Interactions Between Grazing Herbivores and Herbaceous Vegetation on a Heterogeneous Landscape - Yellowstone National Park

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Spatial-Dynamic Modeling of Bison Carrying Capacity
in the Greater Yellowstone Ecosystem:
A Synthesis of Bison Movements, Population
Dynamics, and Interactions with Vegetation

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INTRODUCTION

The role that herbivores play in ecosystems depends fundamentally on how they influence plant and soil processes, and conversely, how plants and soils respond to herbivory. An understanding of plant and soil responses to herbivory is required to predict herbivore population sizes and productivities. Whether the herbivores are food limited or predator limited or both, herbivore population density and productivity depends upon forage productivity. Forage production is determined by abiotic factors, soil nutrient availability, soil microbial processes, and plant responses to herbivory. Plant responses to herbivory are a complex outcome of interacting processes at ecophysiological, population, and ecosystem levels of organization (McNaughton 1979,1983, Detling 1988, Archer and Smeins 1991, Frank 1998). Plant responses to herbivory are directly related to the loss of photosynthetic leaf area and meristems. Losses of photosynthetic leaf area and meristems could reduce plant growth rate . However many plants coevolved with herbivores (Coughenour 1986, Milchunas et al. 1988), and natural selection has bestowed a variety of traits on such plants which enable them to compensate for tissue loss to herbivory (McNaughton 1983), or resist grazing through avoidance and tolerance mechanisms (Briske 1991). Compensatory growth may partially, exactly, or overly replenish the biomass lost to herbivory (McNaughton 1979,1983). However, benefical effects of grazing on plant growth or fitness have been controversial (Belsky 1986), and clearly, there is some limit to the ability of plants to withstand herbivory, even when they have coevolved with herbivores (Coughenour et al. 1986, Briske 1991).

Herbivores, and therefore plant and ecosystem responses to herbivory, are heterogeneously distributed across the landscape, and it is logical to hypothesize that this heterogeneity plays an important role in ecosystem level outcomes (Coughenour 1991a, Hobbs 1999). Some portions of the landscape inevitably experience heavier levels of herbivory than others. Because plant growth and other ecosystem processes may respond non-linearly to grazing intensity (McNaughton 1979, Detling 1988, Briske 1991), the ecosystem level outcome of spatially heterogeneous grazing intensity will not be equivalent to the response to the spatially averaged grazing intensity. Further complicating the prediction are the heterogeneous distributions of soils and plants across the landscape. Plant growth responses to environmental factors may also be non-linear, resulting in a divergence from plant growth under average conditions.

Spatially heterogeneous plant-herbivore interactions could be central to the functioning of the Yellowstone ecosystem. Large herds of elk (*Cervus elaphus*) and bison (*Bison bison*) move throughout a heterogeneous matrix of grasslands, shrublands, and forests (Meagher 1973,

Houston 1982, Frank and McNaughton 1992, Coughenour and Singer 1996a). Between 1968 and the mid 1990's, elk and bison numbers increased under a policy of natural process regulation (Coughenour and Singer 1996a) (Figure 1). The northern elk herd stopped growing as it reached food-limited carrying capacity in the mid 1980's. More recently, herd size has declined in response to combined hunter offtake and wolf predation, and possibly other less obvious factors (White and Garrot 2005). The two bison herds continued to grow through the 1980's and mid 1990's, supported by an increasingly large forage base as they expanded their ranges, declined during a series of severe winters in the mid 1990's (Meagher 1989, Meagher et al. 2003, Taper et al. 2000), but more recently have increased. Bison have expanded their ranges and have increasingly migrated beyond the park boundaries, suggesting they may have reached their carrying capacity within the park. These herbivores have notable effects on the structure and functioning of vegetation and soils, but herbivory levels and effects are likely quite heterogeneously distributed. the spatial distributions of herbivory and available forage must be characterized. Thus, the spatial distributions of herbivory and available forage must be characterized to the effects of herbivory on plants and soils and the degree to which forage productivity and availability limit the herbivore populations.

There have been few studies of the spatial distribution of herbivory in Yellowstone National Park.Wallace et al. (1995) found that elk and bison feeding was randomly distributed at fine spatial scales, but that ungulates select feeding sites based on forage abundance at landscape scales. Olenicki and Irby (2003) studied bison feeding locations, and sampled offtake intensity over many sample points, but did not develop a generalized explanation for the distribution of herbivory. The spatial distributions of Yellowstone elk and bison have been studied by various researchers. Barmore (2003) and Houston (1982) studied elk, and Meagher (1968) studied bison habitat utilization at both local and landscape scales. These authors found that habitat utilization was responsive to forage, slope and aspect, snow depth, and tree cover. Habitat variables often had different influences in different seasons. Boyce et al (2003) found that elk selected habitats differently at different spatial scales, and that different scales came into play in winter vs. summer. Taper et al. (2000) carried out analyses of aerial survey data to study bison density distributions, but did not relate the densities to habitat features. They did, however, show that bison regulated their density through range expansion responses to population increases.

Forage production across the northern elk winter and summer ranges has been assessed using a landscape carrying capacity model (LCCM)(Coughenour 1994, Coughenour and Singer 1996b). Forage production was estimated based upon a synthesis of data describing characteristic productivity values for predominant habitats, and productivity responses to annual and seasonal precipitation. Plant growth did not respond to herbivory and nutrient cycling and soil processes were not considered. A more complex ecosystem model (SAVANNA) was also used to estimate food-limited carrying capacity over the winter and summer ranges (Coughenour and Singer 1996b). However, plant and ecosystem responses to herbivory and the spatial distributions of herbivory were not closely examined. A spatially explicit modeling of elk foraging (NOYELP) was developed to assess interactions between forage, fire, and herbivory on the elk winter range (Turner et al. 1993,1994). However, as in the LCCMs the plant growth model was primarily

driven by precipitation, plant responses to herbivory were not simulated, and there was no assessment of the spatial distribution of herbivory. Despite differences in model formulations and spatial resolution, the LCCM and NOYELP made similar predictions (Wallace et al. 2004). Notably, in all of these previous studies, only elk have been considered. No ecosystem modeling studies involving bison have been carried out in Yellowstone to date.

Thus, the objectives of this study were a) to assess the distribution of bison and elk herbivory in the Yellowstone National Park ecosystem, and b) to estimate the spatially variable responses of herbaceous plants and soils to herbivory. A spatially explicit, process-oriented ecosystem model was used to integrate information about plants, soils, herbivore distributions, and herbivory across the Yellowstone landscape. The results are relevant to bison and elk management, concerns about ungulate overabundance, the degree to which elk and bison populations are food-limited, and explanations for bison range expansion and migration beyond the park boundaries..

MODEL DESCRIPTION

Overall Model Structure

A spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems (SAVANNA, version 5a)(Coughenour 1992, 1999, 2002) was parameterized and tested for the Yellowstone ecosystem. The model is composed 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. Grid-cell size is scaled to the spatial extent of the simulated spatial domain so as to maintain a sufficient degree of realism in capturing landscape-scale heterogeneity while keeping run-time to an acceptable length. Within each grid-cell the model simulates three vegetation patch types or "facets." These are defined by the fractional covers of herbaceous plants, shrubs, and trees. Within each facet, the model simulates plant growth and soil water budgets. Variables results are scaled-up to the grid-cell level by multiplying the variables by the fractions of the grid-cell area covered by each facet, and summing the products over all facets.

Plant Submodels

The plant growth submodel simulates net primary production (NPP) and the turnover of plant biomass. The plant population submodel represents herbaceous plants in terms of basal cover and woody plants in terms of plant numbers. The growth and population models are described in more detail elsewhere (Coughenour 2005a). Here, I describe the key processes

involved in plant responses to herbivory.

Photosynthesis is simulated affected light, water, temperature, and plant nitrogen concentration. Herbivory may affect photosynthesis directly or indirectly. The direct effect is the removal of photosynthetic leaf area. By removing transpiring leaf area, herbivory may prolong soil moisture availablity, and thus photosynthesis. Light interception is modeled using a Beer's law formulation. Three canopy layers are simulated. Consequently, herbivory may reduce self shading by reducing both live and senescent shoot tissues.

Allocation of photosynthate to roots vs. shoots is affected by phenology, water, and nitrogen. Under increasing water or nitrogen limitation, allocation to roots increases. Thus, herbivory may decrease allocation to roots by alleviating soil water or nitrogen limitations. In later phenological stages, allocation to roots increases. The fractional allocation to leaves, stems, and inflorescences depends upon species or plant functional group.

Phenology normally progresses with time, but herbivory may keep plants in a juvenile growth stage if shoot:root ratio is kept low. This may, in turn, alter root:shoot allocation as just described. Leaf nitrogen concentration declines with advancing phenological state. Irrespective of herbivory, plants go into dormancy at the end of the growing season in response to daylength or cold temperatures. When leaves senesce, nitrogen is retranslocated back into the perenniating root system. Thus, when herbivory occurs during winter, plants loses less nitrogen.

Shoot and root tissues turn over at a nominal rates, but mortality rates increase under increasing soil moisture stress. For example, fine-leaved grass shoots are assumed to have a life span of 200 days, but as soil moisture declines to zero, life span declines to 15 days. Roots turn over every 1.5 years, but when the soil is completely dry, root longevity is reduced to 0.5 year. When leaves senesce, nitrogen is retranslocated back into the perenniating root system. Thus, if herbivory occurs during winter when leaves are primarily senescent, the plant loses less nitrogen than if herbivory occurs during the growing season.

Plants maintain a pool of labile carbon, largely consisting of carbohydrates. Early regrowth in the spring or following grazing is supported by this pool until needs can be met by photosynthesis. The pool is replenished in later phenological stages.

Herbaceous population dynamics are represented in terms of a basal cover index. The basal cover index expands when root biomass is high relative to the root biomass that would be expected given the current basal cover. It decreases when root biomass is low relative to expected root biomass. Maximum shoot biomass is limited by basal cover, thus there is a population constraint on productivity. Through this mechanism, the model can simulate decreases in range condition due to excessive herbivory. If grazing is excessive, root biomass will decline relative to the expected value and consequently, basal cover, and thus maximal shoot biomass will decline. When grazing pressure is alleviated, root growth increases relative to the expected value, basal cover increases, and consequently, so does aboveground productivity. Importantly, rangeland

recovery takes time.

Nitrogen Cycling and Decomposition Submodel

A decomposition and nitrogen cycling submodel simulates the breakdown of dead plant materials and animal feces and urine, and the formation and turnover of soil organic matter (SOM). The decomposition submodel is based upon the CENTURY model (Parton et al. 1987, 1993). Inorganic nitrogen (ammonium and nitrate) is released (mineralized) from decomposing materials if substrate nitrogen concentration is higher than the N concentration of microbial biomass. Mineral N is taken up from the soil (immobilized) if substrate nitrogen concentration is lower than microbial N concentration.

Nitrogen in plant tissues consumed by herbivores is recycled as either urine or feces. It is assumed that 50% of N flows to feces and 50 % to urine. The undigestible fraction of carbon intake flows to feces. Fecal C and N are partitioned to structural and metabolic litter. Urine N flows to inorganic N (ammonium and nitrate).

Herbivory Submodel

Forage intake rate responds to forage biomass according to a functional response (Part 3, this report). Below 2 g/m^2 forage is ungrazable. This refugia is critical in situations of heavy grazing as it allows the plants to persist, albeit at a very low biomass density. As forage biomass increases, forage intake rate increases, with intake rate eventually reaching a maximal value. A type I response is used, which linearly increases from 0 at 2 g/m^2 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^2 forage biomass and above (Hudson and Frank 1987) while for elk it is maximal at 92 g/m^2 (based upon Wickstrom et al. 1984, Hudson and Watkins 1986). While the functional response is important because it predicts forage intake rate, it is also important for plants because it, together with herbivore density, determines total offtake and thus grazing intensity. 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 (Part 3, this report). Forage intake rate declines with decreasing forage quality due to increased rumen retention time (Feist 2000).

Forage intake rate is affected by snow. Above a certain snow depth, intake rate declines linearly with increasing depth. Carbyn (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 parameterize the function so that snow has no effect

below 50 cm depth. Above 50 cm, intake rate declines to 15% of the maximum at 85 cm, and it declined to zero at 150 cm (Coughenour 2005b). Snow has not effect on elk intake rate below 30 cm depth, then it decreases intake to 15% of the maximum at 65 cm depth and to zero at 85 cm depth.

Once forage intake rate is calculated, it is partitioned among plant types and tissue types as affected by preferences and relative availabilities. Diet composition is modeled using dietary preference weights specified by plant type and tissue type, similar to Ellis et al. (1976). The preference weights are multiplied by forage biomass densities and the products are summed and normalized to give a sum of dietary fractions totaling 1.0. Preference weights were calibrated so that simulated diets closely matched observed diets.

Ungulate Spatial Distribution Submodel

The herbivore spatial distribution submodel dynamically simulates animal distributions over the simulated landscape or region. Essentially, it is a dynamic habitat selection model. There are two common approaches for modeling habitat selection. One is to model habitat suitability or habitat effectiveness as a function of key habitat variables. Habitat suitability models have been in use for decades (U.S. Fish and Wildlife Service 1981). The second is what has come to be known as resource selection functions (Manley et al. 2002 , Boyce et al. 2003 , Olexa et al. 2003), which are basically logistic regressions (Keating and Cherry 2004). Here, the habitat suitability approach was taken because it is more intuitive and it has been successfully used in SAVANNA in many applications.

The approach is to compute the habitat suitability index (HSI) of each grid-cell each week. This index is a dimensionless scalar where 0 indicates no use, and 1.0 indicates maximum preference. The HSI's are summed up across all grid cells and normalized so they sum to 1.0. Then animals in the population or herd is distributed according to the normalized HSI. The habitat suitability index of a grid-cell is affected by 0-1 scalar functions of preference-weighted forage biomass, green herbaceous biomass, snow depth, slope, tree cover, range location, and humans. Importantly, what is being modeled here is suitability for foraging, since forage intake rate is multiplied by animal density to determine offtake. Use of forests for bedding, for example, is not represented here. It is also important to realize that what is being modeled is distribution on a weekly time-step, that is, the time-integrated use of an area over a week This is much different than modeling individual movements and habitat selection at time steps of a day or less.

$$\text{HSI} = F(\text{forage}) \times F(\text{green herb}) \times F(\text{snow})$$
$$\times \min[F(\text{slope}), F(\text{elevation}), F(\text{tree cover})]$$
$$\times F(\text{range location}) \times F(\text{humans}) \times F(\text{random variable})$$

The forage function simply takes the value of the sum of the products of dietary preference weights times forage biomass over all dietary items in the grid-cell. If forage biomass was the only variable in the HSI equation and dietary preference weights were not used, the

animal distribution would be in direct proportion to forage abundance, which is also known as matching, or an ideal, free distribution (Senft et al. 1987). The inclusion of the dietary preference weight causes animals to be distributed more heavily towards locations with preferred food items. The function of green herbaceous biomass (Figures 2,3) represents selection for a greater abundance of green biomass. It is known, for example, that elk follow a wave of green up as it moves upslope during snowmelt in the Spring (Frank and McNaughton 1992). The function has a small non-zero value even with zero green biomass so that with zero green biomass, distributions will still be affected by the distributions of total forage biomass.

The effect of snow depth for elk was set based upon previous modeling and literature review (Coughenour 1994, Coughenour and Singer 1996b). The effect of snow on bison habitat selection was calibrated to attain realistic distributions. It was found that deep snow would have to be tolerated in order for bison to winter in places such as Hayden and Pelican Valleys.

The minimum of the slope, elevation, shade cover, and thicket cover effects is taken, hypothesizing that any one of these effects can override the others. For example, if the slope is too steep it doesn't matter what the cover is, and if cover is unsuitable it doesn't matter what the slope is. The effect of slope is parameterized to reflect the fact that bison prefer gentle or level topography (Barmore 2003), but do make use of slope up to 25% (Figure 2, Table 1). Elk are less constrained by topography, making use of slopes as steep as 45% (Figure 3, Table 1), based upon an unpublished habitat preference analysis by K. Symonds and F. Singer. The tree cover effect is used to express a preference by bison for open areas (Figure 3). Bison may use woodlands, but much less frequently that open grasslands. No tree cover effect is used for elk since they commonly use woodlands, especially during summer. Note that these functions are calculated based upon tree cover for 1 km or 500 m grid-cells. It is common for these large grid-cells to be only partly covered by trees, so these grid-cells should not be excluded. Also, the forage function will have an overriding effect on distribution, so if there is more forage in grassland grid-cells, the outcome will be an avoidance of trees.

Elevation was used to affect elk distributions during summer (Figure 3, Table 1). This proved to be necessary to simulate observed densities of elk during summer in Hayden Valley (Olenicki and Irby 2003). This area has a high biomass of forage and is otherwise a highly suitable habitat, yet elk densities are relatively low. Similarly, some explanation is necessary for elk avoidance of the lower elevation winter range during summer. Causes could include avoidance of insects, avoidance of waterlogged ground, or avoidance of predators. However, little is known about these factors so a simple elevation surrogate sufficed.

A uniform random variate (0.8-1.0) is introduced that prevents animals from attaining an ideal free (ie. perfect) distribution. There are many reasons why animals may not achieve a perfect distribution such as imperfect knowledge of resource distributions, physical inaccessibility, and time lags for travel.

The range function is a binary 0 or 1 that represents whether the grid-cell is in or out of

the population's range. Population ranges may be an outcome of knowledge, behavioral density regulation, primary wintering and rutting areas, physical barriers, or geographical constraints on interchange between subpopulations but none of these factors are represented explicitly. Range maps are prescribed to take effect at different times of the year, and to vary over years. For example winter and summer ranges may be specified, and for bison they may change over time due to range expansion (Chapter 7).

After animals are distributed according to the HSI, the model checks to see if densities are either above a behavioral maximum or below a behavioral minimum. The maximum and minimum values are applied to represent social aspects of animal behavior. Maximum values represent behavioral spacing or "mobile territories". Minimum values represent tendencies for group or herd formation as opposed to solitary habits. Maximum densities for bison and elk were set based upon aerial survey data (Taper et al. 2000, Hess 2002 , Coughenour and Singer 1996a). Higher values were used for bison during the rutting season (Table 1). Given both species tend to occur in herds or groups, minimum values were merely set to prevent the occurrence of extremely low densities on a weekly basis (Table 1). Animals in excess of the maximum density or below the minimum density are redistributed according to the HSI of cells with densities below the maximum.

Model Configuration

The simulated study area consisted of the combined ranges of bison and the northern and Madison elk herds (Coughenour 2005a). The spatial resolution of the simulations was 1 km. At this level of resolution, the broad-scale heterogeneities of the landscape are represented well, however, fine-scale heterogeneities are aggregated. The aggregation procedure samples from finer-scale data in such a way as to allocate grid-cells in proportion to underlying areal coverages. Thus, while not every vegetation patch is represented, the total area of coarse resolution vegetation patches was approximately equal to the total area of fine-resolution patches.

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. The model was thoroughly tested with respect to its capabilities for predicting herbaceous biomass production in a wide range of habitats (Coughenour 2005a).

Proportions of graminoids, forbs, willow and other shrubs in the diet were in agreement with data (Part 3, this report). Dietary composition was realistically split among upland graminoids (eg. Idaho fescue, bluebunch wheatgrass), forbs, and mesic graminoids (eg. sedges, Timothy, hairgrass) (Part 3, this report). Small portions of sagebrush, willow, and understory decidous shrubs were utilized. Conifers were very little used by elk, and not used at all by bison.

Two bison herds (central and northern) and three elk herds (northern, Madison, summer

immigrants) were simulated. The simulation for 1969-2001 used observed numbers of bison and elk during this period (Figure 1). Population dynamics were not simulated. Original count data were corrected for sightability based upon literature estimates (Figure 1). A constant number of 800 elk in the Madison herd was simulated. The summer range of the Madison herd was not included, so animals were removed from the simulations those months. A constant number of 7,600 summer immigrant elk was used during summer months. The seasonal ranges of the two bison herds (northern and central) were delineated from aerial survey data collected between 1969 and 1999 by Mary Meagher (Taper et al. 2000) between 1997 and 1999 by Hess (2002). Bison range expansion (Meagher 1989, Meagher et al. 2003) was represented by using more extensive seasonal range maps in successive years, based upon the aerial survey data (Chapter 7).

The northern elk winter range also expanded northwards during this period (Houston 1982, Coughenour and Singer 1996a), 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 Singer (1991) and Singer and Mack (1993).

Primary grazing areas are shown in Figure 4. Hayden and Pelican Valleys, and the Firehole area, and the west side are used by the central bison herd. Bison ranges expanded westwards during 1970',s 1980's, and early 1990's. The northern bison herd uses the northern winter range. They primarily wintered on the upper winter range until the late 1980's when they started using the lower winter range as well. The northern elk herd winters on the northern range. The Madison herd winters on the west side and Firehole area.

Model experiments were carried out to examine plant and soil responses to varying levels of herbivory. Several to many grid-cells of four different grassland types were simulated. The model was run for 50 years 1969-2018 using actual weather from 1969-2001 and stochastic weather after 2001. In the first experiment bison and elk were co-varied to achieve different levels of total animal unit months (AUMs) per square kilometer, where one AU is the equivalent of one female bison of 450 kg. The ratio of elk to bison was kept constant and similar to actual values. In the second experiment, elk were held constant and only bison numbers were varied.

The model was run using observed weather data for the period of 1969-2001. Stochastic weather for years beyond 2001 was based upon weather randomly from the 1969-2001 data. The model spatially interpolated weather data from individual stations to create monthly maps of precipitation and temperature (Coughenour 2005a). Simulated snowfall, snowmelt, and resulting snowpack dynamics compared favorably with data (Chapter 3). On grid-cells of thermally warmed ground (Figure 4) snow melt rates were accelerated, resulting in reduced or no snow cover. Thermal areas included riparian areas warmed by thermally warmed river water in the Firehole area and along Madison River and Cougar Creek on the west side. Comparisons were made between results in 1969-1981 and those in 1982-2001 to examine time trends. Comparisons were made between simulations with and without bison and elk to assess effects of herbivory.

The effects of bison herbivory were determined in an experiment where elk numbers were held constant, and bison numbers of 1,000-4,000 and 2,000-7,000 in the northern and central herds respectively were simulated. Northern elk were held at 15,000. Madison elk were held at 800. Summer immigrant elk were fixed at 7,600. Bison range extents were based upon observations of 1994-2001 (Taper et al. 2000). The model was run for 50 years with stochastic weather, randomly sampled from the 1969-2001 weather data.

RESULTS

Plant and Soil Responses to Herbivory

Covaried Bison and Elk Densities

On the northern winter range, bison graze year around, while elk mostly graze during winter. However, elk graze portions of the winter range in early spring as regrowth occurs following snowmelt at successively higher elevations (Frank and McNaughton 1992). To bracket the range of grazing regimes imposed in this area, simulations were conducted with year-long bison, and either winter-only (6 months) or year-long elk grazing.

On dry sagebrush grassland sites on the upper northern winter range, as total AUM's were increased from 0 to 563, with elk present only during winter, ANPP (aboveground net primary production) increased asymptotically (Figure 5, Table 2). At the highest AUM, there were 12.4 bison per km2 and 134 elk per km2 (Table 2). Offtake also increased asymptotically, and it increased as a fraction of ANPP. Even at the highest stocking rate, offtake was only just over 50%. When elk were allowed to graze year-around, however, ANPP increased a small amount under light stocking, but as AUM's continued to increase, ANPP decreased (Figure 5, Table 2). Offtake increased, peaked at 475 AUM/km2, then declined as a result of reduced forage productivity. Importantly, because offtake leveled off and then declined with increased stocking, offtake per animal would have declined. Despite the slight increase in ANPP with winter elk grazing, standing crops of grass and forb did not increase (Table 2). Despite the increase in offtake, however, standing crops did not decline, indicating compensatory growth. However with year-long elk grazing, standing crops declined. Grass biomass declined well before forb standing crops due to dietary preferences for grass. Standing crop declined due to offtake and reduced ANPP. With winter elk grazing, nitrogen mineralization from decomposing plant material remained constant (Table 2). However, nitrogen returned by animals increased continuously. Thus, total N recycling, the sum of the two, was enhanced by herbivory. Under year-long elk grazing, however, N mineralization declined with increased herbivory, most likely due to decreased plant growth and transfers to litter. Animal N return increased at first, but declined at the highest stocking rate due to reduced offtake. With winter elk grazing, belowground NPP , root biomass, and soil organic matter (SOM) were not affected by increased stocking rates (Table 3). With year-long elk grazing, BNPP, root biomass and SOM pools decline with increased stocking rates (Table 3).

10

Similar responses were predicted for moist sage grasslands on the upper northern winter range, particularly with elk grazing only during the winter (Figure 6, Tables 4,5). ANPP and offtake decreased sharply above 249 AUM when elk were present year around (Figure 6, Table 4). As with the dry site, the moist grassland grass and forb standing crops were not affected by increased herbivory. N mineralization declined slightly, and animal N return increased (Table 4). With year-long elk grazing, however, grass and forb standing crops declined, along with N mineralization. Animal N return increased and remained basically constant at higher stocking rates. With winter elk herbivory, BNPP, root biomass, and SOM were unaffected by herbivory (Table 5). However, with year-long elk grazing these variables declined with increased herbivory pressure.

The moist sagebrush grasslands of Hayden and Firehole River Valleys and the thermally warmed grassland of the Firehole area are grazed by bison year around. However elk only graze the Hayden Valley during the summer months. The Firehole area is grazed by elk from the northern herd only during summer. However, a smaller resident herd of elk does winter in the Madison and Firehole River Valleys. Here, simulations were of year-long bison and summer only (4 months) elk grazing.

ANPP in Hayden Valley grasslands was stimulated by light grazing, it remained at or above ungrazed ANPP until approximately 400 AUM/km2, above which it declined (Figure 7, Table 6). Offtake increased through 400 AUM/km2 and declined above 600 AUM/km2. Grass and forb standing crops in August were unaffected by herbivory below 200 AUM/km2. Grass biomass declined at higher stocking rates, while forb biomass did not decline until more than 600 AUM/km2. Nitrogen mineralization was unaffected through 261 AUM/km2 and declined above that. Animal N return increased up until 595 AUM/km2 then declined (Table 6). BNPP, root biomass, and SOM were unaffected through 202 AUM/km2 but declined above that rate (Table 7).

The responses for thermally warmed grassland were similar to moist sage grassland, except ANPP was maximal at higher stocking rates (Figure 7). Standing crops and N mineralization only declined above 266 AUM/km2 (Table 6). Animal N return increased up until 608 AUM/km2. BNPP and root biomass was unaffected until 269 AUM/km2 (Table 7).

Elk Constant, Vary Bison Densities

On dry and moist sagebrush grasslands and sedge meadows of the upper northern winter range, with winter elk grazing, herbivory slightly stimulated ANPP under light grazing (Figures 8,9). ANPP peaked at approximately 25 bison per km2 in dry and moist grasslands, and at approximately 40 bison per km2 in sedge meadows. Above these densities, ANPP declined (Figure 8,9). However, on the dry and moist grasslands, at nearly 50 bison per km2, ANPP was similar to that at 5 per km2. On sedge meadows ANPP at 90 bison/km2 was similar to that at 10 bison per km2. Offtake increased over this range of densities, but not as fast as bison numbers, so offtake per bison declined (Table 8). Grass biomass and total standing crop declined slightly as

bison density increased. Forb biomass increased slightly, however, indicating a shift from grass to forbs. Nitrogen mineralization increased, then decreased as bison density increased. Animal N returns continued to increase throughout.

Higher bison densities were examined in Hayden Valley and the Firehole Valley (Figure 10). ANPP increased up to about 25 bison per km2 as in the northern range grasslands. However, ANPP declined continuously between 25 per km2 and 75 per km2. Offtake increased up to about 40 bison per km2 and declined between 40 and 75 bison per km2. ANPP leveled off at a low level above 75 bison per km2, as did offtake. This is likely because bison offtake became limited by low forage biomass and when offtake leveled off, so did herbivory impact on ANPP. On moist sage grasslands, standing crop of grass biomass declined gradually up until 26 bison per km2, and it declined markedly above 26 bison per km2 (Table 9). Forb biomass was little affected until there were more than 64 bison per km2. On the thermal grasslands grass biomass declined gradually between 20 and 30 bison per km2, and it declined markedly above that density. Forb biomass was little affected until 70 bison per km2 was reached. Nitrogen mineralization rates were little affected below 16 or 20 bison per km2, but declined rapidly above 32 and 40 bison per km2 on the two respective grasslands. Animal N return continued to increase through 48 and 50 bison per km2, but declined above those densities on the two grasslands.

Bison and Elk Density Distributions 1969-2001

Mean bison density in Februaries 1969-1981 was 2-5 per km2 over most of Hayden and Pelican Valleys (Figure 11A). A few of the 1 km2 grid-cells were above that. These were primarily located on more productive mesic habitats or thermal habitats. For example the thermal grid-cell north of Pelican Valley and the thermal cell in northwest Hayden Valley had mean densities of about 24 per km2. Higher densities were estimated for the Firehole area, and were largely in the 15-25 per km2 range. Much of this area was thermally warmed (Figure 2), with less snow cover. There was no use of the west side during this period. On the northern range bison densities were 2-4 per km2 on uplands and 5-6 per km2 in mesic lowlands. The most productive riparian areas supported upwards of 25 bison per km2. There was no use of the lower winter range during this period.

During the period of 1982-1993, bison increased in number and their ranges expanded (Figure 11B). Despite the increased range size, bison densities were higher in Hayden and Pelican Valleys, and in the Firehole area than during 1969-1981. Densities of 6-7 per and 4-5 per km2 in Hayden Valley and Pelican Valleys, respectively. There were more cells in the 15-20 per km2 range than earlier. In the Firehole area densities increased to 25-30 per km2 in some places. Along the Madison River bison occurred at 15-20 per km2. Further west, densities of 5-15 per km2 were simulated. Certain cells outside the park boundary had 4-5 bison per km2 on average. On the northern range, bison expanded westwards and occurred at 3-6 per km2 on portions of the lower winter range. More cells were occupied in the Blacktail Plateau area, on the central portion of the upper northern range.

Densities declined during 1994-2001, reflecting the decrease in population size during 1996-1997. Densities in Hayden and Pelican Valleys were mainly in the 105 per km2 range. , except for certain thermal and productive habitats. Densities in the Firehole areas remained high however (25-30 per km2 in some cells). Use of the west side was similar to that in the previous period. During February, densities were lower outside the park. There was one cell outside the park with 15 per km2. Cells along the boundary had 3-6 bison per km2. Use of areas along the road from Norris to Mammoth (or between the Firehole area and the northern range) expanded. There was more expansive use of the Gardners Hole area (southwest tip of the northern range).

In Augusts of 1969-1981 the central bison herd used Hayden Valley at densities of 25-30 per km2 (Figure 12A). Two cells had much higher densities (40-80 per km2). Some bison from the central herd utilized the Mirror Plateau (between the northern range and Pelican Valley) at densities of 2-10 per km2. The northern herd was mostly located at higher elevations of the upper northern range including the upper reaches of the Lamar, Cache, and Calfee River drainages. Densities were mainly in the 1-10 per km2 range but a few cells had densities of 20-75 per km2.

During Augusts of 1983-1993, the central herd expanded to the Firehole area (Figure 12B) where they mainly occurred at 7-20 per km2, but with one cells reaching 48 per km2. They also used the Madison River riparian areas (along the road to the west entrance). One cell in that area had 54 per km2. Densities in Hayden Valley were mostly similar to those in 1969-1982, however more grid-cells were occupied. Use of the Mirror Plateau by the central herd was more expansive than in 1969-1982 and densities were slightly higher (2-10 per km2). The northern herd expanded summer use to lower elevations on the upper northern range. Densities were largely 5-20 per km2. However isolated areas of high production had 50-90 bison per km2.

During 1994-2001, densities and distributions in Hayden Valley and Firehole were similar to those in 1983-1993 (Figure 12C). However, use of the Mirror Plateau was much reduced, almost to nil. Use of the upper northern range was similar to that in 1983-1993.

Year-long densities in Hayden Valley in 1969-1982 averaged 2-10 per km2 for the most part with a few cells in the 12-16 per km2 range (Figure 13A). Pelican Valley supported 2-3 per km2 and Mirror Plateau supported 1-2 per km2. Use was distributed through the central to eastern portions of the upper northern range at 1-3 per km2 for the most part. However, some cells supported 10-15 bison per km2.

Bison densities rose to 7-10 per km2 in Hayden Valley in 1983-1993 (Figure 13B). Some scells had 10-15 per km2. Densities in Pelican Valley were at 3-5 per km2. On the Mirror Plateaus densities were 1-5 per km2. More cells were occupied in the Firehole area than in 1969-1982. Use of the west side was significant, with densities of 1-5 per km2 in most areas and with higher densities of 12-15 per km2 in productive and thermally warmed areas along the Madison and Gibbon Rivers. Densities outside the west boundary were in the 1-2 per km2 range. Use of the northern range expanded west and to lower elevations, with 1-3 bison per km2 throughout. Several cells supported 10-15 bison per km2.

In 1994-2001, bison densities in Hayden Valley declined to 3-6 per km2 in most cells, However several cells had 10-15 per km2. Densities in Pelican Valley declined to 1-3 per km2. Densities on the Mirror Plateau were similar to 1983-1993. Densities on the west side were also similar to 1983-1993. Densities on the northern range were slightly lower than in 1983-1993, however distributions were similar.

Elk densities in Februaries 1969-1982 were highest in the valley bottoms of the northern range (Figure 14A), reaching 50-90 elk per km2. Densities on the lower northern range were 15-25 per km2 and on higher elevations of the upper range they were 0-15 per km2. The Madison herd used the Firehole and Gibbon River valleys primarily at 10-20 per km2. Lower densities were predicted for the west side (0-2 per km2). Densities rose in 1983-1993 (Figure 14B). More areas of the valley bottoms were grazed at densities of 70-90 per km2. Areas receiving 10-20 elk per km2 also increased. The winter range expanded northwards during this period. During 1993-2001 areas with 50-75 elk per km2 increased, but areas with 75-90 elk per km2 decreased (Figure 14C). The area with 1-10 elk per km2 expanded considerably particularly along the southern fringes of the range. The change in distribution between 1983-1993 and 1994-2001 is consistent with greater numbers of elk and milder winters with shallower snow depths at higher elevations. Similarly, the Madison elk were predicted to be primarily concentrated at higher elevations in 1994-2001.

In Augusts, elk were scattered widely (Figure 15). Pockets of high elk densities (50-80 per km2) occurred on high elevation grasslands. Wet forests south of Lake Yellowstone also supported high densities. Densities generally increased between 1969-1982 and 1983-1994. However, densities in 1994-2001 were similar to those in 1983-1993.

Year around elk densities were mainly in the 1-10 elk per km2 range in 1969-1982 (Figure 16A), with densities in the 10-30 per km2 range at lower elevation of the northern range. Densities increased to 20-40 per km2 at lower elevations in 1983-1993 (Figure 16B). Densities in 1994-2001 were similar to those in 1983-1993 (Figure 16C).

Herbaceous Offtake and Plant Responses 1969-2001

Herbaceous biomass offtake by bison and elk in 1969-1982 was greatest in the productive riparian meadows of the upper northern winter range (Figure 17A). Offtake at lower elevations was greater than at higher elevations on the northern range. Offtake in Hayden Valley was 20-40 g/m2 and in Pelican Valley it was 20-30 g/m2 in most places. There was 40-60 g/m2 offtake in a limited number of grid-cells in the Firehole area. Offtake on the northern range and in the Firehole area in 1983-1993 was similar to that in 1969-1992. However, offtake in Hayden and Pelican Valleys rose to 40-60 g/m2 (Figure 17B). Offtake declined slightly on the northern range in 1994-2001 (Figure 17C). Offtake in Hayden and Pelican Valleys declined to levels similar to those in 1969-1982 (Figure 17C).

Offtake is usually measured by comparing biomass inside grazing exclosures to that

outside exclosures and grazing intensity is computed as the ratio of offtake to ungrazed biomass. Here it is computed as the ratio of offtake in a simulation with observed numbers of animals to biomass in a simulation with no animals. In 1969-1982, grazing intensity was highly variable over the northern range (Figure 18A). Most upland areas were grazed at 5-20%. Some valley bottoms were grazed at 40-50%. Some areas were grazed in the 50-70% range. Hayden and Pelican Valleys were mostly grazed at 10-30%. The Firehole area experienced grazing intensities of 20-40%.

In 1983-1993, a larger portion of the northern range was grazed at 40-50% (Figure 18B). However, the area grazed at 50-70% declined. Grazing intensity in Hayden Valley and Pelican Valleys rose to 30-50%. In the Firehole area, grazing intensity also rose into the 35-50% range in most places.

In 1994-2001, grazing intensities on the northern range were slightly reduced (Figure 18C). The heaviest grazed areas of the upper northern range and near the north entrance were grazed less intensively than in 1969-1982. Grazing intensities in Hayden and Pelican Valleys were in the 15-30% range for the most part. Grazing intensity in the Firehole area remained high, however, and more locations were grazed than in 1969-1993.

Offtake as a fraction of aboveground net primary production (ANPP) was less than offtake as a fraction of ungrazed biomass (Figure 19). This is because ANPP exceeds standing biomass due to the continuous transfer of shoots to litter. For example, while grazing intensity was 10-30% in Hayden Valley in 1969-1982, only 10-20% of ANPP was consumed. While grazing intensity in Hayden Valley in 1983-1993 was 30-50%, the fraction of ANPP consumed was 25-35%. Less than 50% of ANPP was consumed throughout, while grazing intensity was 60-70% in some areas.

The frequency distributions of grazing intensity across all of the bison ranges, inclusive of the entire northern winter range, are shown in Figure 20. In 1969-1982 the distribution was a negative exponential. Approximately 34 km2 was grazed at or above 50% intensity. About 85 km2 was grazed in the 35-50% range. The distribution changed in 1983-1993, with an increased area grazed between 35-50%. Approximately 57 km2 was grazed more than 50%. In 1994-2001, the area grazed at 20-25% increased markedly. The area grazed at more than 50% dropped to 25 km2. The reason there was less heavily grazed area in 1994-2001 than in 1969-1982 despite there being more bison and elk in 1994-2001, is likely due to the expansion of the bison ranges over that time period.

Frequency distributions of grazing intensity and fraction offtake of ANPP for the four primary bison grazing areas are shown in Figure 21. Including areas not grazed, the mean grazing intensities were 0.14, 0.24, 0.27, and 0.37 for the non-forested areas of the northern range, Hayden Valley, Pelican Valley, and the Firehole area respectively. Excluding areas grazed less than 1%, the means were 0.14, 0.28, 0.30, and 0.37. Including areas not grazed, the mean

fraction of ANPP consumed was 0.11, 0.17, 0.18 and 0.27 for the four respective areas. Excludeing areas grazed less than 1% the means were 0.13, 0.20, 0.21, and 0.31 respectively.

Time trends in ANPP were examined by taking the difference between ANPP in 1983-2001 and ANPP in 1969-1982 (Figure 22). With no bison or elk, the model predicted that there were decreases in ANPP over the period on non-forested habitats of the northern range (Figure 22A,B). The decreases were generally less than 20 g/m2/yr. Since there were no animals, it is most likely that the decreases were due to climate, for example increased water stress. In forests, there were generally increases in ANPP over the period. With bison and elk, similar changes in ANPP were predicted (Figures 22C,D), suggesting that herbivory had little effect on trends in ANPP between 1969 and 2001. This comparison demonstrates the importance of separating the effects of climate and herbivory in interpreting changes in rangeland condition.

The effect of herbivory is seen by examining the difference between ANPP in simulations with and without herbivores (Figures 23A,B). The responses were mixed. In some locations ANPP was stimulated by herbivory while in others there was no effect, or it was depressed. ANPP in non-forested areas was enhanced 10-30% by herbivory in portions of the northern range and over most of Hayden and Pelican Valleys and the Firehole area (Figure 23B). ANPP was depressed by herbivory by 5-15 g/m2 in some non-forested areas of the northern range. The absolute quantity of increase or decrease (g/m2) is difficult to assess without knowing the total amount of ANPP. The ratio of ANPP with herbivores to that without herbivores measures the herbivory effect relative to ANPP (Figure 23C,D). Increases of 5-20% were common in many areas on the northern range and in Hayden and Pelican Valleys, and the Firehole area. Where there were seemingly large depressions in ANPP in g/m2, the relative depression was very minor (<5%).

Root biomass was also variably affected by herbivory (Figure 24). Most changes were in the range of 0-15 g/m2, either positive or negative (Figure 24A,B). A greater area experienced small decreases than increases throughout the area. Relative impacts were less pronounced, however (Figures 24C,D). Root biomass was stimulated by less than 5% or it was depressed by less than 5% over most of the area. Root biomass was stimulated by 5-15% in some areas, and it was depressed by 5-20% in others.

Average responses of ANPP to herbivory by habitat type and location are shown in Table 10. ANPP in dry grasslands was stimulated by 3-5% in most areas. However it was depressed by 3-5% in the Firehole area. ANPP of moist sagebrush grasslands of the upper northern range was unaffected in 1969-1981 but it was depressed in 1982-2001. In Hayden and Pelican Valleys ANPP in this habitat type was stimulated by 7-13%. ANPP of hairgrass meadows was stimulated by 21-29% on the northern range and in Hayden Valley, but by only 0-2% in the Firehole area. Similarly, ANPP of sedge meadows was stimulated by 21-27% on the northern range and in Hayden Valley by only 2-17% in the Firehole area. ANPP of thermal areas was stimulated by 20-

24% on the northern range and 14-16% in Hayden Valley, and 2-17% in the Firehole area. ANPP of thermal areas was stimulated by 16-47% ANPP in high meadows was stimulated by 2-3%.

In contrast, root biomass in dry grasslands was depressed by 3-5% (Table 10). Root biomass of moist sagebrush grasslands was depressed by 0-4%. Root biomass in hairgrass meadows was stimulated by 0-7% on the northern range and in Hayden Valley but it was depressed by 9% in the Firehole area. Sedge meadow root biomass was depressed by 1-4% except in the Firehole area in 1982-2001 where it was stimulated by 2%. Root biomass in thermal areas was not affected in the Firehole area, and it was depressed by 1-5% in Hayden and Pelican Valleys. Root biomass decreased 1-2% in high meadows.

Effects of Varying Bison Density on Herbaceous Offtake, ANPP and Root Biomass

Using the ranges of 1994-2001, with 1000 and 2000 bison in the northern and central herds respectively, densities were primarily 1-3 per km2 on the northern range (Figure 25A, Table 11) except for sedge meadows that supported 10-25 per km2.. Portions of Hayden Valley and most of Pelican Valley had densities of 3-5 per km2. Densities of 10-15 per km2 were predicted to occur on thermally warmed ground in the Firehole area, as well as a Pelican Valley and along the Gibbon River. Sedge meadows supported 10-25 per km2 in these areas.

When bison numbers were raised to 2000 and 4000 in the two herds, densities rose proportionately to 2-3 per km2 over most of the northern range, to 4-5 per km2 in Hayden Valley and 5-8 over much of Pelican Valley. Some parts of Hayden Valley had 9-11 per km2, parts of Pelican Valley had 10-13 per km2 , there were 13-15 bison per km2 on thermally warmed ground in the Firehole area and Pelican Valley. Further increasing numbers to 3000 and 5000, and 4000 and 7000 in the two herds resulted in proportional increases (Figure 25 , Tables 12,13). However, it was evident that more grid-cells became occupied at higher densities. Interestingly, at the highest population levels, density in Hayden Valley decreased, while more grid-cells became occupied.

Seasonal dynamics of bison densities were pronounced (Tables 11-13), as would be expected given the seasonal uses of different ranges. As total numbers increased, changes in densities in different habitats were not necessarily proportional. A detailed description of these subtleties is beyond the scope of this report. However, as total numbers increased, it is likely that certain habitats became overly utilized, resulting in lower production, and then, less use by bison, which would then have shifted bison to other habitats despite the increase in total numbers.

Total graminoid consumption increased significantly as bison numbers increased (Figures 26,27). With 1000 and 2000 bison in the northern and central herds as existed in the early 1980's, offtake as a percent of ANPP was in the 1-20% range for much of the northern range, but areas receiving 20-50% offtake were common. Highest offtake was on the valley bottoms of the upper northern range. In Hayden and Pelican Valleys offtake was in the 15-30% range. In the Firehole

area offtake was more intense, reaching 30-50% of ANPP. When bison numbers were elevated to 2000 and 4000, percent offtake on the northern range increased, particularly areas with offtakes of 30% or more. In Hayden Valley, offtake was mostly in the 30-45% range. In Pelican Valley a significant fraction of the area was grazed at 30-35%. Percent offtake in the Firehole area rose to 40-62% in several areas. The increases were greater with 3000 and 5000 bison in the two herds. At the highest population sizes of 4000 and 7000, percent offtake rose to 60-70% in some areas of the upper northern range. Offtake rates in Hayden Valley reached the 60-65% level and in Pelican Valley offtake was 50-55% of ANPP in most places. In the Firehole area, offtake rose into the 65-72% range in some areas.

Frequency distributions of percent offtake shifted towards higher values with increased numbers of bison (Figure 27). The number of 1 km2 grid-cells grazed at 30-50% rose markedly when bison numbers were increased from 1000 and 2000 to 2000 and 4000. At that level approximately 34 km2 was grazed at 50% or more offtake. With 3000 and 5000 bison the number of grid-cells grazed to 45-50% rose markedly, and the area grazed in excess of 50% rose to about 140 km2. With the highest numbers of 4000 and 7000, approximately 230 km2 was grazed at 50% or above.

The impacts of bison grazing on herbaceous shoot biomass in April with 1000 and 2000 bison in the northern and central herds respectively (Figure 28) was to reduce it by 1-5% over most of the northern range, by 5-10% in Hayden Valley and Pelican Valley. The Firehole area had areas where biomass was 20-25% lower. With 2000 and 4000 bison, April biomass was 25-25 % lower in Hayden than without bison. On the northern range it was mostly 5-10% lower with a few exceptions. The reduction was higher with 3000 and 5000 bison. With 4000 and 7000 bison April biomass was 25-35% reduced on much of the northern range. It was 50-60% lower in most of Hayden and Pelican Valleys, and 50-70% reduced in some portions of the Firehole area. As population sizes were increased, offtake did not increase proportionately, particularly at the highest densities. For example, while bison numbers were 1.75 times higher in the Central herd run D than in run B, April biomass was approximately 1.4 times higher in run B than in run D.

Reductions in October biomass were not as large as reductions in April biomass (Figure 29), October values represent end-of-growing season values, while April values represent end-of-winter values. During the growing season, plants can partially or fully compensate for herbivory losses. During winter, there is no compensation and biomass is simply reduced. With population sizes of 1000 and 2000 bison, reductions were very small, being mostly less than 3% with a few areas rising to the 5-15% range. With 2000 and 3000 bison reductions rose to the 2-5% range over much of the northern range with some areas experiencing a 10-25% reduction. In Hayden and Pelican Valleys biomass was 10-15% lower in most places, but it was 15-35% lower in a few locations. October biomass was 12-15% reduced in several and 20-30% reduced in two locations locations in the Firehole area .

Impacts of bison grazing on herbaceous ANPP were mostly positive (Figure 30). ANPP was increased by 0-10% on much of the northern range with 1000 bison in the northern herd.

With 2000 bison in the central herd, ANPP was increased by 10-25% over much of Hayden Valley. In Pelican Valley it was increased by 2-10%. In the Firehole area some areas had increases of 15-30%. Increases were greater in mesic habitats throughout. Peak productivity values were predicted with 2000 and 4000 bison. As population sizes were raised above those levels, the stimulation of ANPP declined except in the most mesic and productive habitats on the upper northern range and the Firehole area.

In contrast, root biomass was primarily negatively affected by bison herbivory (Figure 31). With 1000 and 2000 bison, roots were largely unaffected. In some areas roots were reduced by 1-5% and in other roots were increased by 1-5%. Reductions of 5-10% occurred in some areas of the northern range and in Hayden Valley with 2000 and 4000 bison. A few locations in Hayden Valley and the Firehole area had 10-15% reductions. Withe 3000 and 5000 bison, reductions of 5-10% and 10-15% became more widespread. Root biomass was stimulated by 5-10 % in a few locations in the Firehole area. With 4000 and 7000 bison, much of the northern range had 5-10% less roots and some areas had 10-20% less. Roots in Hayden Valley were reduced the most, by 10-15% over most of the area.

DISCUSSION

Simulated responses to herbivory during 1969-2001 were consistent with the relatively large number of studies of plant responses to herbivory have been carried out in Yellowstone, particularly on the northern winter range. Over a vast majority of the area, ANPP was unaffected or was stimulated by herbivory by 0-13% in dry and moist habitats and by 2-47% in mesic and thermally warmed habitats. Similarly, the overall picture that has emerged from the data is that the herbaceous component of the northern range has not been negatively affected by herbivory, and in some cases, herbivory has been shown to increase primary production. Frank and McNaughton (1993) found 50-75% growth stimulation in mesic habitats and 10-30% stimulation in dry habitats. Frank et al. (2002) found that grazing stimulated ANPP by 21%. Studies of long term grazing exclosures revealed less green biomass in grazed plots in 1988, but no grazing effect was observed in 1988 (Coughenour 1991b). It was unknown if the lower green biomass was due to grazing removal in early spring, and only standing biomass rather than actual net primary production (NPP) was measured. Merrill et al. (1994) found more green biomass in ungrazed plots in early spring due to offtake. However by the end of the season there was no difference in grazed and ungrazed plots. Likewise, Singer (1995) found less green herbage in grazed plots, likely due to early spring offtake and an early snowmelt. Frank and McNaughton (1992, 1993) found that ANPP was greatly stimulated by herbivory in mesic *Phleum pratensis* (introduced Timothy) grasslands, and was slightly stimulated by herbivory (10-30%) in drier native grasslands.

In the simulations, herbivory during 1969-2001 decreased root biomass by 0-5% in most areas, but there were cases, such as in some *Deschampsia* and sedge meadows, where it was increased by 2-7%. Grazing has been shown to stimulate belowground root production (Frank et

al. 2002). In that study, which used mini-rhizotron technology, grazing stimulated root growth by 35%, but also increased root mortality by 22%. Merrill et al (1994) observed increased root mortality due to early spring grazing however root biomass fully recovered later in the growing season. Similarly, Frank et al. (2000) found that grazing stimulated root mortality, but it also stimulated root production. However, total root biomass inside and outside of long-term grazing exclosures was unaffected by herbivory (Coughenour 1991b). If live root biomass was in fact 5%-10% lower in grazed plots it would have been difficult to detect the change. This is because of sampling variance, but also because total, not live root biomass was sampled. Live root biomass could be 40% or less of total root biomass. Thus model predictions of slightly lower root biomass under grazing were consistent with data. Predictions of increased root biomass in some habitats were also consistent with data, but further investigation is required to determine the exact causes for such increases.

The model indicated that at light to moderate grazing intensities, nitrogen cycling is enhanced by herbivory, primarily through the added amount of nitrogen that is returned in dung and urine rather than by an increase in N mineralization from decomposing plant material. Studies carried out on the northern range have shown that grazing promotes nitrogen (Frank et al. 1994, Frank and Groffman 1998a,b, Frank et al. 2000). Unlike the model predictions however, these authors believed that grazing increased nitrogen mineralization, nitrification, and denitrification. Their studies measured total mineral nitrogen absorbed by buried ion exchange resins and did not distinguish between N recycled by animals and N. The N returned to the soil by animals shown in Tables 2,4,6,8 consisted of N in urine (50%) and feces (50%). The N in feces was transferred to soil surface "litter", while urine N was transferred to mineral N. Another study suggested that grazing may cause plants to stimulate soil microbial populations, and thus increase nutrient cycling and plant available nutrients (Hamilton and Frank 2001). It was unclear if the increased carbon transfer from roots to microbes was due to increased fine root mortality or exudation. The effect was only observed in the first 24 hrs after defoliation, and disappeared by 7 days. The model here did not represent short-term root mortality or increased exudation due to herbivory because the mechanisms are unknown. Very little is know about root exudation rates or how they are controlled. It would be important to incorporate this effect when it is better understood, however.

Simulated grazing intensities (offtake divided by ungrazed summer biomass) in 1994-2001 were comparable to observations on the northern winter range. The model predicted an average 14% reduction, but there was considerable spatial heterogeneity. Many areas were grazed less intensively and fewer areas were grazed more intensively (Figures 18, 21). Including areas grazed 5% or more the mean reduction was 20%. Comparisons of total biomass inside vs. outside long-term grazing exclosures showed an approximate 45% reduction (Coughenour 1991b) and a 39% reduction (Singer and Harter 1996) in biomass due to herbivory. These exclosures are located on the most heavily grazed portions of the winter range. Close examination of model outputs showed that in these locations, the model predicted reductions of 33-42%. While 40% reduction is not the mean, it is nearly the median simulated value (Figure 21A). Similarly, the model predicted variable fractions of offtake as a percentage of ANPP on the northern range.

Mean offtake was 14%, but offtake rates in the range of 15-35% were common. In comparison, Frank and McNaughton (1992) observed 21% offtake of ANPP and Tracy (1996) found 15% offtake of ANPP on northern winter range sites.

In Hayden Valley, the model predicted a 24% reduction in biomass overall, and a 28% reduction excluding areas with <1% offtake. Olenicke and Irby (2003) reported a mean year-long offtake of 31% based on 175 fixed plots, and 35% based on 166 paired plots. However in mid summer there was just 5.5% less biomass outside mesic exclosures and 7.7% less outside silver sage exclosures, There was 41% less biomass outside big sage exclosures. They termed these "adjusted percent offtakes", because they truncated negative offtake values to 0. This would inflate the actual offtake because negative values would be expected if biomass amounts were normally distributed. Calculating the mean unadjusted offtake as the weighted mean of "not grazed" and "grazed" plots (their Table 6) results in an actual mean offtake of 8% in fixed plots and 31% in paired plots. Unadjusted offtake was much less than adjusted offtake - 7% in mesic habitats, -1% in silver sage, and 18% in big sage. The model predicted herbivory would increase ANPP in Hayden Valley by 15-20% in most places. Two of the sites studied by Frank et al. (2002) were in or near Hayden Valley. Values for individual sites were not given, but across all their sites grazing stimulated ANPP by 21%, and ANPP was positively correlated with grazing intensity.

In the Firehole area, the model predicted a mean 37% reduction, with a 45% reduction in areas receiving more than 5% offtake. However, some grid-cells had 50-58% reductions. Dawes (1998) found 68% less biomass outside than inside fixed cages in 1996, and 84% less in 1997. However, out of 92 paired comparisons of biomass inside vs. immediately outside each exclosure, only 11 were significant ($p<0.05$) and 12 were near significant ($0.05<p<0.1$). Five of the significant and two of the near significant differences were in May, reflecting winter rather than summer utilization. In July and August, there were no differences in biomass inside versus outside of fixed cages in 1996, and only 2 out of 12 comparisons in 1997 were significant. This spatial variability in grazing is the probable cause of the large discrepancy between observed and predicted biomass amounts in the Firehole/Madison area. The reported large offtake percentage (68-84%) is inconsistent with the low number of significant paired comparisons (Dawes 1996). Large standard deviations (SD) were reported in standing crops. On average, the SD was 67% of the mean inside exclosures and 164% of the mean outside exclosures, which probably explains why no statistical differences were reported between mean biomass inside and outside exclosures. The model represented a realistic density of herbivores in this area, with realistic offtake rates. It is possible that within 1 km grid-cells certain areas could have been grazed more heavily than the 50-58% reductions simulated. However, using such rates to extrapolate over wider areas would be unwarranted.

Reported differences between standing biomass inside and outside exclosures have been spatially and temporally variable, and it has not always been clear that the differences have been due to offtake or to differences in plant growth. On the northern range Singer and Harter (1996) observed 0% difference between biomass inside and outside exclosures in spring and summer.

21

Coughenour (1991) found 48% less green grass biomass outside than inside one exclosure 1987 but no difference at three others. There was on average 17% less green grass plus forb outside exclosures on the upper winter range. Of all exclosure dates, there was more live grass inside exclosures in five cases, more outside in one case, and no difference in six cases. In 1988 there was 46% less green grass biomass outside exclosures on the upper winter range, but this was felt to be primarily a result of the combined effects of early spring grazing and the early onset of dry conditions that year. The unusually short growing season likely prevented compensatory growth. For example, Merrill et al. (1994) found more green biomass inside exclosures in May 1990, but by the end of the season there was no difference.

The model prediction of no impact of grazing on soil organic matter carbon was consistent with the findings of Binkley et al. (2002) and Schoenecker et al. (2002) who found no differences in total organic C inside vs. outside of long-term grazing exclosures in Rocky Mtn. Nat. Park. It is also consistent with other findings, that grazing does not necessarily reduce soil C or N. The effects of grazing on soil C and N are variable, and no consistent pattern has been detected (Milchunas and Lauenroth 1993, Burke et al. 1997). Grazing can decrease, have no impact, or increase soil C and N depending on conditions. It is often expected that grazing will decrease soil C and N, inasmuch as it decreases plant growth and C inputs to the soil (Holland and Detling 1990, Archer and Smeins 1991, Holland et al. 1992). When grazing is heavy enough to significantly reduce plant cover, plant production, and carbon inputs into the soil relative to carbon lost in microbial respiration, soil carbon must decline (Parton et al. 1987). It did so here, but only at high grazing intensities. At grazing levels where roots declined markedly, SOM declined in response.

In general, the model results as well as empirical data indicate that Yellowstone grasslands are capable of supporting recent bison densities, which have gone as high as 1000 in the northern herd and 4000 in the central herd (Figure 1). At these levels, with the current range area, bison densities are at levels where herbaceous ANPP is primarily stimulated or unaffected and root biomass is decreased to a small degree. However, a closer inspection of the model results reveals that these densities are likely to be near the upper end of sustainability for certain key portions of the landscape. While on average, recent grazing intensities may be sustainable, grazing intensity is heterogeneously distributed, with some areas receiving intensities well above the average. Responses of these key areas to herbivory may be viewed as being more sensitive indicators of sustainability than the average response to herbivory. On the other hand, a native grazing ecosystem may be expected to feature a range of grazing intensities, with some areas being grazed to the point of having reduced plant cover and productivity. Such a range of disturbance levels promotes a higher diversity of habitats, which may in turn promote higher diversities of flora and fauna. Thus, this grazing ecosystem may be near a point of optimality, but caution is warranted.

The model experiments in which grazing intensity was varied (Figure 5-10) indicated that primary production is optimal over a range of approximately 25-35% offtake, particularly under year-long grazing. Above 50% offtake of ANPP, and thus likely at grazing intensities of 35-45%

reduction of ungrazed standing crop, ANPP declines. The model also showed that root biomass declines at lower grazing intensities than ANPP. Two mechanisms of resilience were revealed in these experiments. The first was the fact that grasslands are more tolerant of winter grazing than year-long grazing. Those areas that are only grazed by elk in winter, primarily the northern range, tolerate herbivory by being grazed primarily when leaves have senesced and nutrients are stored belowground. However, bison graze the northern range year around, as well as Hayden Valley and the Firehole area. Areas that are grazed year-around are therefore most likely to be key areas to monitor. The other mechanism of resilience is the fact that offtake leveled off in the 40-50% offtake range. This means that herbivores are likely to become food limited at approximately the same rate of offtake that the plants can sustainably support. At higher levels of offtake, per-capita offtake diminishes rapidly, largely because ANPP has peaked at lower grazing intensities and declines at higher grazing intensities. Thus, herbivore densities would equilibrate with plant productivity.

In a spatially heterogeneous grazing ecosystem such as this, however, some areas may be grazed at higher densities than would otherwise be achieved in an equilibrial plant-herbivore system. This is because herbivore density is non-uniformly distributed and it is not distributed in proportion to primary production. In other words, the distribution is not an ideal, free distribution. Although the herbivore distribution model included a function which would distribute herbivores in proportion to forage availability, other factors also affect herbivore distributions such as snow cover, topography, and selectivity for certain dietary items and habitat types. It is possible in such a situation, that herbivores might occur at a higher density on some habitats than would be supported by the forage production in those habitats. The Herbivore densities may be maintained at a higher level by forage production in other habitats.

This is exactly what may occur in the case of thermally warmed habitats. These areas clearly attract bison and elk during the winter due to reduced snow cover (Meagher 1973, Garrot et al. 2002). Bison and elk densities could be maintained by forage production in other habitats, mainly by highly productive sedge meadows which support high levels of intake during summer, and subsequent storage of fat reserves which carry bison through the winter. Indeed, the model predicted that the Firehole area in particular, with its widespread thermally warmed ground, would experience the highest grazing intensities and be most likely to subject to grazing intensities which reduce plant cover. A significant area is grazed above the 0.5 grazing intensity level under recent bison densities (Figure 21G). However, as a fraction of ANPP, offtake was below 50% (Figure 21H), and root biomass was largely little reduced (Figure 24C).

However, there was one area where root biomass was markedly reduced. This was in the area of the lower geyser basin, also known as Fountain Flats (brown grid-cell along the west side of the road in the Firehole area in Figure 24C). Interestingly, this is an area where there is photographic evidence for a reduction in plant cover since the 1980's (Taper et al. 2000, Meagher and Houston 1998, Plates 32.1-3). Taper et al. (2000) hypothesized the decline in plant cover was primarily due to trampling rather than high levels of herbivory, however. They suggested that the unique soil properties of this habitat result in reduced water infiltration rates when soils are

23

trampled.

Because of the spatial heterogeneity of herbivory and the possibilities for non-ideal, free distributions, it is important to base assessments on the frequency distributions of grazing intensity and plant responses across the landscapes rather than mean responses. With bison numbers of 800-1000 in the northern herd and 3000-4000 in the central herd as occurred in the 1990's, the distribution of grazing intensities was reaching a limit, such that more areas were beginning to be grazed at high rates, above a 50% reduction of ungrazed aboveground biomass. With higher densities of 2000-3000 in the northern herd and 4000-5000 in the central herd, the number of heavily grazed sites increases sharply. It is suggested therefore that monitoring be based either upon an adequate sample that covers the range of variability over the landscape, or upon samples of key areas that are known to experience disproportionate grazing intensities, or both.

In summary, the spatial heterogeneity of grazing and primary production were central to the assessment of herbivory in the Yellowstone ecosystem. The spatial dynamics of seasonal range shifts, and range expansion by both bison and elk over time were important for determining grazing intensities and rangeland responses to herbivory. The grasslands are resilient to recent levels of herbivory, but herbivory levels are likely at a point above which close attention should be given to key habitats where grazing intensities are disproportionately high.

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