (DEM), data on vegetation distribution, and point data on snow distribution. Using the DEM and the snow data, an initial grid is created using interpolation and regression. Then, this grid is readjusted for the effect of slope, aspect, and vegetation cover. Using slope and aspect, the more the cell tilts toward the sun, the more it is melted off; conversely, the more it is tilted away from the sun, the more snow accumulates. Using the vegetation data, the grid is adjusted for less snow accumulation under conifers. The bigger the trees and the denser the stand, the less snow accumulation.

Digital Elevation Model
A digital elevation model (DEM) was obtained from NREL researchers working on a similar project in the Greater Yellowstone Area. The DEM is at 30-meter accuracy and covers the entire study area. In Arcview GIS, the DEM was clipped to the study area and exported as an ASCII file for use in the snow model. The DEM was then converted into a slope grid using Arcview's "Spatial.Slope" function, and converted into an aspect grid using Arcview's "Spatial.Aspect"

function. Arcview's Spatial.Aspect command assigns the value "-1" to flat areas. Because the snow model will not read "-1"s, these areas were reassigned the value "300" which results in no multiplier being used in the snow model. These two grids were then converted into integer grids to decrease file size and then exported in ASCII format for use in the snow model.

Vegetation Data
The snow model merged three different vegetation grids. The grids were from Utah State University (Homer 1995), Grand Teton National Park, and the National Elk Refuge. Each of the three grids had relevant codes to use in the snow model. The Utah State University coverage had a code titled "canopy percent"; the GTNP coverage had a code for "forest successional stage"; and the NER coverage only had one applicable forested area. These codes were converted into codes readable by the snow model using a crosswalk table (Appendix C: Table C-4). We assumed dense conifer stands would result in less snow on the ground under those stands, therefore an adjustment is made by the snow model when estimating snow cover in Lodgepole Pine, Subalpine Pine, Douglas Fir, and Englemann Spruce. This adjustment is a multiplier that decreases SWE based on the size of the trees and the density of the stand.

Snow Data
The model interpolates the snow station data provided by Farnes. Several types of data are available in the Jackson Valley including snow courses, SNOTEL sites (an extensive, automated network of sites administered by the Natural Resources Conservation Service to collect snowpack and related climatic data in the Western United States), and climatological stations. In addition, Farnes collected monthly data at over 75 stations beginning in water-year 1996. After the large study area was chosen, snow stations within that area were identified. The snow model incorporates data from six long-term stations that have daily data beginning by 1980, and uses monthly data (Feb, Mar, Apr) from 56 additional stations, primarily in the Jackson Valley. Snow sampling locations are shown in Figure 1 (Part I.). The snow model also requires a file containing UTM location and elevation of each station. This data was taken from the DEM by overlaying the snow station locations on the DEM and assigning the elevation attribute of the DEM to each station.

The six long-term stations ranged from the highest, Togwotee Pass--9580 feet, to the lowest, Jackson--6230 feet. The other four stations were: Moose--6468 feet, Moran--6798 feet, Base Camp--7030 feet, and Phillips Bench--8200 feet. The 56 additional stations contained monthly data collected February, March, and April 1st in 1996, 1997, and 1998. The names, locations, and elevations of all stations are listed in Appendix C: Table C-5.

Data at the six daily sites existed from water-year (WY) 1980 to present. Because WY 1981 had one of the lowest SWEs on record and WY 1997 had one of the highest (Farnes et al. 1999), a 20-year (1980-1999) stretch of time provided ample variability for useful modeling. At the time of this report, 1999 was the last year of data processed by Farnes and Heydon that was available for analysis.

We modeled snow through the entire winter--roughly November 1st to July 1st. This required year-round daily data estimates for all 19 years for the 56 stations where data were only collected on February, March, and April 1st of 1996-1999. We developed a regression technique to estimate the missing data at these sites. Because snow varies due to elevation and location throughout the study area, each of the original daily stations could be used as independent variables in a regression function to predict the missing data at the monthly sites. This process was carried out with these steps:

1. We assembled a matrix of data in S-plus statistical software that contained SWE on Feb, Mar, and Apr 1st in 1996, 1997, and 1998 at all 62 locations. These 9x62 data points contained measured SWE at all locations.
2. A correlation matrix was constructed to determine which of the independent daily stations would serve as best predictors for the dependent monthly stations.
3. Using this matrix, and a more subjective analysis of snow patterns and elevations, a table was constructed which divided the six daily stations into three groups. Group 1 contained Jackson, Group 2 contained Moose and Moran, and Group 3 contained Base Camp, Phillips Bench, and Togwotee Pass. Each monthly station was assigned to one of these three groups. There were roughly three snow patterns in all the data. The first contained sites that increased on March 1st and then melted to "0" or near "0" on April 1st. The second contained sites that increased on March 1st and decreased on April 1st but not to near "0". The third consisted of sites that increased on March 1st and then increased again on April 1st. The assignment appears in Appendix C: Table C-6.
4. A regression equation was developed in S-plus using stepwise linear regression with "0" as the Y-intercept for each of the 56 monthly stations from the independent predictors in each group. This particular method was developed after several attempts at using other regression methods and switches. Forcing the Y-intercept to "0" provided the best fit of the data at the tails of the curves. (The output -- r^2, equations, etc -- is available for review). In these cases, we used the predictor site with the highest correlation, despite the lack of significance. Additionally, a few of the regressions did not yield a significant relationship with any predictor site.
5. These regression equations were pasted into an Excel spreadsheet that contained the daily data for the six stations. Daily data were then predicted for the 56 monthly stations.
6. The predicted versus observed values were compared for Feb, Mar, and Apr 1st 1996-8, for the 56 dependent variables. Predictions were very good. (This output is also available for review).

After the process was completed, Farnes pointed out that Gros Ventre Summit is a long-term daily site rather than a supplemental site. Its daily data were located on a disk from Coughenour and substituted for the predicted data. Because its snow pattern is similar to Togwotee Pass, Phillips Bench, and Base Camp, we saw no need to rerun the regressions that used those sites. Thus, there are seven long-term stations, and 55 supplemental sites used in the final snow model.

With the predicted daily data for all 62 stations over the 20-year time span, the snow model allows us to run a simulation of SWE for any day of the snow-year during those 20 years. The primary output of that model is an ASCII file with SWE for each of the cells in the original input grids. Additional output includes a fit-comparison of observed versus predicted SWE at each site, and a file containing r^2, slope, and intercept of the regression function used in the model.

The output ASCII file was imported into Arcview and converted to a grid for visual inspection. The grid was then smoothed twice with a 5x5 filter using Arcview's "FocalStats" function. This smoothing is recommended by Coughenour and causes most of the banding and striping remnant from the DEM to disappear. Adjusting the legends to create any SWE threshold provides the needed visual reference for the migratory switch used in the forage utilization model. A dynamic snow map was also created which visually steps through the winter on a weekly basis in 1997, 1998, and 1999.

Although SWE grids currently begin when depth hits 2 inches, they can be generated anytime snow is present. Grids were modeled four times per month for each snow-water-year on the 1st, 8th, 15th, and 23rd. Grids were begun when SWE was ≥2” at any station and continued until SWE was <2”. The earliest occurrence was October 15th; the latest was July 15th. Grids have a 30-meter pixel size and have 1851 rows and 2425 columns for a total of 4,488,675 cells.

The Gros Ventre River Valley Snow Correction

At meetings in Jackson in August 2000, it was agreed that the snow model over-estimated SWE in the Gros Ventre River Valley because it did not account for the snow shadow effect downwind of the Tetons. This effect was not detected in the available data used to calibrate the snow model because there were no daily or supplemental sites for the Gros Ventre River Valley, the closest being Gros Ventre Summit. To test the theory that the snow model was, indeed, overestimating SWE in the Gros Ventre drainage, Farnes' team used supplemental SWE data collected in the Gros Ventre River drainage during the winter of 2000. Two dates, February 1st and March 1st, provide enough data points to feed the snow model and check its results. The model was run using all the data for those two dates and the results were discussed with Farnes at a meeting in Fort Collins in October 2000.

Although these supplemental data provided a different snow picture than the previous modeling, it is not clear how well data from WY2000, which had very light snow, represents a typical year. In particular, the predictions at Darwin Ranch in the Gros Ventre River Valley were well below the actual measurements. Also, the correction provided a broad and sharp SWE reduction over vast areas in the Gros Ventre River drainage. During a meeting in October 2000, Farnes described different data, not yet analyzed, from snow stations at Darwin Ranch and from the feedgrounds in the Gros Ventre River Valley (Alkali, Patrol Cabin, and Fish Creek Feedgrounds) collected by the U. S. Forest Service. These data were sent to Fort Collins in late November 2000 and fed into the snow model and to be used in two ways. First, we checked the WY2000 snow correction map against these dates, and found that the WY2000 correction was indeed overcorrecting, especially at Darwin Ranch. Because the new data covered 1996-1998, they provided measurements from deeper snow years. Second, we substituted these data into the snow model and made a new correction map. At a meeting in December 2000 with Hobbs, Singer, Zeigenfuss, and Wockner, we decided that this newest correction provided the best estimate. Not only did predicted/observed measurements match better at all sites, but it also provided the needed correction for the snow shadow in the Gros Ventre River Valley while leaving the higher elevations with greater snow. The model and the correction were run on several dates, and all provided a reasonable fit.

Maps of snow model projections on January 14, 1998 both before (Fig. B-1) and after (Fig. B-2) including the new data, clearly depict that the new data provide a very different SWE picture for the Gros Ventre River Valley. The results for several other dates are not shown here but have the same pattern. Figure B-3 is the actual correction map; the details of its creation are below.

Creating the Gros Ventre River Valley Snow Shadow Correction Map

The correction map was created using these steps:

1. Run the snow model with and without the Gros Ventre River drainage data for 12/20/1996 and 01/14/1998. These two dates were picked because they had the highest SWE of the additional dates. Because the larger carrying capacity model is driven by depth-of-winter forage needs in above average snow winters, these highest SWE dates provide the best estimation of severe conditions.
2. Calculate multipliers for each point in the grid as the ratio of the model estimated SWE with the Gros Ventre data to the value estimated without the Gros Ventre data.

Thus, if the 'before' SWE grid had a cell that was "7" and 'after' was "4", then a new grid is created with the "multiplier" of "0.5714" in that cell.

3. Average the "multiplier grids" from the two different dates to best take advantage of the temporal data, thus creating an "average multiplier grid."
4. Define a geographic area around the Gros Ventre River Valley in which SWE are measurably different in the "before" and "after" grids and select out the "average multiplier grid" in this area. This area was defined as the Gros Ventre watershed from GIS coverage.
5. Create a final "correction grid" in which all cells in the broader study area are "1" and the Gros Ventre River Valley selection area has the value of the "average multiplier grid."

Finally, in the Forage Accounting Model loop, the SWE grid will be multiplied by the "correction grid." The SWE values will be retained in all areas except the Gros Ventre River Valley, which will be adjusted accordingly.

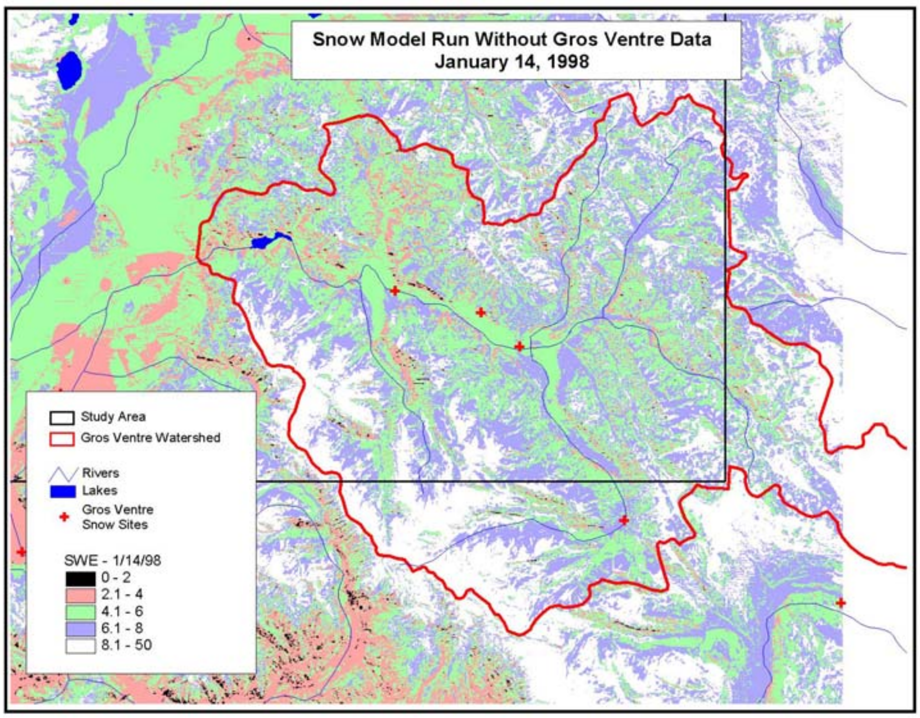

Figure B-1. Predicted snow water equivalents (inches) based on a snow model simulation on January 14, 1998 without specific snow data from the Gros Ventre River Valley, Wyoming.

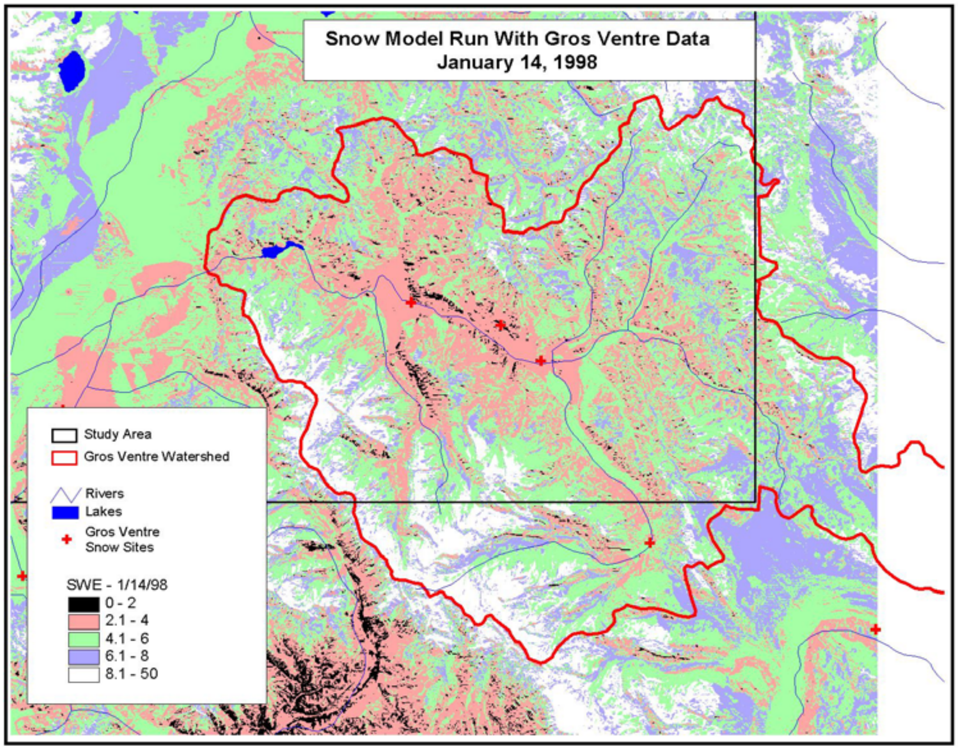

Figure B-2. Predicted snow water equivalents (inches) based on a snow model simulation on January 14, 1998 with specific snow data for the Gros Ventre River Valley, Wyoming.

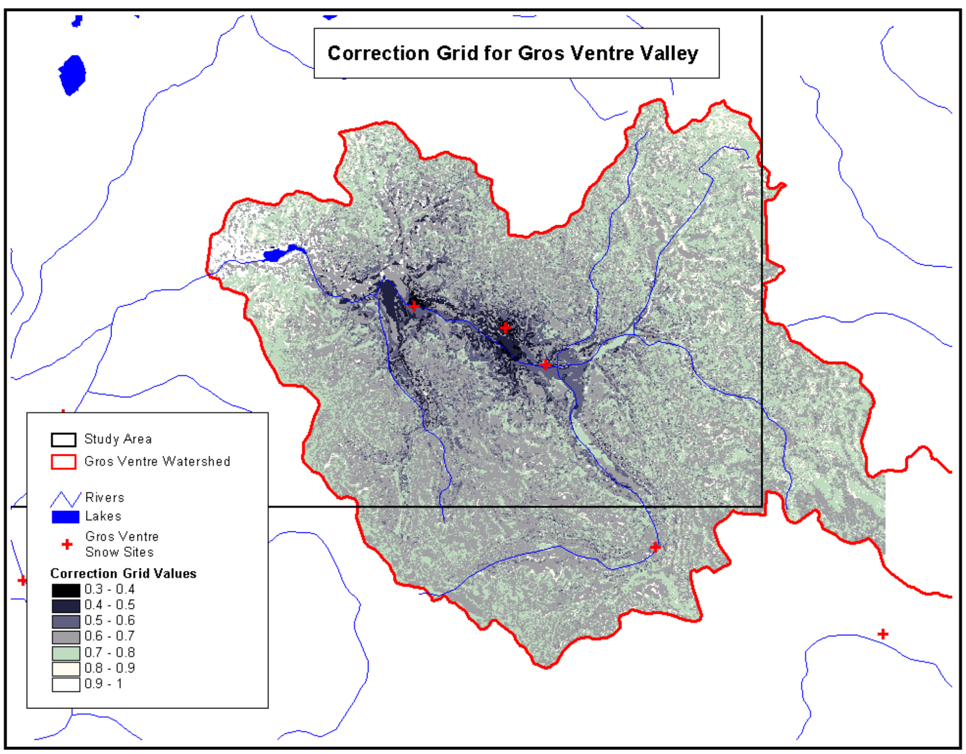

Figure B-3. Correction grid used in the snow model to correct for overestimates of snow accumulation in the Gros Ventre River Valley, Wyoming. These overestimates occurred because a snow shadow downwind of the Teton Range causes decreasing snowfall to the east of the Range and the snow model did not account for this.

Appendix C: Tables

Table C-1. Crosswalk table created to merge and reclassify three vegetation coverages from Utah State University, the National Elk Refuge, and Grand Teton National Park, into one coverage with 15 categories that we used in our forage accounting model for the Greater Teton Ecosystem, Wyoming.

Utah State University			NER		GTNP		Our Model	
CODE	COVER_TYPE	Canopy	CODE	COVER_TYPE	CODE	COVER_TYPE	CODE	COVER_TYPE
	Conifer Trees			**Woodlands**		**Trees (successional stage)**		**Trees**
1	alpine fir	<30%					**1**	Spruce-fir
2	alpine fir	30-59%						
3	alpine fir	>59%						
8	alpine fir/lodgepole pine	30-59%						
9	alpine fir/lodgepole pine	>59%						
10	alpine fir/spruce	<30%			40	Spruce-Fir(0)		
11	alpine fir/spruce	30-59%			41	Spruce-Fir(1)		
12	alpine fir/spruce	>59%			42	Spruce-Fir(2)		
46	spruce, englemann	30-59%			43	Spruce-Fir(3)		
47	spruce, englemann	>59%			44	Spruce-Fir(4)		
14	alpine fir/whitebark	30-59%						
16	doug fir	<30%			20	Douglas-Fir(0)	**2**	Douglas Fir
17	doug fir	30-59%			21	Douglas-Fir(1)		
18	doug fir	>59%			22	Douglas-Fir(2)		
					23	Douglas-Fir(3)		
					24	Douglas-Fir(4)		
23	doug fir/lodgepole pine	30-59%	21	*Pseudotsuga menziesii-Pinus contorta*				
5	alpine fir/doug fir	30-59%						
6	alpine fir/doug fir	>59%						
32	juniper, utah	30-59%	20	*Juniperus scopulorum-Agropyron*	64	Open_Woods/Juniper		
67	maple	>59%						
70	mountain mahogany	30-59%						
71	mountain mahogany	>59%						
37	lodgepole pine	<30%			31	Lodgepole_Pine(1)	**3**	Subalpine Pine
38	lodgepole pine	30-59%			32	Lodgepole_Pine(2)		
39	lodgepole pine	>59%			33	Lodgepole_Pine(3)		
					34	Lodgepole_Pine(4)		
40	lodgepole sapling	>59%			30	Lodgepole_Pine(0)		
48	subalpine pine	<30%			50	Whitebark(0)		
49	subalpine pine	30-59%			51	Whitebark(1)		
64	aspen/conifer	30-59%			52	Whitebark(2)		
					53	Whitebark(3)		
					54	Whitebark(4)		
52	doug fir/limber pine	30-59%						
60	aspen	<30%	16	*Populus tremuloides- Calamagrostis rubescens*	70	Aspen(0)	**4**	Aspen
61	aspen	30-59%	17	*Populus tremuloides-Symphoricarpus*	71	Aspen(1)		
62	aspen	>59%	18	*Populus tremuloides -Salix*	72	Aspen(2)		
			19	*Populus tremuloides - Pseudotsuga*	73	Aspen(3)		
					74	Aspen(4)		

Utah State University			NER		GTNP		Our Model	
CODE	COVER_TYPE	Canopy	CODE	COVER_TYPE	CODE	COVER_TYPE	CODE	COVER_TYPE
111	decidious tree riparian		22	*Populus angustifolia-Poa*	90	Cottonwood(0)	**5**	Riparian Forest
			23	*Populus angustifolia –Artemisia tridentata*	91	Cottonwood(1)		
			24	*Populus angustifolia* –Mixed shrub	92	Cottonwood(2)		
			25	*Populus angustifolia* –deciduous shrub	93	Cottonwood(3)		
					94	Cottonwood(4)		
112	riverine riparian				81	Mixed_Forest(1)		
					82	Mixed_Forest(2)		
					83	Mixed_Forest(3)		
					84	Mixed_Forest(4)		
	Shrubs			**Shrublands**		**Shrubs**		**Shrubs**
75	big sagebrush		9	*Artemisia tridentata -Poa* (on flats)	13	Dry_Sagebrush	**6**	Sagebrush
			10	*Artemisia tridentata - Artemisia tripartita* (grass on slopes)				
			15	*Artemisia tridentata- Bromus*				
82	mountain big sage				12	Moist_Sagebrush/Cinquefoil		
					15	Moist_Sagebrush		
114	shrub riparian		12	*Salix/Carex*	11	Tall_Shrub	**7**	Shrub Riparian/Willow
			13	*Salix/Bromus*	14	Low_Willow		
					81	Tall_Shrub (>7400')		
			5	Subirrigated *Poa*				
113	herbaceous riparian							
81	montane shrub		14	*Symphoicarpos-Rosa*			**8**	Montane Shrub
76	bitterbrush							
77	burn shrub							
80	low sagebrush							
83	mountain low sage							
86	silver sage				57	Shrub-dominated_Avalanche_Chute		
	Herbaceous			**Grassland**		**Grasses**		**Grasses**
87	alpine shrub				63	Krumholtz		
90	alpine herbaceous				34	High_Elevation_Grassland	**9**	Alpine Herbaceous/Shrub
					51	Tundra		
92	burn herbaceous						**10**	Dry Montane Meadow/Grassland
93	clearcut herbaceous							
94	dry meadow		7	*Agropyron-Stipa* (Gros Ventre hills and slopes)	24	Dry_Forb_Meadow		
					74	Dry_Forb_Meadow (>7400')		
95	perennial grass		6	*Agropyron- Poa* (on flat)				
96	perennial grass slope		8	*Agropyron /Poa* (Miller Butte)	35	Dry_Grassland/Meadow		
97	perennial grass montane				42	Dry-Moist_Forest_Opening		
					33	Moist_Grassland/Meadow		
					73	Moist_Grassland/Meadow (>7400')		
98	tall forb montane				21	Forb_Dominated_Seep		
					22	Wet_Forb_meadow		
					82	Wet_Forb_Meadow (>7400')		
					23	Moist_Forb_Meadow		
					58	Graminoid/Forb-dominated_Avalalanche Chute		
99	wet meadow		11	*Potentilla fruticosa/Carex*	32	Wet_Meadow	**11**	Wet Meadow
					72	Wet_Meadow (>7400')		
					41	Wet_Forest_Opening		
	Wetland			**Wetlands**		**Wetland**		**Wetland**

Utah State University			NER		GTNP		Our Model	
CODE	COVER_TYPE	Canopy	CODE	COVER_TYPE	CODE	COVER_TYPE	CODE	COVER_TYPE
120	deep marsh						**12**	Wetland/Sedge Marsh
121	shallow marsh		3	CattailL/ (*Typha scirpus*)	71	Marsh/Fen (>7400')		
			4	*Carex-Juncus*	31	Marsh/Fen		
122	aquatic bed							
123	mud flat							
	Miscellaneous			**Other**		**Other**		**Other**
107	water		1	Pond	55	Water_Body	**13**	Water/Rock/Snow
			2	Stream	54	Water_Course		
101	barren				56	Cliff		
104	rock				52	Bedrock		
					53	Talus		
108	snow							
	Land-use			**Cultivated Fields**		**Agricultural**		**Agricultural**
126	agricultural		26	*Bromus inermis -Medicago sativa*	59	Agricultural	**14**	Agricultural
			27	*Bromus inermis* –Mixed grass				
			28	*Elymus junceus*				
			29	*Elymus cinereus*				
			30	*Poa pratensis*				
			31	*Agropyron* -Mixed grass				
			32	*Alopecurus arundinaceus*				
			33	*Phleum pratense-Poa*				
			34	*Agropyron intermedium*				
			35	*Agropyron elongatum*				
129	disturbed, high						**15**	Developed/disturbed
130	disturbed low							
131	urban, high density				60	Human_Development		
132	urban, low density							

Table C-2. Conversions of U.S. Forest Service production classes to forage production estimates for vegetation categories used in the forage accounting model for the Greater Teton Ecosystem, Wyoming.

Class	Production range (lbs/acre)	Midpoint used for analysis (lbs/acre)
0	No production	0
1	1-50	25
2	50-300	175
3	300-500	400
4	500-750	625
5	750-1200	975
6	1200-2500	1850
7	2500-4000	3250
8	4000+	6000

Table C-3. Estimates of forage offtake by three ungulate species at varying population levels in the Greater Teton Ecosystem, Wyoming.

Species, Sex, and Age Class	Number of Animals	Average Weight (lbs)	Total Animal Pounds	Daily Offtake	Weekly Offtake	Elk % of Total
			Actual numbers Year 2000 -- 12,771 elk			
Elk						
Juveniles	1,915	200	383,000			0.1499491
Yearlings	646	350	226,100			0.0505834
Adults (F)	8,354	500	4,177,000			0.6541383
Adults (M)	1,856	675	1,252,800			0.1453293
Total	12,771	1,725	6,038,900	120,778	905,835	
Moose						
Calves	162	200	32,400			
Cows	466	700	326,200			
Bulls	261	1,300	339,300			
Total	889	2,200	697,900	13,958	104,685	
Bison						
Calves	50	350	17,500			
Yearlings	100	600	60,000			
Cows	150	1,350	202,500			
Bulls	200	2,000	400,000			
Total	500	4,300	680,000	13,600	102,000	
			Total Weekly Offtake		**1,112,520**	
			With 6,000 Elk			
Juveniles	900	200	179,938			0.1499491
Yearlings	304	350	106,225			0.0505834
Adults (F)	3,925	500	1,962,414			0.6541383
Adults (M)	872	675	588,583			0.1453293
Total	6,000	1,725	2,837,162	56,743	425,574	
Moose						
Calves	162	200	32,400			
Cows	466	700	326,200			
Bulls	261	1,300	339,300			
Total	889	2,200	697,900	13,958	104,685	
Bison						
Calves	50	350	17,500			
Yearlings	100	600	60,000			
Cows	150	1,350	202,500			
Bulls	200	2,000	400,000			
Total	500	4,300	680,000	13,600	102,000	
			Total Weekly Offtake		**632,259**	

Table C-4. Crosswalk table used to relate vegetation categories in forested vegetation types for three vegetation coverages to the snow model used to estimate winter forage availability to ungulates in the Greater Teton Ecosystem, Wyoming.

Vegetation Type	Percent Cover (Successional Stage)	Snow Model Code
Utah State University		
alpine fir	<30%	21
alpine fir	30-59%	22
alpine fir	>59%	24
alpine fir/Douglas fir	30-59%	22
alpine fir/Douglas fir	>59%	24
alpine fir/lodgepole pine	30-59%	22
alpine fir/lodgepole pine	>59%	24
alpine fir/spruce	<30%	21
alpine fir/spruce	30-59%	22
alpine fir/spruce	>59%	24
alpine fir/whitebark	30-59%	22
Douglas fir	<30%	41
Douglas fir	30-59%	42
Douglas fir	>59%	44
Douglas fir/lodgepole pine	30-59%	42
lodgepole pine	<30%	33
lodgepole pine	30-59%	31
lodgepole pine	>59%	32
lodgepole sapling	>59%	30
spruce, Englemann	30-59%	22
spruce, Englemann	>59%	24
subalpine pine	<30%	51
subalpine pine	30-59%	52
Douglas fir/limber pine	30-59%	42
aspen/conifer	30-59%	34
GTNP		
Lodgepole Pine	(0)	30
Lodgepole Pine	(1)	31
Lodgepole Pine	(2)	32
Lodgepole Pine	(3)	33
Lodgepole Pine	(4)	34
Spruce/Fir	(0)	20
Spruce/Fir	(1)	21
Spruce/Fir	(2)	22
Spruce/Fir	(3)	23
Spruce/Fir	(4)	24
Douglas Fir	(0)	40
Douglas Fir	(1)	41
Douglas Fir	(2)	42
Douglas Fir	(3)	43
Douglas Fir	(4)	44
Whitebark Pine	(1)	50
Whitebark Pine	(2)	51
Whitebark Pine	(3)	52
Whitebark Pine	(4)	53
Whitebark Pine	(5)	54
NER		
Pseudotsuga menziesii/Pinus contorta		32

Table C-5. Location and elevation of snow sampling sites used to create a snow model for the Greater Teton Ecosystem, Wyoming.

Site #	Elevation (meters)	UTM east	UTM north	Site Name
1	1895	519300	4814300	Jackson
2	1966	522900	4833400	Moose
3	2075	533100	4855800	Moran
4	2148	544800	4865500	Basecamp
5	2574	508200	4818100	Phillips bench
6	2900	575000	4844600	Togwotee pass
7	1974	519180	4831640	Boys Ranch
8	1973	518910	4831620	Death Canyon
9	1955	518330	4830630	R Lazy S
10	1962	517360	4829690	Wilson Road
11	1965	522980	4833440	Moose W.S.
12	2017	521470	4836720	Beaver Creek
13	1986	524570	4834260	Blacktail Butte
14	2092	531120	4844660	Deadman's Bar Rd
15	2072	536830	4848150	Moosehead Ranch
16	2047	539250	4852900	N. Elk Ranch
17	2048	539180	4854300	Buffalo R.S.
18	2056	536480	4856860	Oxbow Bend
19	2092	544870	4853780	Buffalo Valley R
20	2083	545740	4854830	Road 30083
21	2107	546590	4855490	Buffalo Run
22	2072	548180	4853110	KOA Picnic Area
23	2100	552210	4852300	Black Rock R.S.
24	2013	527170	4834620	Antelope Flat
25	2067	529600	4835550	Mailbox Corner
26	2046	529620	4837780	Schwering Studio
27	2108	531930	4834670	Lobo Hill
28	2026	530450	4829060	Highlands Jct
29	2024	528200	4828730	Highlands Loop
30	1958	521490	4827770	Airport
31	1976	524720	4827510	Gros Ventre River
32	1939	521550	4823160	Gros Ventre Turn
33	1900	521580	4820200	Fish Hatchery
34	1895	519420	4814490	Jackson W.S.
35	1908	520480	4814080	NER HQS
36	2044	522090	4839860	Lupine Meadows
37	2099	522290	4847720	Jenny Lake Lodge
38	2115	524050	4848370	N. Jenny Lake Jct
39	2098	530950	4852040	Sewage Ponds
40	2065	520700	4857000	Moran Bay SC
41	2102	533860	4860760	Pilgrim Creek
42	2084	529440	4861970	Coulter Bay
43	2070	529790	4835310	Hunter Hay WE
44	2100	530990	4835510	Hunter Hay NS
45	1977	522120	4834280	Bar BC Road
46	2023	523420	4838230	Bar BC Road B
47	2022	523920	4838180	Bar BC Mid

Site #	Elevation (meters)	UTM east	UTM north	Site Name
48	1983	524770	4837980	Bar BC FP
49	2025	523020	4838280	Bar BC Mid RD
50	2094	531450	4851700	RKO Road Flats
51	2095	536450	4859500	RKO PL
52	2040	535500	4851200	RKO Willow Flat
53	1938	513860	4825940	Ski Area Base
54	1954	511080	4820820	Phillips Canyon
55	2138	532700	4835100	Elbo Ranch
56	2393	558800	4852100	Four Mile Meadows
57	2106	558200	4856100	Turpin Meadows
58	2668	570500	4804200	Gros Ventre Summit
59	2312	519600	4811900	Snow King Mountain
60	2243	525000	4876800	Huckleberry Divide
61	2150	521100	4882800	Glade Creek
62	2456	502700	4816300	Teton Pass W.S.

Table C-6. Station assignment for regression function correlating daily weather monitoring stations (predictor stations) with monthly monitoring stations (predicted stations) in the Greater Teton Ecosystem, Wyoming. The regression functions were used to determine snow patterns in the snow model developed to predict forage availability to ungulates.

Predictor Stations	Predicted Stations
Jackson	Buffalo Valley Road, Fish Hatchery, Jackson W.S., NER H.Q.
Moose, Moran	Death Canyon, Boys Ranch, Wilson Road, R Lazy S, Buffalo R. S., Moose W.S., Beaver Creek, Blacktail Butte, Deadman's Bar, Moosehead Ranch, N. Elk Ranch, Road 30083, Buffalo Run, KOA campground, Blackrock, Antelope Flat, Mailbox, Schwering Studio, Lobo Hill, Oxbow Bend, Highlands Jct., Highlands Loop, Airport, Gros Ventre River, Gros Ventre Turnout, Lupine Meadows, Sewage Pond, Pilgrim Creek, Coulter Bay, Hunters Hayfield WE, Hunters Hayfield NS, Bar BC Road, Bar BC Road B, Bar BC Mid, Bar BC FP, Bar BC Mid Road, RKO Road Flats, RKO PL, RKO Willow Flat, Ski Area Base
Base Camp, Phillips Bench, Togwotee Pass	Jenny Lake Lodge, N. Jenny Lake Jct., Moran Bay S.C., Phillips Canyon, Snow King Mountain, Huckleberry Divide, Glade Creek, Teton Pass W.S., Gros Ventre Summit