

## 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),

$$\begin{aligned} \text{Etrv}_{\text{snow}} &= \text{Etrv} * (1.0 + \text{Fsnw}) \\ \text{Fsnw} &= (\text{Ftrv}_{\text{brk}} * \text{Fsnw}_{\text{brk}}) + ((1 - \text{Ftrv}_{\text{brk}}) * \text{Fsnw}_{\text{unbrk}}) \end{aligned}$$

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.

$$\begin{aligned} \text{Snden} < 0.3 & \quad F_{snw_{unbrk}} = 0.0071 * Ru * e^{0.019 * Ru} \\ & \quad F_{snw_{brk}} = 0.0071 * Rb * e^{0.019 * Rb} \\ \text{Snden} \geq 0.3 & \quad F_{snw_{unbrk}} = 0.0123 * Ru * e^{0.0223 * Ru} \\ & \quad F_{snw_{brk}} = 0.0123 * Rb * e^{0.0223 * Rb} \end{aligned}$$

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

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

where  $Sndp_{brk}$  and  $Sndp_{unbrk}$  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  $MJ/d = 0.294W^{0.75}$ , 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  $-10^{\circ}\text{C}$ , 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,  $\text{Female}_i$  is the number of females in age class  $i$ ,  $\text{Birthrt}_i$  is the maximum birth rate by age class, and  $\text{CI}_{\text{gest}}$  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

$$\text{Deaths}_i = \text{Animals}_i * \max[\text{Deathrt}_{\text{Nom}}, \text{Deathrt}(\text{CI})]$$

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.