

Thus, feeding should be prohibited by regulations that are strongly enforced, and education of tourists to the problems caused by feeding is important.

Thirdly, mesocarnivores can be an umbrella species in the SNP ecosystem, especially because *Martes* species have comparatively large home ranges (Powell 1994; Xu et al. 1997) and take various food items (Murakami 2003). In addition, as most *Martes* species are known as forest dwellers (Buskirk and Powell 1994; Buskirk 1996), existence of Japanese sable may mean there is a healthy forest ecosystem. In order to evaluate the effectiveness of Japanese sable as an umbrella species, relationships between habitat preference among different forest types by Japanese sable should be studied. Currently, the dense sika deer population has changed tree composition in Shiretoko (Okada et al. 2000). Thus, it can cause cascade effects on Japanese sable ecology by reducing the supply of food resources. Evaluation of deer effects on sable ecology is important to predict future sable populations and forest ecosystem in SNP. In addition, a reforestation program, in the Shiretoko 100 m<sup>2</sup> Forest Trust, has been conducted inside SNP since 1997 (Ishigaki 2005). Reforestation progress of this program can be monitored by demonstrating changing habitat use by Japanese sable.

Contrary to Yellowstone National Park (12 native species, Buskirk 1999), SNP has low diversity of mesocarnivores (five native species). However, mesocarnivore roles in the natural ecosystem of SNP are as important as in Yellowstone National Park. We should strongly proceed with mesocarnivore management in SNP.

## 11. Ecosystem Research and Modeling in Protected Areas with Large Mammals Yellowstone as a Case Study

Michael Coughenour

### Abstract

Ecosystem research includes investigations of the direct and indirect interactions of soil, water, decomposition and nutrient cycling, plant growth, herbivory, and predation. These processes can be integrated in ecosystem models to make predictions of the complex outcomes of climate change, fire, hunting, herbivore population sizes and spatial distributions, and loss or reintroduction of predators. Much research has been conducted in Yellowstone on large herbivores, plant and soil responses to herbivory, and predator-prey interactions. Here, I describe how an ecosystem model has been used to integrate this information to provide a basis for explaining numbers and distributions of elk and bison as outcomes of climate, forage supply, winter foraging conditions, hunting, removals, and predation. The model has provided explanatory simulations of plant responses to herbivory and climate, elk (*Cervus elaphus*) and bison (*Bison bison*) population dynamics, bison migrations outside of the park, and indirect interactions between hunting pressure outside the park and climate and predation impacts inside the park. Therefore, it is a useful tool for interpreting ecosystem dynamics and deciding amongst alternative management strategies. I suggest that managers of parks and protected areas such as Yellowstone and Shiretoko consider supporting ongoing efforts to develop, maintain, and evolve ecosystem models to make better use of research findings, to improve decision making, and to enhance capabilities for interpretations of observed changes.

### 1. Introduction

Conservation of park ecosystems requires understanding processes and interactions at the ecosystem level of organization. The ecosystem was defined by Tansley (1935) as a system that includes interactions among organisms and between organisms and the physical environment (Golley 1993). Conservation involves, to a large extent, the protection of natural ecological processes from adverse effects of human activities. It follows therefore, that effective conservation requires a capability to predict the direct and indirect effects of human activities on ecosystem processes and interactions. Unless we can predict the outcomes, we cannot anticipate the direct,

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and indirect consequences of human activities, including management interventions. Without a predictive capability, we cannot anticipate whether management interventions will create more problems than they solve, or if they will endanger the intrinsic capacity of the ecosystem to withstand disturbances and adapt to changing conditions.

Computer simulation modeling has long been central to the ecosystem approach, as a method of understanding, and as a tool for prediction. Simulation modeling can be used to formalize our hypotheses about the way ecosystems function in quantitative terms. Models are particularly useful for understanding the dynamics of complex systems where the number of interactions makes it difficult to make predictions with mental models. Models may be used for research purposes, or they may be used to guide management decisions. An important benefit of ecosystem modeling is the ability to carry out experiments, or "what if" scenarios, to predict outcomes of alternative management practices, climatic change, land use change, and other possibilities. Experiments can be carried out that would be impossible or infeasible to carry out in the real world. Model predictions represent our "best knowledge" of the way the ecosystem functions. The predictive capability of a model is limited by our own understanding, rather than by the model itself. Thus, models also play a useful role in helping us identify knowledge gaps.

Ecosystem level processes are central to many of the natural resource and conservation issues in Yellowstone National Park, particularly those involving large herbivores. Concerns about overabundant elk and resultant overgrazing on the northern winter range began decades ago (McCullough this volume; Gogan et al. this volume). Arguments for overabundance have been rooted in beliefs that elk populations were controlled by predators, which were eliminated in the case of wolves (*Canis lupus*), or depressed in the case of grizzly bears (*Ursus arctos*), and that elk dispersals to lower elevation winter ranges outside the park were inhibited by land use and hunting (Coughenour and Singer 1996b; Singer et al. 1998). This was the justification for culling the herd through 1968. However, the natural regulation policy put in place in 1968 was based upon a hypothesis that the population could regulate itself through food limitation, and that the resultant population density would not lead to rangeland degradation. The reintroduction of wolves has more recently led to questions about their impacts on elk numbers, and the offtake of elk by hunters outside the park boundary may consequently be affected. This is an ecosystem level problem, in that it involves interactions among soil, plants, herbivores, predators, and humans. It also involves the concept of negative feedback, a systems level interaction.

Similarly, bison management involves ecosystem level processes. Over the last two decades the bison population has grown considerably, and its range has expanded from core areas within the park to beyond the park, and bison are subsequently out-migrating from the park. The out-migration is problematic because bison carry brucellosis, which many believe poses a threat to the livestock industry in neighboring states (see review of Cheville et al. 1998). However, if bison dispersal is inhibited by management actions, bison could increase to unnatural densities inside the park, with subsequent negative effects on plants and ecosystems. This situation raises questions such as "why are the bison expanding their range?" Are they exceeding the carrying capacity and overgrazing? What would be the outcomes for plants and soils if bison were confined to the park? Is it possible that bison could ever be regulated by predators?

In this paper, I demonstrate an approach to assessing large herbivore ecology and management using ecosystem modeling (Coughenour 2000, 2002, 2005).

## 2. The Ecosystem Approach

The ecosystem approach integrates ecosystem components through transfers and cycles of matter and energy above and below ground (Figure 2-11-1). The ecosystem includes abiotic (physical and chemical) as well as the biotic components. Climate is traditionally taken as a "driving variable;" more recently, however, we have come to appreciate the importance of feedbacks from the earth's surface to the climate system, effectively making the atmosphere a part of the ecosystem. Ecosystem processes involve transformations and interactions with water and mineral compounds in the soil profile. Soil development and functioning is an ecosystem process involving biotic as well as abiotic processes acting over long periods of time. The decomposer

group, consisting of soil microbes, is an important agent of nutrient recycling as well as soil organic matter formation. Interactions between plants and herbivores have been a central focus of many ecosystem studies. Plants clearly affect herbivore abundance, but there are also important feedbacks of herbivory onto plant growth, causing it to increase or decrease. Herbivores interact with the soil by recycling nutrients. Herbivores affect predator abundance, and predators conversely affect herbivore abundance. Interactions may form a "trophic cascade," with predators influencing herbivores, and with herbivores then affecting plants and even decomposers.

Interactions among ecosystem components give rise to emergent outcomes at the ecosystem level of organization. For example, a nutrient cycle is clearly an ecosystem level phenomenon, because it is the emergent outcome of interactions among the organisms and abiotic components involved in the cycle. Feedback loops and mutual causality produce emergent outcomes in interactive systems. Organisms modify their environments biotically and physically, and these alterations feedback to influence organism behavior and condition.

While ecosystem studies have historically focused on cycles and flows of matter and energy, it has always been clear that these flows are mediated by biotic processes at physiological, organismal, population, and community levels of organization. Cycles of matter and energy are the frameworks for integration; however, a diverse array of biotic and abiotic processes is woven together within these frameworks. For example, ecosystem studies may involve ecophysiological studies of plants that quantitatively explain photosynthesis, respiration, transpiration, and nutrient uptake processes. Ecosystem studies may be concerned with the feeding behavior of herbivores and predators. Or, they may involve population processes and resultant population dynamics.

### 3. Large Herbivores in the Yellowstone Ecosystem

Yellowstone National Park harbors one of the last spatially extensive native grazing ecosystems in North America (Houston 1982; Frank and McNaughton 1992; Coughenour and Singer 1996b). Since 1968, elk and bison have followed population trajectories that have been primarily the result of natural processes. Two bison herds and the northern elk herd grew between 1968 and the mid-1980s. The northern elk herd stopped growing as it reached food-limited carrying capacity (Gogan et al. this volume). The bison herds continued to grow through the mid-1990s, supported by an increasingly large forage base as they expanded their ranges (Meagher 1989; Meagher et al. 2003; Taper et al. 2000). These population increases have resulted in concerns that densities could have reached levels that cannot be sustainably supported by the forage base. More recently, elk numbers have declined due to a combination of severe winters, heavy hunting pressure outside the park, and wolf predation. Bison numbers declined due to severe winter weather, but have increased again since a low in 1998-1999. To date, bison are little affected by wolves.

Elk and bison have seasonal ranges, migrating in response to snow cover and forage availability. Within these seasonal ranges, herbivory is heterogeneously distributed in response to a wide variety of vegetation communities and habitats. Plant growth varies markedly among habitats due to differences in soil moisture, soil fertility, and length of growing season. Some attempts have been made to estimate total forage production across the entire northern elk range (Coughenour 1994; Coughenour and Singer 1996a), however, these were based upon very simplified forage production models. In these models, forage production was primarily driven by precipitation. Plant growth did not respond to herbivory, and nutrient cycling and soil processes were not considered. This showed the utility of the approach, but left considerable work to be done (Coughenour and Singer 1996a).

A relatively large number of studies of plant and soil responses to herbivory have been carried out in Yellowstone, particularly on the northern winter range. The overall picture that has emerged 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 plant growth. If grazing negatively affects plant growth, there would be less green biomass outside of fenced grazing exclosures compared to inside grazing exclosures. Studies of long-term grazing exclo-

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tures revealed less green biomass in grazed plots in 1988, but no grazing effect was observed in 1986-1987 (Coughenour 1991). However, a reduction in green biomass outside exclosures does not necessarily indicate reduced plant growth. For example, 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. Total annual plant growth was measured by Frank and McNaughton (1992, 1993). Plant growth was greatly stimulated by herbivory in mesic grasslands, and was slightly stimulated by herbivory (10-30%) in drier grasslands. Grazing promoted nitrogen cycling rates and nitrogen retention (Frank and Goffman 1998; Frank et al. 2000; Frank et al. 2004). Grazing has also been shown to stimulate root growth (Frank et al. 2002). Grazing caused increased root growth, possibly root exudation, and stimulated soil microbial populations and nutrient cycling rates (Hamilton and Frank 2001). Notably, these studies have involved ecosystem processes such as primary production, nutrient cycling, and plant-soil water relations.

#### 4. Assessing Large Herbivores in Ecosystems with Ecosystem Modeling

Food limitation was the mechanism by which herbivore populations were hypothesized to be regulated in nature, according to the natural regulation hypothesis that was the basis for ungulate management in Yellowstone National Park (Houston 1982; Coughenour and Singer 1996b). If an important predator is absent, as wolves were absent from Yellowstone, and if predation limited herbivores before their extirpation, then food-limited carrying capacity may still be possible. However, it may not be "natural." In some ecosystems, such as the Serengeti, large herbivores do appear to be food rather than predator limited, particularly where the herbivores are migratory (Fryxell et al. 1988). This is because the herbivores escape predation by moving out of predator territories during their migration. In contrast, nonmigratory herbivores do not escape predation in this manner, so they are more likely to be predator-limited. Although elk in Yellowstone are migratory and may escape predation during the summer months when they are highly dispersed, they may still be affected by predation during the winter and in the spring calving season. Thus, if the goal is to manage for natural processes, we must be able to predict the extent to which herbivore populations would be limited by food, or predators, or both, in an undisturbed ecosystem. This requires an integrative approach which represents soil-plant-herbivore interactions and predatory-prey interactions simultaneously.

Ecosystem modeling can be usefully applied to understand and predict the dynamics of this four-component system. The role of large herbivores (e.g., deer, elk, bison) in the ecosystem can be assessed by considering herbivore interactions with soil, plants, and predators. An ecosystem modeling approach can be used to predict herbivore numbers if they were limited by their forage supply. This is often termed ecological carrying capacity (Caughley 1979). Alternatively, the ecosystem model may be used to assess the possibility of that predators may limit herbivores, with subsequent effects on plants and soils.

#### 5. How the SAVANNA Ecosystem Model Works

The first version of the model was an application to a pastoral ecosystem in Kenya (Coughenour 1992). Subsequently, several versions have been developed and the model has become both more refined and more comprehensive. A full description of the model was provided by Coughenour (1993). Here, I will provide a general overview of the model and its workings.

SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems. SAVANNA is normally used to simulate ecosystems at landscape through regional spatial scales over five to 100 year periods. The model is comprised of site water balance, plant biomass production, plant population dynamics, and litter decomposition; and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, and ungulate energy balance; and ungulate population dynamics, predation, and predator population dynamics submodels (Figure 2-11-2). The time-step of the model is one week, meaning that each week a new set of conditions are calculated. This time-step is optimal for representing the important seasonal variations that occur in most ecosystems.

SAVANNA is a spatial model. It simulates a "grid" of square "grid-cells" that cover the landscape. Within each grid-cell the model simulates three vegetation patch types. These are defined by the fractional covers of herbaceous plants, shrubs, and trees. Since shrub and tree covers are simulated variables, facet cover is a dynamic outcome of vegetation growth and mortality. Vegetation patch type locations are not modeled, only the fractions of grid-cells that are covered by the patch types. Within each facet, the model simulates plant growth and soil water budgets.

The vertical spatial structure of the model is defined by soil and plant canopy layers. The soil is divided into three layers. The top soil layer is a zone of evaporation as well as plant water uptake. The second layer is generally the deepest layer that is exploited by herbaceous roots. The bottom layer is generally occupied only by shrub and tree roots. Plant canopies are organized into herb, shrub, and tree strata. In turn, each of these is divided into three substrata to compute shading by leaves and resulting light intensities on photosynthetic leaf areas.

SAVANNA is driven by monthly weather data. Each month, a precipitation map is generated from weather station data. A linear regression is performed between precipitation and elevation. The rate of increase in precipitation with elevation is used to correct for elevation differences between a location and each station. The elevation-corrected weather station data are then spatially interpolated using inverse distance weighting. A snow submodel simulates the accumulation and melting of snow based upon precipitation and temperature. Snow depth maps are generated every time-step.

The water budget at each site is calculated from precipitation, interception, runoff, infiltration, deep drainage, bare soil evaporation, and transpiration. 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).

The net primary production (NPP) submodel simulates the production and flows of plant biomass, and resultant plant biomass dynamics. Plant growth depends fundamentally upon photosynthesis. Photosynthesis is affected by light, water, temperature, nitrogen, and leaf area. Photosynthate is allocated to leaves, stems, and roots. Plant tissue death rates are affected by water and temperature stress, completion of flowering, or triggering of dormancy by temperature or day length. A woody plant population model represents six age classes of shrubs and trees, recruitment of new plants, and death of old or stressed plants.

The herbivory submodel represents forage intake rate and how it varies in response to forage quantity and quality (Wickstrom et al. 1984; Hudson and Watkins 1986; Hudson and Frank 1987), and snow 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 determined by using preference weights, similar to the approach advanced by Ellis et al. (1976).

The herbivore energy balance submodel simulates the body weight of the average animal in each herd or subpopulation, based upon differences between energy intake and energy expenditure (Figure 2-11-3). The energy balance model is partly based upon the models of Coppock et al. (1986) and Hobbs (1989). The net outcome of energy intake and expenditure is a change in stored energy reserves in the animal's body.

The herbivore spatial distribution submodel dynamically simulates animal distributions over the simulated landscape or region in response to the changing distributions of forage biomass, green herbaceous biomass, snow depth, slope, and tree cover.

The herbivore population dynamics submodel represents one age class for each year, for each sex. A simplified diagram of the model is contained in Figure 2-11-3. A key feature of the model is that recruitment rates and death rates are affected by animal condition indices. The effects of condition index, therefore, 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 the population growth rate of the species in question. This provides a process-oriented, mechanistic linkage between foraging condition and population

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The predator submodel simulates predation on ungulates and resultant predator population dynamics. It is derived from a model that was first developed to assess wolf reintroduction into Yellowstone National Park (Boyce and Gaillard 1992; Boyce 1993). The model simulates predation and population dynamics of one or more groups for each predator species. For each species, the model reads a map that shows the ranges for all of the groups of that species. The number of prey animals killed depends on the relative densities of prey and predators within these ranges.

#### 6. Using the Ecosystem Model in Yellowstone

The ecosystem model has been used to assess the bison and elk in Yellowstone National Park (Coughenour 2005). The simulated area included the combined seasonal ranges of bison and elk inside and adjacent to the park (Figure 2-11-4). Because the study was focused on bison and elk, there was no need to model areas that they do not utilize. The bison population comprises two herds that have limited interchange. The central herd inhabits the central portions of the park, particularly the grasslands and shrublands of Hayden, Pelican, and Firehole River Valleys. Originally this herd had a much smaller range and made little use of the Firehole area. It made no use of the western corridor and areas outside the western park boundary. The central herd was originally comprised of two subherds (Meagher 1973), but there has been extensive interchange among these two subherds for decades and they are now considered to be effectively a single herd. The northern herd winters on the northern winter range along with the park's major elk herd. Both herds' winter ranges have expanded over the last two decades, along with their populations (Meagher 1989; Taper et al. 2000; Meagher et al. 2003). These range expansions were represented in the model by applying a series of increasingly large range maps over time.

The study area included a wide variety of topographically complex landscapes (Figure 2-11-5A) ranging in elevation from less than 1600 m to over 3000 m. A long valley complex in the north-central part of the study area is that of the Yellowstone and Lamar Rivers. This area comprises the winter range of the northern elk and bison herds. The central bison range is at higher elevations. There are a variety of vegetation types in the study area (Figure 2-11-5B). The bison and elk primarily utilize grasslands and shrub-grasslands. These habitats occupy large areas in the valleys mentioned above, as well as smaller areas spread out through the extensive forest mosaic that covers most of the park. A variety of forest types occur, but most are dominated by lodgepole pine (*Pinus contorta*) in various stages of postfire succession. Lower elevation forests also include Douglas fir (*Pseudotsuga menziesii*). The forest understory is utilized by elk to some degree, especially in summer. Bison and elk habitats overlap on the dry grasslands and shrublands (Singer and Norland 1994). However bison make much more use of the mesic sedge and grass meadows than elk do.

The spatial heterogeneity of vegetation types and forage quantity and quality was simulated based upon vegetation and soil maps that are read into the model. Each soil type has a number of attributes such as soil water holding capacity and nitrogen and carbon contents. Each vegetation type was characterized by the abundance and composition of major plant functional groups. Upland graminoids were differentiated from sedges, for example, not only because they have different water requirements, but also because they have different digestible energy and nitrogen contents for the bison and elk.

The model was used to simulate the period of 1968 to 2001. This was the period following the implementation of the natural regulation policy during which elk herd grew to its ecological carrying capacity and the bison herds markedly expanded their ranges. The objective was to predict bison and elk population dynamics based upon simulated quantities, qualities, and availabilities of forage within the seasonal ranges of the herds. If the model was successful in predicting the observed dynamics over this time frame, it is likely that it would accurately predict dynamics under a range of management scenarios that might occur in the future. Many elements needed to be correctly simulated, including plant growth patterns over a wide range of habitat

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conditions, herbivore spatial distributions and forage requirements, and herbivore population responses to per-capita forage availability over a wide range of habitats. Plants had to use water at the correct rate and their growth had to be limited when soils dried up. Nitrogen had to be correctly recycled through decomposers to plants and herbivores and back again. If the recycling rate was incorrect, the plants would not grow at the correct rate, with consequences for the herbivores.

Simulated aboveground plant biomass dynamics are shown in Figure 2-11-6, for a single plant functional group (graminoids) at a single location in the study area. Green leaf biomass increased during the early growing season, but then as it senesced due to moisture, cold temperature, and age, it was transferred to standing dead biomass. Stems were also represented. Standing dead biomass was transferred to litter on the soil surface. These dynamics have important implications for herbivores, because they determine the quantity and quality of forage at different times of the year.

The model had to be able to represent the ways plants and soils respond to herbivory. We have learned that plants may exhibit "compensatory growth" to replenish tissues that are removed by grazing (McNaughton 1983). This is often an ecosystem level response as much as a plant level response, because it involves the water and nitrogen cycles. That is, grazing effects on plants may reduce plant water demands, for example, and the conserved water can subsequently be used to support compensatory growth. Alternatively, grazing may promote nitrogen recycling, which also contributes to increased plant growth (Detling 1988). Plants may respond in a variety of ways, including increased photosynthetic rate due to increased light, or younger tissues with higher nitrogen concentration, altered root:shoot allocation, or increased tillering. Of course, compensatory growth only works up to a point. At excessively high grazing intensities, plant growth must be diminished because the compensatory mechanisms are overwhelmed.

An example of how the model represented plant growth responses to herbivory is shown in Figure 2-11-7. At light to moderate grazing intensities, compensatory growth mechanisms at the plant and ecosystem level were effective, and total plant growth (net primary production or NPP) was even slightly stimulated. However, at increasing grazing pressures, NPP began to decline. Notably, the NPP did not decline to zero because when plant biomass was low, offtake rate became limited by the availability of forage biomass in the functional response for forage intake rate. Essentially, plant growth and offtake came to equilibrium, albeit at a lower NPP than under lower grazing intensities.

Forage intake by bison was not constant throughout the year, but instead, varied with foraging conditions (Figure 2-11-8). Intake rate increased in the spring as the snow melts and green biomass density increases. Forage intake declined in the winter. This was due to the decrease in forage biomass caused by transfer of biomass to litter and grazing offtake. It was also caused by snow accumulation, which made forage less accessible.

Seasonal and annual variations in forage intake rate are the root cause of changes in animal body condition (Figure 2-11-9). As forage intake declined, animals were less able to meet energetic requirements. The deficit was made up from body reserves; consequently, weight was lost, and body condition decreased. In the spring and summer, forage intake exceeded energy expenditure, the animals gained weight, and condition increased. An important detail of this figure is that minimum body condition declined from 1968 to 1983. This is a result of increased interspecific competition for forage, as population size increased. This is how density-dependent population regulation occurred. It is also notable that the minimum body condition was lower in some winter than in others. This was due to snow, and to a lesser extent to annual variations in forage biomass. In winters when body condition was lowest, mortality was highest, and calf survival the following spring was also depressed.

Bison and elk population dynamics cannot be modeled without considering removals by humans. The observed numbers of bison removed (Figure 2-11-10) were specified to the model and the simulated population dynamics reflected this. As bison began to emigrate beyond the park boundaries in winter, they were removed to prevent transmission of brucellosis to livestock. Re-

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removals each winter depended upon how many animals left the park. This in turn was dependent upon foraging conditions and the level of interspecific competition for available forage inside the park. It was determined that bison in the northern herd out-migrated in severe winters when the population approached or exceeded 3,000 (Cheville et al. 1998). A large number of animals were removed in 1996 and 1997 due to harsh winter conditions and large numbers of bison.

The model successfully predicted the population growth of the central bison herd between 1968 and 1993 (Figure 2-11-11). The model did not reach as high a level as suggested by data in 1995 and 1996, suggesting either that the model underpredicted population growth or that the data estimates were too high. It is possible that the model underestimated the positive effects of finding new habitat through continued range expansions in those years. However, the sightability correction that was applied in 1995-1996 was only approximate and sightability could have been higher in those years.

The model appeared to underpredict the rapid decline indicated by the data between 1996 and 1999, resulting in about 500 to 900 more animals in 1998 and 1999 than indicated by the data. The counts of 1998-1999 were intensive, and sightability was estimated using radio-collared animals (Hess et al. 2002). The numbers of bison that were removed in early 1996 and 1997 were accurately known (344 in 1996 and 358 in 1997, Figure 2-11-10) and that many were removed from the simulated population. The count data (Taper et al. 2000) indicated 532 fewer bison on January 6, 1997 than on October 31, 1996, while only about 110 were removed during that period in early winter (Gogan et al. 1998). In winter of 1997-98 only 11 animals were removed and the winter was not severe, yet the data indicated a drop of 773 animals from early 1997 to August 1998.

The rate of population increase between 1997 and 2000 indicated by the data was very high. It was puzzling that the data indicated an increase from 1,316 counted bison in September 1999 to 1778 counted in January 2000, which translates into 567 sightability corrected animals being added over winter while the calving season is in spring. As parameterized, the model could not predict such a rapid recovery. However, ungulate populations have been observed to achieve unusually high rates of recovery following a die-off in response to herbaceous vegetation recovery and reduced competition for forage (D. R. McCullough, personal communication). The other possibility is that sightability was lower than estimated in 1998 and 1999. These possibilities all merit further study. Despite these inconsistencies, the model predicted the correct number of bison in 2000 and 2001.

The number of bison found outside the western park boundary was predicted to vary among years (Figure 2-11-12). Significant numbers of bison first started to use this area in the late 1980s when the herd finally expanded its range to include that area. The highest numbers outside the park were predicted in winters 1995-96 and 1996-97. These are years that the herd was at an all-time high (Figure 2-11-11), and they were years with severe winter weather. Bison were responding to simulated snow depth distributions by moving to lower elevations where snow was less deep. These are also the winters (early 1996 and early 1997, Figure 2-11-10) when many bison had to be removed from this area due to the perceived threat of brucellosis transmission.

Ecological, or food-limited carrying capacity was determined by letting the model run for 50 years with no removals, in seven different simulations with different stochastic weather patterns (Figure 2-11-13). The model predicted that on average, the number of bison in the central herd would be limited to about 3,500. Sightabilities for this herd between 1968 and 1997 were on average 88% (Taper et al. 2000), meaning that if similar counting techniques were used, approximately 3,000 bison would be counted. However, there was a considerable range of variation depending upon the weather. A run of mild winters could send the population above 4,500, while severe winters could reduce the population to about 2,500.

At food-limited carrying capacity with no management removals, large numbers of bison may be expected to be found outside the park (Figure 2-11-14). Finding 200 to 400 animals outside the park would be fairly commonplace. Because the population can increase to large numbers during a sequence of mild winters, subsequent severe winters would find many more bison outside the park. The model predicted that 600 to 900 bison could be found outside the park three times in

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50 years in this particular simulation.

The model was useful for portraying distributions of bison and their impacts on plants. Mean bison densities over 50 years with a numbers fixed at 4,000 animals in the central herd and 2,000 in the northern herd are shown in Figure 2-11-15A. This was close to the mean number bison at food-limited carrying capacity. Highest densities were predicted for the wet meadows and riparian areas in the Firehole River area. This area contains many thermally warmed areas of hot springs vegetation. The model predicted increased snow melt rates on such areas, making them more attractive to the bison. Moderately high densities were predicted for Hayden Valley and portions of Pelican Valley. Bison on the northern range were generally less dense except in certain locations such as sedge meadows. Of course, this was just a mean density distribution and it is useful to remember that distributions dynamically respond to snow, forage, and population size.

The resultant distribution of grazing impact roughly follows the density distribution, but the correspondence is far from perfect (Figure 2-11-15B). This figure shows the percent of above-ground plant growth that is eaten, thus it is a measure of grazing intensity. Notably, it is very heterogeneous, demonstrating the great oversimplification of assuming that  $N$  number of bison will result in  $X$  percent offtake. In reality, certain portions of the landscape will be heavily utilized while others will be lightly utilized. Percent offtake is also affected by plant productivity, which is also spatially variable. Thus, in areas with high bison densities and high plant production, grazing intensity will be less than in areas with high densities and low plant production. Hayden Valley, in the center of the park, was clearly the most heavily utilized habitat. This area is moderately productive, but it experiences large numbers of bison year around. Grazing intensity was high in certain portions of Pelican Valley in the southeast, and in the upper portion of the northern winter range. Certain locations in the Firehole area were also heavily grazed.

Impacts on plants are illustrated in Figures 2-11-15C and 2-11-15D, which show the ratios of shoots and roots in the simulation with bison to that in a simulation with no bison, but the same number of elk. These figures thus show the incremental effect of bison, controlling for elk numbers. Shoot biomass in April reflected offtake over the winter as well as the previous summer. Over winter, plants were dormant so there was no compensatory growth. The added effect of bison was particularly apparent in Hayden and Pelican Valleys, and in the Firehole area. In most areas shoot biomass was reduced by 40 to 60%. Over the northern range, the added effect of bison was to reduce shoot biomass by 10 to 20%, except in sedge meadows where shoot biomass was reduced by 25 to 30%. Over most of the area, bison only reduced shoot biomass by 5 to 10%. Effects on root biomass are of interest because this variable is a fundamental index of plant cover; therefore, it can be indicative of longer-term trends in rangeland condition in perennial grasslands. Effects on root biomass were smaller than on shoots. Bison reduced root biomass in some areas by 10 to 15% but effects were negligible over most of the ranges. Similarly, root biomass was not decreased by elk grazing on the northern range (Coughenour 1991). In a few places roots were increased slightly due to a stimulation of plant growth. This tended to occur in moist habitats with low tree cover. Despite the decreases in root and shoot biomass, grazing stimulated aboveground productivity, indicating that grazing shifted carbon allocation from roots to shoots, and that since the shoot biomass was grazed, nutrients were recycled at a greater rate, thus sustaining further plant growth (Coughenour 2005). Grazing thus alters the appearance of the grassland as well as its function, but it does not necessarily result in a permanent loss of plant cover. Indeed, the model predicted lower shoot and root biomass under grazing, but this was a stable condition because bison population size became limited by food availability.

The potential effects of predation should be also considered. The predation model, carefully parameterized based upon observed wolf population growth rate and spacing and the available information on predation rates (Smith et al. this volume), suggested that wolves could reduce the northern elk population and maintain it at about 10,000 to 12,000 elk, with no additional offtake by hunting (Figure 2-11-16). This is below the strictly food-limited carrying capacity of 20,000 or so. This has implications for the level of hunting offtake that can be sustained when the elk

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move outside the park boundary. Indeed, elk numbers have declined since 2001, and hunting quotas have had to be adjusted, most likely due to wolves. In addition, the model only considered the numerical effect of predators, and it did not represent effects of wolves on elk spatial distributions (Gogan et al. this volume) or foraging rates, which could provide additional impacts.

Currently, wolf predation on bison in Yellowstone is limited, but it does occur. It is well known that wolves can learn to hunt bison under the right conditions (Carbyn et al. 1993). So it is possible that predation on bison could increase over time. Because of the higher abundance of elk on the northern winter range, predation on bison is less likely. However, the central herd winters in areas where there are no elk, making bison more vulnerable. Based upon current information, and the assumption that wolves will learn to hunt bison, the model predicted that wolves could maintain the central bison herd at about 3,000 (Figure 2-11-17), in comparison to the food-limited carrying capacity of approximately 3,500. These predation impacts would have cascading effects on plants and soils. Predation impacts on elk would reduce offtake of herbaceous biomass, but because the herbaceous vegetation is adapted to this pattern of herbivory, responses would be muted. In contrast, reduced browsing of willow could lead to significant increases in willow cover in some locations.

### 7. Conclusions

To understand the causes and consequences of bison population dynamics and spatial distributions in Yellowstone, many different pieces of information needed to be integrated. Clearly, population increases and decreases are somehow linked to range and forage availabilities. However, the linkage was nontrivial. Forage availability was determined by several interacting factors. First, the landscape itself is complex, with a variety of different habitats and vegetation communities. Habitat variations are related to variations in soil properties and the redistribution of water on the landscape. Climate is spatially variable due to topographic influences. Spatial variations in precipitation, temperature, and snow cover influenced plant growth. Available forage was affected by spatially and temporally variable snow cover through the effects of snow on bison foraging and spatial distributions. Available forage for bison was influenced by the presence of elk, whose numbers varied over time. The spatial juxtapositions of bison, elk, forage, and snow on a complex landscape influenced net forage availability in complex ways. Temporal variations in forage availability were important on interannual as well as seasonal time scales. Forage variations were driven by seasonal and interannual variations in climate, by the seasonal progression of plant growth, senescence, and transfer to litter, and by the temporal pattern of herbivory. Moreover, bison herbivory influenced plant growth and recycled nutrients, and these processes needed to be factored into the assessment.

The assessment indicated that the concept of carrying capacity is an oversimplification. One of the primary objectives was to determine whether bison have filled up their habitats within the park, which could explain the increased out-migration that has occurred over the last decade. The question was posed as "are bison at their carrying capacity?" Ecological carrying capacity has been defined as the number of herbivores that is in dynamic equilibrium with forage production. At that point, further population growth is limited by the lack of additional forage. The model was used to determine what that population level could be. It was shown that bison had not reached their ecological carrying capacity either during the period of range expansions, or during the recent period of increased out-migrations. Yet, the ranges did expand, and the out-migrations continue. The conceptual model of "when bison reach ecological carrying capacity they will then expand their range and out-migrate" is too simple to explain the observed dynamics. Instead, the model suggests that bison have tended to expand their ranges before food-limited carrying capacity is actually reached. This is a logical outcome. As food starts to become limiting, and as animal body conditions reach lower levels, the bison respond behaviorally to avert the undesirable outcomes of starvation. The behavioral response is to search elsewhere for food. This searching takes place before, not after carrying capacity is reached. It is important to be able to assess the point at which this might occur, and this requires a capacity to calculate how much available forage there is, how much forage is required, and what the net outcome is

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in terms of the bison's energy balance.

The implications for management are equally complex. The model predicted that bison should continue to be found outside of the park boundaries. The number will be variable, depending upon snow depth and bison population size. Movement beyond the park boundary is to be expected because areas outside the park boundary are at lower elevations, and they consequently have less snow. Plants commence growth earlier in the spring at these lower elevations. Thus, in late winter to early spring, there is green forage outside the park while ranges inside the park are either not green or are still covered with snow. If it were possible to cease all management removals and stop bison out-migration by hazing the animals back into the park or the ranges adjacent to the park, the population would be expected increase to ecological carrying capacity. However, it would be difficult to argue that this would be a natural state of affairs, given that under natural conditions bison would have dispersed before that point is reached. Furthermore, if removals are stopped before brucellosis is eliminated, the management problem escalates because at ecological carrying capacity much larger numbers of brucellosis infected bison will be found outside of the park. It can be more logically argued that management removals or hunter harvests outside of the park boundary would both simulate the dispersal sink that would have existed presettlement, and keep out-migrating bison numbers to a manageable level.

The model predicted that at current population densities bison will alter range condition, but the condition is sustainable. In a grazing ecosystem, it is to be expected that there is less herbaceous shoot biomass. This does not indicate a reduction of total plant production, but instead, that the production is being utilized. Localized areas should be expected to be grazed more heavily than others, perhaps to the point of having significantly reduced plant cover. Intermediate levels of disturbance result in a greater variety of habitats for plants and other animal species.

There are many reasons why it is necessary to carry out ecosystem level assessments to meet the conservation objectives of national parks. It is now well established that effective conservation strategies must be based upon the conservation of ecological processes. McNaughton (1994) stressed the importance of conserving self-sustaining ecological systems, in contrast to collections of non-self sustaining biological specimens, for example. Since 2000, an ecosystem approach has formed the primary framework for the Convention on Biodiversity (<http://www.biodiv.org/programmes/crosscutting/ecosystem/default.shtml>). The concept of ecosystem management that became popular in the 1990s was a step in the right direction, in recognizing that ecosystems need to be conserved to conserve species. However, in practice, ecosystems have often been simply equated to "habitats." While the original definition of an ecosystem has not been forgotten, examples of true ecosystem level research and assessments are uncommon. Boyce (1998) and Sinclair (1998) argued that national park ecosystems should be used as ecological baselines to assess of the degrees of departure of non-protected areas from naturally functioning ecosystems. Going one step further, it is also necessary to understand how those baseline systems function. Such knowledge can be used to conserve and sustainably manage protected and unprotected areas alike. Conservation biology must be enlarged to include ecosystem concepts, ecosystem research, and ecosystem modeling.

Ideally, every protected area would construct, maintain, and evolve an ecosystem model, as part of a process of adaptive management. I suggest that managers of parks and protected areas such as Yellowstone and Shiretoko consider supporting ongoing efforts to develop, maintain, and evolve ecosystem models to make better use of research findings, to improve decision making, and to enhance capabilities for interpretations of observed changes. The ecosystem models would embody and formalize current understanding, identify what is and what is not known and what is and is not important to know, and be used to hypothesize outcomes of alternative management scenarios.

**Abstract**

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の生態系レベルの調査研究や評価の例はあまりない。Boyce (1998) や Sinclair (1998) は、国立公園の生態系は非保護地域の評価に際し、それがどの程度本来の生態系から劣化しているかを対比する生態学的ベースラインとして用いられるべきだと主張した。一歩前へ進むと、これらのベースラインのシステムがどう機能しているかを理解することも必要である。そのような知識は保護地域か否かにかかわらず、生態系の保全と持続的な管理に用いることができる。保全生態学は生態系概念、生態系調査、そして生態系モデルを包含していくべきである。

理想的には、順応的管理の一環として、全ての保護地域に生態系モデルが構築され、維持され、そして改良されていくべきだろう。イエローストーンや知床のような公園や保護地域の管理者は、調査研究の結果をよりよく活用し、意思決定能力を向上させ、そして観察された変化を解釈する能力を高めるために、生態系モデルを開発、維持し、そして進化させる努力を支持することを提案したい。生態系モデルは現在の理解を具体化して正式なものにし、既知のものと未知のもの、そして知ることが大切なものとそうでないものを見分け、そして複数の管理手法の結果を仮説として考えることに使われるだろう。

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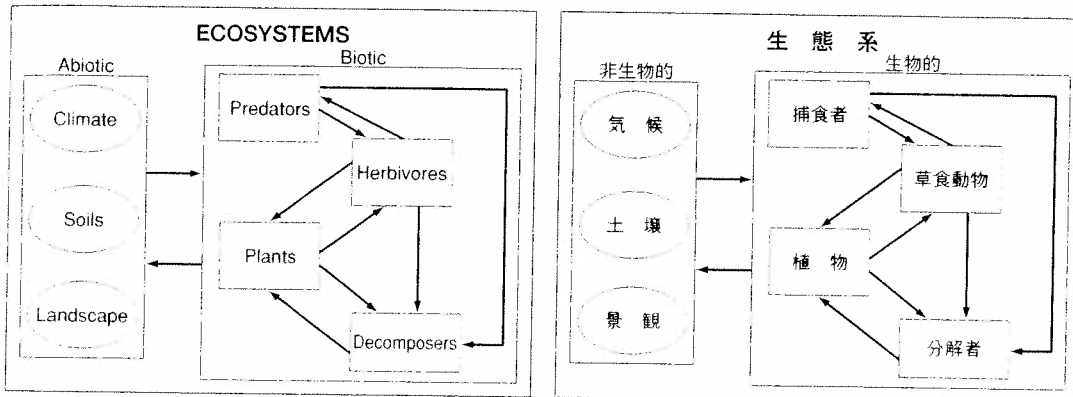


図 2-11-1 一つの生態系の主要要素とそれらの相互作用を表した単純な影響のダイアグラム。矢印は一つの要素から他の要素への作用を表す。

Figure 2-11-1 A simple influence diagram showing the major components of an ecosystem and their interactions. Arrows represent the effects of one component upon another.

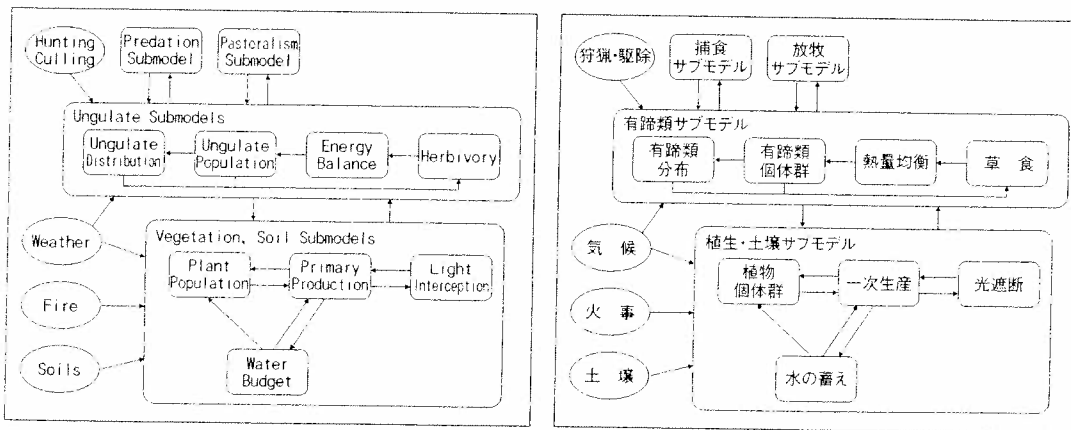


図 2-11-2 SAVANNA 生態系モデルの全体構造  
Figure 2-11-2 The overall structure of the SAVANNA ecosystem model.

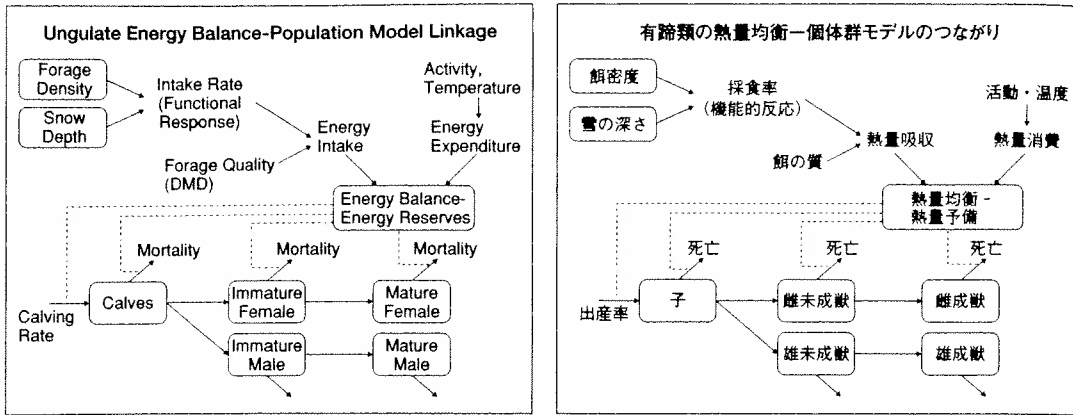


図 2-11-3 有蹄類の熱量均衡、単純化した個体群動態モデル、そして個体群動態間のつながりに影響する主要プロセス  
 Figure 2-11-3 The major processes affecting ungulate energy balance, a simplified representation of the population dynamics model, and the connections between energy balance and population dynamics.

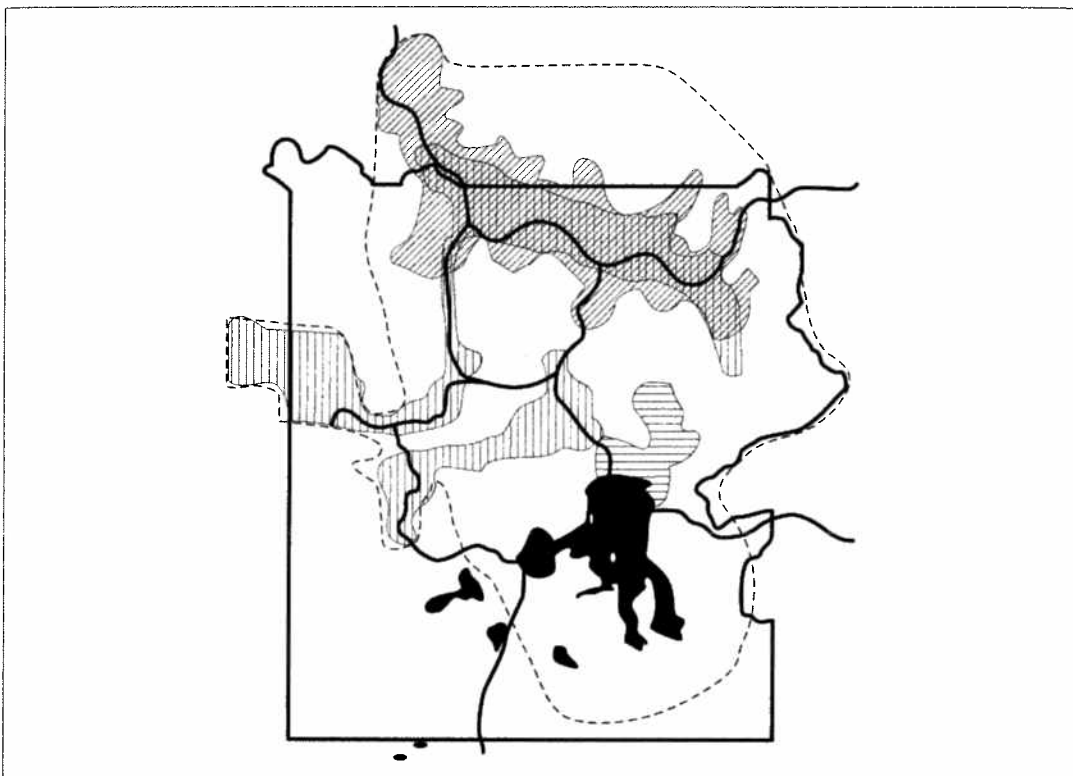


図 2-11-4 調査区域境界 (点線)、公園境界と主要道路 (太実線)、湖 (塗りつぶし)、北のエルク越冬地 (斜線)、北のバイソン越冬地 (北のエルク生息地に重なる縦線部分)、ペリカン谷のバイソン越冬地 (横線部分)、ファイアホール、ヘイデン、及び、西側のバイソン越冬地 (縦線部分)  
 Figure 2-11-4 Study area boundary (dashed line), park boundary and main roads (thick solid lines), lakes (solid fill), northern elk winter range (diagonal hatching), northern bison winter range (vertical bars overlapping northern elk range), Pelican Valley bison winter range (horizontal hatching), Firehole/Hayden/West bison winter ranges (vertical hatching).

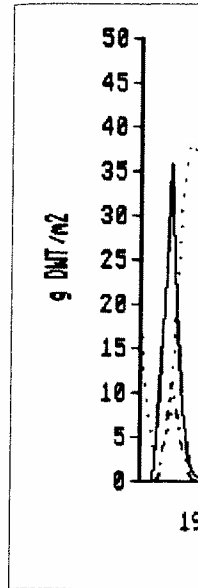


図 2-11-6 シュミレーション。Grn-Lfは緑  
 Figure 2-11-6 Simul: in the study area. Gr

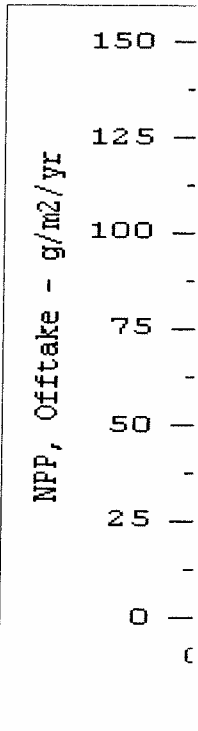
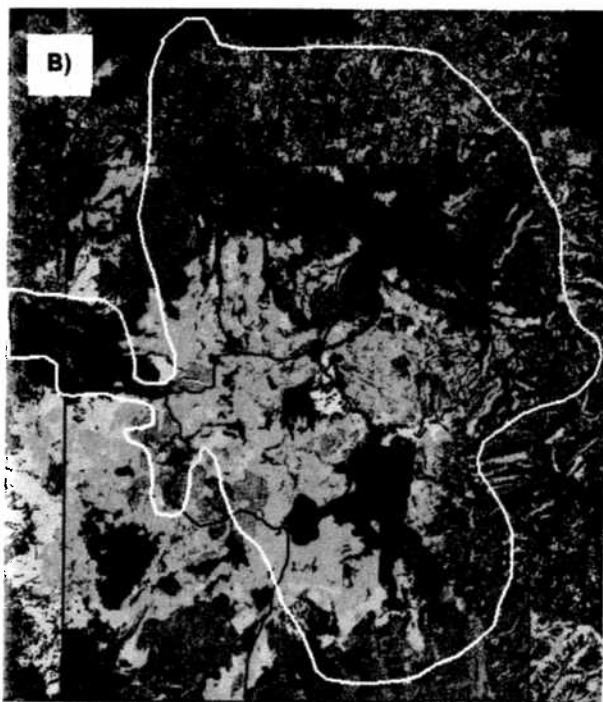
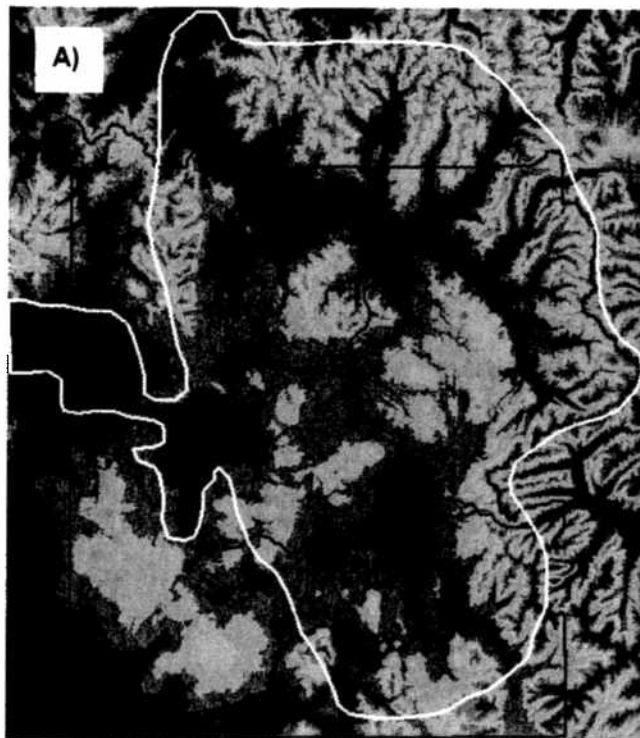


図 2-11-7 草食動物密度。これはバイソンは年中頭に換算した1ヶ月あ。  
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イエローストーン国立公園および  
周辺地域のデジタル標高モデル  
Figure 2-11-5A  
Digital elevation model of  
Yellowstone National Park  
and surrounding areas.



- TFG - moist big sage, idaho fescue
- KF - silver sage, fescue
- TF - dry sage/fescue
- PPX - pitchstone plateau complex
- DW - tufted hairgrass
- WV - willow-sedge
- FD - fescue/hairgrass
- FN - fescue-bearded wheatgrass
- FNG - moist fescue/bearded wheatgrass
- HS - hot springs vegetation
- 2LL - subalpine fir/grouse whortleberry
- 2FO - subalpine fir- meadowrue
- 2L3- subalpine fir/grouse whortleberry whitebark pine phase
- 2LG- subalpine fir/grouse whortleberry phase - pinegrass phase
- 2CL- subalpine fir/twinflower, grouse whortleberry phase
- 2EE - subalpine fir/globe huckleberry, globe huckleberry phase
- 2GO - subalpine fir / pinegrass
- 2DO - wet forests
- 3HO - whitebark pine/feik sedge
- 4PO - lodgepole pine/bitterbrush
- 5NO - douglas fir/snowberry
- 5GO - douglas fir/pinegrass

No.48 図2-11-5B Despain (1990)の生息地地図で認識された生息地クラスの集合に基づき、Trettin(1986)の土壌調査で標本採集された生息地タイプに呼応するようにした単純化した生息地地図。森林生息地は極相の植生の点から見て分類されていることに注意。大部分の森林はトウヒ-モミよりはむしろ遷移途中のコントラマツの林分である。調査地域の外郭線、道路、そして公園境界も表されている。

Figure 2-11-5B Simplified habitat map based upon an aggregation of habitat classes recognized on the habitat map of Despain (1990), to correspond to those habitat types sampled in Trettin's (1986) soil study. Note that forest habitats are classified in terms of climax vegetation. Most forests are seral lodgepole pine stands rather than spruce-fir. Also shown is the outline of the study area (white), roads, and the park boundary.

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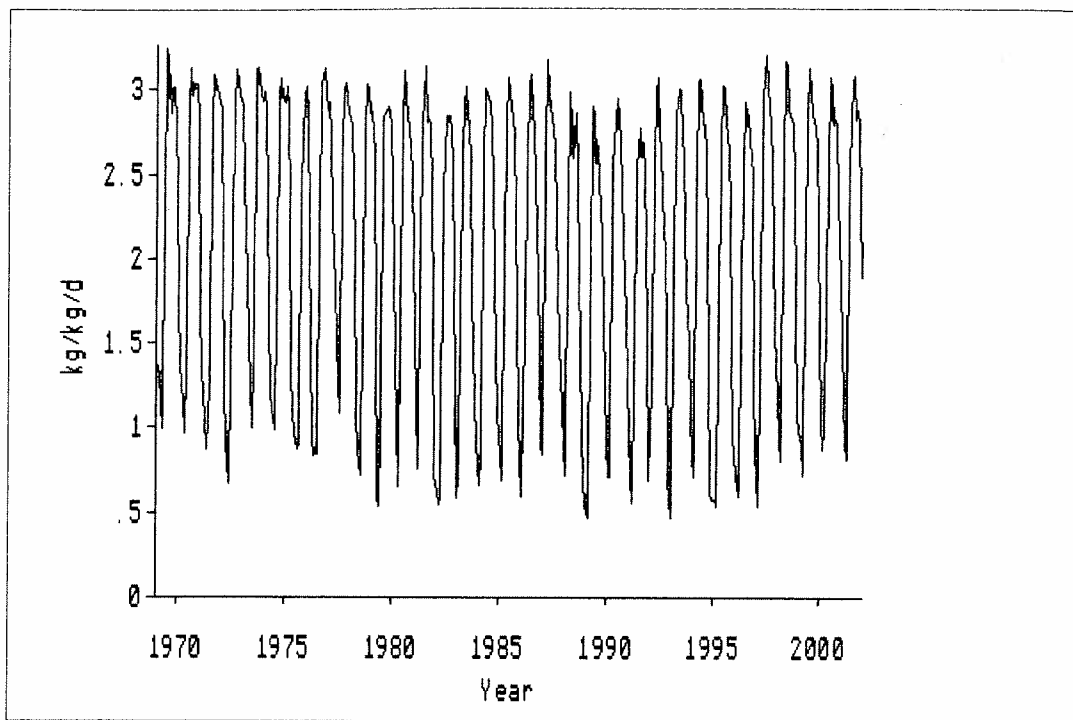


図 2-11-8 長期間のバイソンの餌摂取率の季節変動  
Figure 2-11-8 Bison forage intake rate over time showing seasonal fluctuations.

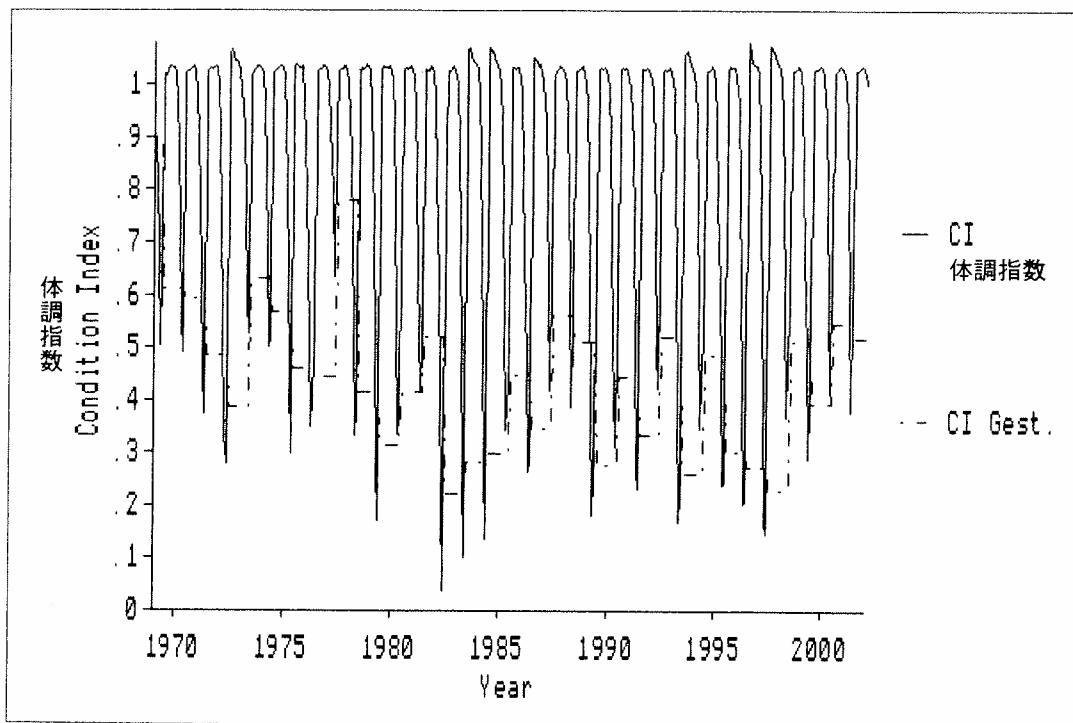
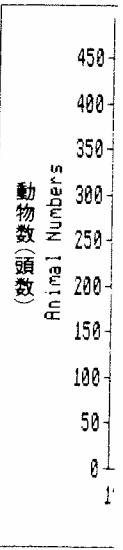
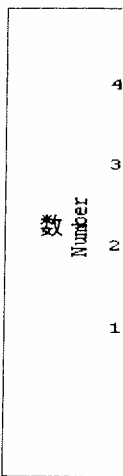
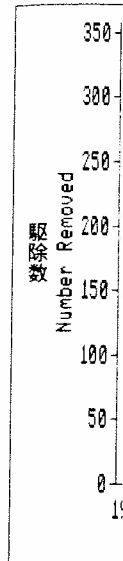


図 2-11-9 長期間のバイソンの体調指数 (実線)、そして、妊娠休止期間中の体調 (点線)  
Figure 2-11-9 Bison condition index over time (solid line). Also, the condition during the gestation interval (dashed line).



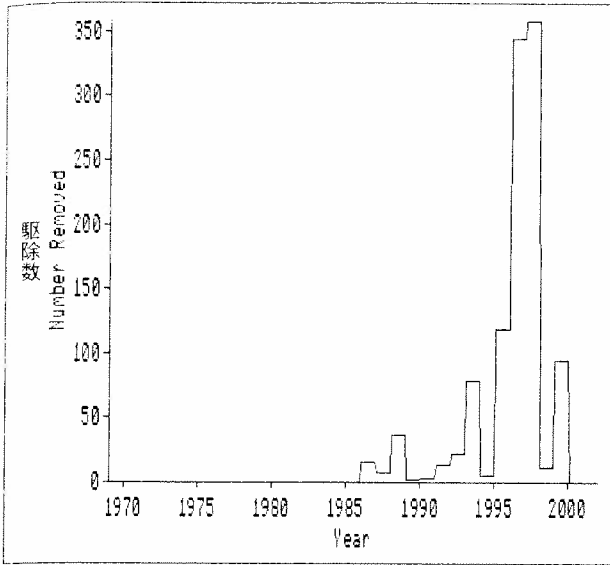


図 2-11-10 中央群から駆除されたバイソンの数  
Figure 2-11-10 Number of bison removed from the central herd.

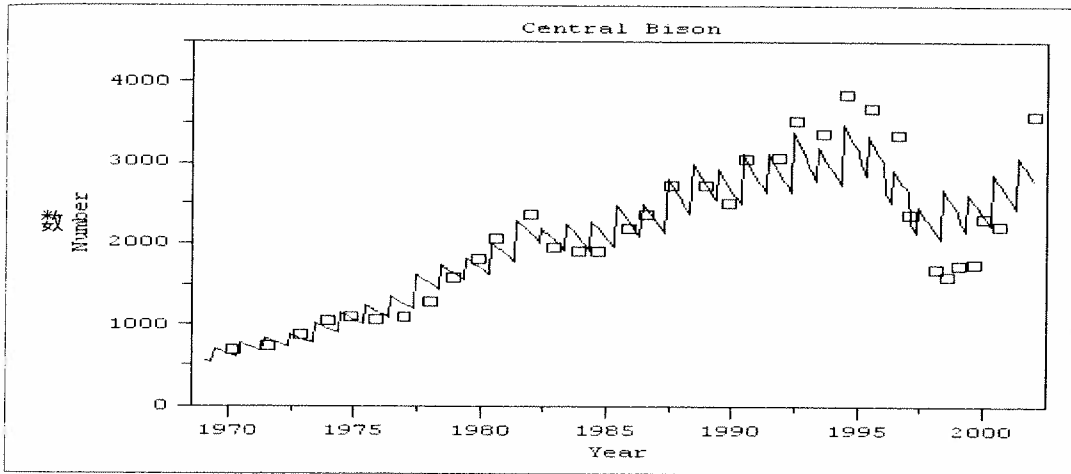


図 2-11-11 中央群のバイソンの観察数(四角)と予測(線)の個体群動態  
Figure 2-11-11 Observed (squares) and predicted (line) population dynamics of the central bison herd.

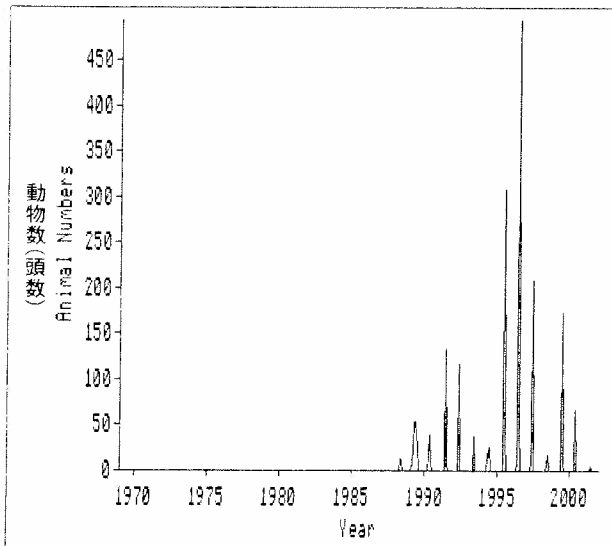


図 2-11-12 1969~2001年に公園の西側境界外で予測されたバイソンの数  
Figure 2-11-12 Predicted number of bison outside the western park boundary 1969-2001.



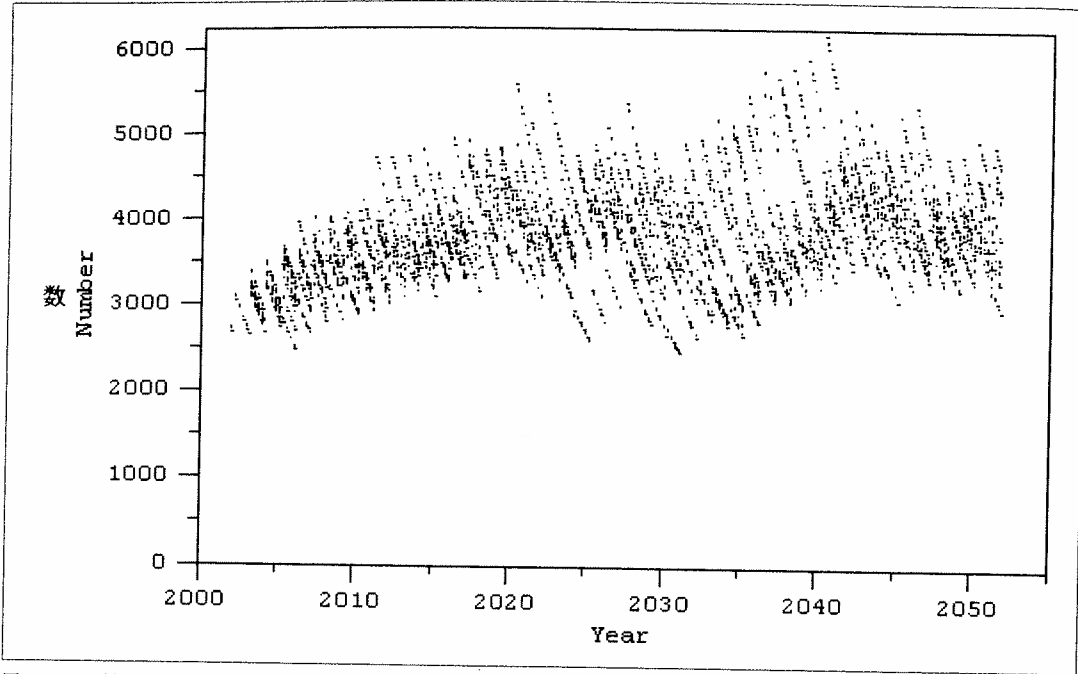


図2-11-13 様々な気候パターン、そしてバイソンを駆除しないと仮定して50年に8回シュミレーションしたバイソンの数  
 Figure 2-11-13 Simulated numbers of bison in eight runs of 50 years with different weather patterns, and with no removals of bison.

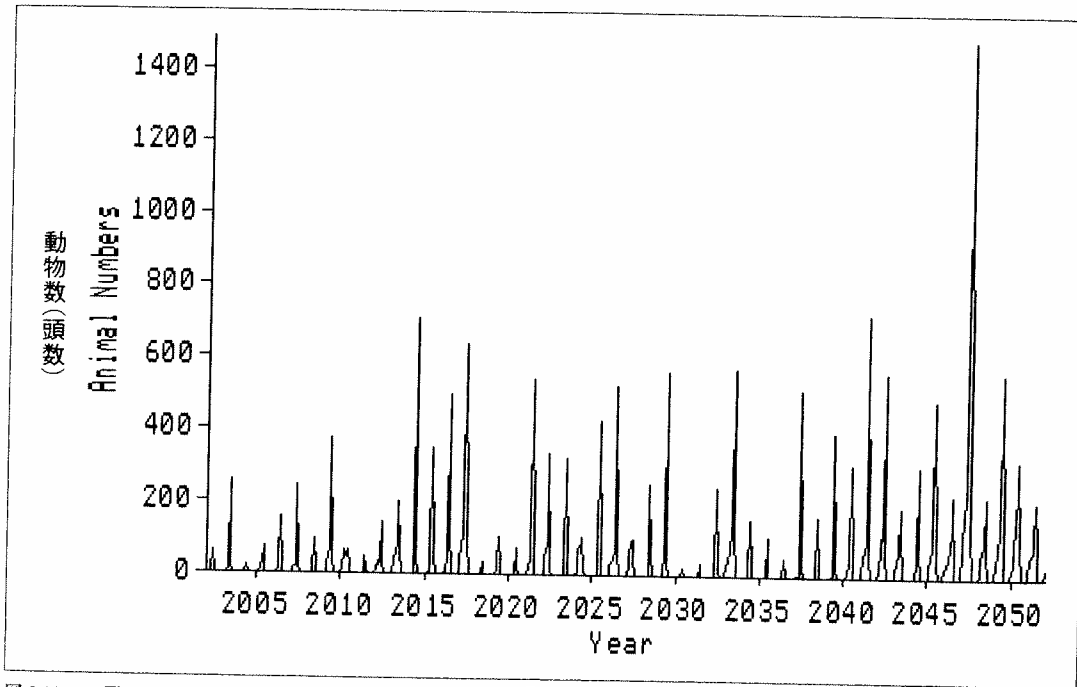


図2-11-14 図2-11-13に示されたシュミレーションの一つで公園の西側境界外で予測されたバイソンの数  
 Figure 2-11-14 Predicted numbers of bison outside the western park boundary in one of the simulations shown in Figure 2-11-13.

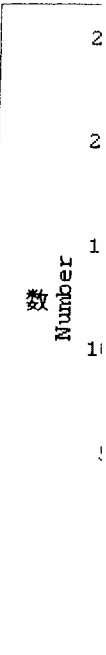


図2-11-16 様々な気候パターン、そしてバイソンを駆除しないと仮定して50年に8回シュミレーションしたバイソンの数  
 Figure 2-11-16 Simulated numbers of bison in eight runs of 50 years with different weather patterns, and with no removals of bison.

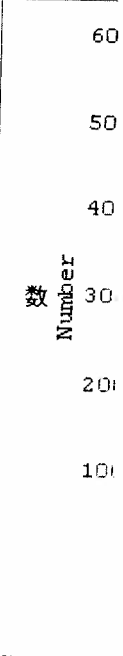
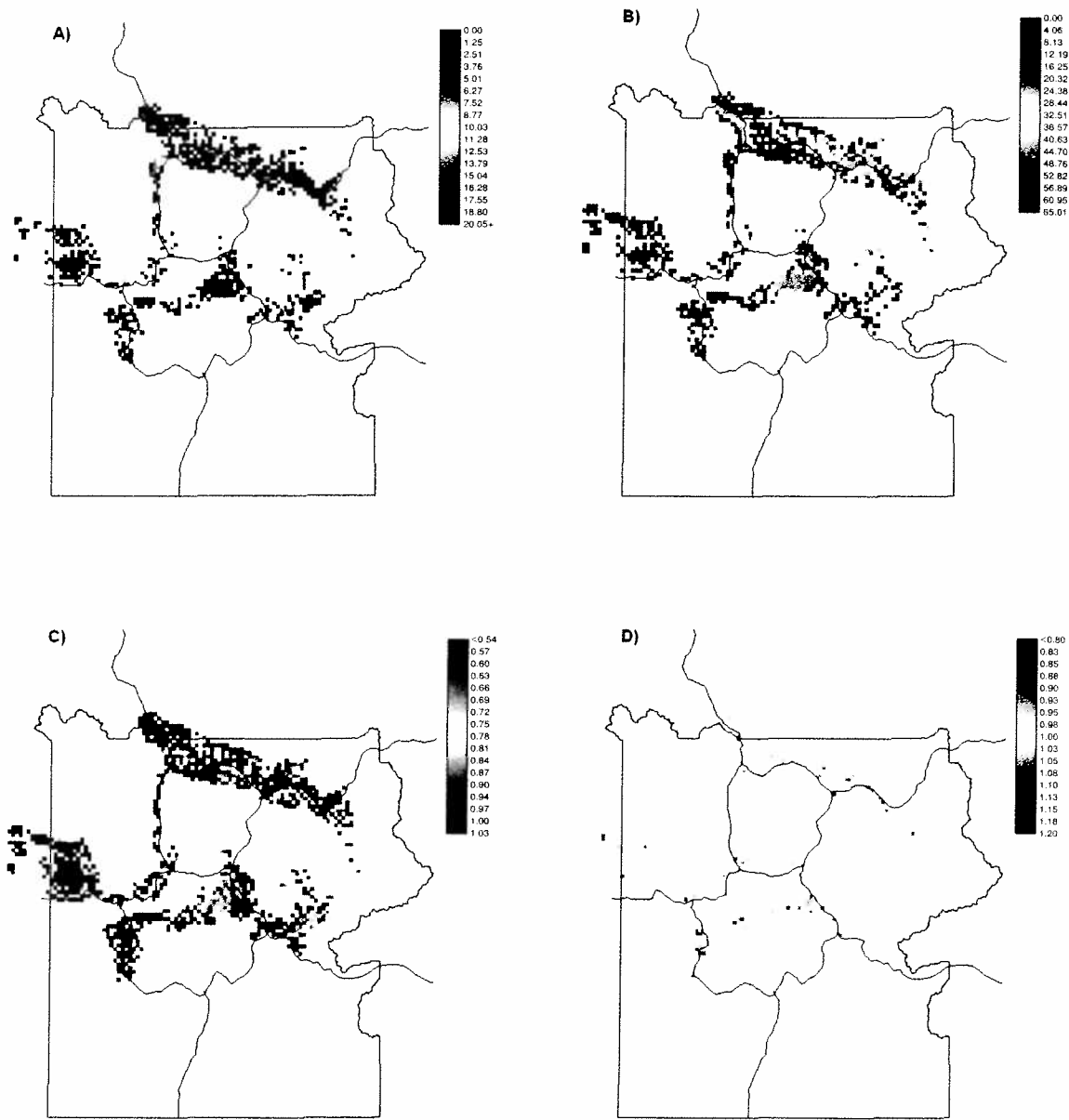


図2-11-17 様々な気候パターン、そしてバイソンを駆除しないと仮定して50年に8回シュミレーションしたバイソンの数  
 Figure 2-11-17 Simulated numbers of bison in eight runs of 50 years with different weather patterns, and with no removals of bison.



No.49 図2-11-15 北の群でバイソン2,000頭、中央の群でバイソン4,000頭のシミュレーションの結果

A) バイソンの平均密度(1Km<sup>2</sup>あたりの数)、B) バイソンとエルクの組み合わせによるグラミノイド地上部生産量の平均オフテイクの割合、C) 10月と、バイソンはいないが同数のエルクがいる模擬実験での平均グラミノイド新芽バイオマスの割合、D) 8月と、バイソンはいないが同数のエルクがいる模擬実験での平均草本根のバイオマスの割合。

Figure 2-11-15 Results from a 50-year simulation with 2,000 bison in the northern herd and 4,000 bison in the central herd.

A) Mean bison density (number per km<sup>2</sup>). B) Mean percent offtake of graminoid aboveground productivity by bison and elk combined. C) Ratio of mean graminoid shoot biomass in October to that in a simulation with no bison, but the same number of elk. D) Ratio of mean herbaceous root biomass in August to that in a simulation with no bison, but the same number of elk.

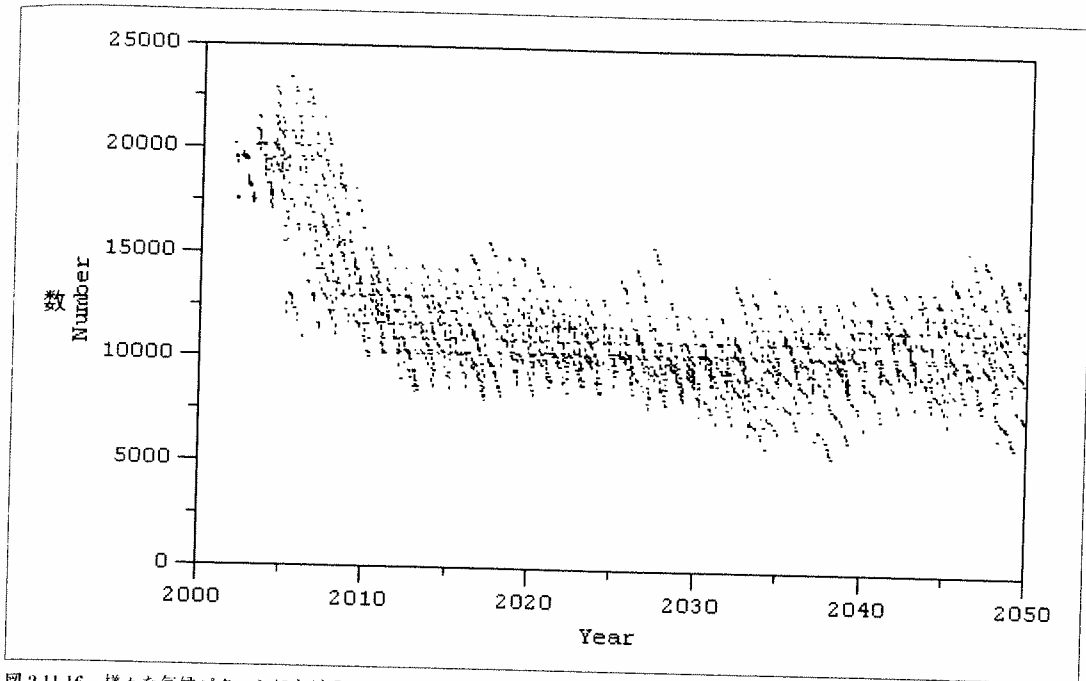


図 2-11-16 様々な気候パターンにおける8つのシミュレーションでのオオカミによる捕食と公園外での狩猟の継続によるエルクの数  
 Figure 2-11-16 Elk numbers with wolf predation, and continued hunting outside of the park in eight simulations with different weather patterns.

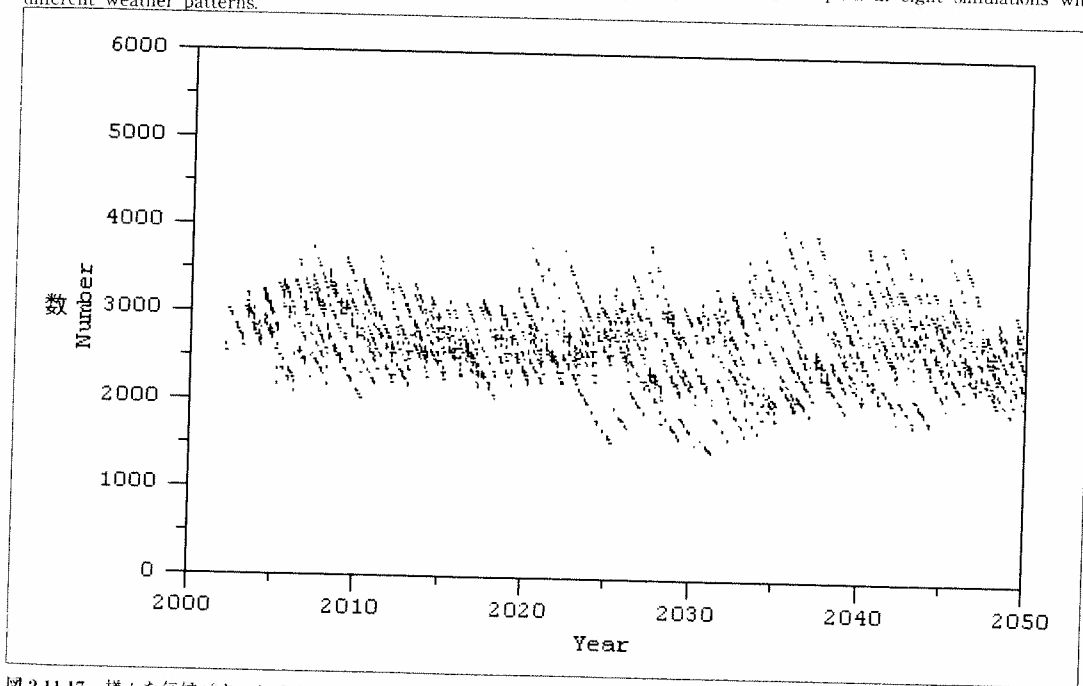


図 2-11-17 様々な気候パターンの8つのシミュレーションにおいて、もしオオカミがエルクを狩ることを学び、公園外でのバイソンの駆除を継続した場合の中央群のバイソンの数  
 Figure 2-11-17 Central bison numbers if wolves learn to hunt bison and with continued removals of bison outside of the park boundary in eight simulations with different weather patterns.