

**Bison and Elk in Yellowstone National Park -  
Linking Ecosystem, Animal Nutrition,  
and Population Processes**

**Part 2 - Final Report to  
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**Project:  
Spatial-Dynamic Modeling of Bison Carrying Capacity  
in the Greater Yellowstone Ecosystem:  
A Synthesis of Bison Movements, Population  
Dynamics, and Interactions with Vegetation**

**Michael B. Coughenour  
Natural Resource Ecology Laboratory  
Colorado State University  
Fort Collins, Colorado**

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## INTRODUCTION

Over the last three decades bison in Yellowstone National Park have increased in numbers and expanded their ranges inside the park up to and beyond the park boundaries (Meagher 1989a,b, Taper et al. 2000, Meagher et al. 2003). Potentially, they have reached, if not exceeded the capacity of the park to support them. The bison are infected with brucellosis, and it is feared that the disease will be readily transmitted to domestic cattle, with widespread economic repercussions. Brucellosis is an extremely damaging disease for livestock, causing abortions and impaired calf growth. After a long campaign beginning in 1934 and costing over \$1.3 billion (Thorne et al. 1991), brucellosis has been virtually eliminated from cattle and bison everywhere in the conterminous United States except in the Greater Yellowstone Ecosystem. Infection of any livestock in Montana, Idaho, or Wyoming would result in that state losing its brucellosis-free status, leading to considerable economic hardships resulting from intensified surveillance, testing, and control (Thorne et al. 1991). Management alternatives that have been considered include hazing animals back into the park, the live capture and holding of animals that leave the park, and culling or removal from within the park. The management policy that was adopted includes testing of animals as they leave the park, killing infected ones, and holding uninfected ones up to the capacities of the holding facilities (National Park Service 2000). Above a threshold number of total bison in the park, all emigrating bison may be killed. This number is currently set to minimize risk of movement beyond the park boundary, rather than being based on any estimate of ecological carrying capacity. Nevertheless, a central question for setting wildlife and disease management policies is whether the bison have reached or will reach ecological carrying capacity (Cheville et al. 1998). Ecological carrying capacity (ECC) has been defined as the number of herbivores that is in dynamic equilibrium with the forage base (Caughley 1976, 1979). However ECC is influenced by several interacting processes including forage production, habitat utilization, foraging and diet selection, and energy utilization. An ECC has not been determined for the Yellowstone bison.

Prior to 1968 bison numbers were apparently managed to prevent overpopulation and overgrazing, but it is difficult to ascertain what the scientific basis was for determining appropriate population sizes. Three bison herds were recognized prior to 1968: a herd that wintered mainly in Pelican Valley; the Mary Mountain herd that wintered in the Hayden and Firehole River Valleys; and a northern herd that wintered in the Lamar River Valley (Meagher 1973). An early estimate of forage-based carrying capacity for the Lamar herd was 1000 bison (Rush 1932). The Lamar herd was maintained at 600-800 from 1936 to 1943, but a series of management actions from 1943-1954 reduced to herd to 148 and it was kept between 66 and 212 animals by occasional reductions from 1955 to 1965. It is unclear if there was any attempt to estimate the carrying capacity of the Mary Mountain herd, but managers were apparently alarmed by the rapid increase in herd size from 340 in 1948 to 858 in 1954. Large reductions of the Mary Mountain herd were subsequently carried out in 1955-1957, resulting in a total removal of about 1000 animals. The Mary Mountain herd was managed to 76-488 animals from 1957-1968. There were only two small management reductions of the Pelican herd, in 1956 and 1965. In all, total bison numbers in Yellowstone N.P. were reduced from a high of 1477 in 1954, to 366 in 1966.

The population grew steady between 1968 and 1994 despite a few removals after The winter of 1988/89 was severe and the 1988 fires reduced forage supplies (Coughenour and Singer 1994, Wallace et al. 2004). Legalized hunting was reinstated and several hundred bison were killed by hunters as they crossed the northern boundary. In the winters of 1994/95, 1995/96, and 1996/97 considerable numbers of bison were killed in management actions as they moved outside of the northern and western park boundaries. Numbers dropped through 1999 but the population rebounded in 2000-2002. Management removals and outmigration have been minimal since 1998, but there has not been a severe winter during that time.

Rapid population growth during the early years was a result of semi-domestication (bison ranching), re-establishment of historic ranges, and periodic favorable climatic conditions while later increases appeared to be offset by reductions and occasional severe winters (Meagher 1973). Winter-kill was the main cause of mortality, particularly, long winters, periods of prolonged cold, and deep and sometimes crusted snow (Meagher 1973). The energetic cost of traveling between foraging areas in deep snow was thought to be especially significant. Meagher hypothesized that wild bison showed a much lower pregnancy rate (62%) than the semi-domesticated herd of 1940-41 (90%), due to a “complex of environmental factors” including winter severity. Given that numbers were at a historical low in 1966 and were starting to increase, Meagher predicted that with no further reductions (under the new natural regulation policy), population numbers would increase but would eventually establish a state of equilibrium with natural environmental conditions. Meagher (1973,1976) felt that total forage was not limiting on bison winter ranges, but forage could be limiting in restricted, key winter habitats such as thermal areas.

ECC has often been calculated using empirically parameterized, density-dependent models of population growth rate (eg. Merrill and Boyce 1991, Coughenour and Singer 1996a, Taper and Gogan 2002). The actual limitations are not explicitly represented, but the implicit assumption is that density-dependence is an outcome of competition for increasingly limited forage, space, or some other limiting resource. The models are numerically solved to simulate population dynamics. When forage production or mortality is driven by variable weather, a dynamic equilibrium is predicted, which can be interpreted as ECC (eg. Merrill and Boyce 1991, Coughenour and Singer 1996a). Using the population modeling approach, Merrill and Boyce (1991) calculated a provisional ECC of 350 for the northern bison herd. The estimate was based upon an empirical equation linking annual population rates of increase to population densities 1971-88, winter severity indices, and summer range forage biomass. Bison population responses to alternative management scenarios were modeled by an unidentified worker for the final bison management environmental impact statement (National Park Service 2000). An empirically parameterized deterministic model predicted that under continued implementation of the interim management plan (alternative 1), total bison numbers in the park would increase at 4% per year before leveling off at approximately 3,100. Under minimal management, with essentially no removals (alternative 2) bison would increase to 3,500. A stochastic version of the model predicted bison would vary between 3,600-3,942 after 8-18 years under alternative 1. Under alternative 2, bison would vary between 3,892-5,247. Taper et al. (2000) used the population modeling approach to estimate that ECC is on the order of 2800-3200 animals. However their

analysis was complicated by the fact that bison ranges were expanding throughout the period, thus density was down-regulated, thus reducing the likelihood that densities increased to levels where population growth rate would have declined.

While these models suggest that there should be density-dependent limitations on bison population growth, Cheville et al. (1998) found no evidence for density dependent limitations on bison population growth rate, even in the late 1990's when populations were at all-time highs. Instead, they found a constant annual increment of 145 bison. They observed that territorial species often grow by constant increments rather than exponentially. The constant annual increment is simply a result of the fixed area and thus fixed rate of production of the territorial area. However, because YNP bison ranges have been expanding, the explanation may not be that simple. Cheville et al. suggested that there may either be a few good habitats available where females can recruit calves and/or dominant females displace others from the good habitats. This explanation is problematic given range expansion, which would likely have added good habitats for calf recruitment. Cheville et al. concluded that there is little evidence of inadequate forage available to YNP bison. They presumably based this conclusion upon their analysis of the continued rate of population growth. Since there was no evidence of reduced population growth at higher densities, the population modeling approach would inevitably be incapable of identifying an ECC. Instead, they suggested that a source-sink model is more appropriate (Pulliam 1988). Yellowstone N.P. will simply continue to function as a source of constant population growth, feeding dispersion out into sink habitats outside the park where they are inevitably removed by humans to control brucellosis, among other reasons.

Despite the assumption that density-dependence is a result of forage limitation, none of the models or analyses just mentioned explicitly link population growth to forage productivity. In interactive plant-herbivore models, in which forage intake is a function of forage abundance, and forage abundance is determined by the net outcome of forage production and forage utilization (Noy-Meir 1975, Caughley 1976, Caughley and Lawton 1975). The feed-back of herbivory onto forage growth rate is central to these models. These plant-herbivore models can be analytically or numerically solved for the population density at which there is an equilibrium between the rate of forage production and the rate of forage utilization. Weather-induced fluctuations in forage production or mortality produce dynamic equilibria, and if weather fluctuations are sufficiently unpredictable, the plant-herbivore system may be disequilibriumal (Caughley 1987, Ellis and Swift 1988).

The complexities of estimating food limitation or carrying capacity for large herbivores can be reduced to fundamental processes involved in nutrition, linkages between habitat qualities and nutrition, and linkages between nutritional status and population responses such as recruitment and survival. Nutritional status is at the core of this set of interacting processes. Consequently, a key component of an explanatory approach must be a dynamic model of animal energy balance, where energy balance is modeled as the net outcome of energy intake through foraging, and expenditures resulting from metabolism and activity. Such energy and nitrogen balance models have been constructed for many years (Moen 1973, Swift 1983, Hudson and

White 1985, Coppock et al. 1986, Hobbs 1989, Ilius and Gordon 1992). The second key component is the linkage between nutrition and population processes. Linkages between nutrition and population models have gradually evolved over the last decade. Hobbs (1989) modeled deer energy and nitrogen balances and used resulting energetic status to predict deer mortality rate. They surmised that below a certain critical level of stored body reserves, survival would be unlikely. They assumed a normal distribution of stored energy reserves in the population, and based upon the mean and standard deviation, calculated the fraction of the population below that survival level. This idea was used to estimate food-limited elk carrying capacity in Yellowstone (Coughenour 1994, Coughenour and Singer 1996a). It was assumed that no more than a 10% mortality rate could be tolerated to support the elk population, on average. The energy and nitrogen available in the forage could then be combined with forage intake rate to determine how many animal-days could be supported by the forage at that mortality rate. Forage intake rate depended upon forage biomass and snow cover. The calculation of supportable animal-days was integrated over time and space to estimate season-long carrying capacities.

Explicit linkages between herbivore nutritional status and population dynamics have been made by W. Getz and N. Owen-Smith, in an approach they call metaphysiological modeling, or growth-metabolism-mortality modeling (GMM) (Getz and Owen-Smith 1999, Owen-Smith 2002a,b). Their approach is a natural extension of the Caughley and Noy-Meir plant-herbivore models. Notable advancements include a) making mortality rate a function of the ratio of the rate of energy intake to expenditure, b) modeling important seasonal variations in forage quality and quantity rather than total or mean annual forage production, c) incorporating heterogeneity among different vegetation components. The incorporation of seasonality and vegetation heterogeneity produced stable plant-herbivore dynamics under conditions where the earlier, more aggregated models were unstable (Owen-Smith 2002a).

A slightly more detailed approach has been developed by Ilius and O'Connor (2000). Their model explicitly simulates the energy balance and fat reserves of the herbivore population using a simplification of an earlier ruminant nutrition model (Ilius and Gordon 1992). As in Hobbs (1989) and Coughenour and Singer (1996a), the nutritional status was assumed to be normally distributed with mortality occurring in the animals in the distribution with zero or less fat reserves. Birth rate was assumed to be a function of body condition score, the ratio of fat reserves to maximum fat reserves. They modeled two vegetation resource areas representing a wet season area and a dry season area with seasonal movements of animals between them. The model supported earlier assertions (Ilius and O'Connor 1999) that population size is limited by dry-season ranges (key resources), and that as the dry season range decreases in size relative to the wet season range, the intensity of herbivory on the wet season range increases because the dry season range determines animal numbers. Their identification of resource bottlenecks on the landscape is interesting, but it is not a new idea. It has long been known that if winter ranges or dry season ranges are small, less productive, or consist of lower quality forage relative to summer or wet season ranges, these ranges will be the most limiting.

Animal energy balance modeling was incorporated into a spatially explicit ecosystem

model to provide insights into the nutritional stress dynamics experienced by pastoral livestock in northern Kenya (Coughenour 1992, Ellis et al. 1993). Energy balance was modeled as the difference between intake and expenditures, giving rise to a dynamic condition index, which was the ratio of stored energy reserves to maximum stored reserves. Shortly thereafter, linkages between animal energy balance and population dynamics were introduced into the model by making animal birth and death rates functions of their condition indices (Coughenour 1993, Buckley et al. 1995, Coughenour and Singer 1996a). The ecosystem model has been used to estimate food-limited carrying capacity and ungulate population dynamics in a wide range of environments (Coughenour and Singer 1996b, Coughenour 1999, 2002, Weisberg et al. 2002, Boone et al. 2002). In this approach, ecological carrying capacity can be determined by simply running the model until it reaches a dynamic equilibrium with no animal removals. ECC is the mean number of animals in long-term dynamic equilibrium with other components of the ecosystem, particularly plants and soils.

Spatially explicit ecosystem modeling offers a number of other advantages for interactions between large herbivore populations and other components of the ecosystem (Weisberg et al. 2006). As pointed out earlier (Coughenour 1991a) and as shown in models (Owen-Smith 2002a, Ilius and O'Connor 2002), spatial heterogeneity plays a critical role in most grazing ecosystems. What has been recently termed “key resources” (Ilius and O'Connor 2002) has been readily represented in spatially explicit models of forage production, snow cover, dynamic spatial distributions of herbivores, and linked nutrition and population models (Coughenour 1999, 2002). In contrast to other efforts (Ilius and O'Connor 2002, Owen-Smith 2002a,b), the ecosystem modeling approach is based upon actual landscapes as represented in geographic information systems (GIS) data. Modeled spatial-dynamic distributions of weather, soils, vegetation, plant growth, and herbivores are temporally variable and realistically portrayed. The ecosystem modeling approach represents links plant growth, nutrient cycling, and soil water budgets using process-based realism, thus permitting explanatory assessments of the impacts of spatially heterogeneous grazing intensities on plants and soils across the landscape (Chapter 4).

The overarching objective of this study is to assess the role of bison and elk in the Yellowstone grazing ecosystem. Specific objectives are to a) assess whether or not bison have or will reach a food-limited carrying capacity, b) provide explanations for bison population dynamics and densities through linked nutrition and population processes, c) provide nutrition and population-based explanations for bison utilization of lands outside the park boundaries, d) assess the possible causes and consequences of bison range expansion, e) assess elk population dynamics and interactions between elk and bison. To accomplish these objectives, a spatially explicit ecosystem model is used to integrate abiotic variables such as soil nutrients, water, topography, and weather, with biotic processes such as plant growth, herbivore nutrition, and herbivore population dynamics.

## **MODEL DESCRIPTION**

## **Ecosystem Model Overview**

A spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems (SAVANNA, version 5a)(Coughenour 1992, 1993, 1999, 2002) was parameterized and tested for the Yellowstone ecosystem (Chapters 1,2). The model consists of site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics, predation, and predator population dynamics submodels. The time-step of the model is one week. The model is spatially explicit (i.e., it is sensitive to spatial position) in that it uses geographic information systems (GIS) data for soils, vegetation, topography, and other variables. A mosaic of grid-cells covers landscape- or regional-scale ecosystems.

The model is driven by monthly weather data from 29 different weather and SNOTEL stations located inside and outside of the park. Precipitation and temperature maps are generated while the model is running using elevation-corrected spatial interpolation. A snow model simulates the accumulation and melting of the snow pack, thus generating spatial maps of snow depth and snow water content every week.

Nine functional groups of plants were simulated including: fine-leaved graminoids, coarse-leaved graminoids, forbs, sagebrush, deciduous shrub species found in forest understories, *Vaccinium* shrub species found in forest understories, and coniferous trees. Although aspen and willow were simulated, they were not the focus of this study. Two bison herds (central and northern) and three elk herds (northern, Madison, summer immigrants) were simulated. The plant soil models were described and tested in Parts 1 and 2 of this report.

## **Herbivory Submodel**

Forage intake rate responds to forage biomass according to a functional response (Holling 1959, Caughley and Lawton 1975). As forage biomass increases, forage intake rate increases, with intake rate eventually reaching a maximal value (Figure 1A,B, Table 1). A Type-I response is used, which linearly increases from 0 at 2 g/m<sup>2</sup> forage biomass up to the maximal intake rate at some saturating value of forage biomass. Bison forage intake rate is maximal at 156 g/m<sup>2</sup> forage biomass and above (Hudson and Frank 1987) while for elk it is maximal at 92 g/m<sup>2</sup> (based upon Wickstrom et al. 1984, Hudson and Watkins 1986). A maximal forage intake rate of 3.5% of body weight per day was used for both bison and elk. Peden et al. (1974) cite a reference where 3.5-6% per day intake was observed in wisent (Boroski 1967). Feist (2000) suggested 3% is the maximal intake rate for bison, based upon data from beef cattle. Watkins et al. (1991) observed 2.7-3.1% per day intake rates in elk. Model values were set at 3.5%, which resulted in simulated maximal intake rates of 3-3.1% averaged for the population. The maximal intake is only achieved for a very brief period during summer, declining during fall and winter to a minimum at the beginning of spring (Chapter 5). Forage intake rate declines with decreasing forage quality due to increased rumen retention time (Feist 2000). The function was set for both bison and elk,

to reduce intake rate to 70% of normal at a mean DMD of 0.3, increasing to 100% of normal at a mean DMD of 0.6. Except for early in the growing season, forages are most often mixtures of live and dead leaves and stems, so digestibility is rarely maximal.

Forage intake rate is affected by snow (Figure 1C,D, Table 1). Above a certain snow depth, intake rate declines linearly with increasing depth. Fine-grained topographic variation leads to the occurrence of wind-blown areas in the particular landscapes of Yellowstone elk and bison winter ranges. This fine-grained variation is not represented in the model. For this reason, the effect of snow was set more liberally than data would suggest. Carbyn et al. (1993) observed that snow had no effect on bison foraging below 40 cm depth, while foraging essentially impossible above 75 cm snow depth. For Yellowstone bison, it was necessary to set the snow effect so that snow has no effect at 50 cm, declining to a low value at 85 cm, and declining to zero at 150 cm. A synthesis of data suggested that elk intake declines above 20 cm, and become severely constrained by 75 cm (Cassier et al. 1992, Coughenour 1994). Elk intake rate was parameterized to decline above 30 cm to a low rate at 65 cm, and declining further to zero at 85 cm.

Forage intake rate is partitioned among plant types and tissue types as affected by preferences and relative availabilities. Diet composition is determined by using preference weights, similar to Ellis et al. (1976). Preference weights are multiplied by biomass densities and the products are summed and normalized to give a sum of fractions totally 1.0. Preference weights were calibrated to match observed diets (Table 2)..

## **Herbivore Energy Balance**

The herbivore energy balance submodel simulates body weight of the mean animal of each herd or subpopulation, based on differences between energy intake and energy expenditure. The energy balance model is partly based upon the models of Coppock et al. (1986) and Hobbs (1989). Energy intake depends on forage biomass intake and forage digestibility. Expenditures depend on body weight and travel patterns. The body weight of the mean animal is used to derive an animal condition index, which affects ungulate population dynamics.

Metabolizable energy intake from forage consumption is the product of kg total forage intake per animal per day, the mean digestibility of the forage, the gross energy content of digestible plant matter, and its metabolizability. Dry matter digestibility values are specified by plant functional group and tissue type. The DMD of live tissues is assumed to be positively correlated to leaf tissue nitrogen (protein) concentration, which declines from a maximum value in early growth stages to a minimum value mid-way through the growing season. Leaf nitrogen and thus DMD are also increased in the regrowth following herbivory,

Energy requirements consist of a "base cost" (not basal metabolic cost) metabolic energy demand per unit body weight per day plus optional added energetic costs of travel, thermoregulation, and gestation. To compute the base cost, a minimum and maximum energy



requirement is specified, with the minimum corresponding to a resting metabolic rate. The maximum includes energy for activities, not counting travel costs if those are specified. Energy use varies between the minimum and maximum in relationship to condition index, according to a function “Enuserate:”. If the condition index is high, animals use more energy on activity. If condition index is low, animals conserve energy by reducing activity.

Gestation costs are calculated based on the equation in Robbins (1983), also used by Hobbs (1989). The percentage increase in energy costs above the base cost is

$$\text{Gest (\%)} = 0.000024 * \text{Pergest}^{3.13}$$

where Pergest is the percentage of gestation period completed. This is applied to the fraction of the herd that is comprised of pregnant females.

Thermoregulatory costs are calculated using the same approach used by Hobbs (1989). Below a specified lower critical temperature, the animal loses heat energy at a rate determined by the temperature difference below critical and the thermal conductance of the animals coat. Different critical temperatures and conductances can be specified for bedded vs. non-bedded activity.

Travel costs may be computed in three different ways - 1) based upon specified distances traveled per day, 2) based upon computed distance to water, or 3) based upon specified times spent walking and feeding per day and mean rates of travel for both activities (Hobbs 1989). The third option was used here. The distance walked per day is computed as the product of a speed of walking or walking during feeding (m/min) times minutes per day spent walking or feeding. The latter are specified by month of year. The cost of walking is then computed from body weight and distance walked, using an equation developed by Parker and Robbins (1984). Travel cost per kg body weight is

$$\text{MJ/km/kg} = 0.012 / (W^{0.34})$$

with W in kg of body weight. Total travel cost per km is then

$$\text{MJ/km} = \text{MJ/km/kg} * W$$

and total energetic cost per day is

$$\text{Etrv (MJ/d)} = \text{MJ/km} * \text{km/d.}$$

The fractional increase in travel costs associated with traveling in snow (Fsnw) is also based upon an equation from Parker et al. (1984),

$$\text{Etrv}_{\text{snow}} = \text{Etrv} * (1.0 + \text{Fsnw})$$

$$F_{snw} = (F_{trv_{brk}} * F_{snw_{brk}}) + ((1 - F_{trv_{brk}}) * F_{snw_{unbrk}})$$

where  $E_{trv}$  is cost of travel on bare ground,  $E_{trv_{snow}}$  includes the cost of travel on snow,  $F_{trv_{brk}}$  is the fraction of travel that is broken vs. unbroken snow, and  $F_{snw_{brk}}$  and  $F_{snw_{unbrk}}$  are the fractional increases in cost due to travel in broken and unbroken snow.

$$\begin{aligned} \text{Snden} < 0.3 \quad & F_{snw_{unbrk}} = 0.0071 * Ru * e^{0.019 * Ru} \\ & F_{snw_{brk}} = 0.0071 * Rb * e^{0.019 * Rb} \end{aligned}$$

$$\begin{aligned} \text{Snden} \geq 0.3 \quad & F_{snw_{unbrk}} = 0.0123 * Ru * e^{0.0223 * Ru} \\ & F_{snw_{unbrk}} = 0.0123 * Rb * e^{0.0223 * Rb} \end{aligned}$$

where  $Snden$  is snow density (mm/mm) and where  $Ru$  and  $Rb$  are relative sinking depths in unbroken and broken snow, defined as

$$\begin{aligned} Ru &= 100 * Sndpu_{brk} / Brht \\ Rd &= 100 * Sndp_{brk} / Brht \end{aligned}$$

where  $Sndp_{brk}$  and  $Sndpu_{brk}$  are snow depths in broken and unbroken snow and  $Brht$  is brisket height. It is assumed that snow depth in broken snow is one half of brisket height.

The net outcome of energy intake and expenditure is a change in stored energy reserves. If energy intake exceeds requirements, then the animals convert the excess energy to fat. If energy intake is less than requirements, the deficit is drawn from fat reserves. The level of stored energy reserves is indicative of body condition. Animal condition index is a number that varies between 0.0 and 1.1, and is calculated as the ratio of kg's below maximum body weight to the difference between maximum and minimum body weights (kg). At condition index 0.0, animals are at the minimum weight while at condition index of 1.0, animals are at maximum weight. Above 100% of maximum body weight, forage intake rate is reduced due to satiation.

## Energy Requirements

### *Bison*

Mean body weights were assumed to be 160 kg for calves, 300 kg for yearlings, 450 kg for cows, and 650 kg for bulls. Podrunzny et al. (2002) found that irrespective of sex or age, bison lost 18.4% of body mass from January to April. When weight loss is >20%, there are negative effects on calving (Feist 2000). Green (1998) assumed a maximum 20% loss based on Gates and Hudson (1981) and Parker et al. (1993). Here, body weight was assumed to fluctuate between -15% and +15% of the mean as absolute lower and upper bounds.

The metabolic base costs were assumed to vary between a minimum of 0.08 MJ/kg/d and a maximum of 0.16 MJ/kg/d (Table 1). Ravndal Vanderhye (1979) used the Kleiber equation

$\text{MJ/d} = 0.294W^{0.75}$ , which results in 0.66 MJ/kg/d for a 400 kg bison. She assumed activity costs would add 50% to the costs, bringing the total to 0.1 MJ/kg/d. Christopherson et al. (1979) found a rate of 0.16 in bison calves in the winter and 0.24 MJ/kg/d in summer for a 454 kg cow. They found that bison were unique in being able to reduce their metabolic rate in response to cold temperature. Feist (2000) suggested a total requirement of 0.116 MJ/kg/d in winter and 0.207 MJ/kg/d in summer, and stated that lower requirements in winter are due to hormonal responses to shorter days. Although temperature or daylength effects are not explicitly modeled here, the reduction in energy costs at lower body condition, as represented in the Enuserate function, result in reduced energy costs in winter. The Enuserate function was set so that energy use was minimal value at a condition index of 0, and maximal at a condition index of 0.5

Thermoregulatory costs were based on a lower critical temperature of  $-40^{\circ}\text{C}$ , and thermal conductance values given by Parker and Robbins (1985).

Gestation costs were calculated based on the equation of Robbins (1983), with a gestation period assumed to begin in August and last through May.

Travel costs were based on data for time per day spent walking and feeding (Table 1). Time spent traveling for Dec.-May was based upon the findings of Bjornlie (2000) and Bjornlie and Garrott (2001). Values for June-September were based upon a mean of 2 hrs per day spent walking in summer, and 10-12 hrs per day spent feeding year-around in Wind Cave N.P. (Green 1998). Hours per day of walking for Oct.-Nov. were derived by interpolating between the summer values and the Dec. values. Walking rate was assumed to be 60 m/min, and walking rate while feeding was assumed to be 3 m/min.

The fraction of travel in snow that was through unbroken vs. broken snow (Table 1) was based upon the findings of Bjornlie (2000) and Bjornlie and Garrott (2001). It was assumed that 6% of travel time in snow was through unbroken snow, 74% was through broken snow, and 20% was on bare ground, or plowed or groomed roads.

### *Elk*

Mean body weights were assumed to be 114 kg for calves, 162 kg for yearlings, 240 kg for cows, and 330 kg for bulls. Body weight was assumed to fluctuate between -16% and +16% of the mean, based on Watkins et al. (1991).

Metabolic energy costs for elk (Table 1) were based on prior analyses of Hobbs (1982) and Watkins et al. (1991). Hobbs' calculations result in approximately  $0.19 \text{ MJ kg}^{-1} \text{ d}^{-1}$ , including all activity costs. Watkins' data suggest  $0.12\text{-}0.16 \text{ MJ kg}^{-1} \text{ d}^{-1}$  for resting and standing animals. Since activity costs of traveling are calculated separately, I used a range of  $0.1\text{-}0.16 \text{ MJ kg}^{-1} \text{ d}^{-1}$ . The Enuserate function was set so that energy use was minimal value at a condition index of 0, and maximal at a condition index of 0.5

Thermoregulatory costs were based on a lower critical temperature of -10°C, and thermal conductance values given by Parker and Robbins (1985).

Gestation costs were calculate based on the equation of Robbins (1983), with a gestation period assumed to begin in October and last through May.

Travel costs was based upon times spent walking and feeding (Table 1). Hours per day spent walking was based on Craighead et al. (1973), while hours spent eating was from Green and Bear (1990). Walking rate was assumed to be 60 m/min, and walking rate while feeding was assumed to be 3 m/min. It was assumed that the fraction of travel in snow was 33% in unbroken snow, and 77% in broken snow, and 0% in no snow, for lack of better information.

### **Forage Quality**

Dry matter digestibility (DMD) values were based on a synthesis of available data (Table 3, Appendices 1-8). It was assumed that green leaf DMD varies from a maximal value when tissue N is at its peak, to a minimal value when leaf N is at its minimum.

Bison are known to have higher digestive efficiencies than domestic cattle on low quality forage (Peden et al. 1974, Hawley et al. 1981a,b). On average, these studies found that bison DMD was 25% higher than standard cattle values when DMD is 0.48. It was assumed the difference between bison and cattle digestive efficiencies narrows on higher quality forage. Thus the difference between bison and cattle was assumed to be 25% at a standard cattle DMD of 0.48, gradually decreasing to 0% at a DMD of 0.65.

### **Herbivore Population Dynamics**

The herbivore population dynamics submodel is an age-sex class model with one age class for each year, for each sex. Recruitment rates and death rates are affected by animal condition indices. Recruitment rather than birth is simulated, because very early calf/fawn survival rate is not distinguished. As condition index increases, recruitment rates increase and death rates decline. The effect of condition index on recruitment rate is multiplicative. For example, a condition index of 0.2 might reduce recruitment rate to 35% of the maximum. The effect of condition on death rate supercedes the nominal death rate if it is larger. The effects of condition index represent population responses to ecological conditions governing forage availability (e.g., forage production, snow depth) and intra- and interspecific competition. As competing animals can reduce forage supply, forage intake rate, and thus body condition, they can consequently reduce population growth rate of the species in question.

The equation for recruitment is

$$\text{Recruit} = \sum \text{Female}_i \times \text{Birthrt}_i * F(\text{CI}_{\text{gest}})$$

where  $Recruit$  is number of surviving newborns in the season,  $Female_i$  is the number of females in age class  $i$ ,  $Birthrt_i$  is the maximum birth rate by age class, and  $CI_{gest}$  is the condition index averaged over the period of gestation. Recruitment is assumed to occur in a single month each year. For Yellowstone bison and elk, that month is May.

The equation for monthly mortality is

$$Deaths_i = Animals_i * \max[Deathrt_{Nom}, Deathrt(CI)]$$

where  $Deaths_i$  is the number of animals dying in age class  $i$ ,  $Animals_i$  is number of animals in age class  $i$ ,  $Deathrt_{Nom}$  is the nominal death rate, and  $Deathrt(CI)$  is the death rate as a function of the monthly body condition. Different  $Deathrt(CI)$  functions are specified for calves, mature females, and mature males.

The monthly nominal mortality rate is computed from the annual survivorship rate as follows.

$$Deathrt_{Nom} = \min (SurvCal_i * Surv_i^{(1/12)}, 1.0)$$

Monthly survivorship rate is equal to the annual survivorship to the 1/12 power, since the monthly survivorship to the 12<sup>th</sup> power should equal the annual survivorship. The parameter  $SurvCal$  is a calibration parameter that is found by fitting the model to the observed data. A calibration parameter of  $>1.0$  is expected because the nominal survivorships are based upon data from field conditions that include mortalities due to environmental stress while here, stress related mortality is accounted for in  $Deathrt(CI)$ .

Animals can be removed by hunting or culling using a specified “trigger” population size. If the population is at or above that value the population will be reduced to a specified “target” number. This method is normally used to simulated management removals to keep a population within a certain range. Removals can also be prescribed with an observed number of animals per year, or an observed fraction of animals per year. Simulations of historical population dynamics use actual removal numbers. Simulations of hypothetical hunting or culling scenarios usually use removal rates.

An emigration rate can be specified as the fraction of the population per month that leaves subpopulation and moves to another subpopulation with a different geographic range.. The emigration rate is a function of condition index, with higher rates when animals are in poor condition, the logic being that as animals increasingly become food-limited, they will more frequently disperse in order to find forage.

## **Parameterization of the Herbivore Population Dynamics Model**

Age class distribution data were obtained from Yellowstone bison and elk studies were

used to estimate age and sex class nominal survival rates.

Pac and Frey (1991) reported age/sex compositions for 569 bison hunted/removed outside the northern boundary in 1988/89 by using the most reliable source of either dental cementum annuli or in-the-field ageing based upon teeth eruption and replacement. Gogan et al. (1998) reported age/sex compositions for 1996/97 removals based upon dental annuli. A total of 421 removed bison were examined from the western boundary removals and 819 were examined from the northern boundary removals. Their reported age/sex class distributions are shown in Table 8. The mean of these two observation sets was calculated, and annual age-specific survival rates were calculated from the mean distribution as the ratio of fractions in successive age classes. The resultant survival rates were inconsistent among some age classes, for unknown reasons. The mean survivorship rates of age classes 1-5, 5-6, and 10-15 were calculated as “simplified” survivorships for those broader age classes. An idealized, exponentially declining age-specific survivorship curve (“smoothed”) was calculated by applying the simplified rates to successive age classes. Commonly used summary statistics are reported in Table 9.

A similar approach was used to estimate multi-age-class survivorships for elk, based upon the life table analyses of Houston (1982). Means were taken for survivorships in age classes 1-5, 6-12 13-15, 16-17, and 18-21 for females. Means were taken for ages 1-5, 6-10, and 11-15 for males.

The stepwise annual survivorship rates were used as the baseline “nominal” survivorship rates in the model ( $Surv_i$ ). The calibration parameter ( $Survcalc_i$ ) was determined to be 1.068 for bison and 1.02 for elk. The final calibrated survivorships applied in the model ( $Surv_i * Survcalc_i$ ) are shown in Table 10.

The sex ratio of recruited bison calves was set to the value of 58:42 females:males observed by Pac and Frey (1991). Meagher (1971) similarly reported 57% of calves were females. This is slightly different than a fetal sex ratio, because the model does not explicitly treat neonatal mortality or sex differences in either neonatal or calf mortality. The sex ratio of recruited elk was set to 66:44 based upon information given by Houston (1982).

Age-specific bison fecundity rates (Table 10) were based upon data presented by Gogan (1998) who found 5% of one-year olds, 50% of 3-year olds and 87% of 6-15 year old females were pregnant. For comparison, Pac and Frey (1991) recorded a 75% pregnancy rate. Meagher (1973) found a pregnancy rate in 1964-66 of 14% in 2-year olds, 27% in 3-year olds, and 71% in 4-year and older females. Fecundity rates for elk were based upon Houston (1982), with mean reported values for age classes 3-7 and 8-15 applied to all ages in those age brackets.

Alternative bison age/sex class distributions were calculated from the survivorships. Three different possible age class distribution models are presented in Table 11. Commonly reported summary statistics computed from Table 11 are presented in Table 12. In model 1, the idealized exponentially declining survivorships of Table 8 were used as the basis. The female

survivorships were used as-is. An intermediary male survivorship was calculated based upon the birth sex ratio observed by Pac and Frey (1991) of 42 males to 58 females, with relative survivorship of males/females of age class 0 being 0.724 (42/58), rather than 1.0 (50/50). The 0.724 scalar was applied to each of the idealized values in Table 8. The female and intermediary male survivorships were normalized (to sum to 1.0). In model 2, the initial birth sex ratio was assumed to be 50/50. Model 3 assumed a 50/50 birth ratio, but males of ages 4+ were adjusted to give a proportion of 4+ year-old males of 0.135, as reported to have been the case in 1970 by Taper et al. (2000). The results from model 3 were used to initialize the model in 1969.

Initial elk age/sex class distributions were calculated from Houston (1982, Table 5.6,5.7), and a calf/cow ratio of 45/100, and a bull:cow ratio of 42/100 as were observed in 1970 and 1971 (Table 13).

The effect of condition index during the gestation period on bison recruitment rate linearly increases from 0.3 to 1.0 (Figure 2A). The effect on elk recruitment rate increased linearly to 0.6, then more rapidly between 0.6 and 1.0 (Figure 3A). The functions were parameterized to produce calf ratios within the range of observed values, and to provide the best fits to the observed population data.

The effects of condition index on mortality rates were presumed to increase gradually with declining condition, and then at a low, critical condition index, increase markedly (Figure 2C,D,3C,D). Calf mortality rates were assumed to be higher than adult mortality rates. Calf mortality rates were then fit to match observed population growth rates, and rates of recruitment into the adult age classes. Adult female mortality rates were mainly fit to match observed population dynamics. Adult male mortality rates were assumed to be higher than adult female mortality rates at the same mean herd condition index. Although sex differences are embodied in the nominal mortality rates (Table 10), added differences between male and female mortality rates were incorporated to improve fits to observed bull:cow ratios.

Small rates of interchange were assumed to occur between the northern and central herds. The fit of the population model to the data was improved by including these interchanges. From 1969 through 1976 animals from the northern herd were assumed to diffuse to the central herd at a maximum rate of 0.0055 per month when condition index is 0, decreasing to a rate of 0.0023 when condition index is 0.5 and above. From 1977 onwards the diffusion rate is 0.013 at CI of 1.0 declining to 0.0065 at CI of 0.5. From 1983 onwards the central herd was assumed to diffuse into the northern herd at a rate of 0.0065 at CI of 1.0 declining to 0.0033 at a CI of 0.5.

The model was fitted to sightability-corrected population sizes rather than raw count data (Table 14) since the objective was to simulate actual numbers of animals. Bison counts were not corrected for removals since counts occurred prior to removals (Taper et al. 2000). Removals generally occurred in late winter. Pre-removal elk counts were estimated by adding in offtake from the regular hunt from late October to late November. Counts were carried out in early winter (December-January). A late hunt has occurred between mid December through mid-

February during the early 1980's and early January to mid-February during the 1990's (Taper et al. 2002).

Bison count data for 1968/69 - 1996/97 are from Taper et al. (2000). They estimated that sightabilities during 1968/69-1973/74 were 0.46 for the northern herd and 0.7 for the central herd. During 1974/75-1996/97 sightabilities of 0.77 and 0.88 were estimated for the northern and central herds, respectively. Hess et. al. (2002) conducted multiple counts per year during 1996/97-1999/2000. He determined that his sightabilities were 0.92 in winter and 0.97 in summer. Estimates for February 2002 are based upon an published total count of 3300, corrected for winter sightability as in Hess et. al., and a partitioning between northern and central herds as in 2000..

Elk count data from 1968/69-1977/78 are from Houston (1982). Data for 1978/89-1989/90 are from Coughenour and Singer (1996b). Data for 1990/91-99/01 are from Taper et al. (2002). A mean elk count sightability of 0.76 was applied to the counts, which was the average sightability in "good" counts reported by Coughenour and Singer (1996b). The poor elk count of 1975/76 was corrected as in Houston (1982). The poor counts of 1988/89 was corrected as in Coughenour and Singer (1996b). The poor count of 1990/91 was corrected as in Taper et al. (2002). Estimated counts for 1979/80 and 1982/83-1984/85 were interpolated.

A constant number of 800 elk in the Madison herd was simulated (Singer 1991, Singer and Mack 1993). The summer range of the Madison herd was not included, so animals were removed from the simulations those months. A total of 7,600 summer immigrant elk were assumed to use the elk summer range in summer months (Singer 1991, Singer and Mack 1993).

## **Bison and Elk Ranges**

Range locations for bison were determined by drawing circumferences around bison locations based upon aerial surveys carried out M. Meagher 1970-1997 (Taper et al. 2000), and surveys carried out in 1998-2001 by Hess et. al. (2002). Four different seasons were recognized: Winter (November-April), Spring (May-June), Summer (July-August), and Fall (September-October). Range extents have changed over time, mainly expanding (Meagher 1989a,b, Taper et al. 2000). Notable expansions occur over a 1-3 year time frame, but as an approximation, three different periods were recognized for the northern bison herd: 1969-1982, 1983-1993, 1994-2001. Four different periods were recognized for the central bison herd: 1969-1983, 1984-1987, 1988-1993, 1993-2001. The resulting set of range maps, for each season of each period and for the two herds, are shown in Appendices 9-12.

The northern elk winter range also expanded northwards during this period (Houston 1982, Coughenour and Singer 1996b), and this expansion was similarly represented. The summer range of the northern herd was based upon the distribution map in Houston (1982). The summer range of the summer immigrant elk, and the winter range of the Madison herd were based upon estimates of Singer (1991) and Singer and Mack (1993). Elk ranges are shown in Appendix 13.



## **Herbivore Spatial Distributions Within Ranges**

The herbivore spatial distribution model is described more fully elsewhere (Coughenour 2005). Animals are redistributed within specified seasonal ranges on a weekly basis in response to changing forage and snow conditions. Animals select for habitats with higher quantities of preferred forage species, green forage, and shallower snow. Distributions are also affected by slope and tree cover. Densities are constrained to be above a minimum and below a maximum value in any one grid-cell.

## **RESULTS**

### **1969-2001 Historical Simulation**

#### *Nutrition*

Simulated forage intake rates for bison varied seasonally from maxima near 3% to minima of 0.5-1.0% body weight per day (Figure 4). Maximum values were relatively constant among years. However, minimum values varied markedly among years, most likely in response to varied snow conditions. Intake rates of the northern elk herd ranged from minima of 0.4-0.8% to maxima of approximately 2.5% of body weight per day. Minimum values also varied among years.

Dietary composition of the northern bison herd in winter was mostly coarse-textured mesic sedges and graminoids found in the sedge meadow habitats of the northern winter range (Figure 5, Table 4). Finer-textured upland grasses such as bluebunch wheatgrass and Idaho fescue comprised approximately 27-43% of winter diets. Forbs were a minor portion of the diets. Coarse forest graminoids comprised 5-38% and their proportion increased over time. Coarse mesic graminoids comprised 33-54% and their proportion decreased with time. Comparisons to data were favorable (Table 2). Singer and Norland (1994) found 39% fine-leaved graminoids in winter diets and 56% coarse graminoids, and 1% forbs. Diets of the central bison herd in the winter included larger percentages of fine grasses, likely reflecting the smaller proportion of sedge meadows in these habitats. Winter diets of the central herd in 1982-1993 contained increased percentages of moist forest graminoids. Summer bison diets were similar to winter diets (Figure 5, Table 5).

Elk diets were more diverse due to their mixed feeding on shrubs as well as herbs (Figure 6, Table 6). In the winter, northern and Madison elk both had 40-49% fine upland grasses in their diets. The northern herd had 12-14% coarse mesic graminoids such as sedges while the Madison herd had 27-33% coarse mesic graminoids in their diets. This difference was probably due to the greater preponderance of riparian meadows and lower preponderance of upland habitats in the

Madison River Valley. Coarse forest graminoids comprised 6-11% of northern elk winter diets and <1% of Madison elk winter diets. Forbs comprised 7-8% of the winter diets of both herds. Deciduous shrubs of forest understories comprised 12-14% of northern elk diets and about 5% of Madison elk diets. Sagebrush and vaccinium were 2-4% of winter diets. Willow comprised 3-5% of northern elk and 11-14% of Madison elk winter diets. Willow is relatively more abundant in the Madison Valley than on the northern range.

Summer diets of the northern herd included were similar to winter diets except there was less sagebrush and Vaccinium (Figure 6, Table 7). Both species are not preferred items and it is likely that with a greater variety of choices available in summer, they were used proportionately less. Madison elk diets changed more significantly from winter to summer. Summer diets consisted of more mesic graminoids than winter diets and there was a smaller proportion of fine upland graminoids.

Mean dry matter digestibilities of bison varied seasonally from maximum values of approximately 67% in the early growing season to minimum values of approximately 58-60% in the winter (Figure 7A). This variation was mainly due to the change in proportion of green leaves in the diets, and also to the decline in green leaf protein and DMD between the early and mid growing seasons. Northern elk diets also varied seasonally, from maximum values of 65% in the early spring to 45-50% in the winter (Figure 7B). Digestibilities of winter elk diets were likely lower than digestibilities of bison diets because they utilized browse species (shrubs) while bison did not.

The net outcome of seasonal and interannual variations in forage intake rates and digestibilities is a temporally varying pattern of energy intake. Northern bison energy intake rate varied from 0.05-0.15 MJ/kg/d in winter to 0.15-0.30 MJ/kg/d in spring and summer (Figure 8). The energy intake rates of central bison reached lower maximum values than rates for the northern bison, however minimum values were similar. The maximum values are highly transitory, only lasting a single month, so the importance of the value is less than it might seem based upon the high values. The time-integrated value is of more significance for animal energy budgets than the peak value. The maximum occurs in May for the northern herd and June for the central herd. There was an increasing trend over time in the transitory maximum energy intake rate, with lower values in the 1969-1982 era. This is likely an outcome of the range expansions which occurred in the early 1980's. Energy intake by the northern elk herd fluctuated from lows of about 0.05 MJ/kg/d in winter to highs of 0.20-0.30 in spring (Figure 8C). Maximum

Metabolic energy use varied within a relatively narrow range for bison, between 0.13 and 0.17 MJ/kg/d, with low values in winter and high values in summer (Figure 8,B). Requirements varied more markedly in the northern elk, between 0.13 and 0.18 MJ/kg/d. The variable difference between energy use and energy expenditure was therefore a result of temporal variations in energy intake and energy use.

The net outcome was a fluctuation in animal condition index, which is a measure of an

animal's body weight (Figure 9). The condition index of the northern herd fluctuated between 0.4 and 1.05. Notably, the minimum values declined between 1969 and 1985. The condition index of the central bison herd declined to lower values than the northern herd. There was a decreasing trend in the minimum values between 1969 and 1983. Lowest values were simulated at the ends of the winters of 1981/82-1983/84. Northern elk condition index values declined to lower values than bison. There was a decreasing trend in minimum values between 1969 and 1979. Lowest values occurred in the winters of 1978/79, 1981/82, and 1988/89.

### *Populations*

The northern bison population grew steadily between 1969 and 1988 (Figure 10), when the large hunter removal occurred in the winter of 1988/89, resulting in a drop from approximately 1100 to 530. The population then began to grow again, reaching another high in 1995 despite removals in 1992 and 1995. The large management removal of over 700 bison in 1996/97 caused the population to drop to about 200 animals. The model predicted a rapid recovery after 1997, with no removals through 2001. The model fit the data well, except in 1970-1976 when the model predicted fewer animals than were reported. The rates of population growth were realistic in the original growth phase and subsequent recovery periods.

The central bison also population grew steadily between 1969 and 1996 (Figure 11). The model matched the data quite well up until 1995. The apparent reduction in the rate of population growth in 1982-1987 was accurately simulated. The model had difficulty in matching the reported highs in 1996-1997 and the lows in 1998-2000. According to the data, there were 975 fewer animals in 1997 than in 1996, yet only 344 were removed during that time. Between 1997 and 1998 the data indicated 680 animals were lost, while only 358 were removed. This would mean that in addition to the removals, 631 and 322 animals would have died in the two years. The model did an adequate job of simulating different phases of population growth 1969-1994. During 1969-1973 the population increased linearly, followed by a level period in 1974-1977. A rapid growth period occurred in 1978-1981, followed by a decline through 1984. The population increased again in 1985-1988, followed by a level period in 1987-1988 and an increase in 1989-1994. The approximately linear increase over the whole period of 1969-1994 noted by Cheville et al. (1998) was captured by the model.

The rapid growth of the northern elk herd observed in 1969-1976 was matched by the model, as was the cessation of growth in 1976-1977 (Figure 12). The data indicated a decline between 1978 and 1982 that was not quite matched by the model. However, the model and data agreed once again in 1982. Importantly, the model predicted a slower rate of population growth in 1983-1987, followed by a decline in 1988/89 and more or less leveling out in 1990-1994. The increase in 1994-1995 was adequately represented, as was the decrease in 1997-1999 and the increase from 1998-2001. Hunting removals grew nearly in proportion to the population between 1969 and 1990. The large removal in the severe winters of 1988/89 and 1996/97 explained much of the population declines those winters, however it is possible that many of the hunted animals would have died anyway.

Calf:cow ratios in the northern bison herd were high, in the 0.6-0.65 range from 1969-1980, except during and after the severe winter of 1975/76 (Figure 13A). Calf ratios trended downwards between 1977 and 1983. There was a strong upsurge in 1984-1988 but ratios were low in 1989-1991. There were large differences between years in 1992-2001, with no consistent trend.

Calf:cow ratios in the central herd were lower than in the northern herd and they fluctuated more from year to year (Figure 13B). Minimum values were much lower than minimum values in the northern herd. Exceptionally low values were predicted for 1983-1984, 1989-1990, 1993-1994 and 1995-1996.

Northern elk calf:cow ratios fluctuated between lows of 0.17 and 0.55 (Figure 13C). Low values were simulated in 1979-1980, 1989-1990, and 1997-1998. There was a downward trend between 1969 and the mid 1980's.

Bull:cow ratios of the northern bison herd fluctuated between 0.42 and 0.47 (Figure 13A). Bull ratios of the central herd varied between 0.4 and 0.45 and exhibited a slight downward trend (Figure 13B). Bull ratios of the northern elk herd fluctuated about 0.4 from 1969-1975 and declined to approximately 0.34 -0.35 in 1980-1995 (Figure 13C). Bull ratios reached 0.37-0.38 in 1997 and 2000.

Numbers of simulated animals outside the park boundaries can be apportioned to different management zones (Figure 14). Simulated numbers of bison and elk in areas outside the park boundary (Figure 15) revealed interannual variations in response to population sizes and snow cover. The model predicted that there would be no animals from the northern bison herd found outside the park until 1983, simply because it was prescribed that their winter range did not extend to the park boundary until that time (Figure 15A). Once the range had expanded to the boundary however, there was consistent use of lands outside the park, particularly the Eagle Creek area. Use of the areas outside the park decreased markedly in 1997/98 and 1998/99 due to the removals in 1996/1997. Simulated animals tended to begin use of the Eagle creek area as early as November with increasing use until March and April. Animals used the "outside north" area beginning in January, increasing to April.

Use of areas outside the western boundary by the central herd did not commence until their range expanded to that boundary in 1988 (Figure 15B). Use was minimal until the winter of 1995/96 and 1996/97 when it was predicted there would be >300 and >450 animals outside the park. After the removals in 1995/96 and 1996/97 the population declined, resulting in fewer animals outside the park in 1997/98. Very few animals were predicted to be outside western boundary in 2001. Simulated animals used this area in April and May, and sometimes June.

The number of elk outside the northern boundary, but on the lower winter range, increased beginning in 1971, reaching over 4800 animals in the Eagle Creek area and 2400 in the

“out north” area in 1978 (Figure 16). There was considerable interannual variability thereafter. Numbers in the Eagle Creek area varied from 400-5500 and numbers in the “out north” area varied between 250-1800. Elk used these areas all winter, increasing from November to peaks in December through April, depending on the winter.

GIS was used to determine the numbers of bison found outside the park boundaries in the aerial surveys carried out by M. Meagher 1970-1997 (Taper et al. 2000) and S. Hess 1998-2001 (Hess et al. 2002) (Figure 17). In 1983-1991 Meagher usually flew three flights per year in February, May or June, and November or December. In 1992 onwards there were usually 7 flights per year, including all winter months from November through June, and one flight in September. Hess flew Feb.-May 1998, Jan.-Mar 1999 and 2000. Numbers in the Gardiner area (outside north) were nil in most years but reached 120 in 1988/1989. Use of the Eagle Creek area was more frequent, with 75-125 animals in 4 years and 10-50 animals in 3 years. Meagher (1989) noted that approximately 250 bison used areas outside the northern boundary in 1986/87 and 1987/88, and despite various hazing efforts, the bison could not be stopped from moving towards this area thereafter. Thus, the total number of animals predicted by the model to be in the “out north” area was similar to numbers found near Gardiner, but animals were found outside Gardiner much less often than predicted by the model. The model predicted more animals would use Eagle Creek area than were observed, and more frequently than observed. There was better agreement between model predictions and data for numbers of bison outside the western boundary (Figures 15B, 17C). Actual numbers increased from about 50 in 1989 to over 400 in 1996. The model similarly predicted an increase from about 50 in 1989 to 330 in 1995 and 470 in 1996. Low numbers were predicted in that area in 1994, 1998, and 2001 and observed numbers were also quite low in those years.

A regression analysis of observed numbers of bison outside the park 1980-1997 against simulated snow depths on the bison winter ranges and bison population sizes indicated that numbers outside the western boundary were significantly but variably affected by snow, little affected by population size, but strongly affected by an interaction between snow and population size. For animals outside the western boundary, the snow effect became more significant when there were more than 1500 bison in the central herd, but snow had no effect with less than 1500 bison in the central herd. The number of animals outside the northern boundary was, in contrast, highly related to snow depth but not related to the size of the northern herd. Irrespective of herd the size of the northern herd, snow was a significant predictor, but population size was not.

## **Experimental Scenarios**

### *No-Removals*

When the model was run for 50 years with no removals or out-migrations of bison or elk, the northern bison herd increased to a mean of 2,417 animals over 8 simulations using stochastic weather (Figure 17). The range of variation was from 1820 to 3,530 (Table 16). The central bison herd increased to a mean of 3776 animals (Figure 19) with a range of variation between

2,430 and 5,630. The northern elk herd increased to a mean of 23,628 animals (Figure 20) with a range of 12,000 to 42,900. The population trajectories are shown in Figures 21 and 22. It is important to remember that these would be sightability corrected numbers and the numbers that would be counted could be 8% lower for bison and 24% lower for elk based upon sightabilities reported by Hess et. al. (2002) and Coughenour and Singer (1996b).

With no removals, the model predicted there would be 9-231 northern bison outside the park in the “north out” area, and 0-781 in the Eagle Creek area (Figure 22A,B, Table 16). Mean numbers in the 2 areas would be 102 and 300. There would be 0-800 outside the western boundary (Figure 23C). There would be 0-700 elk in the “north out” area and 0-2500 elk in the Eagle Creek area (Figure 23D,E). An example of the dynamics from one of the stochastic runs is shown in Figure 24.

### *Removals of Animals Found Outside the Park*

Regularly removing a proportion of animals found outside the park is one option for management. If 45% of bison found outside the park from November through May are removed on a monthly basis, the northern bison population would average 473 and fluctuate between 288 and 779 animals (Figure 25A, Table 17). A mean of 77, range of 17-214 animals would be removed from the northern boundary area each year (Figure 26B, Table 17), and there would be a mean of 18, range 0-40 animals found in the “north out” area and 37, range 0-164 animals found in the Eagle Creek area (Figures 25C,D, Table 17). The central bison herd would average 1946 and fluctuate between 1440 and 2470 (Figure 26A). An average of 95, range 40-382 animals would be removed per year (Figure 26B). The number that would be found outside the western boundary in January-April would be 2, range 0-119 (Figure 26C). However in May, the number outside would be 554 on average, with a range of 125-1102 (Table 17).

A 9% per month removal rate for northern elk outside the park was derived from a regression of the number of elk removed by hunting vs. the number of elk counted outside the park in the annual census 1969-1991 (Figure 27). On an annual basis, 48% are removed during an approximate 3 month period. If sightability is 76% (Coughenour and Singer 1996b), then 36% of actual numbers are removed. If this is spread over a 4 month period of November-February, this amounts to 9% per month.

If 9% of the northern elk outside were removed on a monthly basis from November through February, the elk herd would average 18476, fluctuating between 9510 and 29300 (Figure 28, Table 17). The number removed/hunted each year would average 1690, fluctuating between 284 and 4230. The number found in the “north out” area would average 2231 and fluctuate between 0 and 7948. The number found in the Eagle Creek area would average 624 and vary between 0 and 2950.

An example of population dynamics and offtake rates from one of the stochastic simulations is shown in Figure 29.

The effects of these alternative management scenarios on elk nutritional status are shown in Figure 30. In all three herds, animal body condition increases when managed through removals or hunting. The mean minimum body conditions increase from approximately 0.25 to 0.45 in the northern bison, from about 0.15 to 0.3 in the central bison and from 0.1 to 0.2 in the northern elk. These improvements would result in fewer starvation caused mortalities. As a result of the improved nutritional status during gestation, recruitment rates would also be improved by reductions (Figure 31). Calf ratios increased in all three herds.

#### *Reduced Elk Abundance, No Bison Removal*

The effect of competition between bison and elk on bison forage-limited carrying capacity was assessed in an experiment where elk were held to 5000 while bison were allowed to reach their ECC (Table 18, Figure 32). With elk reduced, northern bison reached a mean of 3112, as compared to 2417 with elk not reduced (Table 16). Central bison reached 5026 compared to 3776 without elk reductions. Thus, elk clearly affect bison ECC. In addition, more animals were found outside the park boundary.

#### *Limiting Bison Range Expansion*

The effects of restricting bison ranges to limits observed pre-1983, or in the mid-1980s' would reveal the extent to which range expansion has contributed to bison population growth. These experiments restricted ranges to either pre-1983 or mid-1980's ranges limits, during the 1969-2001 historical period. Either no removals, or observed historical removals were applied.

With pre-1983 ranges and historical removals, the northern bison population increased as observed up through 1988 (Figure 33A). However, the imposition of pre-1983 ranges reduced the predicted population below observed values particularly after 1993. With no removals and pre-1983 ranges, the northern bison population increased nearly linearly (Figure 33B). With the mid 1980's ranges and observed removals, the population nearly followed the observed trajectory (Figure 33C). Thus, the increase in range size from pre-1983 to mid-1980's certainly contributed to increased population growth. With no removals and mid-1980's ranges, the population increased to a higher level than with the pre-1983 ranges, also supporting the proposition that range expansion contributed to northern bison herd population growth.

The central bison herd responded similarly (Figure 34). With limitations to pre-1983 ranges and observed removals, the population was kept to a lower than observed level after 1988 (Figure 34A). With pre-1983 ranges and no removals, the population reached higher levels after 1988 (Figure 34B). With mid 1980's ranges and observed removals, the population reached only slightly higher levels than with pre-1983 ranges (Figure 34C). With no removals and mid-1980's ranges the population reached the highest levels of the four scenarios (Figure 34D). These results further show that the range expansions from 1983 onwards contributed to central bison herd population growth.

With no removals and bison restricted to mid-1980's ranges, northern bison reached an ECC that was approximately 85% of the ECC with their current ranges (Figure 35A,B). With restriction to pre-1983 ranges, they reached an ECC that was approximately 45% of the ECC with current ranges (Figure 35C). When the central bison herd was restricted to ranges of the mid 1980's, they reached an ECC that was 65% of the ECC with current ranges (Figure 36A,B). When they were restricted to their pre-1983 ranges, they reached an ECC that was 57% of that with current ranges (Figure 36C).

When ranges were restricted to the habitats predicted by logistic regression analysis (Olexa 2003, Appendices 14,25), the northern bison herd reached an ECC of 67% of that with the current ranges used in the model (Figure 37A). The central herd reached an ECC of 80% of that with the current ranges in the model (Figure 37B). The habitat maps predicted by Olexa for the northern range did not include any lands outside of the park boundary, including the Eagle Creek area. Also, his northern bison habitat map for February-May was restricted compared to the winter and transition season range maps used in the model (Appendices 9D,10C). Olexa's central bison habitat maps did not include areas outside the western boundary, and his winter map (Appendix 15D) did not include areas along the Norris-Mammoth road that were included in the modeled ranges (Appendix 9H).

#### *Bison Responses to Traveling in Unbroken, Broken, or Packed Snow*

An experiment was conducted to assess the potential energetic and population responses of bison traveling on surfaces with alternate snow conditions. Allocations of travel time were apportioned differently to travel in broken snow, unbroken snow, and bare ground (packed snow). Travel in broken snow reflects the fact that lead animals break the trail, creating tracks which other animals then follow. The "control run" was conducted with the proportions as found by Bjornlie (2000) and Bjornlie and Garrott (2001), which was 6% in unbroken snow, 74% in broken snow, and 20% on packed snow. Other scenarios included no travel in packed snow with 92%, and 74% and 26% travel in broken snow vs unbroken snow. The no packed snow, 92% broken snow scenario preserved the same ratio of travel in broken to unbroken snow as was observed by Bjornlie and Garrott. Scenarios with 100% travel on packed snow and 50% travel on packed snow were also examined. The scenarios were all run with the observed numbers of animals removed.

The energy used by bison during winter (November-April) varied amongst these scenarios by relatively small amounts (38A, 39A). In the control run, travel costs amounted to 11.0% and 10.7% of total costs in the northern and central herds, respectively. With 100% travel on bare ground, travel costs were 8.9% and 8.8% of total costs for the two respective herds. With no travel on packed snow and only 26% travel in broken snow, travel costs were 14.4% and 13.6% of total costs. Thus, the difference between the most and least stressful scenarios was a difference of 5.5% of total costs for the northern herd and 4.8% difference in costs for the central herd.



However, the population responses during 1969-2001 were disproportionately larger than the energetic differences (Figures 38B,C 39B,C). The population responses were small for the first 13 years but they magnified after that. Differences were amplified because population processes are multiplicative. Per-capita recruitment and mortality rates were applied to the number of animals present. As the number of animals diverged between scenarios, the small differences in recruitment and mortality rates became increasingly large. The end results in 2001 were, therefore, cumulative effects over 33 years.

The effect of winter road grooming is best assessed by comparing the control run to the run with no travel on packed snow and 92% travel in broken snow. There were 17% fewer bison in the northern herd and 9% fewer bison in the central herd in the 0% packed snow run than in the control run after 33 years. Bison numbers in the 100% packed snow run were much higher than the other runs, but this is a very unlikely scenario. There were 56% and 19% more bison in the northern and central herds respectively with 50% travel on packed snow.

## DISCUSSION

The model simulated nutritional patterns that were consistent with what has been observed in Yellowstone bison and elk. This required integrating data on forage production, forage quality, snow cover, spatial locations of foraging, forage intake rates, and energy expenditures. The most striking temporal pattern was the seasonal variation, from highs at the end of summer to lows at the end of winter. This pattern is consistent with evidence for gradual nutritional deprivation and loss of body mass over the winter in both bison (DelGuidice et al. 1994, 2001, Podruzny et al. 2002) and elk (Del Guidice et al. 1991a, 1991b, 2001). Seasonal variations in forage availability were due to snow, changes in forage biomass and forage quality, and the spatial locations of the animals. These seasonal changes have been shown to be stabilizing to plant-herbivore systems (Owen-Smith 2002). The other striking temporal pattern were trends of decreasing minimum body condition over time in both the bison and the elk, particularly between 1969 and the mid 1980s. This is indicative of increased competition for limited food supplies as the populations grew. It is interesting that a small fraction of forage was eaten in total (Part I, this report), yet the nutritional output indicates forage was nonetheless limiting. This suggests the model was successful in characterizing key resource areas or resource bottlenecks on the landscape. Another point of consistency with data is the simulated difference in nutritional status of the northern and central bison herds, with the latter reaching lower minimum condition. Del Guidice et al. 1994 similarly found that bison in Pelican Valley (the central herd) were more nutritionally stressed than animals on the northern range (the northern herd). It is also noteworthy that simulated population dynamics were consistent with data because this indicates that the model was making the correct linkages from foraging conditions to nutritional status, to population responses. Changes in the rates of population growth or decline were not tied to weather variables in a simple way. Instead, changes in simulated snow cover, forage production, affected forage intake rate, which then ultimately affected population growth

in a chain of process-based cause and effect.

Most of the interannual variations were tied to fluctuations in recruitment rates. Calf:cow ratios fluctuated considerably from year to year. Calf ratios were higher following mild winters due to the effect of winter nutritional stress in the gestating females. Following severe winters, calf ratios were much reduced. The difference in nutritional stress between the central and northern bison herds was also evident in calf ratios, with lower ratios simulated in the central herd. The temporal trend of reduced nutrition over time was, likewise, evident in the calf ratios. Minimum calf ratios, in the most stressful years, declined markedly in all three herds between 1969 and the mid 1980s. Maximum calf ratios in the least stressful years also declined in the central bison and the northern elk, but not in the northern bison.

The most serious discrepancy between the simulated and observed population dynamics was the underprediction of central bison numbers in 1995-1996 and the overprediction in 1998-1999. Nevertheless, the model fit the data well in 2000-2001. This could be a result of a problem with the model, or with the data. If it is the model, it is likely because the model overreduced population growth in 1993-1995. The model predicted a slowing population growth in those years partly due to increased competition for forage. Condition index of the central herd was relatively low in 1993/1994, but not in 1994/1995. Condition indices in 1995-1997 were declining, but did not reach the low levels simulated in the mid 1980s. The removals that occurred in 1993 probably contributed as much or more to the lower growth rate. If the population reached as low a point as suggested by the 1998-99 data, the following recovery was notably rapid. Such a recovery might be possible, given that the bison had access to a considerable area of range that they had expanded into. With fewer bison due to the removals of 1995-1997, competition for forage would have been much reduced. Indeed, the model simulated higher condition indices in 1998-2001. The other possibility is that the data were in error. However, intensive census work was carried by Hess et al. (2002) during 1997-1999, including sightability studies based upon radiotagged animals. The estimates for 1994-1996 could have also been high due to an underestimation of sightability in those years. Only a very simple sightability estimate was applied in years prior to 1998. Nevertheless, this was an interesting pattern in the data, and the fact that the model did not quite match the pattern suggests a need for further refinement of the model or the data inputs to the model.

The model was successful in simulated the near linear increase in the central herd observed in the data, and noted by Cheville et al. (1998). Growth was not exponential, nor did the population show signs of slowed growth or reaching an asymptote as in a logistic model. Instead, growth came to an abrupt halt due to the removals of 1995-1997. It is likely that the model simulated this continued expansion partly for the reasons suggested by Cheville et al. (1998), that the bison may be limited to a set of key forage resources during winter, which then supports a base “capital” of bison that produce offspring in proportion to the number of animals that can be supported by those key resources. However, range expansion likely contributed to the increase as well. Finer-scale dynamics reveal periods of higher and lower population growth

during the long-term linear trend. For example, growth was rapid in 1976-1982 and it was slow in 1974-1977 and 1983-1985. These variations could be tied to periods when ranges expanded or when the population reached a temporary limit based upon the area of range being used.

A linear trend of population growth was less apparent in the data for the northern herd, particularly between 1970-1988. The discrepancy between the model and the data in 1969-1975 was difficult to explain, but in this instance, it seems more likely to be a data problem, possibly in overestimating the sightability in those years. It is difficult to devise an explanation for the flat population growth in 1970-1982. It might be argued that was mainly due to a more limited winter range, however simulated condition indices do not support that view. Condition indices for the northern herd during that time were quite high, indicating little competition for forage. The periods of increasing population size in 1983-1988, 1989-1996 and 1998-2000 all exhibit linear trends. The population dynamic of this herd clearly showed a pattern of linear growth punctuated by catastrophic losses due to removals. It is interesting to ask the question, if the animals had not of been removed, would they have successfully dispersed to more suitable ranges before dying? If they then survived, would they have returned? We cannot know the answers to these questions at this time, but they are central to the philosophical underpinnings of bison management.

Predictions of the number of bison found outside of the park were consistent with data from the central herd. In particular, approximately the right number of animals was predicted to be in those locations, and the number of animals that were outside the western boundary was greater in 1996/97, 1997/98 than in other years. This was a combined result of the spatial distribution model's predictions that bison should move to areas of less snow cover when snow depths reach the point that they severely inhibit foraging, and the fact that the population was at an all time high in those years. The spatial redistribution model simply allocated animals to areas where the habitat was suitable, and because there were more animals, more animals were allocated to those areas. The other more subtle feature of the model predictions was that largest numbers of bison were predicted to be outside the western boundary in very late winter and into early spring. This is likely due to the fact that the snow melts earlier at lower elevations, and as a result, green-up starts earlier. Thus the bison find a situation where there is new green forage in that location at the same time the upper elevations are still covered with snow. This likely contributes to the tendency of bison to move to, and linger in this area at that time of the year.

The model was not quite as successful in predicting the number of animals outside the northern boundary. The model predicted more animals in those areas than were observed in the air censuses. There possibly several reasons for this discrepancy. The model is fundamentally saying that this is relatively suitable habitat in winter based upon snow and forage availability. However, the model does not represent various effects of humans on bison movement. Although the model predicted 250-300 animals would consistently be in this area in the early-mid 1980's, the data found 100-240, and only very sporadically. Interestingly, however, Meagher (1989a) noted that about 250 bison foraged in the Gardiner area in 1985/86 and 1986/87. These animals did not appear in the air census data, but it demonstrates that at least that many bison could make use of the area. Although Meagher (1989a) documented that boundary control techniques were

ineffective in deterring animals from crossing an imaginary line, it is not known to what effects the pervasive presence of humans in this area have had on relative habitat preferences at a broader spatial scale. The other factor that may contribute to the lower use of the area by bison, may be that the bison are well below the point of forage induced stress on most of the upper winter range, and there is less pressure to move outwards than predicted by the model. The model does not have a mechanism for social grouping *per se*, although it does ensure a minimum density in any grid-cell. The model does not represent groups or herds spread out over many grid cells but tied to particular home ranges. A more sophisticated model with group dynamics and movements coupled with better information on bison-human interactions may provide more accurate predictions.

According to the model, neither bison herd is at, or has ever been at, ecological carrying capacity in the traditional sense. More bison could be supported by the forage base, but the bison may not tolerate the increased levels of competition and nutritional stress. Furthermore, it is probably unrealistic to assume that bison can be successfully confined within a park that has no fenced boundary. Yet, the simulations of ECC made the implicit assumption that bison would be contained. If they could be contained, and there were no removals, they would rise to approximately 2500 in the northern herd and 4000 in the central herd (sightability corrected), with a considerable range of natural variation. At ECC, bison body condition indices would be markedly lower than they have been in recent times. This also implies that there would be far more mortalities, to balance the greater number of animals recruited. More importantly, there would be considerably more animals to manage outside the park boundaries.

A more realistic view is that the bison are at an ecological carrying capacity defined by their tolerance of nutritional stress. This is consistent with their range expansion responses, in which they have apparently regulated their density below their “comfort level” (Taper et al. 2000, Meagher et al. 2003). It also makes sense biologically, that bison would try to avoid starvation by moving in search of food. Bison evolved in a spatial and temporally variable climatic environment, the Great Plains, and they adapted to this variability through large-scale movements.

The model showed that interactions between bison and elk are significant for predicting bison population growth, nutritional status and ecological carrying capacity. Although bison and elk do exhibit a considerable degree of niche partitioning dietarily (Singer and Norland 1994), they also exhibit a significant degree of dietary overlap, particularly with respect to their uses of fine-leaved upland graminoids. Since 2001, elk populations have declined for various reasons (White and Garrott 2005). This decline is likely to increase bison population growth rates as well as their ecological and behavioral carrying capacities. Notably, the model showed that the northern elk herd is, and has been largely below ECC and has not totally self-regulated. Removals by hunters have had marked impacts on elk numbers, and have largely kept populations below their ECC. Thus, the combined effects of hunting and wolf predation on bison are important components of the overall bison management milieu.

An increased proportion of travel on packed snow led to minor energetic savings over an entire winter. However, the model showed that the cumulative effects of these small changes could be significant. Over the course of three decades, the small instantaneous population responses were compounded. Thus, the possibility that the energetic savings could have accelerated population growth cannot be dismissed. More subtle considerations might also be considered. While the energetic savings is small when averaged over all of the animals in the population and over the winter, the effect on instantaneous decision-making by bison should be considered. Individual animals to travel or not based upon the immediate stress imposed by deep snow conditions. Another aspect worth considering is that animal movements may be directionally biased by the tendency to move along a path of least resistance. Even though bison readily travel in unbroken snow (Bjornlee and Garrott 2001), they may be effectively “guided” by roads when they do make use of them.

Yellowstone bison were heavily managed through 1968, and following the cessation of artificial reductions, both the northern and central herds began to grow. Model predictions were consistent with this fact. One conceptual model is that the central herd has grown according to a “domino effect” (Meagher et al. 2003), in which the most central portion of the herd, the former Pelican herd, reached its carrying capacity, which then put pressure on the former Hayden herd, which then expanded increasing westward into the Firehole and Madison River Valleys. This is one way to conceptualize the process. However, more simply put, the central herd simply grew, following the cessation of removals, to a density where nutritional stress was high enough to elicit increased competition for key resources and subsequent behavioral responses to search for additional range. Once the new ranges were found, carrying capacity was increased in a positive feedback cycle. It is possible that road grooming contributed to the rate at which this process occurred, but on the other hand the model supported the idea that the herds did in fact reach levels of increased, and likely intolerable, nutritional stress when they were limited to their historical ranges deep within the interior of the park. This, combined with their mobile, nomadic nature (Meagher 1973) and their capacity to travel in relatively deep snow (Bjornlee and Garrott 2001), makes it likely that range expansion was an inevitable outcome.

Bison ecology in Yellowstone National Park has changed markedly since 1969, probably irreversibly so. It is likely that the bison herds will continue to grow until a severe winter elicits movements to lower elevations at the northern and western boundaries. At that point, brucellosis infected animals will be removed. The larger the herd is, the more brucellosis infected animals will be found outside the boundary and thus that many more animals will be removed.

The modeling approach used in this study proved to be useful for understanding and explaining the causes of population growth, range expansion, and bison dispersals to the boundary areas. The model should be updated periodically with new data, and refined based upon improved understanding.



## LITERATURE CITED

- Baker, D.L. and N.T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. *J. Wildl. Manage.* 46:694-703.
- Bjornlie, D.D. 2000. Ecological effects of winter road grooming on bison in Yellowstone National Park. M.S. Thesis, Montana State University, Bozeman.
- Bjornlie, D.D. and R.A. Garrott. 2001. Effects of winter road grooming on bison in Yellowstone National Park. *Journ. Wildl. Manage.* 65:560-572.
- Boone, R.B., M.B. Coughenour, K.A. Galvin, and J.E. Ellis. 2002 Addressing management questions for Ngorongoro Conservation Area, Tanzania, Using the Savanna Modeling System. *Afric. J. Ecol.* 40:1-14.
- Boroski, S., Z. Kransinski, L. Milkowski. 1967. Food and role of European bison in forest ecosystems. *Acta Theriol.* 12:367-376. 1967
- Buckley, D.J., F. Schreiner, M. Coughenour, and C. Blyth. 1995. The Ecosystem Management Model: Integrating ecosystem simulation modeling and Arc/Info in Parks Canada. In: GIS and Environmental Modeling: Progress and Research Issues: Proceedings of the Second International Conference on Integrating GIS and Ecological Modeling, Breckenridge Colorado.
- Carbyn, L.N., S.M. Ososenbrug, and D.W. Anions. 1993. Wolves, Bison and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. *Circumpolar Res. Ser. Num. 4.*, Canadian Circumpolar Inst., Univ. Alberta, Alberta, Canada.
- Cassier, E.F., D.J. Freddy and E.D. Ables. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildl. Soc. Bull.* 20:375-381.
- Caughley, G.H. 1976. Wildlife management and the dynamics of ungulate populations. pp. 183-246 in: T.H. Coaker (ed.), *Applied Biology*. Vol. 1. Academic Press, New York.
- Caughley, G. 1979. What is this thing called carrying capacity? Pp. 2-8 in M.S. Boyce and L. Hayden-Wing (eds.), *North American elk - Ecology, behavior, and management*. Univ. Wyoming Press, Laramie.
- Caughley, G. and J.H. Lawton. 1975. Plant-herbivore systems. pp. 132-166 in: R. May (ed.), *Theoretical Ecology*. Blackwell Scientific Publications, Oxford.
- Caughley, G. 1987. Ecological relationships. pp. 158-187 in: G. Caughley, N. Sheperd, and J.

- Short (eds.), Kangaroos: Their ecology and management in the sheep rangelands of Australia. Cambridge University Press, Cambridge.
- Cheville, , N., D.R. McCullough, L.R. Paulson. 1998. Brucellosis in the Greater Yellowstone Area. National Academy Press, National Academy of Sciences, Washington, D.C.
- Christopherson, R.H., R.J. Hudson and M.K. Christophersen. Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Can. J. Anim. Sci.* 59:611-617.
- Coppock, D.L., D.M. Swift, J.E. Ellis, and K. Galvin. 1986. Seasonal patterns of energy allocation to basal metabolism, activity, and production for livestock in a nomadic pastoral ecosystem. *J. Agric. Sci., Cambridge* 107:357-365.
- Coughenour, M. B. 1991a. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *J. Range Manage.* 44:530-542.
- Coughenour, M. B. 1991b. Grazing responses of upland steppe in Yellowstone's Northern winter range. *J. Appl. Ecol.* 28:71-82.
- 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 user's guide. Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins.
- 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: *Plants and Their Environments: Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem*, Mammoth Hot Springs, 1991. D. Despain (ed.). Technical Report NPS/NRYELL.NRTR-93/XX. USDI/NPS. Denver.
- Coughenour, M.B. 1999. Ecosystem modeling of the Pryor Mountain Wild Horse Range. Final Report to USGS. Biological Resources Division, National Park Service, and Bureau of Land Management. 55 pp. + 100 Figs. (Externally reviewed).
- Coughenour, M.B. 2002. Elk in the Rocky Mountain National Park Ecosystem - A Model-Based Assessment. Final Report to USGS Biological Resources Division, Ft. Collins, Colorado and U.S. National Park Service, Rocky Mtn. Nat. Park. 125 pp. 116 Figs. (Externally reviewed).



- Coughenour, M.B. 2005. Bison and Elk in Yellowstone National Park - Linking Ecosystem, Animal Nutrition, and Population Processes. Part 3 of a Final Report to U.S. Geological Survey, Bozeman, Montana.
- Coughenour, M.B. and F.J. Singer. 1996a. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecological Applications* 6:573-593.
- Coughenour, M.B. and F.J. Singer. 1996b. 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.
- Craighead, J.J., F.C. Craighead Jr., R.L. Ruff and B.W. O’Gara. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage as determined by biotelemetry. *Wildl. Monogr.* 33.
- Del Guidice, G.D., U.S. Seal, and L.D. Mech. 1991. Indicators of severe under-nutrition in urine of free ranging elk during winter. *Wildl. Soc. Bull.* 19:106-110.
- Del Guidice, G.D., F.J. Singer, and U.S. Seal. 1991b. Physiological assessment of winter nutritional deprivation in elk of Yellowstone National Park. *Journ. Wildl. Manage.* 55:653-664.
- Del Guidice, G.D., F. J. Singer, U. S. Seal, G. Bowser. 1994. Physiological responses of Yellowstone bison to winter nutritional deprivation. *Jour. Wildl. Manage.* 58:24-24.
- Del Guidice, G.D., R. A. Moen, F.J. Singer, and M.J. Riggs. 2001. Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988. *Wildl. Monogr.* 147:1-60.
- Ellis, J.E., J.A. Weins, D.F. Rodell, and J.C. Anway. 1976. A conceptual model of diet selection as an ecosystem process. *J. Theor. Biol.* 60:93-108.
- Ellis, J.E. and D.M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *J. Range Manage.* 41:450-459.
- Ellis, J. E., M. B. Coughenour and D. M. Swift. 1993. Climate variability, ecosystem stability, and the implications for range and livestock development. pp. 31-41 in R.H. Behnke Jr., I. Scoones and C. Kaven (eds.), *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas*. Overseas Development Institute, London.
- FEIS. Fire Effects Information System. U.S. Department of Agriculture, U.S. Forest Service.

<http://www.fs.fed.us/database/feis/index.html>

- Feist, M.. 2000. Basic Nutrition of Bison. Saskatchewan Agriculture and Food Extension Research Unit, Saskatoon, Canada..
- Gates, C.C. and R.J. Hudson. 1981. Weight dynamics of wappiti in the boreal forest. *Acta Theriol.* 26:407-418.
- Getz, W.M. and N. Owen-Smith. 1999. A metaphysiological population model of storage in variable environments. *Nat. Res. Model.* 12:197-230.
- Gogan, P.J.P., W. Clark, E.M. Olexa, J.A. Mack. 1998. Population characteristics of Yellowstone National Park bison. Annual Report. U.S. Geological Service, Montana State University, Bozeman.
- Green, R.A. 1998. Nitrogen distribution in a perennial grassland: the role of American bison. PhD. Dissertation. Colorado State University, Fort Collins.
- Green, R.A. and G.D. Bear. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. *J. Wildl. Manage.* 54:272-279.
- Hawley, A.W.L., D.G. Peden, H.W. Reynolds, W.R. Stricklin. 1981a. Bison and cattle digestion of forages from the Slave River lowlands, Northwest Territories, Canada. *Jour. Range Manage.* 34:126-130.
- Hawley, A.W.L., D.G. Peden and W.R. Stricklin. 1981b. Bison and hereford steer digestion of sedge hay. *Can. J. Anim. Sci.* 61:165-174.
- Hess, S.C., R.A. Garrott, J.J. Borkowski, and L L. Eberhardt. 2002. Aerial survey methodology for bison population estimation in Yellowstone National Park. Final Report to U.S. Geological Service, Biological Resources Division. Montana State University. Bozeman.
- Hobbs, N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildl. Monogr.* 101.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91:385-398.
- Hudson, D.E. and R.G. White. 1985. Computer simulation of energy budgets. Pp. 261-290 in: *Bioenergetics of Wild Herbivores*. R.J. Hudson and R.G. White (eds.). CRS Press, Inc. Boca Raton, Florida.
- Houston, D.B. 1982. *The Northern Yellowstone Elk - Ecology and Management*. Macmillan

- Publishing Co. New York. 474pp.
- Hudson, R.J. and S. Frank. 1987. Foraging ecology of bison in aspen boreal habitats. *Journal of Range Management* 40:71-74.
- Hudson, R.J. and W.G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. *Canadian Journal of Zoology* 64:1705-1708.
- Ilius, A.W. and I.J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecol.* 89:428-434.
- Ilius and Gordon, A.W. and I.J. Gordon. 1998. Scaling up from functional response to numerical response in vertebrate herbivores. Pp. 397-427 in: H. Olff, V.K. Brown and R.H. Drent (eds). *Herbivores: Between Plants and Predators*. Blackwell Science.
- Ilius, A.W. and T.G. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* 89:283-294.
- Marcum, C.L. 1979. Summer-fall food habits and forage preferences of a western Montana elk herd. Pp. 54-62 in: M.S. Boyce and L.D. Hayden-Wing (eds.), *North American Elks: Ecology, Behavior and Management*. University of Wyoming, Laramie.
- Meagher, M.M. 1973. *The Bison of Yellowstone National Park*. National Park Service Scientific Monograph Series Number One. U.S. Dept. Of Interior, National Park Service. U.S. Government Printing Office, Washington, D.C. 161pp.
- Meagher, M.M. 1976. Winter weather as a population-regulating influence on free-ranging bison in Yellowstone National Park. Pp. 29-28 in: *Research in the Parks: Transactions of the National Park Centennial Symposium*. (Symp. Ann. Mtg. Amer. Assoc. Adv. Sci., Dec. 1971). National Park Service Symposium Series no. 1. U.S. Government Printing Office. Washington, D.C.
- Meagher, M. 1989a. Evaluation of boundary control for bison of Yellowstone National Park. *Wildl. Soc. Bull.* 17:15-19.
- Meagher, M. 1989b. Range expansion by bison of Yellowstone National Park. *Journal of Mammalogy* 70:670-675.
- Meagher, M., M. Taper, C. L. Jerde. 2003. Recent changes in population distribution: the Pelican bison and the domino effect. pp. 135-147 in: *Yellowstone Lake: Hotbed of Chaos or Reservoir of Resilience?*. Proceedings of the 6th Biennial Scientific Conference on the Greater Yellowstone Ecosystem. R. J. Anderson and D Harmon (eds.). A joint publication of the Yellowstone Center for Resources and the George Wright Society.

- Merrill, E.H. and M.S. Boyce. 1991. Summer range and elk population dynamics in Yellowstone National Park. Pp. 263-274 in: R.B. Keiter and M.S. Boyce (eds. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press, New Haven, Connecticut.
- Merrill, E.H., N.L. Stanton, J.C. Hak. 1994. Responses of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park. *Oikos* 69:231-240.
- Moen, A. 1973. *Wildlife Ecology*. W.H. Freeman, San Francisco.
- Noy-Meir. 1975. Stability of grazing systems: an application of predator-prey graphs. *J. Ecol.* 63:459-481.
- National Park Service. 2000. Bison Management for the State of Montana and Yellowstone National Park: Executive Summary. NPS D-655a/August 2000. U.S. Government Printing Office, Washington D.C.
- Pac, H.I. and K. Frey. 1991. Some population characteristics of the northern Yellowstone bison herd during the winter of 1988-1989. Final Report to U.S. Geological Survey, Bozeman, Montana.
- Parker, K.L. and C.T. Robbins. 1984. Thermoregulation in mule deer and elk. *Can. J. Zool.* 62:1409-1422.
- Olenicki, T.J. and L.R. Irby. 2003. Determining forage availability and use patterns for bison in the Hayden Valley of Yellowstone National Park. Final Report to U.S. Geological Service, Bozeman, MT.
- Olexa, E., K.A. Keating, P.J. Gogan. 2003. Landscale-level habitat selection by bison in Yellowstone National Park. Report to U.S. Geological Survey, Bozeman, Montana.
- Owen-Smith, N. 2002a. A metephysiological modelling approach to stability in herbivore-vegetation systems. *Ecol. Model.* 149:153-178.
- Owen-Smith, M. 2002b. *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments*. Cambridge University Press.
- Peden, D.G., G.M. Van Dyne, R.W. Rice, R.M. Hansen. 1974. The trophic ecology of Bison bison L. On shortgrass plains. *Journal of Applied Ecology* 11:489-497.
- Parker, K.K., M.P. Gillingham, T.A. Hanley, and C.T. Robbins. 1993. Seasonal patterns in body mass, body composition, and water transfer rates of free ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska. *Can. Journ. Zool.* 71:1397-1404.

- Ravndal Vanderhye, A.V. 1985. Interspecific facilitation: do bison benefit from feeding on prairie dog towns? M.S. Thesis. Colorado State University, Fort Collins.
- Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York.
- Rush, W.M. 1932. Northern Yellowstone elk study. Montana Fish Game Commission, Helena, Montana.
- Singer, F.J. 1995. Effects of grazing by ungulates on upland bunchgras communities of the norther winter range of Yellowstone National Park. Northwest Sci. 69:191-203.
- Singer, F.J. and J.E. Norland. 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming following release from artificial controls. Can. J. Zool. 72:1383-1394.
- Singer, F.J. and R.A. Renkin. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. Great Basin Naturalist 55:201-212.
- Singer, F.J., M.B. Coughenour, J.E. Norland. 2003. Elk biology and ecology before and after the Yellowstone fires of 1988. Pp. 117-142 in: L.L. Wallace (ed.), After the Fires. Yale University Press, New Haven.
- Singer, F.J. 1991. The ungulate prey base for wolves in Yellowstone National Park I. Pp. 323-348. In: The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage, R.B. Keiter and M.S. Boyce (eds.). Yale University Press, New Haven, CT.
- Singer, F.A. 1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National; Park. Northwest Science 69:191-203.
- Singer, F.J. and J.A. Mack. 1993. Potential ungulate prey for grey wolves. Pp. 75-102 in: Ecological Issues on Reintroducing Wolves into Yellowstone National Park. R.S. Cook (ed.). Scientific Mongoraph NPS/NRYELL/NRSM-93/22. U.S. Department of Interior, National Park Service. Denver.
- Singer, F.J. and Harter, M.K. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecol. Appl. 6:185-199.
- Swift, D.M. 1983. A simulation model of energy and nitrogen balance for free-ranging ruminants. J. Wildl. Manage. 47:620-645.
- Taper, M.L., M. Meagher, and C.L. Jerde. 2000. The phenology of space: spatial aspects of bison density dependence in Yellowstone National Park. Final Report, U.S. Geological Service.

Biological Resources Division. Bozeman, Montana State University.

- Taper, M.L. P.J.P. Gogan. 2002. The northern Yellowstone elk: density dependence and climatic conditions. *J. Wildl. Manage.* 66:106-122.
- Thorne, E.T., M. Meagher and R. Hillman. 1991. Brucellosis in free ranging bison: Three perspective. Pp. 275-287 in: R.B. Keiter and M.S. Boyce (eds. *The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage*. Yale University Press, New Haven, Connecticut.
- Vore, J.M. 1990. Movements and distributin of some northern Yellowstone elk. M.S. Thesis. Montana State University, Bozeman.
- Wallace, L.L., M. Coughenour and M. Turner and B. Romme. 2004. Fire patterns and ungulate survival in Northern Yellowstone Park: The results of two independent models. Pp. 299-317 in L.L. Wallace (ed.), *After the Fires*. Yale University Press, New Haven.
- Watkins, W.G., R.J. Hudson and P.L.J. Fargey. 1991. Compensatory growth of wapiti (*Cervus elaphus*) on aspen parkland ranges. *Canadian Journal of Zoology* 69:1682-1688.
- Weisberg, P., N. T. Hobbs, J. Ellis, M. Coughenour. 2002. An ecosystem approach to population management of ungulates. *J. Environ. Mgmt.* 65:181-197.
- Weisberg, P., M. Coughenour, and H. Bugmann. 2006. Integration of Large herbivore - vegetation processes in a landscape context. In: Kjell Danell and others (eds.), *Large Herbivore Ecology and Ecosystem Dynamics*. Cambridge University Press. (In Press).
- White, P.J. and R.A. Garrott. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. (In press).
- Wickstrom, M.L., C.T. Robbins, T.A. Hanley, D.E. Spalinger, and S.M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *J. Wildl. Manage.* 48:1285-1301.