# THE ECOLOGY OF BISON MOVEMENTS AND DISTRIBUTION IN AND BEYOND YELLOWSTONE NATIONAL PARK

## A Critical Review
## With Implications for Winter Use and Transboundary Population Management

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# EXECUTIVE SUMMARY

*Collaboration is necessary to define what is acceptable;*
*science is necessary to define what is possible;*
*organizing people to use knowledge to design and implement*
*management in the face of uncertainty is fundamental*

In 1968, Yellowstone National Park (YNP) moved from a 33 year (1934-1967) period of culling ungulate populations for achieving predetermined stocking levels to a regime of ecological management under which populations of bison and other ungulates are allowed to fluctuate in the park without human intervention. With growing numbers of bison, management has become dominated by two major linked controversies; namely, the risk to livestock of transmission of brucellosis from bison moving beyond the park boundary, and criticism of the effects of winter use by snowmobiles on bison movements and range expansion, including transboundary movements, bison condition and population dynamics.

This project was initiated to: 1) provide a thorough, independent assessment of the state of knowledge of the ecology of bison movements and distribution within the context of current published concepts and theories; 2) provide recommendations for adaptive management of uncertainties and gaps in reliable knowledge within an adaptive environmental assessment and management framework, which involves organizing people to link science to management.

The principal investigators, based at the University of Calgary, Faculty of Environmental Design, were chosen because of their lack of previous association with issues related to YNP bison ecology or winter use management, allowing them to assess the state of knowledge and adaptive management from an unbiased perspective. The project was commissioned by the National Park Service. The research contract was administered by the Rocky Mountains Cooperative Ecosystems Studies Unit (RM-CESU) at the University of Montana.

The assessment entailed review of 1) literature on ungulate distribution, including Yellowstone National Park publications and planning documents, 2) key informant interviews for gaining rapid understanding of the system and unpublished knowledge, 3) development of a strategic level bison population and winter distribution model, and 4) key informant technical workshops to refine the model. In addition, 5) a workshop was held with environmental non-government organizations to review the concepts and knowledge upon which the assessment and model are based.

The assessment is summarized below. We first present key findings derived from key informant knowledge and interpretation of empirical data on population and spatial ecology. Secondly, we provide a summary of key findings derived from a systems model. Then we summarize key uncertainties and data gaps that may be addressed through monitoring and basic research. To be effective, adaptive management requires learning from key management experiments defined with the agreement of stakeholders and carried out under scientifically rigorous experimental designs. We identify key challenges for adaptive management, including how agencies are organized to collaborate on and coordinate policy development, management experiments, and procurement of scientific research and monitoring data in the long term. Finally, we offer recommendations for addressing these challenges.

## Key Findings

### *History*

- Distribution, movements and population dynamics of large mammal populations need to be viewed at spatial scales significantly larger than Yellowstone National Park itself in the context of historic spatial patterns, habitat composition, and landscape configuration and connectivity. Also, ecological processes play out over many decades so management actions cannot be fully comprehended at shorter time scales.
- Yellowstone National Park is the only area in the lower 48 States where bison have existed in a wild state since prehistoric times.
- Bison occupied the region encompassing the park from shortly after recession of the last glaciers 10,000 to 12,000 years ago, until they were nearly extirpated by market and subsistence hunting, and poaching by 1900.
- The Lamar Valley and the Yellowstone River Valley north to Livingston was an important area for bison and Native peoples throughout Holocene prehistory. This system can be considered the original Northern Range of Yellowstone bison.
- A resident population in the central interior in the Hayden Valley and the Firehole valley was extirpated by the late 1800s.
- The expansive grasslands of the Madison Valley and Snake River Plains were likely the source of some bison moving into the central interior of the park in summer.
- Yellowstone National Park is not a self contained ecosystem, covering only 8,983 $km^2$ or slightly more than 10% of the Greater Yellowstone Ecosystem (80,503 $km^2$).
- Historical records for 1902 indicate the persistence of a small remnant bison population in the eastern central interior of the park (22-30 individuals). The foundation stock for Yellowstone bison also included 18 cows imported from Montana and 3 bulls from Texas.
- Northern Range bison were restored in YNP through captive breeding (1902-1915), followed by gradual release and eventual elimination of husbandry by 1952.
- Interchange between Central Range bison in the Pelican Valley and Northern Range bison was suspected as early as the 1920s, related to common summer range in the Mirror Plateau and western slopes of the Absaroka Mountains (Upper Lamar Valley).
- Bison were reintroduced to the central interior of the park in 1936; 35 were released in the Fountain Flats and 36 in the Hayden Valley.

- Interchange between bison in Hayden Valley and the Firehole via the Mary Mountain Trail was first documented in winter 1945 but probably occurred earlier. The bison using the two areas became known as the Mary Mountain herd.
- Movements in winter between the Pelican Valley and Hayden Valley historically occurred when wintering populations were high in the Pelican Valley and Hayden Valley, e.g. in winter 1956.
- The Northern Range herd was managed more consistently by population reductions during the 1920s to the 1960s than Central Range populations. Management reductions of the Central Range herd began in the early 1950s and ceased in 1967.
- Culling of bison in interior YNP for population and brucellosis management ceased with the advent of the 'ecological management' in 1968.
- The risk of brucellosis transmission to cattle from bison exiting the park has influenced bison management in YNP since the 1920s.

## *Population Ecology*

- Ecological conditions are different on the Northern and Central bison ranges, requiring separate assessment of population and spatial ecology.
- Significant areas of geothermally-influenced habitat in the Central Ranges provide refugia for bison in severe winters and reduce snow cover, resulting in reduced costs for accessing forage, travel, and possibly thermoregulation.
- Extensive grasslands and typically low snow cover in the Gardiner basin (the Yellowstone River Valley from Gardiner to Yankee Jim Canyon) provides winter refuge habitat on the Northern Range outside the park. The importance of this area for ungulates in winter has been recognized since the 1920s and perhaps earlier.
- Bison in Yellowstone attempt to compensate for declining per capita food resources by range expansion, thus maintaining a relatively stable instantaneous density. However, compensation is not exact; population growth rate declines with density because high quality foraging patches are limited in overall area, are patchily distributed, and depleted first, forcing bison to shift to poorer quality patches as density increases. The likely demographic responses are decreased fecundity and increased juvenile mortality.
- In the absence of culling, all YNP bison ranges provide environmental conditions supporting long term growth and persistence of bison populations.
- At low to moderate densities, observed growth capacity was highest for the Mary Mountain herd (13% to 16% annually), and was lower for the Pelican Valley and Northern Range herds (5% to 6% annually).
- Based on data collected since 1970, population rate of increase was significantly inversely related to population density for Central Range bison (population growth decreased with increasing population size), but not for the Northern Range population. Northern Range bison may be unresponsive until now because of the dominant effect of forage competition by a large elk population.

- There was no evidence to suggest that groomed roads have changed population growth rates relative to what may have happened in the absence of road grooming.
- Culling of bison exiting the park in the Gardiner MT area sporadically reduced the Northern Range population, but boundary removals did not begin to affect the Central Range population until the mid 1980s.
- YNP is a forage-limited system. As the bison population increases, they compensate for declining per capita forage availability through range expansion, thus maintaining a relatively stable instantaneous density in winter.
- Predation may become increasingly important as wolves learn how to kill bison. We suggest that wolf predation on bison will continue to increase in the Central ranges, but not on the northern range as long as elk are relatively more abundant there. In systems where wolves show a numerical response to an abundant prey species that is difficult to kill, predation rate on easier prey can be inversely proportional to their density. Non-migratory elk may therefore be reduced to very low abundance in the Central Range.

## *Distribution and Movements*

- Key informants defined five winter ranges. The Central herd uses Pelican Valley (55 km$^2$), Mary Mountain (e.g. Hayden/Madison-Firehole, 152 km$^2$), and West Yellowstone (80 km$^2$). The Northern herd occupies Lamar Valley (234 km$^2$), and Gardiner Basin (98 km$^2$).
- As defined by key informants, these ranges are inter-connected by five primary movement corridors including Firehole-to-Mammoth (59 km), Firehole to West Yellowstone (21 km), Gardiner Basin to Lamar (river route 15.2 km; road route 11.4 km), Mirror Plateau (Pelican to Lamar, 30 km), and the shortest corridor Pelican to Hayden (8 km).
- The Mary Mountain Trail (19 km) connecting the Hayden and Firehole Valleys has been used by bison since the mid 1940s and is considered by key informants an integral part of the Mary Mountain Range rather than a corridor in the sense of other corridors. The authors deduced that the Mary Mountain Trail is a corridor maintained in winter by bi-directional movements of large numbers of bison.
- When population subunits were small, there were four semi-isolated primary wintering areas: the Pelican Valley, Hayden Valley, Firehole Valley, and the Lamar Valley.
- Apparent isolation of bison in separate winter ranges when populations were small likely reflected high per capita availability of forage, low pressure to move or expand, fewer animals to break and maintain a trail.
- Exploratory movements by mature bulls, which subsequently establish annual migration paths to and from peripheral ranges, likely precede range expansion by cow/juvenile groups.
- Range expansion was gradual, rather than pulsed as described for another erupting bison population in northern Canada. Differences in landscape composition and configuration between YNP and the Mackenzie Bison range is offered to explain the near absence of pulsed expansion in YNP.

- Learning the presence of destination habitat (familiar areas) likely played a significant role in the development of calculated migration and increasingly fluid movements of bison between ranges.
- Anecdotal information suggests that bison can break trail for considerable distances through deep snow (> 1 m), but in addition to forage limitation, knowledge of destination is likely an important condition.
- The density of bison in adjacent ranges likely determines the ability of bison to maintain trails that connect them in winter.
- Dispersal (one way movements from natal ranges) of cow/juvenile groups to unoccupied ranges rarely occurs in the YNP system. Cow/juvenile dispersal would likely be more prevalent in the absence of culling on boundary ranges.
- Mid winter survey data provide strong evidence that range expansion is density driven; more bison use more space. This holds for both the Northern and Central bison ranges.
- As populations increased, the area used expanded, and distributions eventually coalesced.
- Movements between winter ranges in central YNP have become increasingly fluid in recent years with bison moving between Pelican Valley and the Madison/ Firehole.
- Presently, YNP supports 2 bison subpopulations (Central and Northern herds) reflecting differences in ecological conditions and use of space between ranges, genetic differences, fetal growth rates, and tooth wear patterns.
- Interchange between the Central and Northern Ranges occurred historically since the 1920s, primarily via a movement corridor over the Mirror Plateau.
- Movement between the Pelican Valley and Lamar Valley in winter via the unroaded Mirror Plateau is likely constrained in most winters by snow depth, steep terrain and the long distance between these winter ranges.
- Since the early 1990s Central Range bison have migrated in increasing numbers north to Blacktail Deer Plateau and the Gardiner basin in winter using a new route associated with the road allowance between Madison Junction and Mammoth. It was speculated that most migrants return to the Hayden Valley for the rut.
- The calculated migration of Central Range bison to the Northern Range would likely not have developed in the absence of the groomed road between Madison Junction and Mammoth.
- Other groomed road segments facilitate movements within and among winter range units, but inter-range movements in winter in the Central Ranges would likely have developed in the absence of road grooming as the density of bison increased, because road segments are aligned with natural movement pathways.
- There is no documented movement of Northern Range Bison to the Central Range via the road corridor.
- Yellowstone bison are most widely dispersed in late winter then return to one of three rutting areas by mid July. The largest rutting aggregation is in the Hayden Valley, the second largest in the eastern Lamar Valley, and a small aggregation occurs in small high elevation grasslands on the Mirror Plateau and Cache/Calfee Ridge.

- Most movements are confined within Yellowstone National Park, except in winter when large numbers of bison may move into Montana near West Yellowstone and Gardiner.
- The level of boundary removals (representing transboundary movements) is strongly related to population size above 1500 bison for the Central Range and 550 for the northern Range.
- Snow pack had a smaller contributory influence on the level of boundary removals than population size, except in the unusually severe winter of 1996-1997 when an exceptionally deep and hard snow pack forced > 1000 bison to western and northern boundary ranges.
- Bison move beyond park boundaries in winter in response to forage limitation caused by interactions between population density, variable forage production (driven by spring/early summer precipitation), snow conditions, and herbage removal primarily by bison and elk.
- The Gardiner basin has been considered important winter range for bison since at least the 1940s and is an important component of the Northern winter range. In contrast, the Hebgen Lake area north of West Yellowstone offers no unique ecological value as winter range. It can be considered an expansion area for the Central subpopulation with the capacity to support 100 to 130 bison at the instantaneous density typical for Central Range bison (approximately 4 per km$^2$).

## Key Findings Based On Systems Modeling

- Based on the systems dynamics paradigm, a strategic-level model was developed to facilitate collaborative learning about bison population, range use dynamics, and management alternatives.
- The systems model was based on empirical data and key informant knowledge. The model identifies key knowledge gaps and easily accommodates new empirical data and relationships emerging from existing and future research.
- Bison population and spatial dynamics are expressions of complex interactions best understood using a systems approach.
- Forage availability was a sensitive driver of bison movements in the model. The three key variables determining winter forage availability were previous summer precipitation, snowpack characteristics, and elk and bison density (i.e., forage demand).
- Inter-range movements of bison were generally not constrained by winter snowpack in non-road grooming scenarios during most winters. The notable exception to this rule was the Firehole-Mammoth corridor that was a barrier during all non-road grooming scenarios.
- Road grooming had a greater influence on movement of bison between interior ranges (Lamar-Mary Mountain, Mary Mountain-Pelican) than to the boundary ranges (West Yellowstone, Gardiner Basin). Therefore, grooming of winter roads may reduce the variation in and total numbers of bison departing for boundary ranges during winters of inadequate forage.
- Bison movement between winter ranges was projected to range from 100 to 4,000 animals, influenced most by per capita forage availability. An average movement

of ~1,000 bison occurred in non-road grooming scenarios, and 1200 in road-grooming scenarios.

- Average simulated annual winter mortality was ~180 bison (5%) for the non-road grooming and 225 for the road-grooming scenario (7%) of the YNP herd. However, mortality during occasional extremely harsh winters exceeded 25% of the population.
- The predicted maximum cull under current boundary management policies periodically exceeded 500 animals, and rarely exceeded 750 animals.
- Culls exceeded 10% of the total YNP herd in 15% of years in non-road grooming scenarios and 6% of the herd during road grooming scenarios.
- Cumulative culls during ten 100-year stochastic runs ranged between annual average culls of 50-90 bison for the non-grooming scenario, and 60-100 for road grooming scenarios. On average, 75 bison would be culled each year from boundary ranges with or without road grooming.
- Increasing bison habitat exterior to YNP is an effective strategy to increase the total regional population, but would not reduce the number of bison that would need to be culled annually in the regional landscape surrounding the park. Although the number of bison to be culled at the boundary of YNP was significantly reduced in a “repatriation” scenario, a greater number of bison were culled in the surrounding region. For example, the annual culls at the margins of the expanded range were projected to be as follows: (2,500 $km^2$ = 1,250 bison, 5,000 $km^2$ = 2,500 bison, 7,500 $km^2$ = 3,750 bison, 10,000 $km^2$ = 5,000 bison).

## Key Uncertainties

Bison population and spatial dynamics are sensitive to variation in several key variables and interactions between variables. Among them is a subset for which the least amount of empirical data are available. They are, therefore, characterized as Key Uncertainties deserving further research:

- Threshold depth/density of snow at which low and high density forage-limited bison cannot move through corridors in search of better foraging conditions.
- Terrain characteristics (slope, ruggedness) that affect the above snow depth/density threshold preventing movements.
- Snowpack characteristics in the Pelican Valley in relation to other ranges.
- The relationship (shape and scale of the curve) between winter forage availability, bison density and bison over-winter mortality.
- The relationship (shape and scale of the curve) between winter forage availability and probability of bison movement.
- There was contradictory opinion whether the unroaded Mirror Plateau Corridor is a functional barrier to movements in winter between the Pelican Valley and the Lamar Valley when bison numbers are high and per capita forage is limited.
- Inter-range variability in forage productivity in response to precipitation and growing season length. In particular, one key informant suggested the growing season is shortest in the Pelican Valley range because of a long period of snow cover typically followed by spring flooding.

- Relationship between incidence of sero-positive bison and proportion of the herd that has been vaccinated.
- Systematic research has not been carried out on the ability of bison to move through snow under the variety of circumstances present in Yellowstone National Park.
- Snow conditions in the Pelican Valley are limited to subjective observations rather than consistent records from strategically-placed snow stations. Two modeling efforts thus far have not been able to precisely model the dynamic of snow conditions in this isolated valley of the park. Calibration of models in one location of the park does not allow large scale inference.
- The future role wolf predation plays in bison population dynamics is uncertain in Central Yellowstone ranges and is likely increasing at present. Mechanisms underlying how YNP wolves limit bison abundance and distribution have received limited attention.
- There is uncertainty of the extent of the interchange between the Northern and Central bison herds. This information is important for understanding how to conserve the spatial and genetic structuring of this population and maintenance of bison on the Northern Range under current boundary management.
- Data now being obtained from GPS collars will allow key questions about movement ecology to be addressed, including the timing and extent of movements in relation to plant phenology, snow conditions, forage production and utilization. In addition, with this technology research is now possible to address questions about the effects of roads and other anthropogenic or natural features on movements about which some uncertainty remains.

The YNP bison population will continue to experience wide long term fluctuations providing opportunities to study ecological dynamics at varying densities. A systems-based approach to understanding the dynamics of the YNP bison subpopulations can exploit environmental and management perturbations to learn about key uncertainties.

## Key Challenges

- Empirical data on the effects of snow pack on bison movements and foraging in YNP is weakly represented in available literature.
- The two snow models developed for YNP yield discordant results.
- Herbivory (bison and elk), primary productivity and plant community structural responses have been poorly studied on ranges in central YNP.
- Competition and antagonism among some scientists and research groups impede data sharing, collaboration and research coordination.
- The YNP bison monitoring program is poorly defined and has been inconsistent since 1997, making it difficult to analyze changes in vital rates, population structure, and spatial responses in relation to environmental variation and management interventions since then.
- Migration of Central Range bison north to the Gardiner basin could result in management actions (removals) that jeopardize the viability of the Northern Range population.

- The humaneness of mechanized hazing of bison back into the park in winter is strongly challenged by some environmental non-government organizations and some park personnel.
- Government agencies compete for influence over bison management based on differences between individual agency mandates, disciplinary biases and institutional cultures.
- The USDA and Montana Department of Livestock remain deeply committed to eradication of brucellosis from wildlife and eliminating all risk to the livestock industry, and appear unresponsive to public interests in bison conservation and ecosystem management.
- The singular focus of these agencies on bison as a vector of brucellosis is poorly understood by the public, which sees a much larger reservoir in elk associated with feed grounds in Wyoming and inconsistent policies by which agencies deal with bison emigrating from the park.
- Efforts to deal with the linked issues of bison/brucellosis management and winter use/bison movements suffer from fractured governmental jurisdiction, inefficient and ineffective policy processes, and have been unable to define the common interest.
- Existing organizations and decision processes addressing the two issues have not been effective in defining the common interest or producing stable, broadly supported management plans.
- The agency-based planning processes used to address the issues and the low level of public involvement required under NEPA, have generated conflict and reduced public trust in governance.
- Decision processes followed by federal and state agencies to develop the Joint Management Plan appear a divisive, deeply-rooted power-balancing struggle to protect fragmented and overlapping jurisdictions and avoid risk.
- Many publics are frustrated with their low level of participation in decision processes but are willing to collaborate with government agencies to define common interests and to participate in decision-making.
- There is confusion about the appropriate role of science in value-based decision-making.
- There is resistance within some agencies to increasing public involvement in decision-making.
- Previous decision-making documents, formal assessments and environmental planning documents have not improved policy processes or provided organizational structures necessary to achieve enduring solutions acceptable to a broad range of affected stakeholders.
- Both the bison/cattle/brucellosis issue and the winter use issue are highly charged conflicts with public interests having no mechanism for meaningful participation. The affected publics are willing to use the courts and sometimes more extreme actions to be heard. The result is ongoing conflict, substantial annual and incremental costs for the agencies in time and resources, and promotion of the notion that more science, more information, will somehow result in wiser outcomes.

## Recommendations

### *Monitoring and Science*

1. Yellowstone National Park should implement an internally funded bison population monitoring program that collects and manages data on population size, vital rates, and winter distribution in the long-term.
2. Yellowstone National Park should define a minimum viable bison population for the Northern Range.
3. Yellowstone National Park should encourage and coordinate research focused on reducing key uncertainties over a full range of densities as the population fluctuates in response to environmental stochasticity or management actions.
4. An adaptive management experiment should be designed to test permeability of the Firehole to Mammoth corridor under varible snow conditions with a specific focus on the road section between the Madison Administrative Area and Norris Junction.
5. Yellowstone National Park should install a SNOTEL or Snow course station in the Pelican Valley, monitor snow conditions in the Pelican-Hayden Corridor, and re-evaluate the two existing snow models.

### *Adaptive and Collaborative Management Structures and Processes*

6. Engage the U.S. Institute for Environmental Conflict Resolution in an independent situation assessment that includes advice on designing an integrated agency and public planning strategy to represent the common interest.
7. The Yellowstone Center for Resources should play a lead role among agencies and researchers in coordinating data sharing, research and monitoring of bison and other research relevant to bison ecology and management, by developing a stable collaborative science and management framework.
8. Develop or refine appropriate systems models and other decision support tools to help agencies and other stakeholders to understand key uncertainties and system properties, and to evaluate outcomes of management scenarios defined through value-based decision processes.
9. The National Park Service should increase its support for the appropriate agencies to secure agreements for key winter range for bison and other wildlife adjacent to the park in the Northern Range.

# GLOSSARY OF TERMS

**AEAM** Adaptive Environmental Assessment and Management
**AM** Adaptive Management
**AHP** Analytical Hierarchical Procedure
**APA** Administrative Procedure Act
**APHIS** Animal and Plant Health Inspection Service
**BTNF** Bridger-Teton National Forest
**CEQ** Council on Environmental Quality
**CMP** Comprehensive Management Plan
**DFWP** Department of Fish, Wildlife and Parks
**DOL** Montana Department of Livestock
**EA** Environmental Assessment
**EIS** Environmental Impact Statement
**ENGO** Environmental Non-Government Organizations
**ESA** Endangered Species Act
**FACA** Federal Advisory Committee Act
**FMC** Firehole to Mammoth Corridor
**FWC** Firehole to West Yellowstone Corridor
**GAO** General Accounting Office
**GIS** Geographic Information Systems
**GLC** Gardiner Basin to Lamar Valley Corridor
**GTNP** Grand Teton National Park
**GYA** Greater Yellowstone Area
**GYCC** Greater Yellowstone Coordinating Committee
**GYE** Greater Yellowstone Ecosystem
**GYIBC** Greater Yellowstone Interagency Brucellosis Committee
**IBMP** Interagency Bison Management Plan
**IENR** Institute for Environmental and Natural Resources
**IHD** Impact Hypothesis Diagram
**ISMA** International Snowmobile Manufacturers Association
**JBEMP/EIS** Jackson Bison and Elk Management Plan and Environmental Impact Statement
**MOU** Memorandum of Understanding
**MPC** Mirror Plateau Corridor
**OSV** Over snow vehicle
**PHC** Pelican Valley to Hayden Valley Corridor
**NAS** National Academy of Sciences
**NEPA** National Environmental Policy Act
**NER** National Elk Refuge
**NPS** National Park Service
**NOI** Notice of Intent
**RM-CESU** Rocky Mountain Cooperative Ecosystem Research Unit, University of Montana
**SWE** Snow Water Equivalence

**USDA** United States Department of Agriculture
**USDOI** United States Department of Interior
**USFS** United States Forest Service
**USFWS** United States Fish and Wildlife Service
**USGS** United States Geological Survey
**USGS-BRD** United States Geological Survey – Biological Research Division
**USIECR** United States Institute for Environmental Conflict Resolution
**WGFD** Wyoming Game and Fish Department
**YNP** Yellowstone National Park

# 1

# INTRODUCTION

Prehistorically, Yellowstone National Park (YNP) bison ranges were probably linked by migration to expansive grasslands surrounding the Yellowstone Plateau, particularly the Northern Range. Historical accounts indicate that interior ranges also supported resident bison. Market and subsistence hunting extirpated bison from the Greater Yellowstone Area by the late 1800s, except for a small remnant population in the remote interior of the park. Eventually, legislation and enforcement provided protection allowing the population to increase slowly. Bison from Montana and Texas were imported to restore the species to the Northern Range of the park in 1902, which together with the wild herd formed the foundation stock for the present day population. Intensive management limited the size of the population until the mid-1960s when a policy change of ‘ecological management’[1] allowed large mammal populations in the park to self regulate in relation to ecological conditions. This form of management has been popularly referred to by the confusing term ‘natural regulation’.

As the bison population increased, their range expanded, resulting in increasing numbers moving to contiguous habitat on the western and northern boundaries of the park. The YNP bison population carries the pathogenic bacterium *Brucella abortus*, which is infectious to cattle and people causing the disease brucellosis. Originating with cattle, the organism has been the subject of a national eradication program spanning 70 years and costing an estimated $3.5 billion in public and private funds. Fearful of the risk of transmission of brucellosis from wild bison to cattle, federal and state agencies negotiated the management of bison moving from the park into Montana at West Yellowstone and near Gardiner. Management actions have included hunting, culling by government personnel, capture and slaughter and hazing bison back into the Park. All have been controversial, especially when the combination of a large population and severe winter conditions induce migration of significant numbers of animals to the Montana boundaries where large removals have occurred. In one particularly harsh winter in 1996-1997, more than 1,000 bison were removed from the boundary ranges.

Since the early 1990s, concern has been expressed that grooming of roads in the park for oversnow vehicle (OSV) use has facilitated bison movements within and between ranges, including boundary areas, and that energy saved by bison travelling on packed snow in combination with better access to foraging habitat, results in enhanced population growth. Opponents of road grooming have sought to eliminate the practice, arguing impairment of the park. Protection of the park environment represents one set of interests in the debate over winter use; recreation and business interests are another. Since 1949, the public has had the opportunity to visit the park during winter using OSVs. A

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[1] ‘Ecological management’ was the original term used in the document *Administrative Policies for Natural Areas, 1968*, which defined the new policy for management of plant and animal resources in national parks.

substantial winter recreation industry has developed around winter access to the park, contributing significantly to the regional economy. Proposals to restrict this activity are met with vigorous opposition from this sector.

The bison/cattle/brucellosis and the winter use/bison movement issues are functionally linked highly charged conflicts with public interests and agencies willing to engage in confrontation to protect their interests. Yellowstone National Park (YNP) was established by an Act of Congress in 1872 setting aside 2 million acres “dedicated and set apart as a public park or pleasuring-ground for the benefit and enjoyment of the people...” and "for the preservation, from injury or spoilation, of all timber, mineral deposits, natural curiosities, or wonders. . . and their retention in their natural condition.". The current controversy over the effects of winter use of groomed roads by bison reflects the inherent tension between the NPS’ dual mandates to accommodate public recreational enjoyment while protecting park resources. The bison of Yellowstone National Park are ecologically and evolutionarily significant because they are among less than a dozen free-ranging herds exposed to natural regulation and selection and the only free-ranging plains bison population on the continent that exceeds several thousand (Boyd 2002). Conservation of bison and maintenance of its ecological roles within the park system has created difficult relationships with agencies responsible for managing other public interests outside the park, such as disease risk to livestock.

Defining the common interest in a sea of conflicting values is a formidable challenge. To date, research has provided conflicting evidence of how groomed roads affect bison movements, energetics, and population productivity, and no research has provided a clear or convincing answer to the question. The notion that winter road maintenance facilitates bison movement, range expansion and increased population growth, was originally offered for bison on the Northern Range where the road is plowed in winter. The concept was elaborated a short time later for the Central Range where snow on roads is packed in winter.

The underlying ecology of bison movements and the influence of natural and anthropogenic features in the Yellowstone landscape are not well documented in the peer reviewed literature. Much existing knowledge exists in internal agency reports, unpublished manuscripts and data sets held close by researchers, and as expert knowledge gained through observation and experience. The available knowledge has not been systematically compiled or evaluated relative to current theories and concepts of ungulate movements and dispersal, nor have these sources been evaluated for uncertainties and knowledge gaps.

## The Task

Winter use of groomed roads by bison in YNP is controversial, in part because bison moving beyond the boundary of the Park are subject to lethal control and other actions to prevent transmission of brucellosis to livestock. Two recent court orders concerning winter use and road maintenance were apparently contradictory. One on December 16, 2003 (Washington, D.C. federal court) directed the National Park Service to phase-out recreational snowmobiling by winter 2004-2005. The other on February 10, 2004 (Wyoming federal court) restrained NPS from doing so, and required a temporary rule for winter use that would be fair and equitable to all parties. The Washington, D.C. federal court noted that conflicting science exists concerning the effects of groomed roads on bison movements, finding the National Park Service (NPS) must “cogently explain why it has exercised its discretion in a given matter”, and when faced with conflicting evidence [disagreement between experts] the decision-maker must “identify the considerations he found persuasive”.

Consequently, the NPS identified a need for this project, the purpose of which was to: 1) produce a thorough,unbiased and independent assessment of the state of knowledge of the ecology of bison movements and distribution within the context of current published concepts and theories; 2) provide recommendations for adaptive management of uncertainties and gaps in reliable knowledge within adaptive environmental assessment and management and systems frameworks, including institutional structures and processes for adaptive and collaborative management planning to link science and management.

## Structure of This Study

The principal investigators, Cormack Gates and Brad Stelfox (University of Calgary, Faculty of Environmental Design), were chosen because of their lack of previous association with issues related to YNP bison ecology or winter use management, allowing them to assess the state of knowledge and adaptive management from an unbiased perspective. The project was commissioned by the National Park Service (principal contact Dr. G. Plumb). The research contract was administered by the Rocky Mountains Cooperative Ecosystems Studies Unit (RM-CESU) based at the University of Montana (principal contact Dr. L. Broberg). RM-CESU operates independently and in association with a national network of CESUs.

The ecological, social, legal, and political complexities underlying the linked winter use/bison ecology and bison movements/brucellosis risk management issues required an interdisciplinary approach involving the integration of social and natural sciences concepts and methods. Interdisciplinary approaches are distinguished from multidisciplinary and monodisciplinary approaches by the manner in which complex problems are addressed. By interdisciplinary, we mean involving several unrelated academic disciplines in a way that forces them to cross subject boundaries to solve a common research goal. To develop the approach, we drew on concepts and methods from spatial and population ecology, systems dynamics modeling, adaptive environmental assessment and management, collaborative resource management, alternative environmental dispute settlement, and natural resource policy science.

We began by orienting to the problem through a review of documents and interviews of key informants to seek rapid understanding about what was known about the system, what the issues were, and the nature of people’s interests in the issues. We used a broad range of methods to acquire and organize available knowledge, and then integrated results using a dynamic systems model. It was understood from the outset that one of the central causes of ongoing conflict was not a lack of knowledge but a lack of policy process by which people and institutions can be constructively engaged in integrative decision making using the best available science.

For this project, we adopted an Adaptive Environmental Assessment and Management (AEAM) and a systems framework approach, recognizing the need as well for integration of principles and practices from other disciplines noted above. We addressed the issue in a broad sense, defining the ecological and management settings within which the issues are occurring. AEAM can be defined as the process of organizing people and their decisions around systems modeling and iterative hypothesis testing (Holling 1978, Blumenthal and Jannink 2000). Adaptive Management (AM) is the systems-modeling/hypothesis-testing aspect of AEAM that provides for use of the scientific method to test the outcome of management actions against objectives (McLain and Lee 1996). Its most effective form, "active" adaptive management, employs management programs designed to compare selected policies or practices, by evaluating alternative hypotheses about the system being managed (Nyberg and Taylor 1995). Adaptive management also refers to a process in which uncertainty is acknowledged, learning is an integral component of management, and the scientific method forms the basis for management experiments (Lee 2001, Lancia et al. 1996). Adaptive management provides for monitoring and evaluation of resource outcomes relative to objectives at specified intervals (Ringold et al. 1996, McMullin 1999).

Systems modeling emphasizes broad viewpoints, or the "big picture" view, so that interrelationships and interconnectivity are the focus rather than statistical precision, collection of complex data and empiricism. AEAM rejects the notion that all elements and interactions must be fully defined and understood to effectively manage a natural system. Systems modeling is employed to reduce complexity by identifying important components and interactions, thereby limiting the number of possible management options (Walters 1986). As stated by Holling (2000) "There is a requisite level of simplicity/complexity behind complex, evolving systems that, if identified, can lead to understanding that is rigorously developed but can also be lucidly communicated."

The state of knowledge of bison movement ecology was compiled by reviewing published and grey literature and conducting interviews with key informants including past and present agency personnel involved in research and/or management, university researchers, and others with local knowledge of the issues. We searched electronic databases and asked key informants for relevant documents. Literature was accumulated on ungulate movement, relevant research in YNP, pre-historical and historical information on bison in YNP, and legal and management documents relevant to bison management. We conducted semi-structured interviews with key informants to obtain information not available in published or unpublished documents (Robson 1993, Babbie 2001). Initially key informants were identified *a priori* based on their expertise. Additional key informants were identified during the interviews (the snowball method, Babbie 2001). Key informant interviews are considered an efficient method for rapidly learning and integrating local and scientific knowledge (Kloppenberg 1991, Stromquist et al. 1999). Some interviews were conducted with groups when key informants were compatible, e.g. part of the same research group/agency. A list of interviewees is provided in Appendix I.

The interview protocol received approval from the University of Calgary Conjoint Faculties Research Ethics Board. Before release of the final report, key informants had the opportunity to review information or statements attributed to them. They were asked to confirm that we correctly represented the information they provided, and were given an opportunity to modify inaccurate statements to their satisfaction. During interviews, we discussed background to the issues and key elements and processes influencing bison movements in YNP. We used a conceptual system diagram (Impact Hypothesis Diagram or IHD) to aid deliberative dialogue. The IHD identified system variables and interactions (e.g. forage distribution and quality, patch metrics, forage competition, predation), key system indicator variables (e.g. bison density distribution in the park and in relation to the park boundary), and extrinsic drivers (e.g. snow pack, geothermal patterns, and anthropogenic influences). We used the diagram to focus discussion on additional information and insights on feedback loops and interaction behaviors between system components. Maps were used to record spatial information (e.g. location of bison winter ranges and movement corridors) offered by interviewees using a technique known as 'interviewing the map' (Catley 1999). Spatial information was drawn by the interviewee on an acetate sheet overlaying a base map. Spatial data were digitized using ArcView Geographic Information Systems (ESRI 1999).

Information from the interviews was compiled and used as the basis for building a spatially stratified strategic level systems dynamics model representing bison ecology and management relevant to road grooming effects and bison management at the boundaries of the park. Technical validation workshops were held in October 2004 with five groups of key informants, two to three months after individual interviews were completed. A list of key informants invited to and participating in each workshop is listed in Appendix II. Technical Workshop Groups were assigned a unique number, which is not crossreferenced to a specific Group in the report to protect the confidentiality of individual participants in compliance with the policy of the University of Calgary on the Ethical Conduct of Research on Human Subjects.

A draft operating systems model was presented at workshops to seek further input and explore participant's understanding of the system. We used the Analytical Hierarchical Procedure (AHP; Berry 2003) to "weight" some of the key components of the model based on expert opinion. These were the parameters influencing the permeability of winter movement corridors (snow, thermal areas and forage) determined to be important during initial interviews. AHP allows key informants to rank the importance of each component against each other component; a weight defining the relative influence of each parameter is calculated from the ranking matrix. An average weight for a workshop group was calculated and used to attribute a group model. Additionally, key relationships and response surfaces were defined during the workshops. We created individual systems dynamic models that represented how each workshop group perceived the system. Separate models were constructed representing input from each workshop group. Some models were similar, thus an averaged model was produced. We used a standard set of scenarios and compared outcomes between models. Simulations enabled us to identify sensitive and uncertain components of the system and assess their potential influence on bison movement patterns and population dynamics. We identified system key drivers and relationships that require further research. A final technical workshop was held with Yellowstone Center for Resources personnel in late February 2005 to identify any technical inconsistencies or factual errors.

A facilitated workshop was held in Livingston Montana in late October 2004 for representatives of Environmental Non-Government Organizations (ENGO); 13 organizations were represented and 18 people attended (Appendix II). At this workshop, we sought further information on bison movements and ecology in YNP. The nature of the system was discussed using an IHD refined through previous technical workshops, and the graphical user interface from the model. In addition, there was general discussion of stakeholder issues.

## Organization of the Report

A comprehensive review of the worldwide literature on the ecology of ungulate movements and distribution is provided in Chapter 2. It is important to consider environmental and historical contexts of bison in YNP to understand the current situation and identify potential future directions. Chapter 3 provides a review of the environmental setting and history of road and other infrastructure development and levels of use in YNP. Data on baseline conditions presented in Chapter 3 were used in building the systems dynamics model. Pre-historical and historical contexts of the issues, highlighting the history of bison the YNP area and their management, is provided in Chapter 4. Chapter 5 provides an assessment of available knowledge on bison distribution, movements and population ecology in YNP. Results of system dynamics simulations are presented in Chapter 6. In Chapter 7, we provide a synthesis of key findings of the assessment and offer recommendations for adaptive environmental assessment and management, monitoring and basic research needs. Recommendations are offered to improve the process of creating broadly supported management policy and actions, drawing on the theories and practices of environmental problem solving (Endter-Wada et al. 1998, Clark 1999), shared learning (Daniels and Walker 1996), collaborative decision making (Wondolleck and Yaffee 2000, Conley and Moote 2003) and policy process (Clark 2002). Recommendations are offered in recognition of a lack of clarity on the common interest of society, the historical power struggle and remaining deep divisions between agencies, and conflicting world views bearing on the issues of winter use management in YNP and containment of bison to mitigate risk of brucellosis transmission to livestock.

# 2

# REVIEW OF LITERATURE ON UNGULATE MOVEMENTS

This chapter reviews the scientific literature on temporal and spatial distribution and movements of ungulates to provide background for interpreting the movements of bison in and near Yellowstone National Park, where weather, population density, predation, hazing and winter grooming of roads influence movements. The review probes the implications of restricting movements and forced sedentarism.

## Evolution of Movement Patterns

Movement patterns evolved among animal species in response to diverse ecological pressures (Dobson 1982). The fitness of an individual is dramatically influenced by its selection of a place (Alcock 1977), and particular movement patterns will be selected if they have reproductive or survival (fitness) value (MacArthur 1972). Pease and Lande (1989) stated the biogeography of a species is determined by evolution and movements of populations. They suggested the distribution of a species is often more malleable than its morphology or environmental tolerance.

### *Dispersal*

Dispersal is an important process for improving a population’s ability to respond to changing environments. Dispersal has been defined as: travel by individuals beyond their home range boundaries when they do not return (at least in the short term) as they would after brief excursions (Stenseth and Lidicker 1992); individual movements out of an area larger than a home range with no predictable return (Bunnell and Harestad 1983); and one-way movement by a population with no predictable direction (Sinclair 1992). Dispersal plays a major role in population regulation (Lidicker 1975), and spatial distribution (Taylor and Taylor 1977). Species that disperse with a low rate of return likely subsist in habitats subject to a high deterioration rate, but low movement cost, possibly due to short distances between suitable habitat patches (Baker 1978).

According to Murray's “rule of dispersal” (Murray 1967), individuals move to the first suitable uncontested site, and no further, assuming the disperser spends no longer than necessary searching for an empty location, because of the risk of travel or cost in time, or they disperse to avoid sharing home ranges. Selection favours non-dispersal in the absence of competition, but when competition exists, individuals are pressured to disperse (Waser 1985). Instead of attributing dispersal to a single cause, Dobson and Jones (1985) stated that multiple factors should be considered. Even if there is one primary cause, other factors may contribute to the magnitude of dispersal.

For dispersal to be advantageous, fitness gained from exploiting new areas must exceed the costs of moving. Dispersal may reduce disease, predation, and competition for resources (Waser 1985), but there are also potential disadvantages, including uncertainties of finding necessities (e.g. food, shelter, empty habitat, a mate, or appropriate social milieu), greater exposure to predators and competitors, loss of rare phenotypes, and less viable offspring (from breakdown of co-adapted systems, or disadvantageous genetic recombination; Stenseth and Lidicker 1992). Effective fertility may decrease if a disperser must establish a dominant position in an existing hierarchy before it can mate (Bengtsson 1978). Also, increased movement rates can be associated with greater prevalence and spread of disease (Mollison and Levin 1995).

### *Migration*

Movement from one spatial unit to another is the least restrictive definition of migration (Baker 1978). A definition that includes a return component is used most consistently by vertebrate biologists (Stenseth and Lidicker 1992), thus distinguishing it from dispersal. To be adaptive, migratory movements must involve a change in environment, or travel over an "ecological distance" from one environment to another (LeResche 1974). Species with a high incidence of return migration should be those adapted to spatially separate habitat types that fluctuate in relative suitability (Baker 1978). Many ungulates have evolved in grassland, desert or tundra regions where food availability is highly seasonal or erratic because of drought or snow cover. Messier et al. (1988) considered the increasing energy expenditures for migration as a possible regulatory factor for the expanding George River caribou herd. In African grassland, mammal diversity is low, large concentrations of animals are typical, and long distance seasonal migrations are common (Baker 1978). In transitional zones between grassland and forest (i.e. savannah), species diversity is relatively high, animals are not highly concentrated, and migration is rare. When it does occur, migration is for relatively short distances.

Species such as wildebeest (*Connochaetes taurinus*), and caribou/reindeer (*Rangifer tarandus*), which are known for long distance mass migrations, typically also have populations that remain sedentary (McNaughton 1985, Banfield 1954). Migrants may share ranges with residents at certain times of the year. In the Ngorongoro Crater, Tanzania, there are abundant year-round food and water resources and resident wildebeest do not seem compelled to migrate (Talbot and Talbot 1963).

Opportunities to use a complementary range of habitats with limited migration distance is afforded in areas with sharp ecological gradients such as mountains. Altitudinal migration is a feature of the seasonal ecology of many ungulate species throughout western North America. Bison (*Bison bison*) use altitudinal gradients in Yellowstone and similar landscapes but used other gradients such as the prairie-parkland transition in the Northern Great Plains (Morgan 1980). The occurrence of migration in many ecosystems around the world suggests there may be common underlying causes (Fryxell et al. 1988). Large herbivores appear to migrate primarily to access high quality food and/or avoid predators, but also as an effective strategy to avoid thermal stress, insect harassment, and contact with disease and parasite vectors.

### *Dispersion*

Dispersion is defined as the internal distribution pattern of a population (Odum 1971), or the distribution of animals in space, ignoring time, since birth (Bunnell and Harestad 1983). As the mean distance between individuals increases through dispersal, changes in dispersion may result in greater clumping, increased randomness, or more even spacing

(Stenseth and Lidicker 1992). Convergence decreases the mean distance between individuals.

Often, a population undergoes dispersion when departing on a migration, and convergence on return. If an animal migrates as a herd, then disperses into smaller social units at the destination, herding behaviour is assumed to reduce the cost of migration (Baker 1978). Natural selection appears to favour dispersion in animals when food availability is low, or convergence when food availability increases (Leuthold 1977). However, if water or other point resources are limiting, selection seems to favour convergence, whereas dispersion is favoured when water becomes less limiting.

## Benefits of Dispersal

### *Inbreeding Avoidance*

Genetic variation has been generally accepted as necessary for evolutionary adaptation of a species to a changing environment. Restriction of movement may facilitate mating of closely related individuals (Wright 1946). If a population has been outbreeding for an extended period of time, recessive deleterious mutations accumulate and deleterious effects of inbreeding become relatively high (Bengtsson 1978). Pemberton et al. (1988) reported that red deer (*Cervus elaphus*) calves homozygous for two alleles did not survive as well as calves heterozygous for both. Ralls et al. (1979) used juvenile survival of ungulates as a measure of inbreeding depression in zoos. Inbreeding avoidance is most effectively accomplished by female dispersal. Territorial behaviour of males also reduces inbreeding (Spinage 1982).

A population that has been inbreeding for a considerable time would not greatly increase fitness by changing its reproductive strategy (Bengtsson 1978). Genes required for adaptation to a particular environment may be lost or suppressed, and acquired skills appropriate in one environment may not be useful in another (Cockburn 1985). Inbreeding may be advantageous in low fecundity mammals by improving adaptation to local conditions and reducing the cost of meiosis (Shields 1983). Throughout history, bison lived in large mobile populations, which should minimize inbreeding. Inbreeding depression might be expected under the restricted management that has prevailed for the last 150 years. However, there is little evidence of problems, although the number of generations under these conditions is not great. In a recent study of bison gentics at Elk Island National Park where population structure is not manipulated, Wilson et al. (2002) found that individual males were not able to dominate breeding opportunities and successful bulls were not always the largest.

### *Finding Mates*

Animal movements are greatly influenced by mating systems (Greenwood 1980). Ideally, dispersal should occur either at young ages before reproduction or at old ages after the reproductive contribution to the population has been completed (Morris 1982). Typically, males compete for mates and invest relatively little in rearing offspring. Conversely, females typically invest heavily in offspring and are therefore the sex limiting reproduction. In many polygynous and promiscuous mammals, young males are more likely to find mates if they adopt a disperser strategy (Dobson 1982). Males increase reproductive success through contact with many females, which can often be achieved through greater mobility. In most monogamous mammals, both males and females disperse (Dobson 1982).

In Georgia, sexual competition among male white-tailed deer (*Odocoileus virginianus*) appeared to be the primary stimulus for dispersal (Kammermeyer and Marchinton 1976). Most dispersers were young subordinate bucks of breeding age. Nelson and Mech (1999) suggested the recent range expansion and establishment of new wintering areas of white-tailed deer in North America resulted from dispersal of yearlings.

Male dispersal occurs in species that live in permanent herds, such as impala (*Aepyceros melampus*; Murray 1982), or African buffalo (Synerus caffer; Sinclair 1977). Sinclair (1977) found an increasing tendency for male buffalo to depart from mixed herds as they grew older, and those greater than ten years were permanently displaced by dominant breeding bulls. According to Prins (1989), rutting activities in mixed herds diminished a male's physical condition, while males in bachelor herds improved their condition. Distant movements of male muskoxen (*Ovibos moschatus*) on the Seward Peninsula probably improved their prospects for breeding whenever social competition was intense (Smith 1989).

In monogamous and territorial species such as dikdik (*Madoqua rhynchtragus*) and roe deer (*Capreolus capreolus*), all offspring of both sexes disperse to find mates (Hendricks 1975, Bobek 1977). Also, both sexes (although mostly males) disperse in species with loose social organization, such as southern reedbuck (*Redunca arundinum*; Howard 1986) and black-tailed deer (*Odocoileus hemionus columbianus*; Bunnell and Harestad 1983). Conversely, female Uganda waterbuck (*Kobus ellipsiprymus*) are the most active in dispersal, searching new areas for awaiting males (Spinage 1982).

During the breeding season, most mature male bison disperse to gain access to females and displace dominant bulls (e.g. Herrig and Haugen 1969, Petersburg 1973, Lott 1974, and Melton et al. 1989). Because mixed herds of wood bison (*B. b. athabascae*) are small and widely scattered, they are more likely to be encountered by nomadic males (Gates and Larter 1990). Komers et al. (1992) suggested that male wood bison accompany mixed herds for breeding, and disperse to recover from rutting activities. Once body condition is restored, the males rejoin mixed groups where there is a continuous exchange of potential female mates. Lott (1979) observed that male plains bison lose dominance if they become exhausted from rutting activities.

### *Access to New Resources*

When resources become limited, female dispersal has been observed in red deer (Clutton-Brock and Albon 1985), southern reedbuck (Howard 1986), and roe deer (Bobek 1977). Although moose (*Alces alces*) are generally solitary, they do not exhibit female dispersal when resources become limited (Gasaway et al. 1985). Increase in population density stimulates dispersal of white-tailed deer bucks (Nelson and Mech 1984), but not females (Nixon et al. 1991, Nelson and Mech 1992). Social organization of a species influences dispersal rates (Baker 1978). In ungulates that occur in moderate sized herds, such as elk (*Cervus elaphus*) and sheep (*Ovis spp*.), females usually disperse in small groups, splitting off from the parent group and establishing an adjacent home range (McCullough 1985). Wildebeest typically occur in large herds and may disperse in large groups (Sinclair 1992). Although male African buffalo experience higher predation when they are not part of large herds, groups of three or four are able to utilize habitat patches too small for female-dominated groups that aggregate to minimise vulnerability to predation (Sinclair 1977). Gates and Larter (1990) also observed male wood bison foraging in small habitat patches not used by large mixed groups. Movement over wind-packed open habitat would have much higher energetic costs for male bison because foot loadings in snow are much higher in males than females (Telfer and Kelsall 1984). Lott and Minta (1983) suggested lack of group fidelity in bison may facilitate dispersal in a Great Plains environment with fluctuating rainfall and forage resources.

## Benefits of Migration

### *Access to Shifting Resource Availability*

Many migrations occur during transitions between seasons (winter/summer at high latitudes and wet/dry seasons in the tropics) indicating this may be a response to changes in resource availability. Rapid, long distance movements are characteristic of large herbivores that evolved in grassland ecosystems. McNaughton (1985) described the Serengeti region of East Africa, comprised of 27 ungulate species and over three million individuals. The open grasslands receive low annual precipitation that support shortgrass, while wooded grasslands receive higher rainfall that support tall, highly lignified grasses. The primary grazers are wildebeest, zebra, Thomson's gazelle (*G. thomsonii*), buffalo and topi (*Damaliscus korrigum*). Annual movements occur in nomadic herds of wildebeest, plains zebra (*Equus burchelli*) and eland (*Taurotragus oryx*). Although most gazelle (*Gazella spp*.) are nomadic, they travel shorter distances. Buffalo, topi and gazelle occur as resident herds throughout the savannas. Impala, topi, hartebeest (*Alcelophus buselaphus*) and giraffe (*Giraffa camelopardalis*), which include browse in their diet, remain in wooded grasslands year-round (Baker 1978). Some eland also remain, while others migrate with zebra herds. Among seasonal migrants, there is relatively little mortality through starvation, but non-migrants such as impala, giraffe, kudu (*Tragelaphus strepsiceros*) and waterbuck all experienced considerable starvation mortality at the end of a dry season in South Africa (Hirst 1969).Wildebeest migrate to open grassland for the wet season to feed on shortgrasses, which are easily digestible and nutrient rich (Fryxell et al. 1988). When water sources evaporate during the dry season, and the food value of tropical grasses declines (Sinclair 1975), wildebeest must migrate to wooded grasslands for water and green grass.

Migration during the dry season by white-eared kob (*Kobus kob leucotus*) in Boma National Park, Sudan, allowed access to green grass and water when these resources were scarce elsewhere in ecosystem (Fryxell and Sinclair 1988*b*). Because Lechwe antelope (*Kobus spp*.) feed on floodplain grasses and herbs, movements coincided with the annual expansion and contraction of flood waters across broad river basins (Fryxell and Sinclair 1988*b*). These animals disperse during flooding, and then converge when waters subside.

On the Eurasian steppes, east of the Caspian Sea, antelopes such as dzeren (*Procapra gutterosa*) and dzheiran (*Gazella subgutterosa*), and wild asses (*Equus hemionus*) congregate in winter (Formozov 1966). Forage is locally abundant where the ground lacks snow cover. If severe winter reduces food availability, these animals undergo dispersive migration.

In southern California, migratory female mule deer (*Odocoileus hemionus*) used habitats with higher forage quality than non-migratory deer (Nicholson et al. 1997). However, migrants were exposed to increased predation during the seasonal movements and experienced higher mortality during dry years. Moose typically converge on a common range during winter and disperse into separate ranges during summer (Hundertmark 1998). In Laurentides Provincial Park, Quebec, DesMeules (1964) observed that as snow depth increased, moose became more dispersed and confined to coniferous cover. Under deep snow conditions, singles or small groups of moose could use scattered winter forage more efficiently (Houston 1968).

An eastern European tundra moose population formed in the 1950s (Pulliainen 1974) spent the summer on the arctic coast then migrated south to find adequate vegetation for sustenance during winter. In southeastern Norway, migrating moose used habitats of lower quality but higher quantity browse than resident moose (Histol and Kjeljord 1993). There was no data to indicate which strategy provided a nutritional advantage. Mutual cooperation in trail breaking and cratering in snow is an advantage of herding behaviour for caribou and bison (Helle 1984, Telfer and Kelsall 1984). Cooperative trail maintenance in snow to access resources may also be important for white-tailed deer (Telfer and Kelsall 1984, Messier and Barrette 1985).

### *Predator Avoidance*

In many ungulate species, parturition coincides with movements away from predators (Fryxell et al. 1988). Migratory animals tend to outnumber sedentary compatriots, in some cases by an order of magnitude. One explanation for this phenomenon is that migrants are less vulnerable to predators that are unable to follow migratory herds. Also, pregnant females that disperse in a heterogeneous environment before calving force predators to search larger areas. Some ungulates that experience deep snow conditions may converge to evade predators.

Above average grass productivity in the 1970's allowed the migratory wildebeest population in the Serengeti to increase; non-migratory kongoni (*Alcelophus buselaphus cokii*), topi and impala were apparently unaffected (Sinclair 1979) suggesting that wildebeest were regulated by food, while non-migrating species were regulated by predation (Fryxell and Sinclair 1988*a*). The migratory strategy of wildebeest may decrease their vulnerability to regulation by sedentary lions (*Panthera leo*) and hyenas (*Crocuta crocuta*). During the period that their young are immobile and dependent, these predators are limited by resident prey because they are unable to follow migratory herds. Migratory species associated with open grasslands are unreliable prey; therefore predators are restricted mainly to wooded grasslands.

In the Masai Mara National Reserve, Kenya, Cooper et al. (1999) monitored spotted hyenas that fed mainly on resident topi and Thomson's gazelle during the first half of the year. Upon arrival of the migratory herds of wildebeest and zebra, hyenas switched to wildebeest, which provided them a superabundance of food for about three months. After the migratory animals departed, there was a period of reduced prey abundance due to temporary dispersion of resident ungulates. Parturition for zebra, wildebeest and gazelle is December to January. Impala, hartebeest, giraffe and other non-migratory ungulates calve in October while accompanied by seasonal migrants. This suggests an adaptation in parturition time by resident ungulates to minimise predation on offspring.

Bighorn sheep forage in large dispersed groups in open habitat adjacent to steep cliffs as a predator-evasion strategy (Risenhoover et al. 1988). Security depends on sightability of predators and availability of escape terrain. Bleich et al. (1997) studied mountain sheep (*Ovis canadensis*) in California to help determine causes of sexual segregation in ungulates. Mature rams and ewes were segregated from December to July. Mature males usually occupied sites with more abundant and higher quality forage than ewes; however, predators were substantially less abundant on ranges used by ewes with lambs than on those used by mature rams. Mixed groups occupied steeper slopes, rougher terrain and habitats that are more open when lambs were very young. Results supported the hypothesis that female ungulates, which have greater vulnerability to predation due to smaller body size, minimize their risks and risks of their offspring to predation by using habitats with greater opportunities to evade predation than mature males.

Long distance migration of the George River caribou herd of northern Quebec and Labrador reduced its accessibility to wolves (*Canis lupus*) during the four to five months when pup-rearing restricted their movements (Messier et al. 1988). As the herd expanded, sedentary populations of caribou in the region declined (Brown et al. 1986). Barren-ground caribou herds migrate from the boreal forests of Manitoba, Saskatchewan, Alberta and the Northwest Territories, to calving grounds in the tundra of Nunavut. Calving grounds were described by Kelsall (1968) as poor in vegetation and unattractive to males and non-breeders, which selected better vegetated sites at lower latittudes. Calving areas provided some refuge from tundra wolves, which preferred to den closer to the treeline (Heard and Williams 1992). Fancy and Whitten (1991) suggested that female caribou from the Porcupine herd selected calving areas north of the mountain foothills in northeastern Alaska and northern Yukon, primarily to reduce predation exposure. Highest calf mortality occurred in years when calving was closer to the foothills, where wolves and grizzly bears (*Ursus arctos*) were abundant. In Denali National Park, Alaska, offspring from caribou that migrated to calving grounds experienced only half the wolf predation that calves born in other areas (e.g. lowland spruce forests) experienced (Adams et al. 1995). In south-central Alaska, Ballard et al. (1987) determined that calving caribou were usually unavailable to wolves because wolves remained within their territories and did not follow migrating caribou into calving areas.

Maternal female woodland caribou sought high elevation slopes for calving in Spatsizi Provincial Park, northern British Columbia (Bergerud et al. 1984), west-central Alberta (Edmonds and Smith 1991), and Wrangell-St. Elias National Park and Preserve in Alaska (Barten et al. 2001). Calving grounds were partially out of the range of wolves and bears, however, food resources were more limited at those locations compared to lower elevations. These females appeared to sacrifice food abundance and/or nutrition to provide safety for their offspring.

Many caribou populations that disappeared in British Columbia since the early 1900s were non-migratory (Seip 1992). He suggested wolves might have eliminated the sedentary Quesnel Lake herd because wolf numbers were sustained at high densities by moose. In contrast, the neighbouring Wells Gray herd, which migrated to mountainous summer ranges away from moose and wolves, was increasing. Tweedsmuir-Entiako caribou that used low elevation forest had very low calf survival (Seip and Cichowski 1996). In contrast, those migrating into alpine and subalpine areas experienced higher calf survival, and calves born on islands had the lowest mortality. Migratory caribou form large aggregations to “space away” from predators at calving time, whereas less mobile woodland caribou that disperse from each other “space out” from predators (Bergerud and Page 1987). This type of behaviour has been observed in Spatsizi Provincial Park of B. C. (Bergerud et al. 1984), west-central Alberta (Edmonds 1988, Edmonds and Smith 1991), northeastern Alberta (Fuller and Keith 1981), central Saskatchewan (Rettie and Messier 1998), Manitoba (Brown et al. 2000), and Quebec and Labrador (Brown et al. 1986). In 1978, before coyotes arrived, only 15% of parturient female caribou dispersed into the Gaspe uplands. By 2002, this rose to 70% and calf survival improved (Mosnier et al. 2003).

Home range sizes of moose cow/calf pairs became significantly smaller in an experimental area of Alaska after removal of brown bears (Ballard et al. 1980), suggesting these moose used dispersion as a predator avoidance tactic.

The formation of concentrations of white-tailed deer in winter (yarding) may be due to predator avoidance rather than a food acquisition strategy (Nelson and Mech 1981). Reduced philopatry during winter may also be a mechanism for predator avoidance. Trail networks are maintained to access forage and evade predators (Telfer and Kelsall 1984, Messier and Barrette 1985). Parker et al. (1999) suggested that white-tailed deer tend to decrease home range size to a minimum, regardless of forage availability, to reduce encounters with predators. In northeastern Minnesota, deer that converged near human habitation during winter experienced less wolf predation (Hoskinson and Mech 1976). In southern Sweden, roe deer form small matriarchal groups in winter when predation risk is high (Wahlstrom and Liberg 1994). Mountain goats (Oreamnos americanus) occupy some of most rugged terrain in North America, effectively reducing predation from grizzlies, wolves and cougar (Felis concolor; Chadwick 1983). During the period after wolf eradication in the Greater Yellowstone Ecosystem, bison and elk became more sedentary (Berger 1991).

## Use of Space

### *Familiar Area*

Familiar area is the entire range an animal has prior knowledge of, either from direct perception, previously memorized sensory contact, or from social communication. Animals can therefore navigate from one point to any other point within a familiar area (Baker 1978). Once familiarity is developed, elk show high fidelity to seasonal home ranges (Knight 1970, Craighead et al. 1972). The period of delay before moose immigrate into vacated habitat is likely because familiarity needs to be developed (LeResche 1974). There are many ungulate species where few individuals leave the population, including elk (Houston 1982), red deer (Clutton-Brock et al. 1985), reindeer (Skogland 1985), and African buffalo (Sinclair 1977). Winter range of red deer in northern Scotland extended from sea level to 520 m, and summer range was >520 m (Darling 1937). The migration pattern was flexible and they migrated to low elevations in summer if weather became inclement. In spring, daily altitudinal return migrations occurred, from lower elevations at night to higher levels by day. Baker (1978) surmised that these red deer were aware that higher altitudes provided greater shelter from adverse weather, a gradual succession of new food, and protection from biting insects during spring and summer; they responded to prevailing conditions by migrating to the part of their familiar area they assessed would offer optimum conditions for that particular situation.

Male white-tailed deer left their mothers and began making exploratory movements at one year of age (Nelson and Mech 1984). This led to formation of home ranges by their first breeding season; the short dispersal distances were affected by early movement experiences. New white-tailed deer wintering areas can be established when an adult female, possibly with her daughters, abandons the traditional area and spends the winter in a new location (Lesage et al. 2000*a*). Dispersers would likely select new wintering areas near summer range or along migratory routes to former wintering areas. Migration could develop at this intermediate stage of new wintering area formation. Female offspring, and to lesser extent male offspring, establish winter home ranges peripheral of their mothers (Hoskinson and Mech 1976, Nelson and Mech 1999) causing wintering areas to expand over time. Sweeney et al. (1971) radio-collared 64 white-tailed deer and observed their behaviour when pursued by hunting dogs. These deer had relatively large familiar areas; only six travelled more than two kilometers beyond their home range, and all except one individual returned to their respective home ranges after the chase.

Within enclosures, introduced moose and calves born to them died at a faster rate than resident moose (Bailey and Franzmann 1983). This was attributed to increased energy expenditure by the introduced moose while pacing fence lines, indicating a strong desire to return to familiar surroundings.

In South American Vicuna (*Vicuna vicuna*) the basic social units are mixed herds that occupy relatively small home ranges (Koford 1957). Sub-adult males leave mixed herds to accompany bachelor groups. Each male joins and departs these groups repeatedly and ranges widely. This enables a young male to have a large familiar area within which a small home range will be established once a harem is gathered.

Since the mid 1970s, nearly all mixed groups of bison on the northern range of Yellowstone National Park migrate to a wintering area west of the traditional core area in some years. Meagher (1989*b*) suggested acquired knowledge of new foraging areas and the gregariousness of bison, which facilitated learning, were the predominant factors influencing this movement pattern.

### *Home Range*

Home range can be defined as the area traversed by an individual during normal foraging activities, mating and caring for young (Burt 1943) or the total fraction of the lifetime range of the familiar area physically visited by an animal in a given time interval (Baker 1978). For some species, home ranges vary between seasons and for most ungulate species home range selection differs between sexes. Bleich et al. (1997) suggested that male mountain sheep select home ranges with superior forage to enhance body condition and horn growth. Conversely, home range selection by females appeared to be influenced by predation risk. They concluded that sexual segregation likely results from differing reproductive strategies of males and females among sexually dimorphic ungulates. The ultimate factor determining home range size is energetic requirements (McNab 1963). According to Cederlund and Sand (1994), male moose have larger home ranges than females because of higher metabolic requirements related to sexual dimorphism, and a mating system that depends on access to dispersed females. They also stated that with large mammals such as moose, habitat patches are relatively small compared to the home range. During severe winters, the optimum strategy for large bull moose in Denali National Park, Alaska, was to remain solitary, reduce activity levels, decrease travel distances, increase bite size and inhabit a site with high forage biomass (Miquelle et al. 1992). During summer, bull moose tended to aggregate in open areas where higher forage biomass was available, while cow moose with calves dispersed in forested areas to reduce predation risk.

In African buffalo, home range size was related to quality of habitat (Sinclair 1977). Small home ranges occurred in forested or high rainfall habitat, whereas larger home ranges were likely to be in drier open areas. Buffalo density was correlated with the amount of food in patches along riverbanks, in swamps and in forest glades. To learn the locations of these habitat patches, young animals must follow adults for an extended period of time. Mackenzie wood bison used smaller home ranges where populations were expanding their range, probably due to greater access to unexploited forage resources (Larter and Gates 1990). Females had the largest home ranges. Because they aggregated in larger herds than males, females probably required more extensive grazing areas and these were distributed in widely separated patches. In autumn, bison used a greater variety of habitats when forage quality and quantity became more homogeneous on the landscape (Larter and Gates 1991*a*).

### *Territory*

The simplest cited definition of a territory is “any defended area” (Noble 1939). Leuthold (1977) expanded the definition to include “that part of an animal’s home range from which it excludes individuals of comparable social status through active repulsion”, or “a spatially fixed area within which a given animal consistently prevents certain other individuals from engaging in certain activities”. Territorial behaviour appears to be most apparent in tropical ungulates (Spinage 1982). Leuthold (1977) described territorial behaviour of five classes of African ungulates. Small, exclusive browsers with small home ranges occupied year-round, such as dikdik (*Madoqua kirkii*), duikers (*Cephalophus spp*.) and klipspringers (*Oreotragus Oreotragus*), generally have individual or pair territories. Larger browsers or grazers, such as reedbucks (*Redunca spp*.), oribi (*Ourebia ourebia*), sitatunga (*Tragelaphus spekei*), bushbuck (*T. scriptus*) and gerenuk (*Litocranius walleri*), have larger home ranges, and typically only males are territorial. Moderate sized browsers, grazers and mixed feeders such as impala, waterbuck, and several species of gazelle and kob have fairly large home ranges and are typically sedentary but may move seasonally. Diets may change seasonally, for example, reduced foraging on grass as the dry season progresses. Male territories are a small part of the home range, and a large proportion of males occur in bachelor herds. Exclusive grazers, such as wildebeest, are highly mobile and have attenuated territories that continually reform as the herd moves. Sedentary populations of wildebeest exhibit more pronounced territorial behaviour. Buffalo and eland, which consume a wide variety of grasses and/or browse, move across extensive areas and are not territorial.

## Dispersal and Density

### *Saturation Dispersal*

Saturation or enforced dispersal is density dependent and occurs when an animal population fills its habitat to capacity (Lidicker 1975). The dynamic state of the population is stationary and most dispersal in large mammals fits this category (Sinclair 1992). Non-adaptive dispersal occurs when animals are forced from natal or established home ranges by social factors inherent in high density populations (Stenseth 1983). Movements caused by pressure dispersal usually do not extend beyond the first area of favourable conditions encountered (Caughley 1977). In some species, dispersal distance changes with density, not frequency (Cockburn 1985). Food availability is often driven by weather (White 2004) and animals confronted with a sudden drop in carrying capacity because of unfavourable weather may be forced to search for better foraging opportunities.

In Georgia, Kammermeyer and Marchinton (1976) observed that all dispersal of white-tailed deer originated from heavy concentrations around agricultural areas protected from hunting. Dispersal terminated in less densely populated wooded areas often subject to intense hunting pressure. Neither lack of food nor deteriorating habitat were mitigating factors, and dispersers were generally subordinate males. In southeastern Quebec, high-density populations were the most philopatric in winter, and were the source of most dispersers (Lesage et al. 2000*a*). Nicholson et al. (1997) found dispersal to new areas occurred more often from a high density mule deer population than a low density population.

Barren-ground caribou may exhibit a density-dependent response to forage depletion, which could potentially be delayed by a shift in winter range (Ferguson and Messier 2000). On Baffin Island, a mass emigration of caribou from the Foxe Peninsula traditional winter range to Meta Incognita Peninsula occurred. Caribou that remained on Foxe Peninsula's overgrazed range were in poorer physical condition than those migrating to relatively unexploited range on Meta Incognita Peninsula. Periodic recurrence of freezing temperatures during the early stages of spring thaw results in ice formation within snow cover rendering low-growing forage unavailable to Peary caribou (R. t. pearyi; Miller and Gunn 1978). This precursor to starvation may trigger long distance movements across sea ice on the Arctic Archipelago that are important for the survival of these caribou, and recolonization of islands where there have been severe declines. Similarly, mass movements of typically sedentary urials (*Ovis orientalis*) have been reported during times of severe drought (Geist 1971).

After about 75 years of occupying a traditional winter range in northern Yellowstone Park, bison underwent a westward "stress dispersal" during a particularly severe winter of 1975-76 (Meagher 1989*b*). Mackenzie wood bison experienced range expansions when population densities were high, suggesting the animals were responding to environmental stress (Gates and Larter 1990).

### *Pre-saturation Dispersal*

Pre-saturation dispersal is density independent, meaning it occurs before carrying capacity is reached (Lidicker 1975). Movements occur when the population is either increasing toward saturation or decreasing from saturation levels (Sinclair 1992). Ambient dispersal is low level dispersal by young healthy animals and reproductively active adults, independent of population density. Stenseth (1983) included both pre-saturation dispersal and ambient dispersal in adaptive dispersal. Howard (1960) described innate dispersal as emigration of individuals by random diffusion that is predetermined genetically and is not in response to environmental conditions. As opposed to pressure dispersal, distances travelled during innate dispersal may be many times farther than the average home range radius (Caughley 1977).

Dispersal in some expanding populations is not necessarily pre-saturation (Sinclair 1992). Thar (*Hemitragus jemlahicus*) introduced to New Zealand dispersed from a core population that was at or above carry capacity (Caughley 1970*a*). Singer et al. (2000*b*) reported higher rates of dispersal of mountain sheep from rapidly expanding populations not at saturation levels. In contrast to white-tailed and mule deer, roe deer dispersal was inversely related to density (Linnell et al. 1998). Males maintain territories, while females live in what may be more appropriately described as home ranges (Bobek 1977). Both sexes force subordinate animals to leave when social carrying capacity is reached. In Poland, high summer forage availability resulted in smaller territories and home ranges, not density of animals (Bobek 1977). Summer carrying capacity was the determining factor of territory and home range size if winter snow depths were less than 15 cm.

Muskoxen were reintroduced to the Seward Peninsula in 1970. Bulls that wandered from areas of high muskox density served as the vanguard for expansion of traditional habitat (Smith 1989).

Innate dispersal may be operative in wood bison as pioneering mature males encounter unoccupied habitat. Mature bulls were the only segment of the Mackenzie wood bison population found in peripheral habitat patches, and competition for food was an unlikely explanation (Gates and Larter 1990).

## Awareness of Destination

### *Exploratory Migration*

Exploratory migration was defined by Baker (1978) as migration beyond the limits of the familiar area, but the animal retains the ability to return. According to Johnson (1989), exploratory migration may be a precursor to dispersal and permanent change in an individual's home range. Exploration allows an animal to compare its potential success in an alternative setting to its present location. If exploratory movements fail to result in a new residence, the cost may be the loss of the original home range to an intruder. Red deer released in New Zealand in 1861 dispersed more rapidly along valleys than between valleys, suggesting the ability to return to vacated areas was retained (Baker 1978). Climatic changes that varied locally on the Great Plains, and rapidly changed the distribution of resources, favoured a propensity for exploratory behaviour in bison (Lott and Minta 1983).

### *Calculated Migration*

Calculated migration is movement to a specific destination known to the animal at the time of migration, either through direct perception, previous acquaintance, or social communication (Baker 1978). They are usually regular and occur at a fixed periodicity over the course of a year. Ungulates seem to exhibit various behavioural patterns such as contact between adjacent social units and exploratory migration that increase the ratio of calculated to non-calculated migrations. Baker (1978) stated that when ungulates are introduced into unoccupied areas, the rate of movement from the release point is seldom so great that it cannot be attributed to calculated migration. The most common migrational pathway for ungulates is along the slopes of hills and mountains, following an elevation gradient, regardless of latitude (Baker 1978). In temperate regions, animals usually select higher elevations in summer and lowlands where there is less snow in winter. The reverse is true for moose in some areas where snow seldom exceeds critical depths, and calving habitat may be better in lowlands (Gasaway et al. 1983). The north-south migration of barren-ground caribou is more accurately described as perpendicular to the treeline (Banfield 1954). Elevational and latitudinal migrations involve movements along a climatic gradient; however, there are other seasonal and rectilinear migrations not necessarily related to climate.

It is quite probable that several years are required to change traditional movement patterns of moose (LaResche 1974). Calves seem to learn traditional travel routes from their mothers, which is further enhanced by the long lifespan of moose (Pulliainen 1974). Migratory systems should be maintained as long as offspring of moose that established the system persist. In many areas of Europe, summer and winter habitats are adjacent to each other and movements are not extensive. Where seasonal habitats are up to 300 km apart, traditional migration routes may be essential for survival. In Sweden, migration distances of adult moose are directly related to that of their mothers (Sweanor and Sandegren 1988). A traditional migration route in Norway has been used for at least 5,000 years even though habitat has deteriorated on the winter range (Andersen 1991). Pulliainen (1974) found that moose in various parts of Europe migrate in different directions. Moose of western Lapland migrate to the east and northeast. Moose that summer in northern Karelia, Russia migrate east for winter, whereas moose in other parts of Karelia migrate west for winter. In the Pechora River region of Russia, autumn migration occurs in two directions – north to south and east to west; these moose are noted for their uniformity of travel paths. Seasonal migrations in other parts of Russia vary in direction, apparently due to winter food availability.

Wintering female Sika deer (*Cervus nippon*) in eastern Hokkaido, Japan have mixed migration patterns (Mayumi et al. 2003). There are residents, north migrants that occupy summer range at high elevation, and east migrants that summer at lower elevation. White-tailed deer complete calculated migrations between winter and summer range (Aycrigg and Porter 1997, Van Deelen et al. 1998, Nelson and Mech 1999). Some individuals abandon traditional routes to disperse or remain in the same range year round (Nelson and Mech 1984, 1999, Aycrigg and Porter 1997, Nelson 1998). Female white-tail deer appear to transfer knowledge of migratory routes to their offspring (Tierson et al. 1985, Nelson and Mech 1999, Lesage 2000*a*). Female offspring remain closer to mothers into adulthood than males (Nelson and Mech 1984, 1999).

### *Nomadism*

Nomadism refers to movements where no fixed directional pattern or destination is apparent. In the Serengeti, rapid desiccation and senescence of vegetation at the beginning of the dry season results in a sharp decline of food quality (Sinclair 1974).

Movements are directed to any area where rain can be seen or heard by the animals, but only those storms producing rain within the familiar area of a wildebeest herd seemed to initiate movement (Talbot and Talbot 1963). Late in the dry season, nomadic ungulates are usually concentrated in high rainfall locations where green forage persists (McNaughton 1985). In the savannah-grassland environment, there are continuous fluctuations in rainfall, grazing, nutrient availability and fire. These generate pulses in primary production that result in a potentially rich, but temporally and spatially unpredictable food sources for grazing ungulates. The evolution of highly mobile nomadic lifestyles contributes to dominance of grazing ungulates in this ecosystem because this behaviour is essential for effective exploitation of a constantly shifting resource base. In heterogeneous landscapes where high rainfall areas or lakeshores provide dry season refuges, resident herds may duplicate many features of the migrations of the major grazers, but on a smaller scale.

Movements of some ungulate species occur at irregular intervals. In sub-arid or arid regions of Africa, there may be large-scale unpredictable movements of ungulates (Leuthold 1977) such as springbok (*Antidorcus marsupialis*) (Bigalke 1966), addax (*Addax nasomaculatus*), oryx (*Oryx gazella*), and several species of gazelle (Dorst and Dandelot 1970). After evaluating historical accounts from early observers, Roe (1970) was unable to confirm any consistent directional migrations among the large North American bison herds. He defined irregular migration as either movements that were possibly quite regular, but not necessarily associated with any direction or season, or erratic movements that occurred in any direction or season. McCullough (1985) described bison as nomadic with migration apparent in some populations. These patterns have been reconstructed for herds in western Canada (Morgan 1980). Northern Yellowstone bison that move between summer and winter ranges may be at an intermediate stage of migration development (Meagher 1989*b*).

## Range Expansion

Range expansion is the outward dispersal of individuals beyond the limits of the traditional area of distribution for a population. Increases in low density populations may be confused with supposed range extensions (LeResche 1974). Often, range retraction of one ungulate coincides with range expansion of another. When large mammalian herbivore species experienced dramatic population declines in Lake Manyara National Park, Tanzania, compensatory responses of other species resulted in overall constancy of herbivore biomass (Prins and Douglas-Hamilton 1990). As moose extended across most of Labrador during the latter half of the 20th century (Chubbs and Schaefer 1997), the Red Wine Mountains caribou herd coincidentally declined (Schaefer et al. 1999). Caribou formerly existed on Isle Royale. They were replaced by moose that invaded the island in the early 1900s (Allen 1979).

### *Post-Glacial Colonization*

There have been five global cooling periods since the last ice age (John 1977). The most recent, often referred to as the “Little Ice Age”, lasted from approximately 1300 to the mid 1800s. It was followed by a warming period, with a cool interruption from 1900 to 1920. Indirect effects of recent climate change on vegetation through fire may be more important than direct effects on species distribution, migration, substitution and extinction (Weber and Flannigan 1997). As the favourable climatic region for many species shifts northward, large climatic disturbances will disrupt life cycles of the original inhabitants, facilitating entry of new competitors. According to Peterson (1955), Asia was the original centre of moose dispersal and the widely distributed subspecies *Alces alces pfizenmayeri* approaches the ancestral type. Since the last glaciation, moose at their widest distribution covered almost all of Europe excluding the Mediterranean (Kurten 1968). In northeastern Siberia and Alaska, moose of the subspecies *A. a. gigas* remained in Beringia during glaciation (Kistchinski 1974, Peterson 1955). Other moose in North America found refuge in west central U.S.A. (*A. a. shirasi*), south of the present day Great Lakes (A. a. andersoni), and the Atlantic seaboard (*A. a. americana*; Peterson 1955). After glacial retreat, *A. a. gigas* moved into the Yukon, *A. a. shirasi* extended its range northward, *A. a. andersoni* moved north and west from Ontario to the edge of treeline and the Yukon, and *A. a. americana* expanded north on the eastern side of the continent. Before 1875, these subspecies were still geographically separated. Since then, all have colonized huge tracts of land to the point where they now overlap, suggesting that post-glacial dispersal has continued until recent times, or is still progressing.

Kelsall and Telfer (1974) cautioned against assuming moose were completely absent from many regions where low populations may have existed in widely scattered locations. It is possible that moose have always inhabited the same regions in Quebec, or extended their range northward within the last century because of habitat changes (Brassard et al. 1974). Moose may have been sparsely distributed in central British Columbia before undergoing a rapid population increase in the early 1900s (Spalding 1990). LeResche et al. (1974) described moose distribution in Alaska. In the Brooks Range on the Arctic Slope, and on the tundra of northern and western Alaska, moose were apparently very scarce at the turn of 20th century. They did not inhabit Colville River delta on the northern coast until about 1890 to 1910, and then became common by the 1950s. Along the northwestern and western coast of Alaska beyond treeline, where moose were essentially absent at the turn of century, there was a gradual population increase, similar to the central Brooks Range. Much of the Seward Peninsula was devoid of moose until the 1940s. Apparently, moose invaded the coastal rain forest of southeastern Alaska and British Columbia by moving down river valleys before 1900 (Klein 1965).

Since the Second World War, moose have expanded their range in all directions in Europe (Pulliainen 1974). In northwestern Russia, dispersal to the north led to formation of a “tundra population” of moose. In southern Russia, moose extended their range into steppe habitat, of which only a small percentage is forested. Some individuals have wandered to the Caspian Sea, Sea of Azov and the northern Caucasus.

The maximum southerly extension of woodland caribou range coincided with the end of the “Little Ice Age” (Bergerud and Mercer 1989). A moose/white-tailed deer community in Nova Scotia switched to a moose/woodland caribou community during this period of global cooling. After warming recommenced, deer recolonized Nova Scotia and expanded northward and westward in Canada (Telfer 1967). The last lichen-rich habitats caribou occupied in eastern North America were generally the most recent to be invaded by white-tailed deer (Bergerud and Mercer 1989).

Northward range extension of mountain goats (*Oreamnos americanus*) in southeastern Alaska was possibly due to mild winter conditions and cessation of hunting in 1977 (Aumiller and Ballard 1986). There was also a similar black-tailed deer northward range expansion in Alaska (Roberson 1986).

Multivariate morphometric analyses of cranial and post-cranial skeletal data from late Pleistocene, Holocene, and living populations of European and North American bison were used by Van Zyll de Jong (1986) to study bison systematics. Results supported the premise that all forms could be considered as one variable chronospecies, *Bison bison*. A large diverse bison population occupied the Beringia refugium before the onset of the last glacial cycle (Shapiro et al 2004). After the Bering Strait re-established at the beginning of the Holocene, the Siberian bison population became extinct. When the ice-free corridor reopened between Alaska and the North American interior, Van Zyll de Jong (1986) suggested that *B. b. occidentalis* from Beringia probably met and hybridized with the more southerly *B. b. antiquus*. The modern prairie bison, *B. b. bison* evolved from this intergrade, probably during the Hypsithermal (5000-7000 b.p.) when extensive grasslands developed. *B. b. athabascae* displays greater morphometric resemblance to *B. b. occidentalis* and has affinities with woodland habitats more associated with ancestral forms. Shapiro et al. (2004) used ancient DNA and Bayesian techniques to reconstruct the genetic history of bison throughout the late Pleistocene and Holocene. During deglaciation, the first bison into the ice-free corridor were evidently of southern origin, and the authors concluded that modern bison are mainly derived from a clade originating south of the ice sheet, distinct from Beringian bison.

### *Human Disturbance of Habitat*

Human activities on the landscape often modify habitats in ways that result in profound changes in ungulate distribution, often leading to species substitution. Habitat alteration has been an important factor in the widespread distribution of white-tailed deer across North America (Waller and Alverson 1997, Hosley 1956, Kramer 1972). Northward expansion of deer in Ontario coincided with logging and settlement (Dawson 1963). Deer rapidly expanded northward between Lake Superior and the Quebec border after 1900, reaching maximum limits of expansion about 1940. Following fire control and regrowth of forest habitat, deer populations declined and range contracted. Deer expanded their range at the turn of last century from southern Quebec across the Gaspe Peninsula, following human disturbances such as logging, agriculture and wolf control (Lesage et al. 2000*a*). In northern Alberta, white-tailed deer are closely associated with nutritious agricultural crops (Prescott 1974). Similar trends have been reported in Eurasian species of deer. In Yakutia, Russia, agricultural activities have facilitated northerly and westerly expansion of roe deer (Egorov 1965).

Extensive prairie lands of northwestern Minnesota were cleared and drained for agriculture in the early 1900s (Phillips et al. 1973). By the mid-1930s much of the farmland was abandoned and subsequently developed into large expanses of willow, aspen and marsh. Since then, moose have invaded these new habitats and expanded westward.

Kochy and Wilson (2001) detected a strong correlation between anthropogenic nitrogen deposition and forest expansion in several northern Great Plains parks. Where the limiting resource for plants is nitrogen, tall woody species with large receptor surfaces are better able to intercept airborne particulate nitrogen than grasses. Trees, shrubs and browsing ungulates should benefit most, while grazers such as bison would be at a disadvantage. Over the last six decades, forests near large metropolitan centres in high deposition areas, such as Elk Island and Prince Albert National Parks in Canada, expanded ten times faster than forests in low deposition areas such as Wood Buffalo or Jasper National Parks.

Archaeological evidence indicates that bison did not invade the region east of the Mississippi River until some time after the year 1000 (Roe 1970). Bison habitat was enhanced by aboriginal use of fire, which may have contributed to significant range expansion.

### *Translocation*

Wildlife management agencies often remove individuals of a species from one location and place them in another to repatriate a species into former range, augment existing populations with additional animals, or introduce exotic species into new range. Immigrants to islands are usually strong competitors (Ricklefs 1979). Most invaders exhibit ecological release as populations grow rapidly and occupy a variety of habitats, many of which are not inhabited on the mainland. For six species of deer introduced into Victoria, Australia, the number of individuals introduced (propagule size) was a significant predictor of success (Forsyth et al. 2004). Nine introductions of four or fewer individuals failed, whereas six of seven introductions with seven or more individuals succeeded. Migratory species were less likely to become established than non-migratory species, species with wider climatic tolerances were more likely to have wider spatial ranges, species with larger spatial ranges had higher population growth rates, and species with larger original range sizes had larger total range sizes. A similar propagule size threshold (six individuals) was apparent for ungulate introductions to New Zealand (Forsyth and Duncan 2001).

Eruptive oscillation in ungulates occurs when a large discrepancy exists between the number of animals the environment can support and the number of animals actually present (Riney 1964). Most basic interactions between an animal and its environment exist, regardless of whether the species is newly introduced or re-introduced, native or exotic, wild, domestic or feral. In an established population, eruptive oscillation can occur when the environment suddenly becomes more favourable, such as following a disturbance (e.g. logging, overgrazing, fire), or when the number of animals in a population is significantly reduced. Riney (1964) described four stages of a typical ungulate introduction. Initially, mortality is low, the population increases rapidly, and vegetation quality in critical parts of the habitat begins to decline. In the second stage, vegetation quality continues to decline and the population exceeds its carrying capacity. Reproduction remains high because the large proportion of younger age groups in the population creates a reproductive time lag of several years. Even if mortality of young starts to increase, the total population continues to rise. The physical condition of individual’s declines, especially in critical periods of the year, and in the latter part of this phase animals can be in poor condition even at the most favourable times of the year. Large-scale mortality is apparent by the third stage, especially when a critical resource becomes limited, such as water in drought years. Overpopulation continues in the early part of this stage, and later food resources in the most heavily utilized parts of the range begin to recover. In the final stage, the population adjusts to the carrying capacity of the habitat. In the early part of stage 4, a population can be slightly below carrying capacity, but not so low as to initiate an eruptive cycle. The time between the start of stage one and the peak of stage two will be longer if the nucleus population is able to disperse into areas progressively more remote from the release site. In general, the minimum time between initiation of the oscillation and an eruptive peak is 15-20 years for medium sized ungulates (reedbuck, impala). For red deer in New Zealand it is approximately 20 years. The rate of dispersal is an important factor affecting the oscillation period. Caughley (1970*a*) listed several examples of probable irruptive fluctuations of ungulates. When he tested Riney's model on Himalayan Thar, introduced to New Zealand in 1904, results supported the model.

Caribou were repatriated to Southampton Island in northern Canada in 1967. The population increased almost 100 fold by 1983 (Heard and Ouellet 1994). Instead of extending their range radially from a zone of high density, as in Riney's model, caribou spread over the entire island; density increased only after all apparent habitat was occupied.

A bull and cow moose released in 1878 and two bulls and two cows released in 1904 founded the entire moose population of Newfoundland, covering the whole island by 1945 (Pimlott 1953). The spread of moose was characterised by a 25 year period of rapid dispersal and low density, followed by a period of build up to high densities.

Growth of a reintroduced muskoxen herd in the Arctic National Wildlife Refuge of northeastern Alaska occurred in three stages (Reynolds 1998). Slow growth in 1969-70, immediately after release, was followed by a decade of irruptive rapid growth. In the final stage, the population declined and stabilized in the regions of initial occupation, concurrent with emigration of mixed-sex groups into additional regions.

Wood bison repatriated west of Great Slave Lake (Mackenzie Bison Sanctuary) closely followed Riney's model (Larter et al. 2000). Increases in density and intraspecific competition were followed by expansion into new range. The expansion population benefited from better quality forage and lower calf mortality.

## Biophysical Constraints

The range inhabited by a species is generally surrounded by ecological and/or physical barriers (Allee and Schmidt 1966). Dispersal is significantly influenced by the inherent power of movement by individuals (vagility; Odum 1971). Corridors offer relatively little resistance to dispersal, whereas filter routes allow passage of only some species (Vaughn 1972). Beringia filtered ungulates maladapted to temperate conditions, while the Panama isthmus filtered ungulates poorly adapted to tropical conditions.

### *Terrain and Landscape*

High elevation may restrict dispersal because of slope, low temperature, or low atmospheric pressure. Wild sheep, ibex (*Capra sp.*) and yak (*Bos grunniens*) are unable to range much higher than 5800 m because of lack of oxygen, not because of low temperature or food availability (Allee and Schmidt 1966). The direction that mountain ranges extend also has an important effect on dispersal. East-west ranges in Eurasia such as the Pyrenees, Alps, Carpathians, Caucasus, Hindu Kush, Himalaya, Tien Shan and

Altai intensify climatic barriers. During periods of global cooling, higher rates of extinction occurred in Eurasia because these mountain ranges became more of a barrier to animals seeking warmer climates than the north-south New World mountain ranges (John 1977). South of the Sahara in Africa, there are no extensive mountain ranges and species distribution is widespread (Allee and Schmidt 1966). In southeastern Alaska several small moose populations are restricted to river valleys (LeResche et al 1974). Moose invaded the Yakutat area by the Alsek River in the 1920s or 1930s following the retreat of glaciers that previously blocked the valley (Klein 1965). In southcentral Alaska, moose were isolated from Prince William Sound by both glaciers and Miles canyon on the Copper River. A population was established on the Copper River delta through a series of transplants (LeResche et al. 1974).

Waterbodies pose a significant barrier to island colonization unless they freeze, or the distance is short enough for animals to swim. Moose were able to cross to Isle Royale and woodland caribou to the Slate Islands when Lake Superior froze between these islands and the mainland (Allen 1979). Moose were unable to cross to good quality habitat in Newfoundland without human intervention.

### Habitat Type

Geist (1971) described the effect of habitat stability on ungulate movements. *Caprinae* habitat in mountains is typically comprised of stable climax grass communities. Some grassland created by fire is slow to revert to forest. Habitat is discontinuous and patches are linked together by migration routes. During warmer drier periods, montane grassland habitats expanded, then as forest cover spread in cooler, wetter periods, probably allowing mountain ruminants to continue normal movements between shrinking patches. Under natural conditions, virtually all range is occupied. Because dispersal does not usually lead to discovery of new habitat, it is more advantageous for home range knowledge to be transmitted from one generation to the next, and for yearlings to follow other adults after weaning.

Presently, bighorn sheep populations occur in small isolated groups because of catastrophic declines in the late 1800s and early 1900s (Singer et al. 2000*a*). They probably occurred in a naturally fragmented distribution with population centres located on rugged mountainous terrain. When dispersal did occur, it was typically into contiguous habitat already occupied by other bighorns, and rarely into unoccupied habitat. Although they occasionally engage in exploratory behaviour, successful colonization is unusual. Efforts to increase bighorn sheep populations have included extensive translocations, but many have resulted in small, sedentary and stagnant or declining populations that avoid travelling through timber. Despite the low success rate, over half of extant populations are the result of translocations (Gross et al. 2000). Sedentariness is considered one of the largest problems challenging long-term persistence of bighorn sheep populations (Risenhoover et al 1988).

In contrast to bighorn sheep and other mountain caprinids, several species of cervids, such as moose, select fluctuating, early successional habitat, and are more capable of expanding their distribution (Geist 1971). Movements of yearling moose driven off by cows after weaning often appear erratic (Houston 1968). New home ranges are established through individual exploration of transient habitat that is linked to permanent habitat.

According to the Bell-Jarman Principle, body size determines forage selection of ruminant species (Renecker and Schwartz 1998). Forest vegetation tends to concentrate nutrients in leaves, buds and twigs, and provides cover from predators. Ruminants that select dense forested habitats are generally small, solitary and laterally compressed. Small ruminants select for high quality browse that passes rapidly through the digestive system because of relatively high metabolic requirements (Renecker and Schwartz 1998), and they tend to evade predators by hiding (Estes 1974). Open habitats lack high quality food that small ruminants require, and make them conspicuous to predators. An exception to this rule is the moose, the world's largest cervid, that must select food patches that permit high rates of intake, especially in winter, when food quality deteriorates and movement through snow is energetically costly. Another exception to the Bell-Jarman Principle is the giraffe, the world's largest ruminant. Here, dense food patches are individual acacia or other trees.

Open plains may provide extensive food patches, and vigilance behaviour allows escape from predators. Ruminants adapted to open plains are generally large and gregarious. Bison are bulk feeders able to digest large amounts of low quality fibrous forage in voluminous rumens (Houston 1982, Hudson and Frank 1987, Hanley 1982). Plains species often depend on open environments such as grasslands where bulk food is abundant, but low in nutritional quality, and avoid predators by running (Estes 1974). To consume enough forage, minimal time must be spent searching. When nutritional quality of grass reaches intolerably low levels because of desiccation, the mobility required to take advantage of irregularly distributed rainfall that produces fresh grass is facilitated by large body size. In forested habitat, rapid locomotion is hampered, especially for larger mammals. Of the large African ruminants, only the buffalo and okapi occur in the African rain forest (Allee and Schmidt 1966). Dispersal in forest may be limited because of sparsely distributed food and obstructed escape from predators.

### *Human Predation*

Unparalled in the fossil record or on other continents at the same time, the extinction of more than half of the large mammals in the Americas was attributed to direct effects of human predation (Alroy 2001), or a combination of human predation and climate change (Ward 1997). Archaeological evidence indicates large human populations has been present in the Americas since 13,400 years BP, coinciding with the beginning of the mass extinction period. Alroy's simulation of human population growth, hunting patterns, and population dynamics of 41 large herbivores (30 now extinct) indicated that human density had to be less than 0.13/km$^2$ for all species to survive. However, this was an order of magnitude lower than the observed range of hunter-gatherer densities.

The keystone herbivore hypothesis suggests that large grazing mammals maintain open grasslands, and if these herbivores are removed by human predation, grasslands may succeed to other vegetation types such as shrubland or forest (Owen-Smith 1987). Zimov et al. (1995) applied this concept to Siberia, western Alaska and Beringia using a simulation model that suggested human predation could also have indirect constraints on ungulate dispersal. In Beringia, semi-arid grass-steppe largely converted into wet moss tundra after much of the grazing megafauna consisting of bison, muskoxen, horses (*Equus spp*.) and mammoths (*Mammuthus primigenius*) disappeared. This coincided with improved human hunting weaponry at the end of the Pleistocene. Grasslands have high rates of evapo-transpiration that reduce soil moisture and are adapted to grazing. Mosses are lower in productivity, increase soil moisture and are vulnerable to damage by trampling. Human predation may have caused a biome shift from steppe to tundra hindering the re-establishment of grazing ungulates.

Kay (1998) proposed that before their populations were devastated by introduced diseases, aboriginal people of North America were the ultimate keystone predator. Native Americans were highly efficient predators who could rely on a variety of alternate food when meat was unavailable. There is evidence that humans suppressed moose, bison, elk, deer and muskox populations to very low levels in historical times (Fritz et al. 1993, Krech 1999, Isenberg 2000). The shrub-steppe region of western Montana, central Idaho and southeastern Washington was considered a game sink mainly because of human predation (Martin and Szuter 1999). Aboriginal harvest may have limited growth of moose numbers on the Colville River, Alaska, until the 1920s when humans moved to the coast, and hunting pressure on the river was relaxed (LeResche et al. 1974). However, there remains debate and uncertainty about the extent to which human predation altered wildlife populations and distributions (Yochim 2001).

In Norway and Sweden, moose hunting was formerly restricted to nobility, and poachers were severely punished (Markgren 1974). After hunting rights were granted to commoners in Sweden in 1789, the moose population was almost exterminated; this trend was similar in Norway and Finland. Since 1830, hunting restrictions and predator reductions in Scandinavia resulted in moose dispersing to most of the present range limits by the end of the 19th century. During human famines, many moose populations in Europe were severely depleted, and in southern, western and central parts of Europe, they were exterminated by the13th century (Pulliainen 1974). After 1850, when moose distribution was at a minimum, numbers increased when protective measures and wolf control were implemented. Moose reintroduced near Warsaw, Poland have expanded their numbers and wandering individuals have been seen in neighbouring countries.

Moose distribution contracted during the 19th century in Siberia. Subsequent range expansion after the beginning of 20th century may be due to decreased hunting pressure and conservation measures (Kistchinski 1974). Murie (1934) reported that moose from the mainland were prevented several times from becoming established on Isle Royale because of hunting. It was not until the winter of 1912-13 that they successfully colonised the island.

Mountain goats that occupy the most rugged and remote terrain are less vulnerable to hunters (Rideout 1978). The mountain goat population in Glacier National Park is characterised by high density and large group sizes (Singer and Doherty 1985). After reaching peak numbers, introduced herds stabilized with little or no compensatory reproduction for hunter harvests.

Muskoxen populations have increased dramatically since the early 1900s, reoccupying much of their former circumpolar range (Reynolds 1998). Overexploitation by humans and severe weather likely caused earlier declines.

Around the time of human colonization of North America, the *B. antiquus* variety of bison dominated the Great Plains ungulate community (Guthrie 1970). It was possibly extirpated along with other large-sized bison such as *B. latifrons*, by advancing hunting societies. Modern plains bison usurped the vacated niche on the Great Plains as the dominant grazer. This new smaller form was reproductively mature at a younger age, possibly making them better adapted to human predation (Guthrie 1970, Wilson 1992). Limited range extension of plains bison into eastern and western mountain ranges suggested it was a relatively late arrival, and *antiquus* populations on the west coast disappeared without being replaced (Guthrie 1970). Van Vuren (1987) considered human hunters, particularly after obtaining the horse, quite capable of exterminating small bison populations, preventing them from establishing west of the Rocky Mountains. Hornaday (1889) documented that technological improvements in firearms and ammunition accelerated the extermination of plains bison throughout most of its range. Wood bison disappeared from the Yukon and Alaska by the early 20th century, probably because of hunting (Guthrie 1968, Stephenson et al. 2001).

### Land Use Conflict

Human activities on the landscape are often incompatible with wild ungulates. Their presence may not be tolerated, or habitats may be altered in such ways that they can no longer be occupied or traversed by native species. If migrants are culled when they leave protected areas, migratory habits may be eliminated, favouring survival of non-migratory individuals (Leopold et al. 1963).

Since the 1980s most of the deciduous forest and natural open fields in eastern Hokkaido, Japan have been converted to agriculture (Mayumi et al. 2003). Increased forage resources and protection of females from hunting resulted in a Sika deer population irruption. Migrants used agricultural lands less than predicted because of aggressive deterrence by humans. In central Asia, the wild yak has lost most of its preferred alpine meadow and steppe habitat to pastoral activities (Schaller 1998).

The greatest diversity and abundance of African ungulates now occur mainly in undisturbed habitats in eastern and southern parts of the continent. Most game preserves have been established without ample consideration of the spatial movements of wildlife (McNaughton 1985). In a portion of the Kalahari within Botswana, wildebeest previously had access to three main river systems. Fences now restrict them to Lake Xau, where access has diminished because of expanding livestock production and human settlement (Williamson et al. 1988).

In the 19th and early 20th century, large numbers of sheep, goats and cattle pastured in Scandinavian forests competed with wild ungulates for forage (Markgren 1974). Agro-sylviculture, urbanization and infrastructure development, among other human activities, were considered by Perez et al. (2002) as the primary threats to Spanish ibex (*Capra pyrenaica*) conservation. Reservoirs, canals and aqueducts usually impede movements of mountain sheep (Singer et al. 2000*a*). Fences, roads, and towns have severely disrupted movements of desert bighorns (Bleich et al. 1996). Advanced fire suppression has enabled encroachment of tall shrubs and trees into early seral habitats required by sheep.

The dispersal capacity and reproductive ability of tule elk (*Cervus elaphus nannodes*) have made them effective colonizers, but their range includes some of the richest agricultural land in California (McCullough et al. 1996). Conservation measures have rescued them from extremely low numbers and tule elk now survive in scattered populations. In the Greater Yellowstone Ecosystem, about three-quarters of bison, elk and pronghorn migration routes have been lost (Berger 2004), primarily due to lack of tolerance for bison outside of protected areas, winter feeding of elk, an increase in the local human population, and loss of habitat.

### *Competition*

Elton and Miller (1954) identified two principal components of competitive interactions. Exploitation occurs when organisms utilize common resources that are in short supply, and interference occurs when organisms seeking those resources have their access limited by others. Krebs (1972) suggested that the first indication of competition between two closely related species is that their spatial distributions do not overlap. The second indication is when one species is absent and the other occupies a wider range of habitats.

The “Competitive Exclusion Principle” states that complete competitors cannot coexist (Hardin 1960). Competitive exclusion is a transient phenomenon because the poorer competitor is always eliminated (Ricklefs 1979). When it occurs it is likely intermittent and not always evident (Weins 1977). Outcomes of competitive interactions are not always predictable because conditions influencing form and intensity of competition vary locally (Boer 1998). Organisms are able to increase competitive ability if they evolve interference mechanisms or become more efficient exploiters of a common resource. Ungulates of North and South America evolved independently for millions of years until the land bridge emerged five million years ago, allowing faunal exchange. Because northern immigrants to the southern continent were superior competitors they caused the disappearance of many South American ungulates (Simpson 1950).

Within goat (*Capra spp*.) and sheep genera, species often divide mountain ranges in half and restrict overlap to a narrow zone (Schaller 1977). The Kuban ibex and Dadestan tur (*C. cylindricornis*) have partitioned the Caucasus into eastern and western halves. On the Gadabar Ghar massif in Pakistan, the markhor (*C. falconeri*) occupy the western half while wild goat (*C. aegagrus*) occupy the eastern half.

Although elk are primarily grazers, they may also include browse depending on food availability (Houston 1982). Moose introduced to Colorado from 1978 to 1993 compete with native elk herds for willow (Boer 1998). Houston (1968) suggested that moose dispersed at low densities may have a competitive edge over herd species such as elk in winter because moose are able to use scattered forage more efficiently than large concentrations of elk. According to Cowan (1950), when elk were introduced into Banff and Jasper National Parks in 1917 and 1920, moose, mule deer and mountain sheep were the ancestral ungulate community. Elk food preferences overlapped with the original ungulates and competition increased as elk numbers grew. Elk dominated moose and mule deer in competitive interactions probably because of their diversity of diet. Mountain sheep populations remained stable probably because of spatial separation and minimal competition between elk and mountain sheep. Elk apparently out-compete moose in some conditions (Cowan 1950, McMillan 1953, Flook 1964). High elk numbers using riparian habitat in summer may reduce the amount of willow browse available to moose in winter when elk have migrated elsewhere (Martinka 1969, Telfer and Cairns 1986). In the Yakutia region of Russia, well defined competition between elk and moose for willow in streambeds only becomes important at high densities (Egorov 1965).

In Wind Cave National Park, South Dakota, the greatest spatial overlap between mule deer and elk was during summer (Wydeven and Dahlgren 1985). Competition was expected to be low because mule deer selected forbs and browse, while elk consumed graminoids. However, elk may have displaced mule deer from portions of the park through agonistic behaviour and competition for browse during periods of high elk density. During winter there was lower potential for competition because of different spatial distribution and food habits, but competition could be possible if severe winters cause elk to browse more extensively. In central Montana, competition between mule deer and elk appeared to be most intense during spring and summer (Mackie 1970). Direct competition between elk and pronghorn (*Antilocapra americana*) could increase in autumn and winter if increasing numbers of elk fed more extensively on forbs.

In northern Montana, white-tailed deer range expansion into mule deer habitat coincided with decreased mule deer populations (Martinka 1968). Higher deer densities may increase competition between the two deer species during severe winters. In Alberta, much of the southern mule deer range has been invaded by white-tails (Soper 1964). The reverse is evident in the Dos Cabezas Mountains of southeastern Arizona where mule deer appeared to be the superior competitor (Anthony and Smith 1977).

Although Fisher and Gates (in press) found no evidence of wood bison and woodland caribou competition in the Yukon during winter, there is potential for exploitative competition during autumn when significant use of lichens by bison was observed in the Mackenzie Bison Sanctuary (Larter and Gates 1991*a*).

Guthrie (1970) theorized on bison evolution and competition. Bison occupied the large bovid grazing niche in northern Eurasia. In the warmer south (including tropical regions) it was occupied by wild cattle species such as auroch (*Bos primigenius*), zebu (*B. indicus*), banteng (*B. banteng*), kouprey (*B. sauveli*) and gaur (*B. gaurus*), and buffalo genera, consisting of *Syncerus* and *Bubalus*. An exception was the yak, a species of wild cattle that was able to invade the cooler Himalayas. Because of diet similarity between *Bison* and *Bos* they become biotic barriers to each other. Although bison did not penetrate southern Eurasia because of competitive exclusion, there was no such limitation in North America. Bison underwent considerable range expansion and phylogenetic change in the New World that was unparalleled in the Old World. In the northern environment of Eurasia and Alaska, *B. priscus* existed almost unchanged throughout the latter half of the Pleistocene until its extinction by either rapid evolution or elimination (Guthrie 1970). This form of bison appears to have flourished as the dominant ungulate in northern regions (Guthrie 1968). When bison dispersed into the North American interior, the complex ungulate community it encountered (dominated by horses) was not competitive enough to prevent colonization, possibly resulting in the decline of horses during the late Pleistocene (Guthrie 1970). The fossil record suggests that there is insufficient specialization of Bison to allow stable sympatric distribution of more than one form for any extended periods of time. The modern plains bison and European counterparts (*B. b. bonasus* and *B. b. caucasus*) replaced the earlier forms either through direct competition, or passive replacement whereby the indigenous form became extinct and the niche was immediately occupied by a new variety.

### *Alternate Prey*

Two species may be in “direct competition” for resources or exhibit “apparent competition” if they share a common predator (Holt 1977). In a single prey scenario, a predator’s numbers are limited by one feedback pathway. The addition of an alternate prey species may increase the density of the predator by expanding its resource base, leading to heavier predation on the original prey species. Thus survival of the most vulnerable prey can become independent of its own carrying capacity, yet indirectly and critically dependent upon the carrying capacity of the less vulnerable prey. In South Africa's Kruger National Park, Harrington et al. (1999) implicated lion predation as the cause of a roan antelope population crash. Influx of zebra into antelope range during drought conditions may have led to an increase in lions.

Simkin (1965) hypothesized that caribou could decline from apparent competition with moose if wolves are the shared predator. In British Columbia where moose expanded after 1900, providing a greater prey biomass for wolves, subsequent higher predation on caribou may have resulted in local extinctions (Bergerud and Elliot 1986). Seip (1992) suggested that increasing wolf predation was the major cause of the declining caribou populations in the Quesnel Lake and Wells Gray Provincial Park area of southeastern British Columbia.

Alternate prey may include other ecotypes of the same species, such as migratory and resident caribou (Schaefer et al. 1999). The Red Wine Mountains caribou population of central Labrador declined drastically from the 1980s to the 1990s, while the adjacent migratory George River herd grew and expanded its range. Subpopulations of the Red Wine Mountains herd with the greatest range overlap with the George River herd experienced the highest mortality. Schaefer et al. (1999) concluded that refuge from other ungulates, including other caribou, were important for persistence of some caribou populations.

Augmentation of existing endangered woodland caribou populations along the southern parts of its former range in Idaho has been implemented as a conservation measure. In addition to loss of habitat, failure to reverse the caribou decline may be attributed to an increased cougar population resulting from an expanded white-tailed deer prey base (Zager et al. 1996).

While many mule deer populations throughout western North America seem to be declining, white-tailed deer populations are increasing (Robinson et al. 2002). In south central British Columbia, the main cause of mortality in both species was cougar predation. The lower survival rate of mule deer was directly linked to a higher predation rate compared to white-tailed deer. The disparate survival and predation rates were consistent with the apparent-competition hypothesis. Moose appeared to be declining in the Mackenzie Bison Sanctuary while the reintroduced wood bison population was erupting, and wolves were probably increasing (Larter et al. 1994). The proportion of moose in the wolves' diet was significantly higher than its availability. In an adjacent area with less wolf activity, moose densities were twice as high.

### ***Food Availability***

Ungulate distribution and home range size are strongly influenced by habitat productivity and forage resources that are often distributed in a patchy environment (Ford 1983). The botanical environment of Beringia during the late Pleistocene appeared to have inadequate forage productivity to sustain the abundance of large ungulates (Hopkins et al. 1982). According to Laxton et al. (1996), this paradox is reconciled by localized "hotspots" of loess-fed soils conducive to extremely productive grasslands capable of sustaining large ungulate populations in an otherwise impoverished ecosystem.

Winter food profoundly influences moose distribution (Kelsall and Telfer 1974). Even where a variety is available, only a few selected plant species are consumed in large quantities. Some genera such as willow are important at both the southern extremities of moose range, which are characterized by greater food diversity, and the northern periphery where choices are much more reduced. Moose have been observed wintering above the treeline in river valleys where willows are present (Kelsall 1972).

Lyman and Wolverton (2002) reviewed archaeological evidence and concluded that bison were never abundant west of the North American continental divide. Van Vuren (1987) suggested a contributing factor might have been low carrying capacity. Physical barriers are an unlikely constraint as Haines (1967) described potential avenues for bison immigration westward through the Rockies.

Mack and Thompson (1982) discussed the phenology of dominant plant species in intermountain grasslands as an explanation for lack of bison. Grasses and large herbivorous mammals with hypsodont dentition first appeared in the Eocene and evolved together (Stebbins 1981). Basal meristems, small stature, high shoot density, rapid turnover of deciduous shoots, below ground nutrient reserves and rapid growth are characteristics of grasses adapted to convergent pressures of both aridity and grazing (Coughenour 1985). Grasslands east of the Rocky Mountains are dominated by rhizomatous/stoloniferous species (Daubenmire 1978). Tall, tussock-forming caespitose grasses from boreal regions are adapted to conserve energy and immigrated from the north into the intermountain trough (Daubenmire 1975). Much of the ice-free mid-continent east of the mountains was occupied by bison; after the last deglaciation, they proliferated. The chronology of calving and maximum milk production in bison is well suited to staggered phenology of grasses in this part of the continent, where different grasses become available to bison throughout the year (Peden 1976). In contrast, it is unlikely that large herds occurred in open steppe west of the Rockies where dominant grasses aestivate during much of the summer and are intolerant of grazing and trampling. Caespitose grasses may have persisted through the Quaternary because large-hooved congregating mammals did not override macroclimatic selection for this grass form. Although small herds of elk occurred west of the Rocky Mountains (Rickard et al. 1977), their distribution was probably also restricted in similar ways, and only became common in areas after wolves were eradicated (Lyman and Wolverton 2002).

Following livestock and exotic introductions, tussock grasslands of New Zealand have experienced massive replacement by alien rhizomatous grasses since mid-nineteenth century (Godley 1975). No indigenous rhizomatous grasslands in temperate regions display human-induced change to such degree. This suggests that the extent of co-evolution of large mammalian herbivores and plants in these grasslands may be predicted to some extent from characteristics of the dominant grasses. Steppe from Ukraine to Kazakstan is an apparent exception where most dominant grasses are caespitose, despite a long association with saiga (*Saiga tartarica*), camel (*Camelus dromedarius*), gazelle (*Gazella sp*.), wild ass and auroch. Eurasian caespitose grasses have adaptations to mammalian grazers, but little is known about how their selection forces compare with bison.

## *Climate*

**Snow Accumulation**: Snow restricts forage availability, increases energy costs of foraging, alters habitat selection and movement patterns, and increases energy costs of locomotion (Fancy and White 1987). Snowfall effects can be offset by an abundance of food and cover (Edwards 1956), and topography where snow can be blown away or melted (Stelfox and Taber 1968). When Telfer and Kelsall (1984) used chest height, foot loading and behaviour to calculate indices of snow coping ability for several North American ungulates, those with higher indices occurred in snowier regions. Of the species studied, pronghorn, short-grass plains specialists, had the lowest indices. Elk, white-tailed deer and bison tolerate the shallow soft snow of the southern boreal forest. Caribou had the highest indices of snow coping ability and, as expected, subsist further north, where snow cover is deeper and persists longer. On mule deer winter range in Middle Park, Colorado, snow that was over 46 cm deep essentially excluded them from large areas (Gilbert et al. 1970). The capacity of white-tailed deer fawns to survive their first winter could influence species distribution in north eastern North America (Lesage et al. 2000*b*). The quality of winter range would likely be important for maintenance and expansion of northern populations. They did not penetrate the boreal forest biome in Quebec apparently because of excessive snow depths (Prescott 1974).

Moose are uncommon or absent in eastern Quebec where snow depth regularly exceeds 500 cm (Brassard et al. 1974). In nearby Labrador, slow dispersal of moose may be due to deep snow (Mercer and Kitchen 1968). Studies in Canada and Russia suggest that moose travel easily in snow up to 60 cm in depth, but are impeded by soft snow up to 100 cm, which is the approximate chest height of an adult (Kelsall and Telfer 1974). Nasimovich (1955) described areas in Russia where 70 cm of soft snow is prevalent and there are no moose. They may occupy regions of deep snow if there is adequate food or tree canopy, but not at high altitudes and latitudes where trees are open-growing and branched to the ground. Moose are sparsely distributed or absent in high snow fall areas adjacent to the Sea of Okhotsk and Kamchatka (Kistchinski 1974). Singer and Doherty (1985) found a significant negative correlation between mean monthly snow depths and mean monthly elevation of collared mountain goats.

**Aridity**: Extinction of desert bighorn sheep populations in California is more likely in low elevation mountain ranges (less than 1500m), where precipitation is below 200 mm, there are few natural springs, and where there is range overlap with domestic sheep (Epps et al. 2004). These findings suggest desert bighorns are vulnerable to climate warming and it has already affected their distribution. Lower temperatures associated with high elevation mountain ranges alleviate water requirements for sheep and provide a longer growing season. The distribution of desert bighorns has probably fluctuated for centuries, expanding in cool wet periods and contracting to higher elevations as climate became warmer and drier.

In Kruger National Park, severe population declines of roan antelope (*Hippotragus equinus*), sable antelope (*H. niger*), tsessebe (*Damaliscus lunatus*), kudu (*Tragelaphus strepsiceros*), waterbuck, warthog (*Phacochoerus africanus*) and eland occurred during a period of extreme reduction in dry season rainfall from 1977-1996. This coincided with a rise in regional temperature (Ogutu and Owen-Smith 2003). Zebra, giraffe, wildebeest and impala populations remained stable. Species that remained abundant possessed diverse feeding habits. Forage production during the dry season had a greater influence on ungulate population dynamics than forage production during growing season. Grazers were more affected by rainfall variability than browsers because the herbaceous layer is more sensitive to moisture than woody vegetation. The southern limits of Roan antelope, sable antelope, and tsessebe reach Kruger National Park and may have been undergoing range contraction in response to increasing aridity and habitat change. Protected areas are increasingly becoming surrounded by fences and other barriers to movements that otherwise might be made by large mammal populations in response to habitat changes. Habitat use by white-eared kob was constrained by the availability of water as herds were rarely observed farther than 10 km from water sources (Fryxell and Sinclair 1988*b*). The aridity of the hypsithermal period is a possible explanation why moose did not disperse through mountains to occupy the interior plateau of British Columbia at that time (Kelsall and Telfer 1974).

**Temperature**: Many mammals are more sensitive to heat in summer than cold in winter (Allee and Schmidt 1966). The Shirasi moose has not dispersed westward along the corridor of the Okanagan highlands in southern British Columbia and northern Washington to potentially suitable habitat in the Cascade Mountains or the central coastal rain forest (Kelsall and Telfer 1974). The presence of moose in similar habitat in British Columbia and Alaska suggests hot summer temperatures may be preventing them from occupying these areas by high summer temperatures.

## *Disease*

According to Hess (1996), highly contagious diseases of intermediate severity present the greatest conservation risk to wildlife populations. Severe diseases tend to disappear rapidly because either the local population dies out or dispersal is too low to spread the disease across the metapopulation. When a shared parasite effects species differently and influences the outcome of interactions, parasite-mediated competition may be the result. A lack of evidence of elk, moose, or caribou in North America from before the Pleistocene indicates that they were very late immigrants from Asia (Scott 1937). Certain parasites that have evolved a stable relationship with North American deer of the genus *Odocoileus* cause mortality in cervids that invaded the continent during the Pleistocene (Kelsall and Telfer 1974). Examples include *Elaeophora schneideri*, which is benign in mule deer, but causes mortality in elk (Hibler and Adcock 1971), and the meningeal nematode (*Parelaphostrongylus tenuis*), which does not harm white-tailed deer, but is lethal to moose and caribou (Anderson 1972). *P. tenuis* is potentially a limiting factor for woodland caribou in eastern and central Canada (Anderson 1972, Pitt and Jordan 1994). Some translocations of woodland caribou such as at Michipicoten Island in Lake Superior have been considered successful, but no reintroductions have persisted where high white-tailed deer populations exist with meningeal worm (Bergerud and Mercer 1989).

Kelsall and Telfer (1974) noted that moose are conspicuously absent in the deciduous biome and southward extension of the deciduous-coniferous transition of the Appalachian Mountains. South of deep snow regions, white-tailed deer diets consist of a high proportion of mast and herbage (Murphy 1970). There appears to be an empty niche for a browser, however *P. tenuis* may be limiting moose dispersal (Kelsall and Telfer 1974). Whitlaw and Lankester (1994) questioned whether this parasite actually restricted the distribution of moose in Ontario. Although populations consistently declined when deer densities exceeded 5/km$^2$, the effect of *P. tenuis* could not be separated from other factors known to influence cervid numbers. In areas where moose and deer coexisted, and *P. tenuis* was endemic, moose still persisted (often at low densities) and no catastrophic declines or extinctions had been observed.

Bighorn sheep are highly susceptible to pneumonic pasteurellosis from contact with domestic sheep and catastrophic mortalities have resulted (Foreyt and Jessup 1982). Bighorns now occupy about one third of their historic range (Gross et al. 2000). Epizootics are able to kill up to three-quarters of a population in a single year and reduce recruitment for an additional three to seven years. Disease has a more profound influence on sheep survival than habitat loss or fragmentation. Simulated population dynamics in the South Dakota Badlands ecosystem that were subjected to a range of conditions showed that in the absence of disease, extinction rates were low and insensitive to rate of colonization or area of suitable habitat.

## Migration Initiation Thresholds

Factors that stimulate migration are quite dependent upon the animal's expectation of improved environment at a particular time of year, and this would change with the time of year (Baker 1978). Leuthold (1977) stated that migratory populations (or portions of them) may become sedentary as environmental conditions ameliorate.

### *Snow*

The presence of snow has a significant effect on an individual's mobility and food availability. Heavy snowstorms cause mule deer to migrate to winter range (Russell 1932). For most Kaibab mule deer, seasonal migration from high plateau summer range to lowland winter range is triggered by the first persistent snow cover, usually in November (Barlow and McCulloch 1984). Where persistent snow cover occurs, white-tailed deer migrate between summer and winter ranges (Messier and Barrette 1985, Nelson 1995, Van Deelen et al. 1998). Hoskinson and Mech (1976) suspected that in northern Minnesota, fall migration was triggered by a combination of snow accumulation and low temperature. In the Adirondack Mountains of New York, Tierson et al. (1985) observed deer began movements to winter range when snow depths approached 38 cm. In New Brunswick, this occurred when snow depths exceeded 30 cm in hardwood stands (Drolet 1976). Although white-tailed deer typically yard together in winter, concentrations may not develop if snow conditions do not inhibit travel (Moen 1973). In prairie and agricultural habitats of South Dakota, where temperatures are cold and there is little snow, Sparrowe and Springer (1970) reported that up to 30% of white-tailed deer remained dispersed during winter. Where persistent snow cover is absent, white-tailed deer are quite sedentary (Larson et al. 1978, Lincoln 1992, Loudon and Brinklow 1992).

In Wells Gray Park, British Columbia, Edwards and Ritcey (1956) observed that moose spent the summer at high elevations up to the timberline. Autumn migration was triggered by snowfall, and depths increasing faster at higher altitudes caused moose to gradually descend. The critical snow depth appeared to be 75cm. Knowlton (1960) also suggested that winter snow depths in Montana initiated movements of moose downward from upland summer range. Scandinavian moose carry out regular winter migrations from mountains to valleys but if there is little or no snow they may remain at high altitudes (Pulliainen 1974). In the Kisloretsk area of the Russian Lapland Game Preserve, the majority of moose migrate to the southwestern part of the preserve and deep snow is regarded as the primary cause. In the central and southern Ural Mountains, moose that summer on western slopes migrate along valleys to eastern slopes where snow is shallower. Although this movement usually occurs during November and December, migration is as late as February in winters with little snow, and ceases when snow reaches 20-30 cm. Autumn moose migration in Sweden seemed to be triggered by 40 cm of snow (Sandegren et al. 1985).

The first heavy snowfall of the season possibly caused the fall migration of barren-ground caribou to begin (Kelsall 1968). A composite threshold of snow depth, hardness and density for movement within winter range was determined by Pruitt (1959) for barren-ground caribou. They prefer snow that is soft, light and thin and the migration threshold seems to increase as winter progresses.

### *Plant Phenology*

In temperate ecosystems, protein content and digestibility of plant material is positively correlated with latitude and elevation (Van Soest 1983). Although temperate ungulates may not encounter more abundant vegetation by migrating to higher elevations or latitudes, they may obtain higher quality forage (Skogland 1984, Langvatn and Albon 1986). Migrating cervids gain fitness from prolonged access to newly emerging forage along an ascending altitudinal gradient during early summer (Mysterud et al. 2001). Russell (1932) suggested that migration of mule deer from winter to summer range was related to plant growth. Moose increased their use of open lowlands in spring where earlier snowmelt promoted green-up (Hauge and Keith 1981). High quality forage is required soon after winter due to increased demands of cows and the negative energy balance of both sexes. In tropical India, the home range of gaur may be large enough to encompass a valley and surrounding hillsides (Schaller 1967). Migration to higher elevations before the hot season allows the gaur to access green grass. After calving, the timing of migration of female saiga to spring feeding grounds coincides with green-up (Bannikov et al. 1967).

Serengeti ungulates experience a shifting mosaic of available forage that can be exceptionally rich due to localized rain showers, but it is not sustained (McNaughton 1985). These animals concentrate on actively growing grasslands, and then abandon them as grasses desiccate. Lack of correlation among productivity patterns of three stands on the Serengeti plains separated by only 4-10 km demonstrated the low predictability of productivity pulses. Productivity ranging up to $40 g/m^2/day$ in such pulses may provide a substantial food potential to grazers, but its occurrence in space and time is highly variable. The ability of gazelles to track a pulse of productivity was demonstrated by a close relationship between their density and primary production over the duration of such a pulse.

Spring movements of Montana moose from winter ranges to higher elevations may be stimulated by disappearance of snow or by green-up of growing plants (Peek 1962, Knowlton 1960). Migration of Kenai Peninsula moose from winter to spring range, followed by slow dispersal to upland summer-fall ranges is likely related to plant phenology (LeResche 1974).

Blood (1963) and Murie (1944) observed that mountain sheep followed the ascending snowline in spring feeding on fresh sprouting vegetation.

### *Thirst*

Prolonged dry weather may compel ungulate populations to search for water and lush forage. In Montana, Peek (1962) observed greater use of upland habitat by moose during dry summers. Except during brief periods of parturition and breeding herds of saiga are usually migrating (Bannikov et al. 1967). In mid summer there may be continuous movement in search of food and water on the Eurasian steppes. During exceptionally dry summers, migrations extend further westward. Some species are able to direct their movements according to rain events. Wildebeest are adapted to feed on grass less than 10 cm in height, particularly freshly sprouting (Talbot and Talbot 1963). They drink every day if water is readily available, but cannot exceed five days without it. During the dry season, wildebeest may travel more than 80 km/day if food and water are widely separated. Wildebeest react to the sound of thunder 25 km away by moving toward it. Migration may also be initiated toward dark cloud-capped storm columns up to 80 km away. Antelopes and wild asses leave the Gobi desert at the onset of winter because of thirst when open water freezes (Allee and Schmidt 1966).

### *Reproduction*

Movements of some species are influenced by their reproductive condition. Barten et al. (2001) observed that parturient cows of the Mentasta caribou herd in Alaska migrated to elevations higher than the usual range of bears and wolves, whereas non-maternal females remained at lower elevations. Also if females lost their offspring, they rejoined non-maternal females and predators at the lower elevations. Parker (1972) reported that non-pregnant barren-ground caribou were less likely to migrate to calving grounds. Similarly, non-pregnant saiga females often accompany males instead of migrating with females to calving grounds (Bannikov et al. 1967).

In southeastern Oregon, sexual segregation of mule deer supports the hypothesis of sexual segregation (especially around parturition) to enhance reproductive fitness (Main and Coblentz 1996). Maternal females selected areas with adequate food, permanent water nearby to satisfy lactation demands and steep slopes as escape terrain from coyotes. Males travelled more widely to exploit superior foraging opportunities.

### *Group Size*

There may be minimum group sizes that cause animals to undertake movements. In the Pechora River area of Russia, seasonal migrations discontinued when moose reached low densities in the 1920s and 1930s, then migrations resumed after the end of the Second World War when the population rebounded (Pulliainen 1974). Indian elephants (*Elephas maximus*) in Malaya live in discreet home ranges that overlap with other herds (Mohamed Khan bin Momin 1969). If a group was reduced to three individuals or less, they travelled away from the home range to join another herd.

## Multi-Species Resource Use

### *Resource Partitioning*

When two closely related species of similar size meet in the same region they tend to compete for resources and only persist together if they are ecologically separated by habitat and/or food preference (Schaller 1977). The differential use of resources by species is termed resource partitioning (Schoener 1974), and it may ultimately be caused by competitive interactions (Connell 1980). Often, species of prey differ in their vulnerability to predation in a particular habitat. Predator-mediated resource partitioning results when one of the prey species responds by moving to a different habitat (Lingle 2002). Wet season food selection by nomadic grazing ungulates in the Serengeti suggests resource partitioning (McNaughton 1985). Wildebeest concentrated on vegetation forage with a green standing crop of between 40-80g/m2, and gazelles on 20-40g/$m^2$. Buffalo were bimodal in their eating habits using swards of low standing crop and 80-100g/$m^2$. They tend to occupy fairly restricted home ranges and do not undergo extensive movements. Bimodality occurs because some herds experience the onset of the wet season at different times than others. Generally, buffalo resided on the most productive sites, followed by wildebeest, then gazelle on the poorest ranges. During the peak of the rainy season, the three major nomadic grazers (wildebeest, zebra and gazelle) were spatially segregated. Wildebeest and zebra occurred in the wettest areas, while gazelles occupied the driest areas.

Dry season food selection of the four major grazers was separated by species, composition, standing crop and structural properties of the vegetation. Buffalo and zebra fed in tall vegetation where green forage was diffusely distributed, gazelles grazed short vegetation with a low standing crop, and wildebeest used grazing lawns of high biomass concentration. Sinclair (1977) noted that wildebeest were potential competitors with buffalo in the dry season, when both used riverine grasslands. Buffalo were able to use forest glades as an ecological refuge if competition became excessive which wildebeest, topi, kongoni and hippopotamus (*Hippopotamus amphibious*) avoided.

Species also followed one another in grazing succession as new arrivals consumed forage avoided by previous grazers (Vesey-Fitzgerald 1960). For example, dry season feeding patterns of gazelle were closely associated with sites previously utilized by wildebeest (McNaughton 1976). Schaller (1977) summarised ecological separation of Caprinae species in mountainous regions of Eurasia. Although some species generally preferred certain types of forage (e.g. goats selected browse more than sheep) most specialization appeared to be in habitat selection. Where sheep and goat species co-occurred, sheep were found mainly on undulating terrain, while goats were on precipices. In the Himalayas, thar are cliff dwellers that may travel above the timberline, while serow (*Capricornis sumatraensis*) are more associated with dense cover. Where ibex or bharal (*Pseudois nayaur*) occur above the timberline, thar are found mainly in wooded gorges that ibex and bharal avoid. In the Altai, where thar are absent, ibex occupy cliffs in the wooded zone. In the Alps, Ibex live at higher elevations than chamois (*Rupricapra rupricapra*), and where mouflon/urial (*Ovis orientalis*) have been introduced, they occupy the lowest slopes. In the eastern Caucasus, chamois may range higher than the tur, but when they share the same elevation, tur are more often found in shady valleys that chamois avoid. In Baluchistan, markhor (*Capra falconeri*) are on cliffs whereas urial occur on talus slopes, and ibex are on cliffs above argalis (*O. ammon*).

Northern portions of white-tailed and mule deer range overlaps with southern portion of moose range. In parts of western North America, all three share sympatric zones. Because moose are generally associated with boreal coniferous forest, white-tailed deer with deciduous brush forest, and mule deer with more open grassland-parkland, the sympatric ranges may be comprised of marginal habitat for all three species (Prescott 1974). As browsers that consume a number of similar food items, there is potential for competition where they coexist. Differences in food preferences, seasonal spatial segregation and different abilities to cope with snow and cold provide evidence of resource partitioning (Boer 1998). Snow depths of about 30 per cent less than chest heights seriously impeded both white-tailed deer and moose in Nova Scotia and New Brunswick, but moose, being taller, had an advantage in deep snow. Northern and elevational limits for white-tailed and mule deer are influenced primarily by winter conditions, and mule deer can apparently tolerate winters of greater severity (Kramer 1972). The main determinant of moose distribution appears to be browse availability (Prescott 1974). In New Brunswick and Nova Scotia high moose densities tend to be limited to elevations above 150m (Dodds 1974). An altitudinal separation over part of the year may allow moose to survive in areas of deer abundance. Because moose are adapted to cope with deeper snow, they seasonally occupy areas uninhabited by *P. tenuis* infected deer.

In mountainous areas of northwestern North America, moose and deer are more segregated than in other parts of sympatric range probably because of elevational effects on vegetation communities and snow accumulation (Telfer 1978). Moose and deer differ in wintering area selection by choice of overstorey cover and understorey browse. Where moose and mule deer share the landscape, they seldom compete in same area during winter. Mule deer converge in valley bottoms, while moose are more dispersed. In the Maritimes-Maine region, moose and white-tailed deer reduce spatial overlap, as moose winter on upper slopes greater than 180 m in elevation, while deer are more often on lower slopes under 180m in elevation (Prescott 1974).

Elk have less tolerance for snow depth than moose and this may be a determining factor for the proximal distribution of these two species in winter (Stevens 1974). Both have been able to maintain high populations in Elk Island National Park where they reside together in close proximity (Holsworth 1960). In Wind Cave National Park, South Dakota, habitat selection, spatial distribution and food habits of mule deer differed extensively from both bison and pronghorn (Wydeven and Dahlgren 1985). Elk and bison had low distributional overlap and food habits differed. Similar resource partitioning between these two species has been observed in Elk Island National Park, Alberta (Telfer and Cairns 1979).

On Yellowstone National Park's northern range, Singer and Norland (1994) compared niche relationships and diet among elk, bison, bighorn sheep, mule deer, and pronghorn antelope during the periods of 1967-1970 and 1986-1988. By the latter period, total ungulate numbers nearly tripled. Although bison used a wider variety of habitats as their population increased and diet and habitat overlap increased with other species, Singer and Norland (1994) found little evidence of change in competitive interactions between species. Although food habits and habitat use patterns of pronghorn and mule deer overlap where they are sympatric, there was nearly complete spatial segregation and limited opportunities for competition (Wood 1989). Where overlap occurred, it usually resulted from movement of pronghorn into mule deer habitat.

Lingle (2002) studied predation and habitat separation of white-tailed and mule deer in southern Alberta. Although they are closely related species that tolerate a wide variety of habitats and frequently coexist, in this study area mule deer used more rugged and open terrain, while white-tails occupied gentler terrain. In response to coyote predation, mule deer moved to and up slopes, and white-tailed deer moved down and away from slopes, which led to habitat segregation of the two species. Similar mechanisms have been proposed for segregation of African ungulates (Jarman 1974, Sinclair 1975). Risk of predation may also lead to convergence of ungulate species such as Thomson's and Grant's gazelles (*Gazella granti*) (Fitzgibbon 1990).

Although woodland caribou often share the landscape with other ungulates such as moose, deer, elk and bison, they occupy a much different ecological niche. Certain adaptations permit caribou to exploit a nutrient-poor niche on the landscape where other ungulates are unable (Thomas and Gray 2002). According to Kelsall (1968), caribou are physiologically adapted to cope with low protein forage. Lichens, which form the bulk of the winter diet, are high in digestible carbohydrates for energy value, but low in protein and minerals.

The musk deer (*Moschus moschiferus*) of Eurasia shares the landscape with reindeer and also depends on lichen for sustenance. The musk deer is a small cervid that requires shelter during winter and there appeared to be little overlap in distribution with reindeer outside of mountain taiga (Egorov 1965). Cumming et al. (1994) described habitat partitioning by moose and woodland caribou in north western Ontario. Autocorrelation of winter track locations demonstrated that wolf tracks were most often associated with moose tracks, and the two ungulates appeared to disassociate from each other. Cumming (1975) found that predation rates on caribou varied according to distance from wolves.

Results from a study in north eastern Alberta by James (1999) supported the following three predictions of a spatial separation hypothesis: (1) caribou and moose selected different habitat types, while moose and wolves selected the same upland habitat type; (2) wolf predation on caribou was higher near habitats selected by moose (3) scat analysis showed that relative predation on caribou was less than their relative frequency in the environment. In west-central Alberta, wolves selected habitats with young vegetation and waterways with abundant moose (Kuzyk 2002). In contrast, caribou preferred forest 120-160 years of age (Szkorupa 2002), and avoided cutblocks (Smith et al. 2000) and perennial streams (Oberg 2001).

In a study of range relationships of muskoxen and Peary caribou on Banks Island, Northwest Territories when both species were increasing, Wilkinson and Shank (1974) detected little overlap in distribution and most of the feeding time was spent in different plant communities. Similar results were observed in later studies of caribou/reindeer – muskox interactions (e. g. Smits 1989, Biddlecomb 1992, Schaefer et al. 1996, Ihl and Klein 2001).

In the Aishihik Lake area of the Yukon, Fischer and Gates (submitted) observed strong patterns of niche partitioning during winter between woodland caribou and wood bison. Although both species are grazing ruminants, specific morphological, physiological and behavioural adaptations determine foraging niche at the landscape, range overlap, feeding site, and diet composition levels.

### *Commensalism*

Commensalism occurs when populations of two species may interact in such a way that one population benefits but the other is unaffected (Odum 1971). In the Serengeti, long distance migrants follow each other in a sequence led by zebra, then wildebeest which are followed by Thomson's gazelle (Gwynne and Bell 1968). The rapid passage, hindgut digestive system of zebra is relatively efficient for extraction of nutrients from low quality forage. High grass stem consumption and trampling by zebra reduce plant competition for light and stimulate greater production of grass leaf. Because wildebeest feed mainly on grass leaf, they experience improved habitat suitability when following zebra. The combined action of zebra and wildebeest enhances availability of dicotyledonous plant material that gazelles prefer.  Although large grazers may facilitate access to forage for smaller grazers, smaller grazers may drive the succession from behind by high-grading pastures (Farnough et al. 2002). Predation also may partially explain the grazing succession (Sinclair and Norton-Griffiths 1982).

Although waterbuck consume the same types of grass in forest habitat as African buffalo, the smaller waterbuck is able to forage where the grasses are widely scattered (Sinclair 1977). As the buffalo requires large food patches that allow high rates of intake, Sinclair (1977) suggested that its feeding activities in the forest could be both competitive and facilitative for waterbuck. During earlier times, pronghorn may have been at least as numerous as bison in western North America (England and DeVos 1969). Pronghorn underwent dramatic decreases, but there is little reference to excessive slaughter similar to bison. The diet of pronghorn consists mainly of browse and forbs, which may increase under heavy grazing. It is possible that moderate overgrazing by bison improved habitat for antelope.

## Chapter Summary

Animal species move in response to diverse ecological pressures (Dobson 1982). The primary benefit to adopting a movement strategy appears to be the ability to respond to a changing environment. Environments can change through variation in resource availability, which is often weather related, predation pressure, interspecific or intraspecific competition, or disease. These changes ma be atributed to a range of natural variability in the environment and can be modified by human activity. Movement strategies allow species to find new resources, escape predation pressure, find new mates and improve reproductive potential. Movement can be costly, however, because of uncertainties of finding necessities, greater exposure to predators and competitors, loss of rare phenotypes, and less viable offspring (Stenseth and Lidicker 1992).

Success of a movement strategy depends on the environment in which the population persists. Many species of ungulates have populations within the same environment that adopt either a movement strategy, such as migratory movement tracking seasonal changes in resource availability, or are sedentary, adapting to a particular niche in the environment. Both strategies have costs and benefits, yet both can be successful. Changes in the environment can make either of these strategies more successful than the other; however, movement strategies may be best for highly variable environments. Ungulate species will adapt movement strategies, whether long distance migratory movements or sedentary, in response to their environment. Although one particular pressure may be the primary cause of movements, movement strategies are typically an adaptation to multiple pressures.

# 3

# ENVIRONMENTAL SETTING

Ecological conditions, other biota, and terrain modified for human infrastructure needs define the environmental setting influencing the spatial and population ecology of bison in and around Yellowstone National Park. The purpose of this chapter is to describe baseline environmental conditions relevant to bison ecology in YNP. Much of this information was required input for the YNP bison movement and distribution model described in Chapter 6. Here we provide information useful for placing the bison/winter road use and bison/brucellosis issues into an ecological context by reviewing the past and present environmental setting of the park.

## Geography and Geology

Yellowstone National Park is a 8,983 km$^2$ mountainous reserve in the northwest corner of Wyoming, USA (Figure 3.1). It is part of the Greater Yellowstone Ecosystem (GYE), which encompasses more than 7.3 million hectares of public and private land in Wyoming, Montana and Idaho (Keiter 1991). The headwaters of three major continental-scale watersheds originate in the GYE: the Mississippi-Missouri, Snake-Columbia and Green-Colorado (Marston and Anderson 1991). Five percent of YNP is covered by water; major rivers include the Snake, Yellowstone, Gallatin and Madison and major lakes include Lewis, Heart, Shoshone and Yellowstone (Rodman et al. 1996). Mountain ranges in YNP include the Absaroka, Gallatin and Washburn (Rodman et al. 1996). The continental divide traverses YNP from west to southeast (Meagher 1973). Major shrub and grassland valleys in YNP include Lamar (part of the northern range), Pelican, Hayden and the Firehole.

Extensive volcanism and glaciations shaped the landscape of YNP (Meagher 1973). Parts of the Plateau were formed by uplift and erosion during the Precambrian era 2.7 billion years ago (Meagher and Houston 1998). Some of the oldest geologic materials in YNP are Precambrian gneisses and schists (Rodman et al. 1996). The Laramide orogeny, between 100 and 50 million years ago (late Cretaceous through Paleocene), formed the southern Rocky Mountains (Despain 1990, Rodman et al. 1996, Meagher and Houston 1998). The Yellowstone area has existed as a terrestrial environment since 90 million years ago (Despain 1990). Volcanic eruptions further shaped the landscape during the Eocene era 50 to 40 million years ago (Despain 1990, Meagher and Houston 1998). Sixteen million years ago a plume of magma formed below the earth’s crust 600 km southwest of the present Yellowstone plateau (Meagher and Houston 1998). As North America drifted southwest, the plume of magma shifted northeast and eventually became positioned beneath the Yellowstone plateau (Meagher and Houston 1998). Subsequent large volcanic eruptions 2.1, 1.3 and 0.6 million years ago formed three partially overlapping calderas (Meagher and Houston 1998). The Yellowstone calderas (large basin-shaped volcanic depressions more or less circular in form) extend from Old Faithful to Mount Washburn in the north and to Yellowstone Lake in the east (Meagher and Houston 1998). They still provide an active heat source in parts of YNP, giving rise to an unusually high concentration of geothermal features (geysers, hot springs, mud pots and fumaroles; Rodman et al. 1996) and influencing bison habitat. YNP has also undergone at least 3 extensive glaciations that have affected most of the park (Rodman et al. 1996).

Northern and central YNP are characterized by a decreasing elevation gradient from east to west. Northern YNP is generally lower in elevation than central regions of the park. In the northern range, highest elevations occur on the Mirror Plateau and Cache Calfee ridge (2500 m) and decrease through upper (2200 m) and middle (2100 m) Lamar Valley to the Gardiner area (1800 m). The highest elevation in central YNP occurs at Mary Mountain (2500 m). Pelican Valley and Hayden Valley are at 2400 m, and elevation drops in the Firehole (2225 m), to Madison Junction (2100 m) and out to West Yellowstone (2050 m). Along the road from Madison Junction to Mammoth, elevation increases at Norris (2300 m) and Swan Lake Flats (2250 m) before dropping at Gardiner.

## Bison Winter Ranges and Movement Corridors

Bison winter ranges and movement corridors were defined by key informants during semi-directive interviews (see Chapter 1) conducted in Montana and Wyoming in July 2004. A bison *winter range* was defined as a common destination winter foraging area. A *corridor* was defined as a common winter movement pathway connecting two ranges within which foraging habitat and foraging may occur. Ranges and corridors were defined by key informants as areas where the majority of mixed groups (cows and calves) forage and travel, rather than all locations where they may occur. These structures were illustrated on maps by key informants then digitized using a Geographic Information System (GIS). During digitization, habitat classification maps for YNP (Despain 1990) and outside YNP (United States Geological Survey - Land Use Land Cover (USGS – LULC), Anderson et al. 1976) were overlaid on air photos. Classified habitat and unclassified open shrub-grasslands were digitized within the bison range defined by key informants to insure inclusion of all suitable habitats available to bison within that range; non-habitat areas (e.g. forests) were not included in the range. Maps of digitized bison winter ranges and movement corridors were returned to interviewees during validation workshops held in Montana and Wyoming in October 2004 to verify accuracy and modify as necessary.

Key informants identified 5 bison winter ranges and 5 winter movement corridors in YNP (Figure 3.2). In northern YNP, two ranges were identified, Lamar Valley (233.80 $km^2$) and Gardiner basin (98.35 $km^2$). Many key informants considered Lamar Valley and Gardiner basin as one continuous range, i.e. the northern range. However we separated these ranges so we could illustrate bison use of ranges exterior (Gardiner basin) and interior (Lamar Valley) to YNP. One key informant questioned the definition of Lamar Valley range because his telemetry location data for 1995 - 2001 indicated that bison used only flat valley bottoms within Lamar Valley during this period, whereas our delineation of Lamar Valley included steeper upland grassland habitat. However, all other key informants agreed with including upland grasslands. Indeed, one long term data set suggests that bison are increasingly using upland habitat[2].

The portion of the Gardiner basin bison winter range outside YNP was delineated based on current bison management policy documents (United States Department of the Interior (USDOI), National Park Service (NPS) 2000). Bison could move beyond the Gardiner basin boundary to other foraging areas, however, they are not tolerated outside the Gardiner basin range because of concerns about brucellosis transmission risk from bison to cattle. Bison are culled if they travel past the boundary. Additionally, only 100 bison are tolerated within the Gardiner basin range before culling is implemented (USDOI, NPS 2000).

Three bison winter ranges were defined in central YNP: Pelican Valley (55.16 $km^2$), Mary Mountain (151.8 $km^2$, including Hayden Valley and the Firehole), and West Yellowstone which spans the boundary of the park (79.93 $km^2$). Hayden Valley was grouped with the Firehole because of historic continuous movements back and forth between the two valleys over the Mary Mountain trail, throughout the winter (the assumption that the Mary Mountain Trail is unlike other corridors is assessed in Chapter 5). Like Gardiner basin, the portion of the West Yellowstone bison winter range outside YNP was delineated based on bison management policy and reflects where 100 bison are tolerated before culling actions are taken (USDI, NPS 2000) as opposed to where bison could move if allowed to expand freely (see Figure 3.1 for location of capture facilities).

Digitized corridor maps were overlaid on a digital elevation model to illustrate terrain ruggedness (Figures 3.3 to 3.7). Grassland habitat, geothermal areas and linear features (i.e. roads and power lines) are also illustrated on the corridor maps. The 5 corridors (Figure 3.2) are the primary bison movement pathways between winter ranges described by key informants. In the northern range, the Gardiner basin to Lamar Valley corridor (GLC) is located along the Yellowstone River and the road from Cooke City to Gardiner (Figure 3.3). It consists of two routes, one following the Yellowstone River, the other along the paved road. The Mirror Plateau corridor (MPC) extends from southeastern Lamar Valley to northeastern Pelican Valley (Figure 3.4) and was considered by key informants to be infrequently used by bison during mid winter because of deep snow and rugged terrain. The northern range is also connected to central YNP by the Firehole to Mammoth corridor (FMC; Figure 3.5). The FMC has only recently become a significant pathway for bison movement from the central range to the northern range (Chapter 5). The Pelican Valley to Hayden Valley corridor (PHC; Figure 3.6) connects the two interior central bison ranges. Bison exit the western boundary of YNP via the Firehole to West Yellowstone corridor (FWC; Figure 3.7).

The length of each corridor was determined by measuring the distance from one end of the corridor to the other. The FMC was the longest winter movement corridor, almost double the length of the next longest, the MPC; the next longest corridor was the FWC, followed by the GLC and PHC (Table 3.1).

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[2] Interview with Chris Jerde, 24 June 2004, Edmonton, Alberta.

## Climate

The YNP climate can be divided into four seasons (Despain 1990). Spring begins March or April, extends through June, and is characterized by cold to cool nights and warm to cool days, during which snow gradually melts and disappears over time with elevation. Summer is short and occurs during July and August. Fall begins in September and extends through October, and winter begins in November and ends in March - April.

Present winter climate in YNP has been described as severe, long and cold (Meagher 1971, Meagher and Houston 1998). Mean annual temperature is 4.3°C at Mammoth (1900 m) and 0.2°C at Lake Yellowstone (2360 m; Meagher and Houston 1998).

Climate data is collected at various SNOTEL, snowcourse and Climate (CLIM) stations in and around YNP (Figure 3.8). CLIM stations measure daily minimum and maximum temperature, daily precipitation, and snow depth. A snow course is a designated permanent site where snow depth and its water content are measured. SNOTEL stations measure and transmit daily snow water equivalence from snow pillows, total precipitation accumulated from October 1 each year, and air temperatures.

### *Snow*

Most precipitation reaches the GYE along prevailing westerlies (Marston and Anderson 1991), much of it in the form of snow (Despain 1990). Snow accumulation begins mid to late October and persists until late March, to early April (Despain 1990). Mean duration of snow cover is 213 days at 7,000 ft (2,133 m; Despain 1990). Snow water content and total precipitation is typically greater at high elevations and greater in the western portion of YNP compared to the east (Despain 1990, Delgiudice et al. 2001). Previous studies indicate snow conditions are more severe (i.e. deeper) in central YNP than the northern range (Meagher 1973, Delgiudice et al. 2001).

Snow conditions (e.g. depth and density) can have a significant impact on ungulate foraging, movements and survival. In YNP, snow may influence forage availability, energy expenditure during movements and foraging, ability to travel, vulnerability to predators and nutritional status of ungulates, including bison (Meagher 1973, Turner et al. 1994, Mech et al. 2001, Delgiudice et al. 2001, Meagher et al. 2002). The effect of deep snow on reducing forage availability to ungulates, prompting migratory movements to lower elevations, was noted in YNP as early as 1937-38 (Grimm 1939). This is a critical concern in the current management challenge of minimizing contact between bison and cattle as they disperse northward and westward across park boundaries during harsh winters.

Snow Water Equivalence (SWE, cm) and snow depth (cm) was obtained from CLIM stations (National Oceanic and Atmospheric Administration, National Climatic Data Center, http://lwf.ncdc.noaa.gov/oa/ncdc.html. accessed Jan. 11 2005), snowcourses (United States Department of Agriculture, National Water and Climate Center, http://www.wcc.nrcs.usda.gov/snowcourse/. accessed Jan. 11 2005) and SNOTEL stations (United States Department of Agriculture, National Water and Climate Center, http://www.wcc.nrcs.usda.gov/snow/. accessed Jan. 11 2005) in and around YNP. SWE is a measure of the amount of water stored in snow (Farnes et al. 1999); it integrates snow depth and snow density. SWE has been used to assess winter severity in previous studies on ungulates in YNP (e.g. Bjornlie and Garrott 2001, Delgiudice et al. 2001).

We used SWE and snow depth and density data to compare winter severity between years and between bison winter ranges. We compared yearly historical February 15th measures of SWE (Figure 3.9) and snow depth (Figure 3.10) between the northern range (Mammoth, Tower Falls, Lamar Ranger Station climate stations) and central YNP (Hebgen Dam, West Yellowstone, Old Faithful, Canyon, and Lake Yellowstone climate stations). We also compared mean annual SWE (Figure 3.9) and snow depth (Figure 3.10) between climate stations.

We used February 15th SWE to compare snow conditions between ranges and years. SWE on this date is representative of snow conditions for the winter (Figure 3.12). Snow was deeper and SWE was greater in central YNP than the northern range (Figure 3.9 and Figure 3.10). Mean February 15th SWE values for central YNP were approximately 20 cm compared to 7.5 cm on the northern range. Mean snow depth in central YNP was approximately 100 cm. The maximum was approximately 160 cm, close to the maximum at which bison may cease foraging (Turner et al. 1994). The minimum was approximately 40 cm, below the level where snow begins to limit access to forage (Turner et al. 1994). Mean snow depth in the northern range was approximately 40 cm, with maxima close to 90 cm and minima close to 10 cm in some years.

We considered two spatial models of YNP snowpack (Wockner et al. 2002 and Watson et al. (u.d.) (F. Watson, California State University-Monterey, pers. comm.) to predict mean February 15th SWE for each bison winter range and movement corridor. We compared the output of each model to data collected at climate stations (Figure 3.11) to identify the model that most accurately predicted SWE for each bison winter range. The Wockner et al. (2002) model creates historical daily interpolated SWE maps for the entire YNP. It considers characteristics (elevation, slope, aspect, and vegetation) of a location (100 m x 100 m) and interpolates an SWE value for that location based on the actual SWE data measured at SNOTEL stations and data from 28 additional snow measurement sites. The model can create an SWE map for YNP each day from 1981 to 1999. The Watson et al. (u.d.) LANGUR snow model also generates historical predictive snow maps for YNP. Elevation, aspect, slope, land cover type, canopy cover, mean annual temperature and ground heat flux of each location (228 m x 228 m) are used to interpolate SWE values. The LANGUR model also considers maximum and minimum daily temperature and precipitation data from up to 5 SNOTEL sites in and around YNP. The LANGUR model was calibrated with three snow core data sets collected from 2001-2004 and SWE measured at six SNOTEL sites in YNP from 1993-2004. Mean February 15th bison winter range SWE values from each model were compared to actual mean February 15th SWE measured at climate stations. The climate station closest to, or that best represented snow conditions for a particular bison winter range was associated with that range for comparison to the models. The model that best emulated SWE was used to calculate mean SWE values for each bison winter range and movement corridor. Overall, the Wockner et al. (2002) model best emulated actual SWE data at stations (Figure 3.11). The Wockner et al. (2002) model predicted SWE in the northern range and Pelican Valley closer to measured SWE than LANGUR. The LANGUR model estimated SWE higher for the northern range than observed at Mammoth and Tower Falls climate stations. A possible explanation is that snow core measurements used to calibrate the LANGUR model were collected in central YNP and none were collected on the northern range. Meagher (1971) indicated snow in Pelican Valley is deeper than at Lake

Yellowstone where measurements are recorded. However, LANGUR predicted a lower SWE value for Pelican Valley than measured at the Lake Yellowstone climate station, and similar to the northern range. The Wockner et al. (2002) model predicted higher SWE values in Pelican Valley than the LANGUR model. A possible explanation why LANGUR predicted low SWE values in the central range is the model was calibrated with snow core data from 2001-2004, a period of below average snowfall (see Figure 3.9 and Figure 3.10).

We used the Wockner et al. (2002) model to calculate SWE for each bison winter range and movement corridor because it better simulated the difference in SWE between northern and central YNP and the severity of snow conditions in Pelican Valley. Estimated mean SWE for February 15 from the Wockner et al. (2002) model (Table 3.2) was highest in the Mary Mountain range (20 cm), followed by Pelican Valley (19 cm), West Yellowstone (17 cm), Lamar Valley (9 cm) and Gardiner basin (6 cm). Estimated SWE values illustrate the strong difference in snow conditions between the northern range (less snow) and central YNP (more snow). Along movement corridors (Table 3.1), SWE was highest along the FWC (17 cm) and FMC (17 cm). The MPC (16 cm) also had a high SWE value. SWE along the PHC (13 cm) was relatively low and SWE along the GLC (3 cm) was very low.

In addition to snow depth and SWE, other characteristics of snow pack can affect forage availability to ungulates. Key informants identified snow crusting as an important constraint on forage accessibility for bison, making it difficult to crater. Snow hardness (the initial resistance to deformation per square unit area; McClung and Schweizer 1996) is affected by temperature, wind speed, type of snow, rain on snow, and incoming shortwave radiation (Kozak et al. 2002, Pomeroy and Brun 2001). Key informants identified a major crusting event during the winter of 1996-1997, when the temperature increased above 0˚C for about one week, during which time it also also rained. A subsequent decrease in temperature caused the snow to freeze. After this event, many bison moved from interior YNP winter ranges to boundary park ranges, and a precipitous decline in population occurred primarily due to culling (Peacock 1997*a*). Crusting due to December rainfall was also noted in YNP in the winter of 1937-1938 (Grimm 1939).

We were unable to find a published method for predicting snow crusting events from historical climate data, so we developed a method. Data on temperature, snow depth and precipitation from various climate stations in and around YNP are collected by the National Oceanic and Atmospheric Administration National Data Center, (http://nndc.noaa.gov/). We used data from 4 stations, Gardiner, West Yellowstone, Lake Yellowstone and Tower Falls for November, December and January, from 1981 to 2004, except for Tower Falls, which had data for the period 1989 to 2004. Each station was associated with a bison winter range, Gardiner for Gardiner basin, Tower Falls for Lamar Valley, West Yellowstone for West Yellowstone and Lake Yellowstone for Pelican Valley and Mary Mountain. For each station, we identified sequences of days from November 1 to January 31 when initial temperature was below or equal to 0˚C followed by an increase in temperature to > 0˚C for at least 3 days, of which at least one day was greater than 5˚C, followed by a temperature decrease to below or equal to 0˚C. Of those sequences, we identified those that had a snow depth greater than or equal to 30 cm. We considered that 30 cm was a threshold below which snow cover did not influence access to forage. Finally, we identified those sequences where precipitation during the > 0˚C days was > 0 mm. For clarity, the criteria were designed to identify freeze/thaw/freeze events when at least 30 cm of snow was on the ground and precipitation fell as rain. We were unable to use other factors such as wind to predict crusting events because data were not available. Using these criteria, we determined the probability of a crusting event in a year for each bison winter range (Table 3.4). Gardiner basin (0.08) had a very low probability of a crusting event. Crusting events were rare at Gardiner basin because snow is rarely above 30 cm. West Yellowstone (0.29) had the second lowest probability of a crusting event. The central interior bison winter ranges (0.42) had the same probability of crusting events because the same climate data was used. The probability of crusting was highest in the Lamar Valley (0.56). Based on information provided by key informants, crusting events occur more often in Lamar Valley than central bison ranges.

Geothermal activity can also modify snow pack. YNP has the highest density of geothermal features in the world (U.S. Department of the Interior, National Park Service, http://www.nps.gov/yell/pphtml/subnaturalfeatures 23.html). Geothermal features generate heat that can dramatically reduce snow cover and lengthen the growing season, both at geothermal basins and along the banks of streams and rivers influenced by warm water (Meagher 1973, Despain 1990), thus improving forage availability at these sites (Bjornlie and Garrott 2001). Geothermal sites and geothermally influenced shorelines may therefore be key refugia for bison during severe winters (Despain 1990, Meagher et al. 2002).

A digitized map of geothermal areas was provided by the Spatial Analysis Center, Yellowstone National Park (unpubl. data). In central YNP, geothermal areas are common but are uncommon in the northern range. Total area and percentage of area geothermally influenced were calculated for each bison winter range (Table 3.2). Mary Mountain bison (21.9 km$^2$; 14.4%) had the greatest total area and percentage of area geothermal features, with many of them occurring in the Firehole. Pelican Valley (2.7 km$^2$; 4.8%) also had a relatively high amount of geothermally influenced habitat, although notably less than Mary Mountain. Lamar Valley and Gardiner basin had insignificant geothermal influence on bison habitat (< 1%). West Yellowstone had no geothermal influence based on spatial data provided by the Spatial Analysis Center, Yellowstone National Park. In contradiction, Craighead et al. (1973:38) described the importance of geothermal springs in the Duck Creek and Cougar Creek area for elk in winter.

Each bison movement corridor was randomly sampled for geothermal areas 1,000 times using a random point generator (Jenness 2003) in GIS. The proportion of random samples that fell on geothermal areas and associated geothermally influenced rivers was used to calculate relative frequency of thermal areas for each corridor (Table 3.1). Geothermal features occurred most frequently along the FWC (0.092). The FMC (0.052) also had a relatively high proportion of geothermal features. The MPC and PHC had a very low proportions of geothermally influenced areas (0.001), and no geothermals occurred along the GLC.

### *Summer Precipitation*

Summer drought can reduce forage production and thus forage quality and quantity available to ungulates during the subsequent winter (Merrill and Boyce 1991). The sum of June and July precipitation can be used as a relative index of winter forage available to ungulates on winter range (Farnes et al. 1999). Mean monthly precipitation for June and

July was obtained from SNOTEL and CLIM stations in YNP. The Canyon SNOTEL station (data from 1981-2003) was used to calculate mean summer precipitation for the Mary Mountain bison winter range. Madison SNOTEL station (data from 1968-2003) was used to calculate mean summer precipitation for West Yellowstone bison winter range (the West Yellowstone SNOTEL station had only 4 years of precipitation data). Gardiner CLIM station was used to calculate mean summer precipitation for Gardiner basin bison winter range, Tower Falls CLIM station was used to calculate mean summer precipitation for Lamar Valley bison winter range and Lake Yellowstone CLIM station was used to calculate mean summer precipitation for Pelican Valley bison winter range. Mean monthly precipitation for June and July from 1971-2000 was obtained from CLIM stations; raw data was not available. Standard deviation was therefore not available for CLIM stations but was estimated based on the coefficient of variation for the mean at Canyon and Madison SNOTEL stations.

Summer precipitation was highest in West Yellowstone (11.05 cm), followed by Mary Mountain (10.9 cm), Pelican Valley (9.8 cm), Lamar Valley (9.7 cm), and Gardiner basin (6.3 cm), which had the least precipitation (Table 3.6). On average, summers were drier on the northern range than central YNP.

## Vegetation, Forage Production, and Utilization

Two major soil parent materials occur in YNP, rhyolitic and andesitic materials, both derived from bedrock deposited during volcanic events (Despain 1990). Sedimentary deposits also make up some of the soil materials in YNP (Despain 1990). Andesitic and sedimentary soils are richer in nutrients than rhyolitic soils (Despain 1990).

Approximately 80% of YNP is covered in forest, of which 60% are subalpine-fir (*Abies lasiocarpa*)/lodgepole pine (*Pinus contorta*) communities (Despain 1990). These extensive lodgepole pine forests typically grow on nutrition-poor soils derived from rhyolite (Meagher and Houston 1998). Forest at lower elevations (<2000 m) is characterized by Limber pine (*Pinus flexilis*) and Douglas-fir (*Pseudotsuga menziesii*; Meagher and Houston 1998). Lodgepole pine, Spruce-fir-pine and Whitebark pine (*Pinus albicaulis*) are characteristic of higher elevation forests (>2000m, >2400 m and >2800 m respectively; Meagher and Houston 1998).

Nonforested plant communities were described in detail by Despain (1990). Nonforested communities occur throughout the park, typically in areas underlain with andesite or sedimentary rock (Despain 1990). Big sagebrush (*Artemesia tridenta*)/Idaho fescue (*Festuca idahoensis*) is the most abundant sagebrush-grassland type in YNP (Klein et al. 2002). Other grassland communities include Idaho fescue/bearded wheatgrass (*Agropyron subsecundum*), Idaho fescue/Richardson’s needlegrass (*Hesperostipa richardsonii*), Idaho fescue/Bluebunch wheatgrass (*Pseudoroegnaria spicatum*) and Bluebunch wheatgrass/Sandberg’s bluegrass (*Poa secunda*; Klein et al. 2002).

Geothermal activity can produce tropical conditions, providing habitat for tropical plant species (Despain 1990). Plant species growing in geothermally influenced areas vary depending on temperature and include, mosses (50˚F to 65˚F), grasses (25˚F to 50˚F) such as Nuttall’s alkali-grass (*Pucinellia nuttalliana*), thermal western witchgrass (*Panicum capillare*), poverty danthonia (*Danthonia spicata*), winter bentgrass (*Agrostis* spp.), cheatgrass (*Bromus tectorum*) and bluegrasses (*Poa* spp.), and herbs (23˚F to 37˚F) such as hairy golden-aster (*Chrysopsis villosa*), sheep sorrel (*Rumex acetosella*), fireweed (*Epilobium angustifolium*), Canada thistle (*Cirsium arvense*) and spar-leaf fleabane (*Erigeron* spp.; Despain 1990). Plant communities associated with geothermal sites in the Madison-Firehole area consist of aquatic macrophytes (*Myriophyllum* spp., *Ranunculus aquatilis* and *Potamogeton* spp.*)* and spike rush (*Eleocharis rostellata*) communities (Garrott et al. 2002).

Ungulate herbivory has important impacts on grassland dynamics in YNP. In the northern range, grazing stimulates aboveground production of grasslands by promoting nutrient cycling and enhancing N and $NO_3^-$ availability to plants (Frank and Evans 1997, Frank 1998, Singer and Schonecker 2002). Migratory movements of ungulates in the northern range, from lower elevations in the spring to high elevations in the summer, represents tracking nutritionally rich forage as it shifts spatially to higher elevations as the season progresses (Frank and McNaughton 1993, Frank 1998). Seasonal migration allows vegetation to recover from herbivory (Frank 1998).

## Fire

YNP has been shaped by 9 to 12 major fire events over the last 2,000 years and major fires occur at roughly 100-300 year intervals (Klein et al. 2002). The fire of 1988 was considered a major fire in scale. It burned roughly 794,000 acres of YNP (Despain 1990) of coniferous forest and sagebrush-grasslands (Turner et al. 1994). Fires can have significant effects on ungulates up to four years post-fire, although effects diminish within this time (Pearson and Turner 1995). Substantial immediate post-fire ungulate mortality can result because of reduced forage and typical drought conditions reducing forage in unburned areas (Turner et al. 1994). In subsequent years, fire may stimulate primary productivity resulting in improved forage quantity and palatability (Turner et al. 1994).

## Bison Habitat and Forage

Mary Meagher (Bison biologist, retired, Yellowstone National Park, pers. comm.) identified important bison winter habitat from among Despain's (1990) habitat classes for YNP. Important winter habitat for bison included shrub-grasslands consisting of Idaho fescue, bearded wheatgrass, bluebunch wheatgrass, sandberg's bluegrass, shrubby cinquefoil (*Dasiphora floribunda*), richardson's needlegrass, tufted hairgrass (*Deschampsia cespitosa*), big sagebrush and silver sagebrush (*Artemesia cana*). Wet meadows consisting of willows (S*alix* spp.) and sedges (*Carex* spp.) and vegetation associated with thermal areas (hotsprings vegetation) were also identified as important bison forage during the winter (Table 3.5).

Mean annual above ground primary production (forage production) was calculated for each bison winter range (Table 3.2). Tom Olenicki (Montana State University, pers. comm.) provided data on vegetation productivity (mean ± s.d, data collected during summers of 1998, 1999 and 2000) from a study conducted in Hayden Valley. Additionally, he estimated thermal area vegetation productivity as approximately 1,000 kg/ha, with a high degree of variation. Olenicki's data was comparable to data from other studies on vegetation productivity in YNP (Table 3.6). We identified the vegetation class used by Olenicki (Montana State University, pers. comm.) most comparable to each of Despain's (1990) habitat classes and USGS - LULC (Anderson et al. 1976) classes then assigned a corresponding productivity value. For each bison winter range, mean and standard deviation productivity of each habitat class within the range was multiplied by the arial proportion of that habitat class in the range. The proportional mean productivity of all habitat classes was then summed to calculate the annual weighted mean productivity for each bison winter range.

The area of each habitat type and percentage of each habitat type was calculated for each bison winter range (Table 3.5). Mean annual productivity (Table 3.2) was highest in Pelican Valley (1881 kg/ha), followed by West Yellowstone (1613 kg/ha), Mary Mountain (1327 kg/ha), Lamar Valley (1123 kg/ha) and Gardiner basin (1104 kg/ha), which had the lowest productivity. On average, forage production was higher in central YNP than the northern range.

Habitat proportion was calculated for each bison movement corridor by randomly sampling 1,000 pixels (30x30 m) in each corridor using a random point generator (Jenness 2003) in GIS and determining the proportion of the sample that was habitat. Habitat occurred most frequently along the GLC (0.724), followed by the PHC (0.510), MPC (0.431), FMC (0.372) and FWC (0.250), which had the lowest frequency of habitat (Table 3.1).

## Other Wildlife

A variety of ungulate species, in addition to bison, use YNP seasonally or year round, including elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*). Large carnivores in YNP include grizzly bears (*Ursus arctos*), black bears (*U. americanus*), mountain lions (*Puma concolor*), and wolves (*Canis lupus*). Coyotes (*C. latrans*) are also present in YNP.

Habitat overlap between ungulates was compared on the northern range between 1967 to 1970 and 1986 to 1988 by Singer and Norland (1994). Habitat overlap between bison and other ungulate species had increased since the 1960's (the end of population regulation of bison inside YNP), likely due to a rapid increase in populations and range expansion by elk and bison (Singer and Norland 1994). Intraspecific competition for forage also increased between elk and bison (Singer and Norland 1994).

Predation on bison by wolves and grizzly bears occurs in YNP; predation by grizzly bears is extremely rare (Wyman 2002, Varley and Gunther 2002, Smith et al. 2000). Currently, predation by wolves on bison does not limit bison subpopulations in YNP (D. Smith, Wolf Biologist, YNP, pers. comm.). Elk are the primary prey for wolves in YNP because they are more abundant and easier to kill (Smith et al. 2000). However, predation rates on bison vary in the park and are higher in central YNP compared to the northern range because elk are much less abundant in central YNP, particularly during the winter (Smith et al. 2000, D. Smith, Wolf Biologist, YNP, pers. comm.). In central YNP, because of the small and likely decreasing population of elk (Garrott et al. 2002), wolves are taking an increasing number of bison (D. Smith, Wolf Biologist, YNP, pers.

comm.). Therefore, there is potential for this predator prey system to evolve to a state similar to that reported in Wood Buffalo National Park where bison are the main prey and other ungulates occur at low densities (Carbyn et al. 1993). Bison carcasses also provide an important food source for scavengers, particularly grizzly bears (Green et al. 1997, Mattson 1997).

## Anthropogenic Features

YNP was established March 1, 1872 as "…a public park or pleasuring ground for the benefit and enjoyment of the people." (Schullery et al. 1998). Infrastructure development has been ongoing since then to meet demands for increasing use. A summary of development of roads and buildings in YNP is provided below. For a detailed account see Culpin (1994) and Culpin (2003).

In 1872-73 there were two routes entering YNP, one through the north entrance to Mammoth Hot Springs and the other through the west entrance via Madison Canyon to the Lower Geyser Basin. In 1877, the first road over Mary Mountain was "cut" by Maj. Gen. O. O. Howard during his pursuit of Chief Joseph. Superintendent Norris built roads in YNP from 1877-1881 and was credited with building nearly 2/3 of the Grand Loop, including road sections from Mammoth to Lower Geyser Basin, Upper Firehole Geyser Basin to Yellowstone Lake and Mammoth to the west entrance, via Forks, Great Falls, Yellowstone Lake and Forks of the Firehole River. As early as 1883, Lt. Dan C. Kingman of the U.S. Army Corps of Engineers expressed concern about overdevelopment of the park. He prioritized building high quality roads and improving existing ones over building new roads. In addition to improving much of the existing road system, Kingman completed the Golden Gate pass, a new road from the Firehole to Upper Geyser Basin and a road from Norris Geyser Basin to Beaver Lake. The philosophy of developing quality roads over quantity was maintained throughout the history of the park, although often difficult to achieve due to budget constraints.

From 1883 to 1886, the Yellowstone National Park Improvement Company built hotels at Mammoth, Upper Geyser Basin, Canyon and Lake Yellowstone. By 1886 telephone lines were installed to all hotels. Prior to 1924, government buildings and hotels had separate telephone poles and lines, each running down opposite sides of the roads. In 1924, park managers decided to remove the old poles and lines and put up new joint lines away from the roads, cutting through the forest.

In 1910-11, a road was constructed along the Gallatin River, from Taylor's Fork to West Yellowstone by Gallatin County. The road between Bozeman and West Yellowstone was opened to automobiles in 1914. On August 1, 1915 the first automobiles were permitted to enter YNP. 1926 to 1939 was one of the most significant periods in the history of road development in YNP; 249 of the 558 km road system received a bituminous surface, 154 km of which were on the Grand Loop. Development of and visitation to YNP slowed drastically during WW II, but visitation increased rapidly after the war. Subsequent deterioration of the park infrastructure system led to MISSION 66 endorsed by President Dwight D. Eisenhower, cabinet and congress in 1955. MISSION 66 was a program to improve conditions of the national park system to maximize its use and provide protection of assets by 1966, the 50th anniversary of the creation of the NPS. Part of the proposal was to provide adequate roads and trails, facilities and interpretation.

## Motorized Oversnow Vehicle Winter Use History

Motorized Oversnow Vehicle (OSV) use was introduced to YNP in 1949 (Yochim 1998*a*,*b*) but regular OSV use in the park was not established until the 1960's and 1970's. The road from Mammoth to Cooke City was occasionally plowed during the latter 1930's; plowing was more frequent after WW II. By the 1960's, the road was plowed almost daily, as conditions dictated[3]. As early as 1930, local businesses asked the NPS to plow all roads in the park to allow year-round access[4]. The NPS declined the request, citing that roads were too poor to permit extensive plowing, plowing would be too hazardous, and facilities in the park interior were not winterized (Yochim 1998*a*).

The first permit for a snowcoach operator to bring tourists into YNP (Yochim 1998*a*) was granted to a businessman in West Yellowstone in 1955 (Aune 1981, Bjornlie and Garrott 2001). In January 1963, three private snowmobiles entered the park for the first time and the following winter the first snowmobile rally was held at West Yellowstone (Aune 1981, Yochim 1998*b*). By 1967, snowcoaches operated out of both Mammoth Hot Springs and West Yellowstone (Aune 1981). NPS issued regulations to confine snomobiles to snow-covered roadways; they were not allowed in back country areas or on frozen lake surfaces[5]. In 1967, a congressional hearing was held in Jackson, WY (USDI, NPS 1968) in response to public pressure for winter plowing of roads and concerns over winter use in YNP (Yochim 1998*a*). At this meeting, park managers concluded that use of interior roads by OSV's was preferable to park-wide snow plowing of roads, and that OSV travel would be restricted to roads (Yochim 1998*a*).

The actual date when Yellowstone Park Company began grooming roads for snowcoaches is lost to historians, but was probably in the 1960s. In 1971 the NPS assumed responsibility for road grooming to facilitate access to the park and restrict OSV's to roads (Aune 1981, Yochim 1998*a*, Bjornlie and Garrott 2001). In 1971, the snow lodge at Old Faithful was opened for its first winter operation (Aune 1981, Yochim 1998*a*). Most OSV activity was initially concentrated in the west end of the park, therefore grooming only occurred on these roads (Yochim 1998*a*). By 1973, all roads were groomed as needed but grooming occurred more frequently on roads where OSV use was higher (i.e. the west side of the park; Yochim 1998*a*). In 1976-77, more consistent grooming of the east entrance road began resulting in a marked increase in OSV use of east side roads (Yochim 1998*a*). By the late 1970's, all snow covered roads were in constant use, with the exception of the Tower to Canyon route across Mt. Washburn. Public winter use was permitted from December 1st through the third week of March, depending on snow conditions, with highest levels of use over the Christmas holiday season and from February into the first week of March[6]. Spring opening of roads by snowplows began in March. Grooming practices have remained roughly the same since

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[3] Interview with M. Meagher, 15 July 2005, Gardiner MT.

[4] Comment made by M. Yochim in factual review of a draft of this report, 8 April 2005.

[5] Comment provided by Yellowstone Natonal Park personnel in factual review of a draft of this report, 8 April 2005.

[6] *supra* note 3

grooming began, with the entire width of the two lane road groomed[7]. Grooming typically occurs between 3 pm and 2 am (Kurz et al. 2000).

Currently, roads are closed from early November to mid- December to all but YNP personnel (Bjornlie and Garrott 2001), with the exception of the road from Gardiner to Cooke City through the Lamar Valley, which is plowed and open to the public year round. In mid-December, roads are opened to the public and groomed as needed (typically every night) until the end of the OSV season in early to mid-March when all roads are plowed. Then roads are once again closed to all but YNP personnel until mid-April (Bjornlie and Garrott 2001).

Winter use has increased rapidly since YNP began grooming roads (Figure 3.13). Much of the growth has occurred because of increasing numbers of snowmobiles entering YNP. Recently, winter use impacts on park resources and wildlife have become major and controversial issues in YNP. Several studies (e.g. Kurz et al. 2000, Bjornlie and Garrott 2001, Meagher et al. 2002, Davis et al. 2004) have been conducted on the effects of winter use on wildlife and other park resources.

## Conclusions

There were notable distinctions between ecological conditions on the five bison winter ranges and five bison movement corridors in YNP, which may differentially affect bison ecology and movement. The Gardiner basin and Lamar Valley ranges were functionally a continuous range, following an elevational gradient represented in winter severity (SWE). In central YNP, bison range is made up of several distinct shrub-grassland valleys connected by corridors. Climate, particularly snow conditions, was noticeably different between northern and central YNP bison ranges. Snow conditions are less severe in the northern range compared to the central. Additionally, the northern range is drier than central YNP. Predictably, forage production and habitat composition varies between the ranges, with distinct differences between northern bison winter ranges and central ranges. The area and proportion of geothermally influenced areas, which can affect snowpack, was much higher in central ranges compared to the northern range, which had negligible geothermal influence. Assessment of the study area indicated there are distinct and important differences between bison winter ranges, most evident in differences between the central and northern YNP ranges.

Anthropogenic features, such as roads and road grooming, have been present in the YNP landscape roughly as they are now for several decades. Roads and other linear features (i.e. powerlines and telephone lines) have been in place in YNP since at least the early 1900’s. Winter use by humans is a more recent phenomenon, but developed quickly after its introduction in 1949. Infrastructure and other facilitation of winter use (i.e. road grooming) have been in place in YNP since the late 1970’s. Human use of YNP in winter (Figure 3.13) has grown simultaneously with the bison population (Chapter 5), providing opportunity for confusing causes and effect.

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[7] *supra* note 3

Table 3.1. Attributes of bison movement corridors. The proportion of habitat and geothermal features was based on 1000 random samples of 30x30 m pixels in each corridor. GLC: Gardiner basin to Lamar Valley corridor; MPC: Mirror Plateau corridor; PHC: Pelican Valley to Hayden Valley corridor; FMC: Firehole to Mammoth corridor; FWC: Firehole to West Yellowstone corridor.

| | **Bison Movement Corridor** | | | | |
|---|---|---|---|---|---|
| | **GLC** | **MPC** | **FWC** | **FMC** | **PHC** |
| Corridor length (km) | 13.5 | 30.5 | 21.1 | 59.4 | 8.3 |
| % Habitat | 72.4 | 43.1 | 25.0 | 37.2 | 51.0 |
| % Geothermal areas | 0 | 0.1 | 9.2 | 5.2 | 0.1 |

Table 3.2. Attributes of bison winter ranges. Summer precipitation was based years of data from the following stations: 1971-2000 from the Gardiner, Tower Falls, and Lake Yellowstone CLIM stations representing Gardiner basin, Lamar, and Pelican ranges respectively; 1961-2003 from the Canyon SNOTEL station representing Mary Mountain; and 1968-2003 measurements for the Madison Plateau SNOTEL station representing West Yellowstone winter range.

| | **Winter range** | | | | |
|---|---|---|---|---|---|
| | **Gardiner basin** | **Lamar Valley** | **West Yellowstone** | **Mary Mountain** | **Pelican Valley** |
| Area ($km^2$) | 98.34 | 233.8 | 79.93 | 151.83 | 55.16 |
| Geothermal area ($km^2$) | 0.05 | 0.3 | 0 | 21.93 | 2.67 |
| Summer precipitation (cm) ± s.d | 6.3 + 2.8 | 9.7 + 4.3 | 11.1 + 4.3 | 10.9 + 5.3 | 9.8 + 4.3 |
| Forage production (kg/ha) ± s.d. | 1104 ± 534 | 1123 ± 519 | 1613 ± 598 | 1327 ± 627 | 1881 ± 682 |
| Area ($km^2$) sedge meadow | 0 | 11.64 | 2.15 | 14.22 | 4.57 |

Table 3.3. Mean (s.d.), minimum and maximum February 15th SWE values for each bison winter range and movement corridor in Yellowstone National Park. Values were calculated from simulations on February 15th of each year from 1982 to 1999 using the Wockner et al. (2002) snow pack simulation model. All maximum values occurred in 1997. All minimum values occurred in 1987, with the exception of the GLC, which occurred in 1991. GLC: Gardiner basin to Lamar Valley corridor; MPC: Mirror Plateau corridor; PHC: Pelican Valley to Hayden Valley corridor; FMC: Firehole to Mammoth corridor; FWC: Firehole to West Yellowstone corridor.

| Range or corridor | SWE (s.d..) (cm) | Max. SWE(cm) | Min. SWE (cm) |
|---|---|---|---|
| Gardiner basin | 6 ± 2 | 10 | 3 |
| Lamar Valley | 9 ± 3 | 16 | 5 |
| Pelican Valley | 19 ± 6 | 36 | 12 |
| Mary Mountain | 20 ± 7 | 40 | 12 |
| West Yellowstone | 17 ± 6 | 31 | 8 |
| GLC | 3 ± 1 | 4 | 1 |
| MPC | 16 ± 5 | 30 | 10 |
| PHC | 13 ± 6 | 27 | 9 |
| FMC | 17 ± 5 | 32 | 10 |
| FWC | 17 ± 6 | 33 | 9 |

Table 3.4. Annual probability of a snow crusting event in each bison winter range.

| **Station** | **Bison range** | **Years** | **Number of years with $\geq$ 1 snow crusting event** | **Annual probability** |
|---|---|---|---|---|
| Gardiner | Gardiner basin | 1981-2004 | 2 | 0.09 |
| West Yellowstone | West Yellowstone | 1981-2004 | 7 | 0.30 |
| Lake Yellowstone | Pelican Valley | 1981-2004 | 10 | 0.43 |
| Lake Yellowstone | Mary Mountain | 1981-2004 | 10 | 0.43 |
| Tower Falls | Lamar Valley | 1989-2004 | 9 | 0.60 |

Table 3.5. Area (km$^2$) and percent of total range area (brackets) of each habitat type in each bison winter range in Yellowstone National Park.

| Habitat Type | Winter range<br>Gardiner basin | Lamar Valley | West Yellowstone | Mary Mountain | Pelican Valley |
|---|---|---|---|---|---|
| Idaho Fescue/ Tufted Hairgrass | 0 (0) | 0 (0) | 0 (0) | 1.78 (1.18) | 0 (0) |
| Idaho Fescue/ Bearded Wheatgrass | 0 (0) | 5.52 (2.36) | 1.66 (2.08) | 0.14 (0.09) | 0 (0) |
| Idaho Fescue/ Bearded Wheatgrass - sticky | 0 (0) | 44.95 (19.22) | 0 (0) | 0 (0) | 0.15 (0.26) |
| Idaho Fescue/ Bluebunch Wheatgrass | 0 (0) | 6.77 (2.89) | 4.56 (5.70) | 0.81 (0.53) | 0 (0) |
| Idaho Fescue/ Richardson's Needlegrass | 0 (0) | 6.48 (2.77) | 0 (0) | 0 (0) | 0 (0) |
| Big Sagebrush/ Idaho Fescue | 19.66 (19.99) | 57.94 (24.78) | 3.34 (4.18) | 2.63 (1.74) | 1.12 (2.03) |
| Big Sagebrush/ Idaho Fescue - sticky | 0 (0) | 94.17 (40.28) | 11.99 (15.00) | 53.92 (35.51) | 3.66 (6.63) |
| Big Sagebrush/ Bluebunch Wheatgrass | 4.75 (4.83) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Silver Sagebrush /Idaho Fescue | 0 (0) | 0 (0) | 0 (0) | 45.07 (26.69) | 27.27 (49.44) |
| Bluebunch Wheatgrass/ Sandbergs Bluegrass | 6.51 (6.62) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Shrubby Cinquefoil | 0 (0) | 0.29 (0.12) | 0 (0) | 0 (0) | 0 (0) |
| Hotsprings Vegetation | 0 (0) | 0 (0) | 0 (0) | 29.56 (19.47) | 2.30 (4.16) |
| Tufted Hairgrass/ Sedge | 0 (0) | 12.71 (5.44) | 6.82 (8.53) | 8.53 (5.62) | 9.70 (17.59) |
| Tufted Hairgrass/ Sedge - Sedge bogs | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 2.68 (4.86) |
| Sedge Bogs | 0 (0) | 4.98 (2.13) | 2.69 (3.36) | 9.37 (6.17) | 8.28 (15.02) |
| Willow/Sedge | 0 (0) | 0 (0) | 8.15 (10.20) | 0 (0) | 0 (0) |
| Herbaceous Rangeland | 57.67 (58.63) | 0 (0) | 29.26 (36.60) | 0 (0) | 0 (0) |
| Shrub and Brush Rangeland | 9.76 (9.92) | 0 (0) | 0.29 (0.36) | 0 (0) | 0 (0) |
| Mixed Rangeland | 0 (0) | 0 (0) | 6.38 (7.99) | 0 (0) | 0 (0) |
| Nonforested Wetland | 0 (0) | 0 (0) | 4.79 (5.99) | 0 (0) | 0 (0) |

Table 3.6. Annual above ground primary production (APP) measured by several vegetation studies conducted in Yellowstone National Park.

| Vegetation type | APP (kg/ha) | Location of study | Period of study | Source |
|---|---|---|---|---|
| Bluegrasses (Poa spp.)/Sedges (carex spp.) | 708 (forage available) | Gibbon Meadows | October 1996 | Dawes 1998/ Dawes and Irby 2000 |
| Kentucky bluegrass (Poa pratense)/mixed forbs | 240 (forage available) | Terrace Springs | October 1996 | Dawes 1998/ Dawes and Irby 2000 |
| Big Sage (Artemisia tridentata)/bluebunch wheatgrass (Agropyron spicatum) | 288 (forage available) | Four-mile site | October 1996 | Dawes 1998/ Dawes and Irby 2000 |
| Beaked spike-rush (Elocharis rostella) | 492 (forage available) | Fountain Flats Drive | October 1996 | Dawes 1998/ Dawes and Irby 2000 |
| Wetsern wheatgrass (A. smithii)/sedge/rush (Juncus spp.) | 948 (forage available) | Midway Geyser Basin | October 1996 | Dawes 1998/ Dawes and Irby 2000 |
| Beaked spike-rush (Elocharis rostella) | 1509 (forage available) | Old Faithful Interchange | October 1996 | Dawes 1998/ Dawes and Irby 2000 |
| Festuca Idahoensis/Lupinsis sericeus | NA | Crystal Creek | snow-free period 1988 | Frank and McNaughton 1992 |
| Phleum pratense/Poa pratense | 5130 (ANPP) | Lamar Valley | snow-free period 1988 | Frank and McNaughton 1992 |
| Bromus inermis | 2320 (ANPP) | Lamar Valley | snow-free period 1988 | Frank and McNaughton 1992 |
| Carex rostrata | 5390 (ANPP) | Slough Creek | snow-free period 1988 | Frank and McNaughton 1992 |
| Festuca Idahoensis/Lupinsis sericeus | 850 (ANPP) | Crystal Creek | snow-free period 1989 | Frank and McNaughton 1992 |
| Phleum pratense/Poa pratense | 3800 (ANPP) | Lamar Valley | snow-free period 1989 | Frank and McNaughton 1992 |
| Bromus inermis | 2040 (ANPP) | Lamar Valley | snow-free period 1989 | Frank and McNaughton 1992 |
| Carex rostrata | 5890 (ANPP) | Slough Creek | snow-free period 1989 | Frank and McNaughton 1992 |

| | | | | |
|---|---|---|---|---|
| Artemisia tridentata/Festuca Idahoensis | 1014 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Artemisia cana/Festuca Idahoensis | 1245 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Artemisia tridentata/Festuca Idahoensis-Danthonia intermedia phase | 1296 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Artemisia cana/Festuca Idahoensis-Danthonia intermedia phase | 1426 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Artemisia tridentata/Agropyron caninum. | 1650 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Festuca Idahoensis/Agropyron caninum | 867 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Festuca Idahoensis/Deschampsia cespitosa | 1314 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Ridge top Poa sandbergii | 894 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Artemisia tridentata/Poa sandbergii | 894 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Potentilla Fruticosa/Deschampsia cespitosa | 1938 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Artemisia cana/Deschampsia cespitosa | 2001 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Calamagrostis canadensis | 2577 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Deschampsia cespitosa | 1884 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Wet carex spp. | 3315 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Deschampsia cespitosa/Carex | 2832 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Salix/carex | 3074 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Hotsprings Vegetation (estimate) | 1000 | Hayden Valley | 1998/1999/2000 - summer | Olenicki pers. comm. |
| Artemisia tridentata/Festuca Idahoensis/Psuedoroegneria spicata/Poa pratensis/Stipa comata | 1140 | Lamar Valley | Summer 1996 | Tracy and Frank 1998 |

| | | | | |
|---|---|---|---|---|
| Poa pratensis/Phleum pratense/Agropyron caninum/Deschampsia caespitosa/Carex sp./Calamagrostis sp. | 2259 | Lamar Valley | October 1990 | Turner et al. 1994 |
| Artemesia tridentata/Phleum pratensis/Bromus carinatus/Agropyron caninum/Geranium visoscisimum/Potentilla sp./Carex sp. | 1122 | Lamar Valley | October 1990 | Turner et al. 1994 |
| Artemesia tridentata/Agropyron caninum/Agropyron spicatum/Bromus sp./Potentilla sp./Stila ap. | 631 | Lamar Valley | October 1990 | Turner et al. 1994 |
| Artemesia tridentata/Agropyron spicatum/Koeleria cristata/Festuca idahoensis/Chrysopsis villosa/Stipa comata/Danthonia sp./Poa sp./Sedum sp. | 520 | Lamar Valley | October 1990 | Turner et al. 1994 |
| Live grasses | 3030 (aboveground biomass - unfenced) | Lamar Valley | August 1987 | Coughenour 1991 |
| Live grasses | 1550 (aboveground biomass - unfenced) | Lamar Valley | September 1987 | Coughenour 1991 |
| Live grasses | 1790 (aboveground biomass - unfenced) | Lamar Valley | July 1988 | Coughenour 1991 |
| Live grasses | 3380 (aboveground biomass - unfenced) | Blacktail | August 1987 | Coughenour 1991 |
| Live grasses | 2320 (aboveground biomass - unfenced) | Blacktail | September 1987 | Coughenour 1991 |
| Live grasses | 2940 (aboveground biomass - unfenced) | Blacktail | July 1988 | Coughenour 1991 |

| | | | | |
|---|---|---|---|---|
| Live grasses | 2140 (aboveground biomass - unfenced) | Stevens Creek | August 1987 | Coughenour 1991 |
| Live grasses | 1800 (aboveground biomass - unfenced) | Stevens Creek | September 1987 | Coughenour 1991 |
| Live grasses | 1630 (aboveground biomass - unfenced) | Stevens Creek | July 1988 | Coughenour 1991 |
| Grasslands | 4270 (aboveground biomass - unfenced) | Blacktail | May 1998 | Augustine and Frank 2001 |
| Grasslands | 3240 (aboveground biomass - unfenced) | Lamar Valley | May 1998 | Augustine and Frank 2001 |
| Grasslands | 3800 (aboveground biomass - unfenced) | Stevens Creek | May 1998 | Augustine and Frank 2001 |

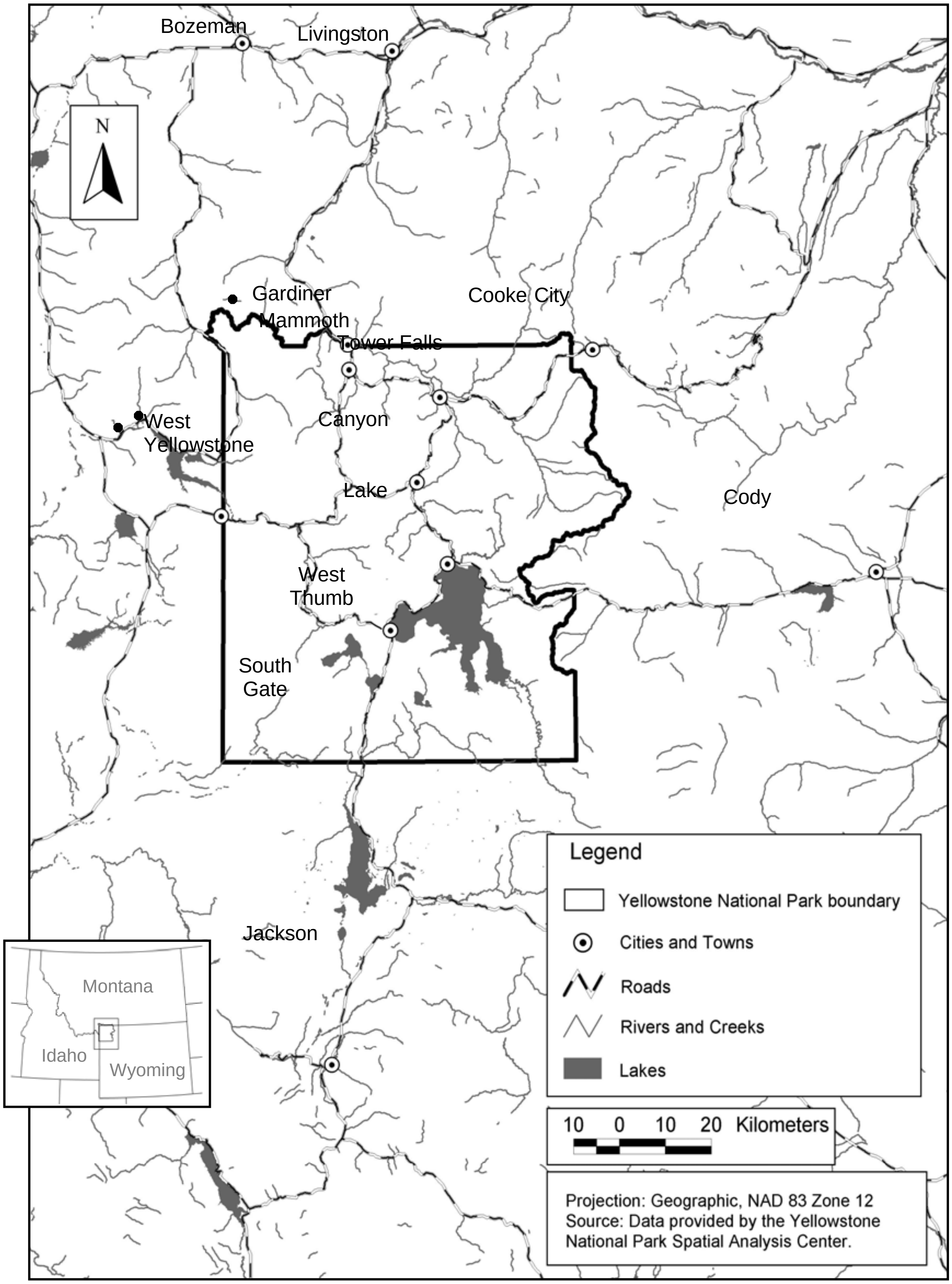


Figure 3.1. The Greater Yellowstone Area (GYA). Inset map (lower left) indicates location of the GYA. Black dots represent locations of bison capture facilities.

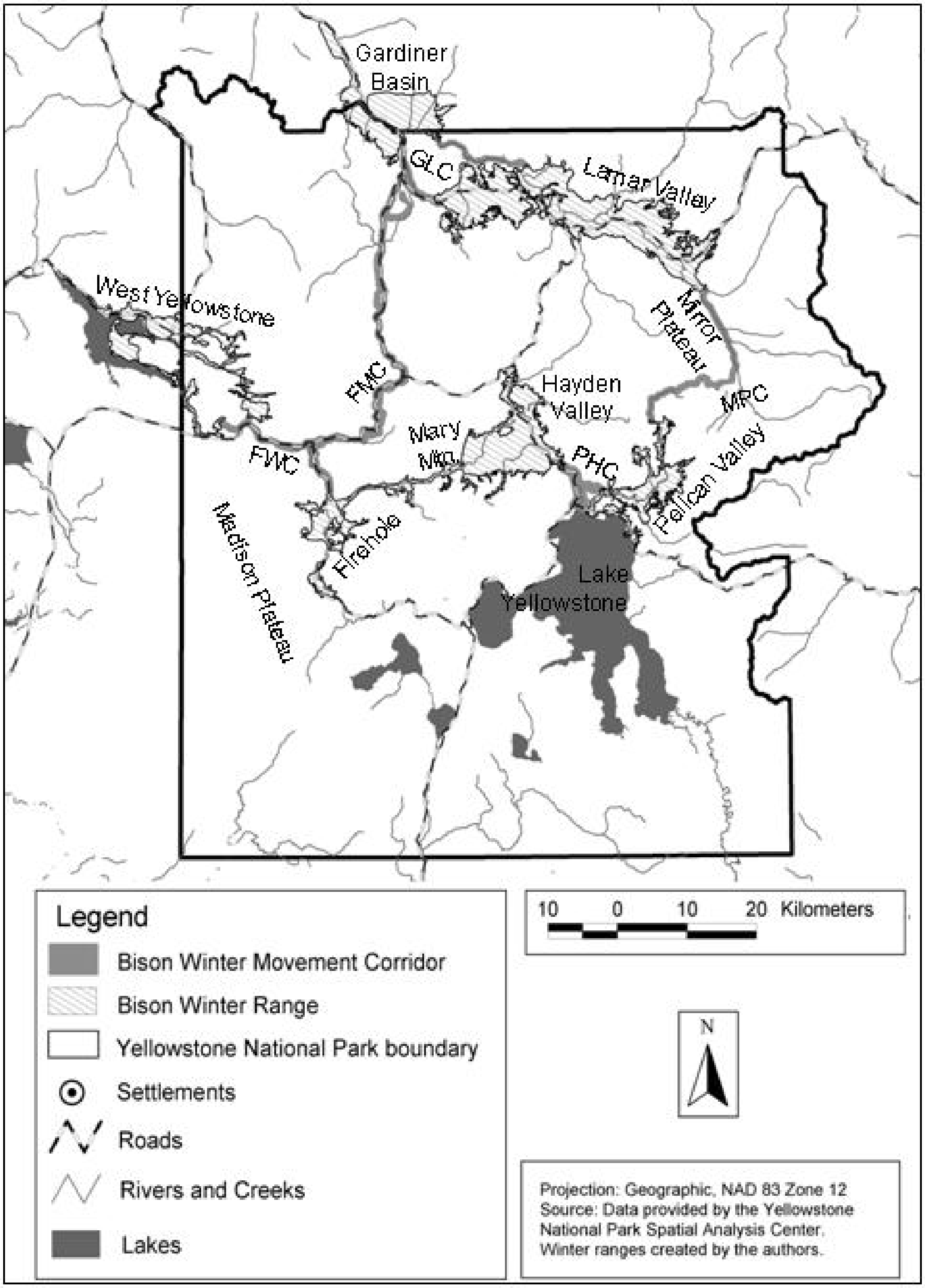


Figure 3.2. Bison winter ranges and movement corridors in Yellowstone National Park. FMC: Firehole to Mammoth corridor; FWC: Firehole to West Yellowstone corridor; GLC: Gardiner Basin to Lamar Valley corridor; MPC: Mirror Plateau corridor; PHC: Pelican Valley to Hayden Valley corridor.

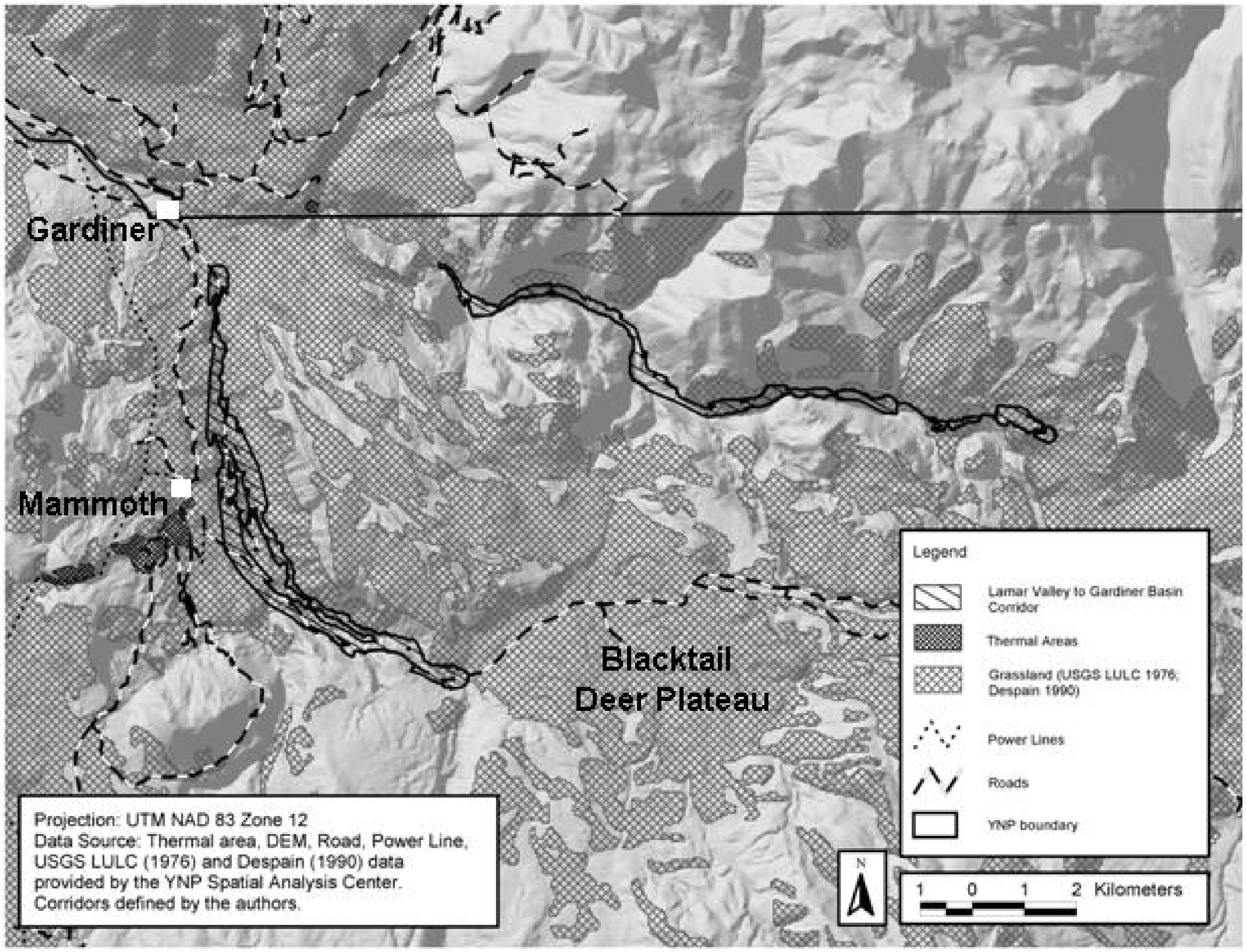


Figure 3.3. The Gardiner Basin to Lamar Valley winter movement corridor. Corridors were delineated based on interviews with Mary Meagher, July 15, 2004, and a workshop with Yellowstone Center for Resources personnel, October 20, 2004.

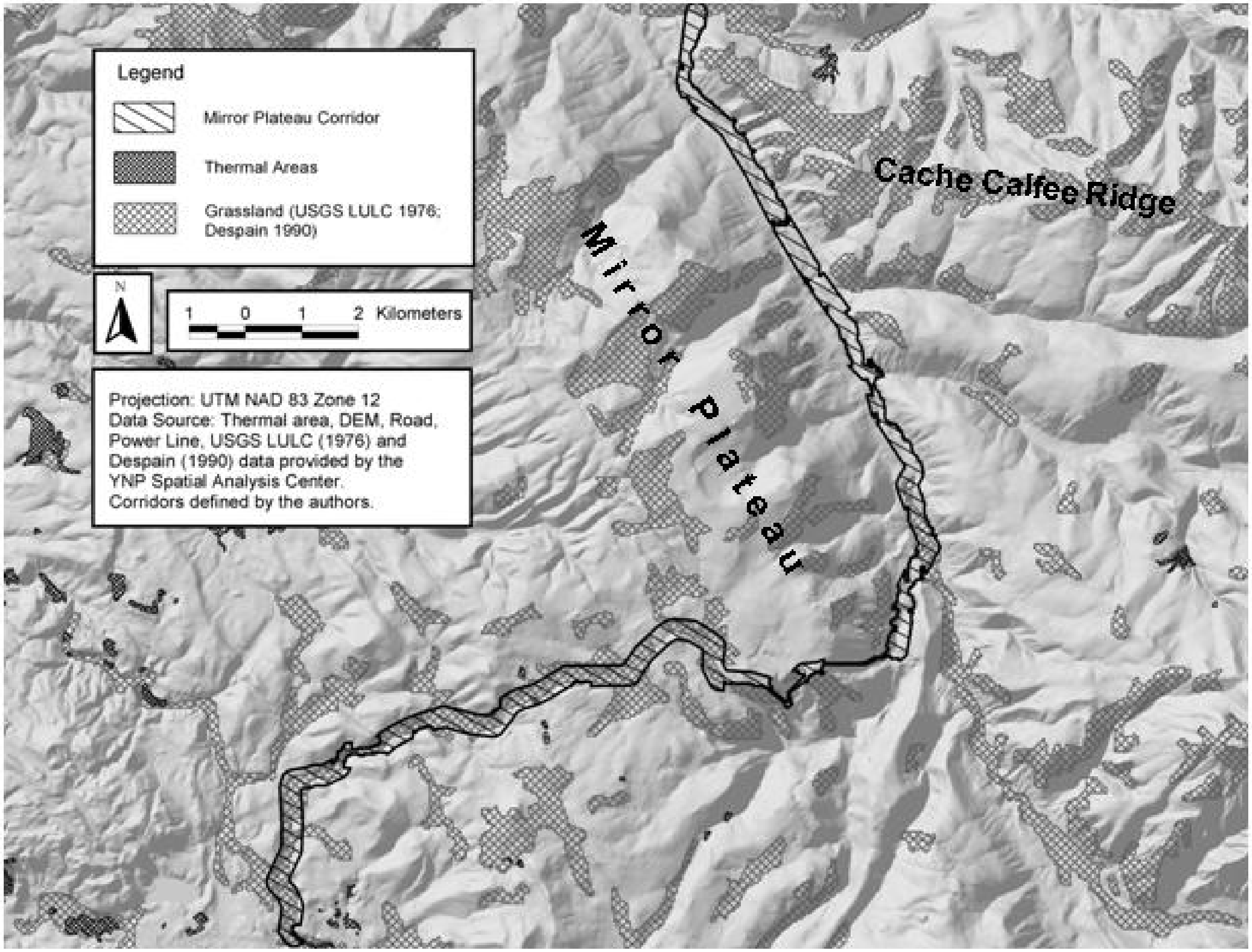


Figure 3.4. The Mirror Plateau winter movement corridor. Corridors were delineated based on interviews with Mary Meagher, July 15, 2004, and a workshop with Yellowstone Center for Resources personnel, October 20, 2004.

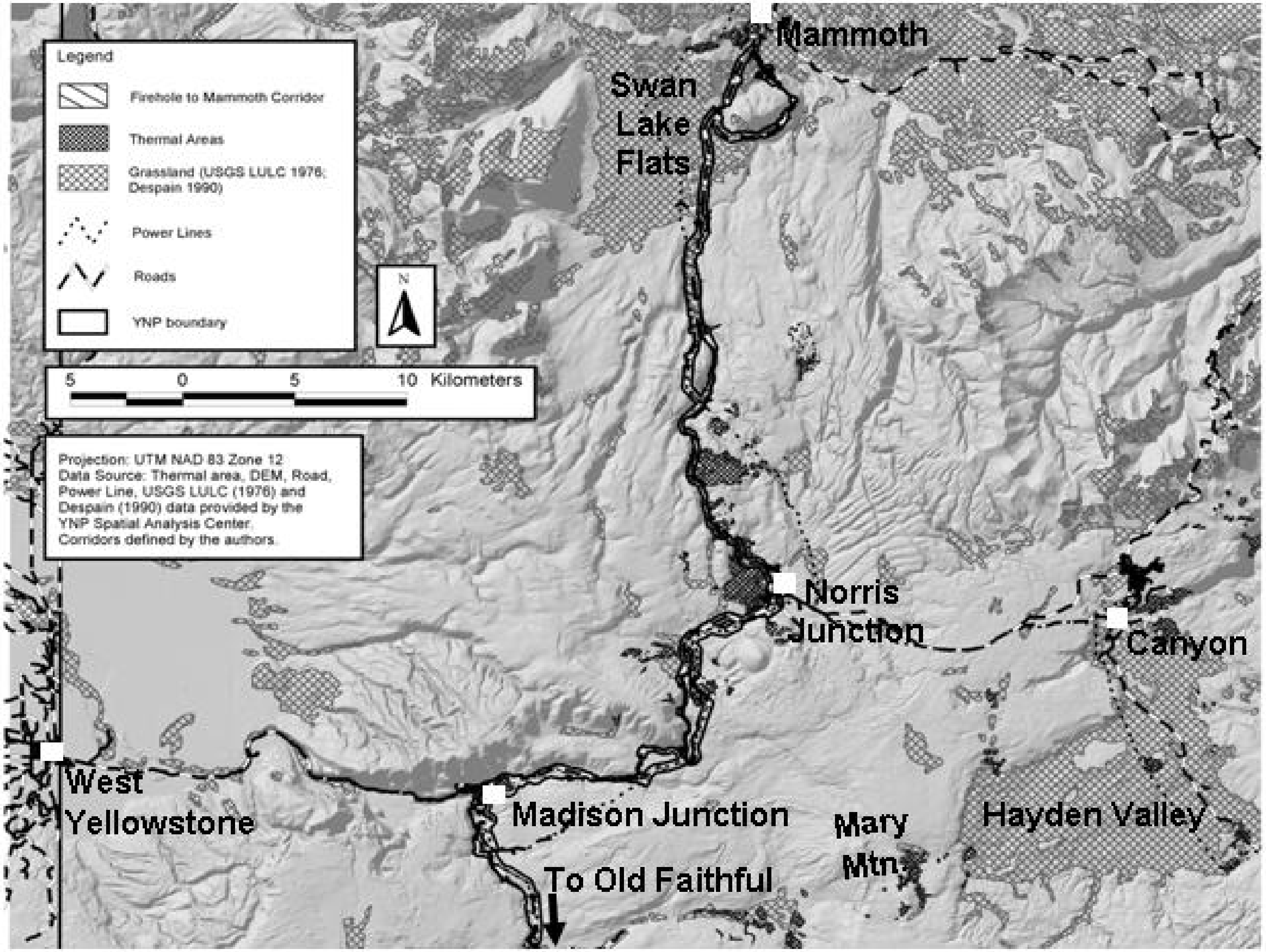


Figure 3.5. The Firehole to Mammoth winter movement corridor. Corridors were delineated based on interviews with Mary Meagher, July 15, 2004, and a workshop with Yellowstone Center for Resources personnel, October 20, 2004.

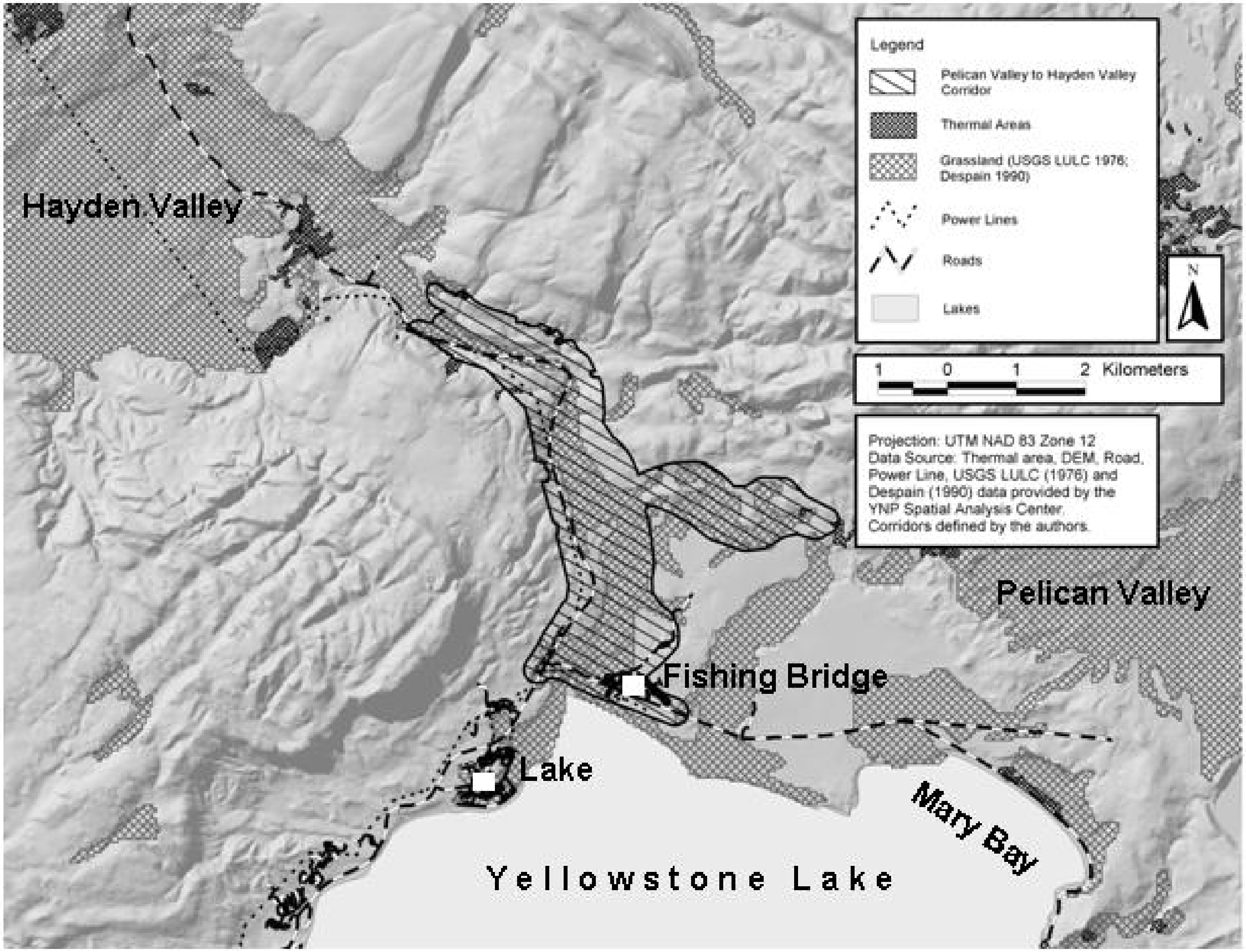


Figure 3.6. The Pelican Valley to Hayden Valley winter movement corridor. Corridors were delineated based on interviews with Mary Meagher, July 15, 2004, and a workshop with Yellowstone Center for Resources personnel, October 20, 2004.

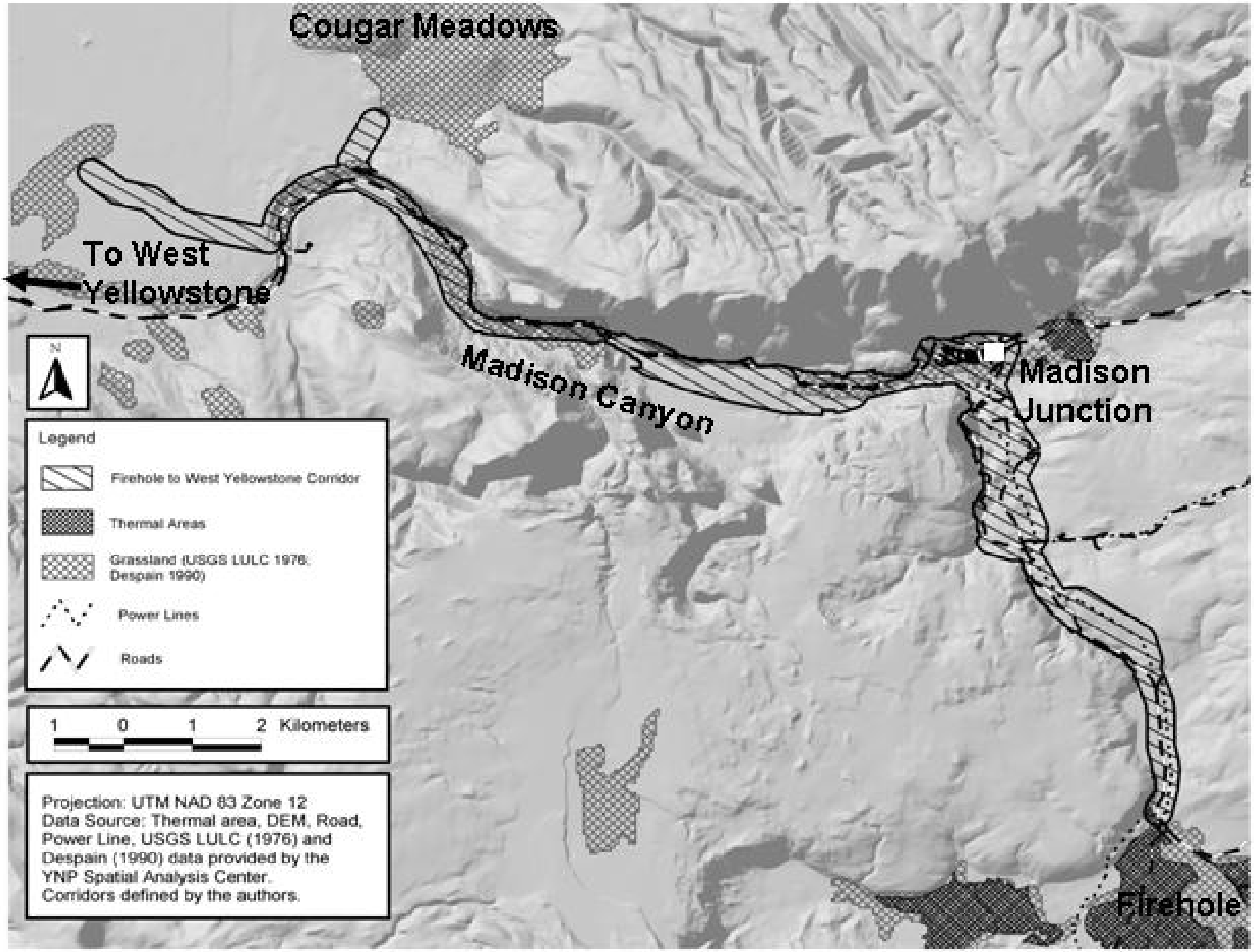


Figure 3.7. The Firehole to West Yellowstone winter movement corridor. Corridors were delineated based on interviews with Mary Meagher, July 15, 2004, and a workshop with Yellowstone Center for Resources personnel, October 20, 2004.

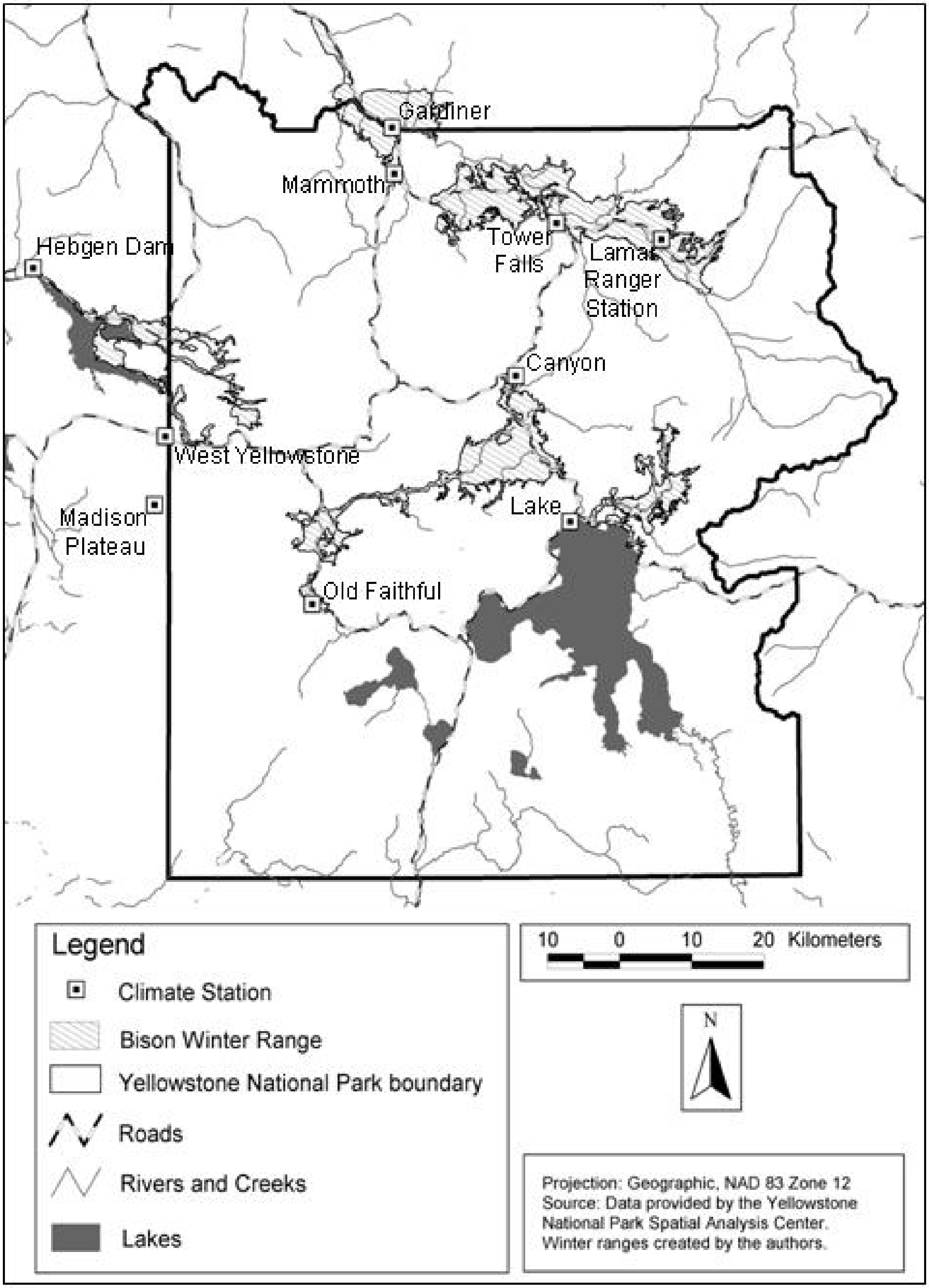
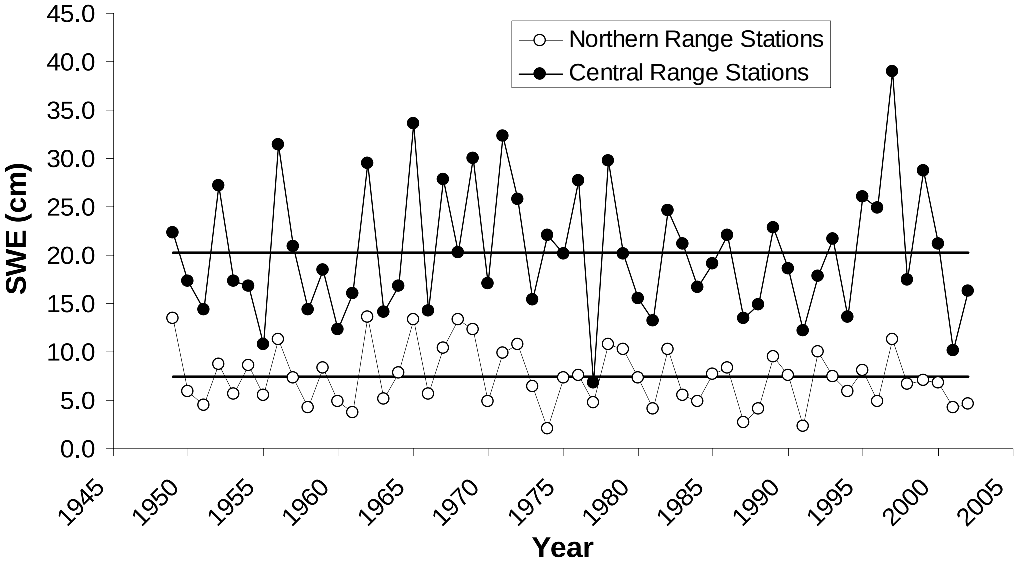


Figure 3.8. Locations of climate stations used for weather data.



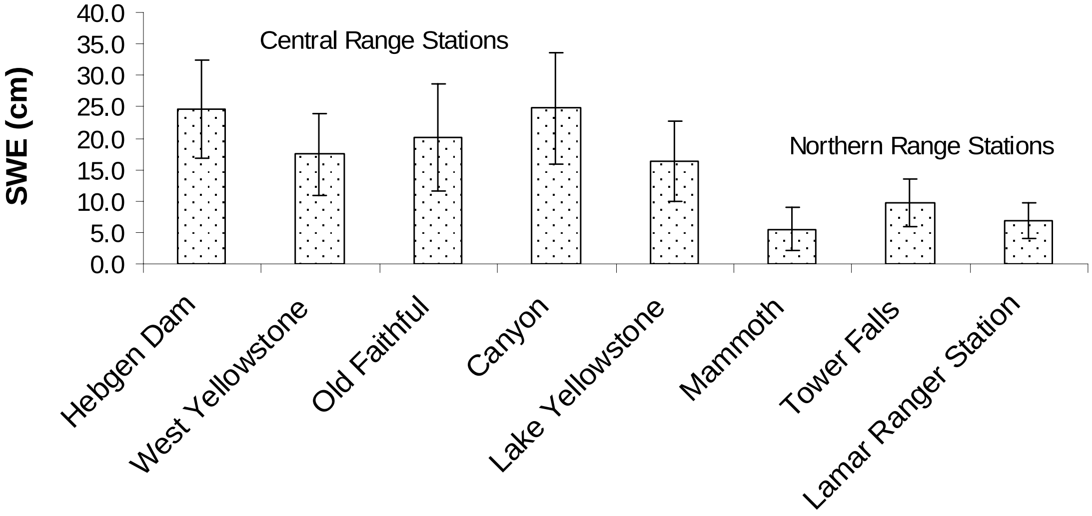
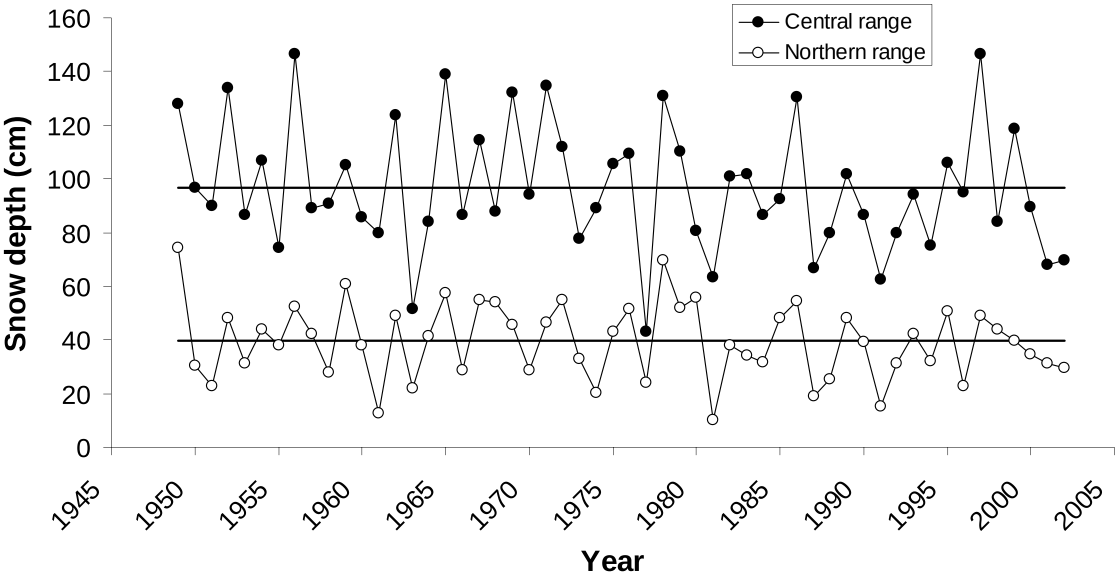


Figure 3.9. Annual and long term average snow water equivalence (cm) ± s.d. in mid-February on Central and Northern bison ranges in Yellowstone National Park based on available station records between 1949 and 2002. Central range stations included west to east: Hebgen Dam, West Yellowstone, Old Faithful, Canyon, and Lake Yellowstone. Northern Range stations included west to east: Mammoth, Tower Falls, Lamar Ranger Station.



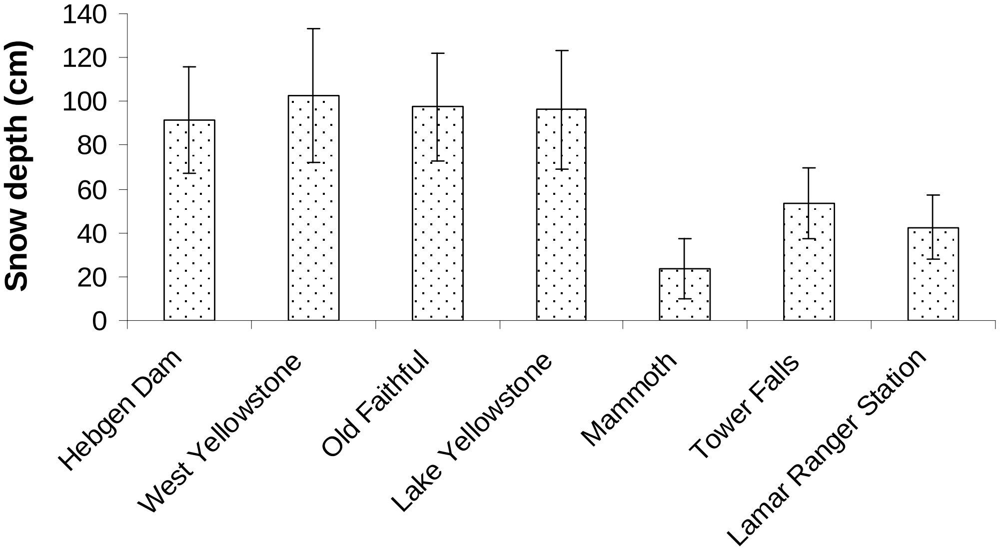


Figure 3.10. Annual and long term average snow depth (cm) ± s.d. on the ground in mid-February on Central and Northern bison ranges in Yellowstone National Park based on available individual station records between 1949 and 2002. Central range stations west to east: Hebgen Dam, West Yellowstone, Old Faithful, and Lake Yellowstone. Northern Range stations west to east: Mammoth, Tower Falls, Lamar Ranger Station.

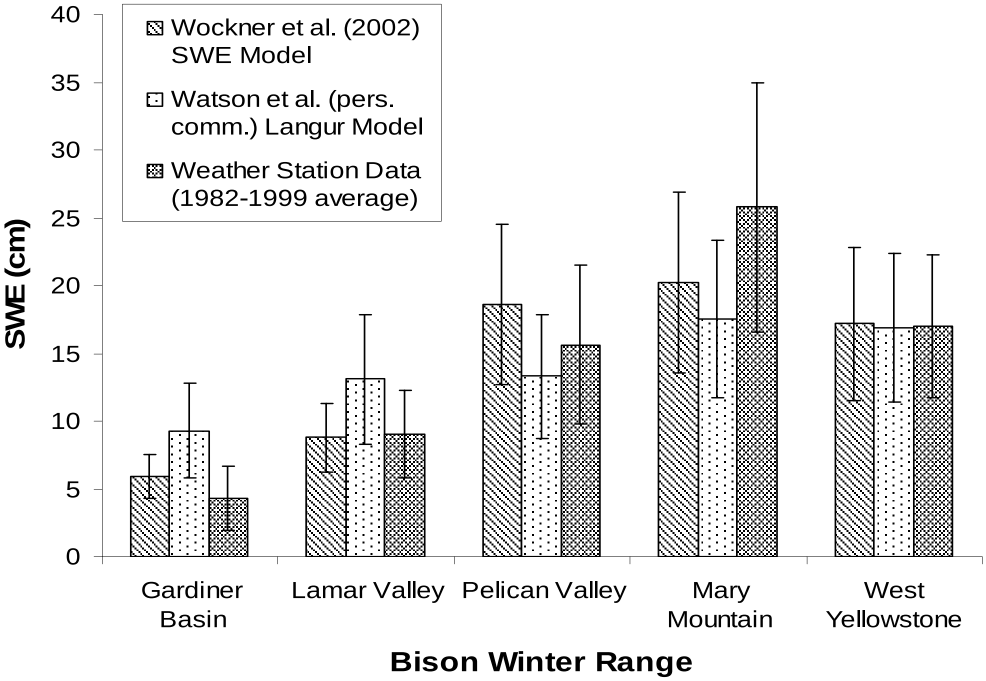


Figure 3.11**.** Mean + s.d. estimated and actual February 15th SWE values for each bison range from 1982-1999. Estimated values were derived from the Wockner et al. (2002) snow model and the Langur (Watson et al. pers. comm.) snow model. Actual data comes from weather stations in YNP. Mammoth CLIM station was used for Gardiner basin range, Tower Falls CLIM station was used for Lamar Valley range, Lake Yellowstone CLIM was used for Pelican Valley, Canyon SNOTEL station was used for Mary Mountain range and West Yellowstone SNOTEL station was used for West Yellowstone range.

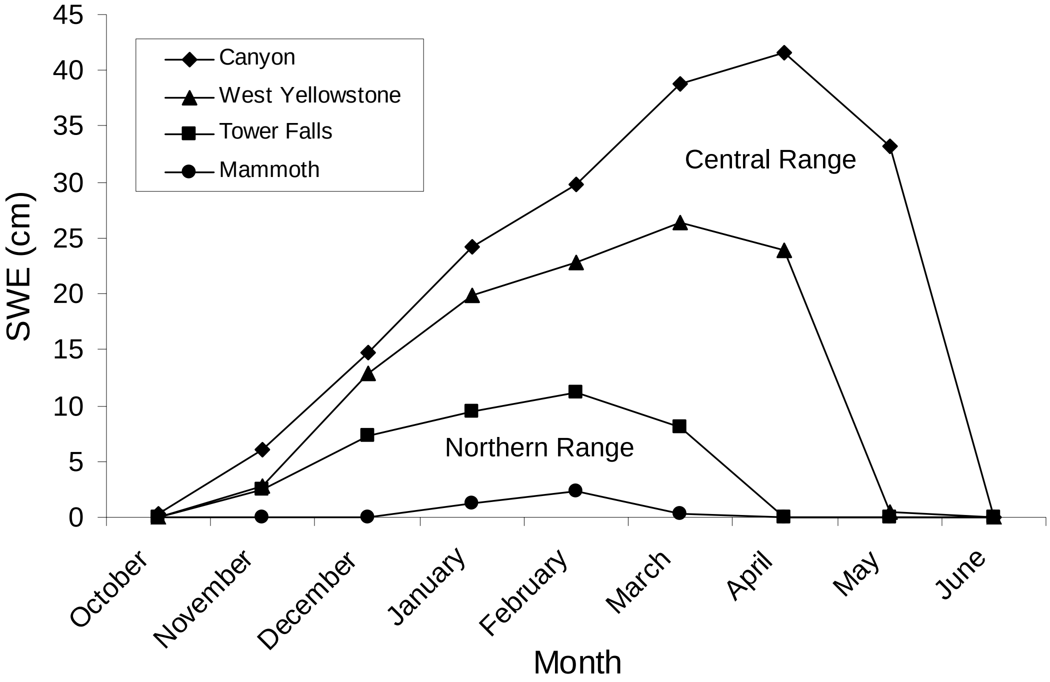


Figure 3.12. Mid-month (15th) SWE at selected climate stations in Yellowstone National Park in the winter of 1994-1995.

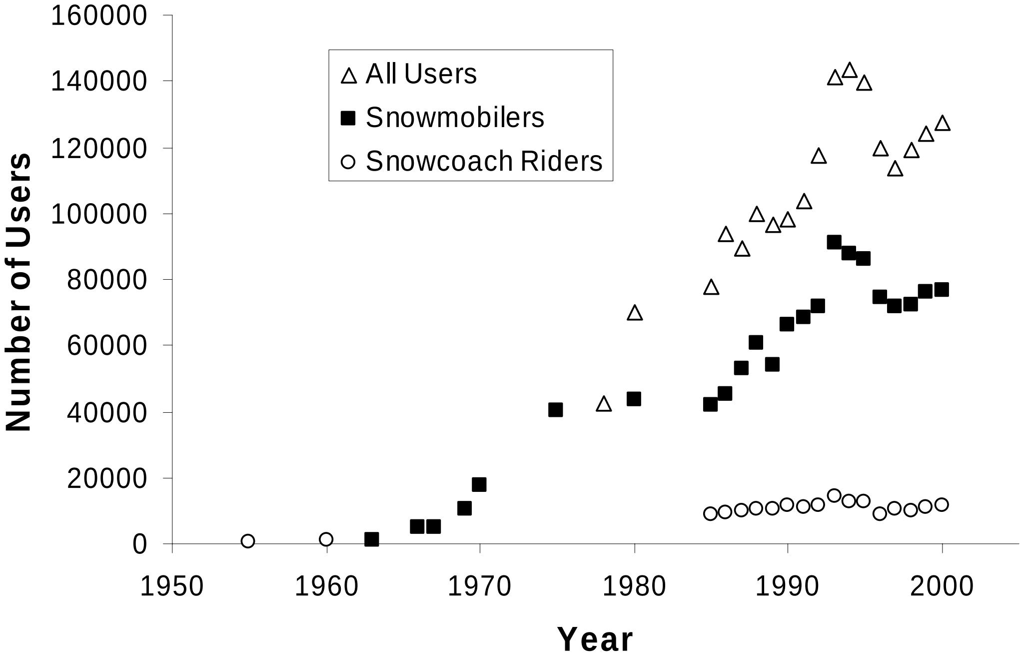


Figure 3.13. Number of winter users, snowmobilers and snowcoach riders entering YNP annually. Data from: USDI-NPS EIS (2000), Greater Yellowstone Winter Visitor Use Management Working Group (1999), Yochim (1998*a*), USDI-NPS (1990), and Snowmobile Briefing Books (1976 to 1978).

# 4

# HISTORY OF BISON MANAGEMENT IN YELLOWSTONE NATIONAL PARK

## Yellowstone Bison in Prehistory

Bison were continuously distributed from eastern Beringia southward into central North America during the interstadial period before the Last Glacial Maximum (LGM, ca. 22 to 18 ky b.p.) (Shapiro et al 2004). The subsequent formation of the Laurentide (eastern) and Cordilleran (western) ice sheets created a barrier to north-south faunal exchange. The formation of an ice free area between the continental ice sheets around 14,000 b.p. provided a corridor for bison to disperse southward and northward from the respective glacial refugia. Southward dispersal of Beringian bison was more limited than movement of southern bison into the corridor. Evidence of temporal overlap of the two clades of bison exists only in the Peace River area in northeastern British Columbia ca. 10, 500 b.p. (Shapiro et al 2004). Grassland habitat rapidly diminished in the north, giving way to coniferous forests (Catto et al. 1996) and peatlands (Halsey et al. 1998) around 11,000 to 10,000 b.p. In the north, bison habitat remained as riparian meadows associated with seasonal inundation plains along river courses and other water bodies (Gates et al. 1992). However, the vast expanse of unsuitable habitat represented a barrier to interchange between northern and southern bison during the Holocene.

Yellowstone National Park is the only place in the lower 48 States where bison have existed in a wild state since prehistoric times. Bison occupied the region encompassing the park from shortly after recession of the last glaciers 10,000 to 12,000 years ago, until the 19th century when they came close to extirpation. *Bison bison antiquus* is represented at early Holocene archaeological sites. The Horner archaeological site southwest of Cody Wyoming yielded a date for a *B. b. antiquus* specimen of 10,000-11,000 b.p. (Frison and Todd 1987). The earliest date (8,000 b.p) for bison bones at an archaeological site north of Yellowstone National Park was obtained for the Meyers-Hindeman site south of Livingston (Lahren 1976). Recent archaeological work in 2003 near Gardiner Montana on the Yellowstone River (site 24YE353) yielded a radiocarbon date of 9,400 b.p. (Cody Complex material). Other bison bones were found at the same level at this site in 2004[1]. A Windlust-type point was found at a site in the Hellroaring area with a date of 9,500 – 10,700 b.p. (site 48YE1025); a right proximal metacarpal bison bone was also found at the site. In the interior of the park, a Cody Complex chert knife, dated to 9,000 b.p., was found at a site (48YE410) on the shore of Yellowstone Lake. Organic residue on the artifact, either blood or sinew, was determined to be of bovid origin (Cannon and Newman 1994). A corner-notched point found at an archaeological site near Tower Junction was 2,000-3,000 years old (Aaberg 1996: 48YE215). Materials at another nearby site were estimated to be 900 to 1,000 years old. Neonatal bison bones were found

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[1] Interview with Ann Johnson, 28 July 2004.

at an archaeological site near the old Buffalo Ranch in the Lamar Valley; the site was dated at 400 to 500 years old (Sanders et al. 1997: 48YE168). Dates for bison bones sampled at the Meyers-Hindeman site south of Livingston ranged from 8,000 b.p. to 700 b.p. (Lahren 1976). In combination, archaeological evidence indicates a continuous association between bison and Native peoples in the Yellowstone area enduring more than 10 millennia.

The Lamar Valley and the Yellowstone River Valley north of the park (Figure 4.1) to Livingston and beyond was an important area for bison and Native peoples throughout the Holocene. This system can be considered the original Northern Range for Yellowstone bison[2], functioning as an ecological continuum of grasslands that likely supported seasonal migrations by bison as far south as the high elevation ranges in the Upper Lamar Valley. Davis and Zeier (1978:224) described the lower Yellowstone Valley as an exceptional area for Native people to gather, drive and kill bison. Eight bison jumps and three kill sites have been documented south of Livingston. The closest jump site to YNP is 25 km north of the park boundary. It was used during the late prehistoric period between 1,700 and 200 b.p. (Cannon 1992). There is evidence of a human use corridor from the Gallatin and Madison River drainages into the interior Yellowstone National Park. Several major bison kill sites are located in the Gallatin Valley outside of Bozeman Montana[3]. Archaeological sites in Fawn Pass provide evidence in support of the hypothesis that Native people moved between the Gallatin drainage and the interior of the park[4]. Chert and obsidian projectile points were found at the Fawn Pass site. The chert implements likely originated west of the park. The obsidian is being fingerprinted to determine its origin. Approximately half the projectile points were the Pelican Lake type, the most commonly represented prehistoric culture in YNP, dating from 1000 B.C. to A.D. 200. Other points were assigned to the McKean Complex, dating to around 3500 B.C. McKeean Complex sites are also quite common in the park. There is an obsidian source at Cougar meadows in west central Yellowstone Park. The material is inferior to the Obsidian Cliff source and was only used for making utility implements like knives and scrapers rather than projectile points. An obsidian artifact found at Yellowstone Lake was determined to be Cougar Creek Obsidian.

Based on the temporal frequency of dated archaeological sites and materials, it appears use of Yellowstone Park by prehistoric peoples increased over time from the early Holocene, reaching a peak between 3,000 and 1,500 b.p.[5] Thereafter, the abundance of dated archaeological materials diminishes, particularly during 600 to 400 years b.p. This period coincides in part with the Little Ice Age (ca. 1450 to 1850 A.D.) during which the severe climate of the park may have deterred human use, except for forays by work parties to acquire resources such as bighorn sheep and obsidian that were not available at lower elevations. Reduced use of the park during the Little Ice Age may also be attributable to a diminished wildlife population, which may have also been a response to severe winter conditions.

Europeans arrived in North America in 1492, bringing with them two significant forces of change for the aboriginal population and for bison: novel pathogens and horses.

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[2] Interview with Mary Meagher, 15 July 2004.

[3] Interview with Ann Johnson, 28 July 2004.

[4] Email from Ann Johnson, 5 September 2004.

[5] *Supra* note 4.

Smallpox, influenza, whooping cough, measles, and the common cold caused devastating epidemics that vastly reduced the immunologically naive indigenous human population (Crosby 1986). Before the arrival of the horse, the abundant bison population of the Great Plains provided part of the subsistence needs of both nomadic cultures living in the grasslands and village-dwelling Indians that migrated seasonally from nearby regions to hunt bison on foot (Isenberg 2000). Resource use was diverse for both traditions, involving gathering a variety food plants, pedestrian hunting of several wildlife species, and crop production in the case of village Indians in regions adjacent to the grasslands (Holder 1970, White 1983). The diversity of resources used and associated land use practices buffered these peoples from drought, fluctuations in wildlife abundance, and reduced the likelihood of overexploitation of resources (Isenberg 2000). Drought, the introduction of horses, and the emergence of a commercial market for wildlife products following European settlement changed the original economies of the Great Plains and contributed to the near extinction of the bison (Isenberg 2000:27, Flores 1996:16).

Horses did not reach the plains until the late seventeenth century, nearly 200 years after they were reintroduced by the Spanish. In the opening years of the 17th century, the Spanish in Mexico attempted to colonize Pueblo Indians in what is now New Mexico. In 1680, the Indians rebelled against oppressive treatment, forced about 2,000 Spaniards to flee, and seized their livestock (Spicer 1962 cited by Isenberg 2000). The ensuing intertribal trade in horses resulted in their rapid spread throughout the plains, reaching northern plains tribes by the 1730s to 1750s. Feral horses reestablished free ranging populations in the former grazing niche of the species. Flores (1996) estimated two million horses roamed below the Arkansas River and others ranged further north, competing with bison for forage. The Great Plains were opened to direct trade with Europeans beginning with the villages along the Missouri River in 1738 (Wood and Thiessen 1985). Located along the Missouri River in present day North Dakota, the Mandan/Hidatsa Indians traded horses, robes and furs to Canadian Fur Companies in return for guns and ammunition. In turn, they traded these goods for other commodities from various Northern Plains Indian Tribes, resulting in a technological revolution on the Great Plains. Beginning in about 1820, Euroamericans established a trade in native-tanned bison hides, soft pliable robes with the hair on. So began an insatiable demand for bison robes in the developed eastern United States and central Canada. By 1825, 25,000 robes were moved to market down the Missouri River. This increased to 85,000 to 100,000 raw hides traded annually at St Louis by the 1840s. Flores (1996) cites an unpublished reference by D. Wishart stating that the Hudson Bay Company trade reached a zenith of 73,278 robes traded in Canada between 1841 and 1845. By the time Euroamerican hide hunters arrived to engage in market hunting plains bison for their skins in the 1850s, the robe trade had been in place for a quarter of a century. Thereafter the extirpation of bison rapidly accelerated to near final conclusion in the mid 1880s. Bison were extirpated from the Snake River plains in Idaho by 1838 (Hornaday 1889). In 1880 the northern plains herd was estimated at 1.5 million animals; Euroamerican commercial hunters secured about 320,000 hides that year. The Blackfeet took 100,000 to 150,000 in 1881 and last hunted bison in 1883 when they took only six (Flores 1996). The last bison were extirpated from the prairies north and east of the Absaroka Mountains surrounding Yellowstone National Park by 1883 (Hornaday 1889). The last wild bison in

Wyoming outside of YNP was killed in 1889 (Blair 1987:27, cited by P. Schullery[6]). So it was that a population of about 30,000,000 or so plains bison present when Columbus arrived on the continent in 1492 (Shaw 1995) was reduced to near extinction at the close of the 19th century, the victim of a brief spasm of commercial exploitation.

Yellowstone National Park is the 8,983 km$^2$ center piece (Figure 4.1) of a large high elevation plateau, a caldera formed by volcanic eruptions, the most recent occurring 630,000 years ago (Smith and Siegel 2000). About 80% of the Yellowstone Plateau is covered by lodgepole pine forest (Despain 1990). Bison habitat (grasslands and meadows) occurs mainly in the Gardiner basin, Lamar River drainage, the Firehole, West Yellowstone to Hebgen Lake, and the Pelican, Hayden, upper Yellowstone River (Thorofare), and Bechler River Valleys (Figure 4.3). The combined area of winter forage producing communities on the Northern and Central ranges is less than 700 km$^2$, or less than 7% of the park and boundary areas used by bison today. In contrast, throughout most of the Holocene the extensive grasslands of the Great Plains, the eastern Columbia River Basin and intermountain grasslands of the Madison, Gallatin and Yellowstone River Valleys were the main grazing systems supporting an immense bison population that may have numbered 30,000,000 during pre-Columbian times (Shaw 1995, Isenberg 2000).

Prehistorically, YNP bison ranges were probably the "tips of the fingers" of seasonal migration from large source populations associated with expansive grasslands (Figure 4.1) lying to the north, west and southwest around the Yellowstone Plateau[7]. The high mountains on the east side of YNP and discontinuous habitat would likely not have supported bison migration. Historical accounts indicate that interior ranges also supported resident bison populations (Meagher 1973: Appendix II). Today, the bison of YNP are a source population with the potential to reoccupy surrounding grasslands systems if incompatible land uses and policies did not constrain expansion. There are no free-roaming bison populations in adjacent areas containing habitat contiguous with the park. The closest contemporary population is in the Jackson Valley, separated from YNP bison ranges by the Continental Divide and an expansive tract of coniferous forest.

Although the exact nature of early historic period bison movements is a matter of conjecture, inferences can be drawn from knowledge of contemporary movement patterns and archaeological evidence. Mary Meagher[8] inferred that prehistorically, during the spring and early summer, bison would have moved into YNP following advancing plant phenology. Depending on snow conditions in the park, most would have moved out to lower elevation ranges during the fall and early winter. However, Meagher (1973:23) provided evidence that some bison wintered in the park in the Lamar, Pelican and Hayden Valleys.

What is now considered the Northern Range (Klein et al. 2002) used to extend from the Upper Lamar Valley to Livingston Montana and beyond. This larger area is considered the prehistoric annual range of northern herd, occupied continuously by bison for ca. 10,000 years. There are a dozen or so buffalo jumps documented between

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[6] Draft manuscript provided by Paul Schullery: Schullery, P. and L. Whittlesey. Draft last revised 5-30-03. Greater Yellowstone bison distribution in the early historical period. This work, combined with Schullery and Whittlesey (1992) support, complement and expand on Meagher (1973), providing readers with the full geographical and historical context, and full citations unavailable in all earlier works.

[7] Interview with Mary Meagher, July 15, 2004.

[8] *Supra* note 7.

Yellowstone and Livingston, indicating the Yellowstone and Lamar Valleys were important for both bison and the original human occupants of the region.

The Gallatin and Madison Valleys and the Snake River Plain contain extensive grasslands that served as habitat for large numbers of bison (Figure 4.1), source populations for bison entering the park from the west. In 1880, Superintendent Norris commented on the presence of about 300 bison on the Madison Plateau and Madison River (Meagher 1973: 118). He speculated that the winter range of this population may have been outside the park. M. Meagher[9] inferred that bison would have migrated into the park from the west in the spring and summer by several routes: the chain of wet meadows along the Bechler River in the southwest corner of the park; diffuse movements across the Madison Plateau; and through Raynolds Pass and other low passes in the Continental Divide west of the Park. There is little available evidence for or against the possible use of the Madison River corridor during prehistoric or the early historic period. Meagher (1973:23) cites Raynolds (1867) who in 1860 saw “bison among the hills” while traveling from Henry’s Lake to the Madison River west of the park. Bison were present in this corridor in the 1950’s (Meagher 1973:23) and the corridor is heavily used by contemporary bison (Bjornlie and Garrott 2001).

A bison movement corridor (trail) across the Mirror Plateau was mapped by Superintendent Norris in 1880 (cited by Meagher 1973:25). Then as at the present time, the high country grasslands of the Mirror Plateau and upper Lamar drainage in the western slopes of the Absarokas were used as summer range. Bison left these areas to winter in the Lamar Valley south of Soda Butte Creek and in the Pelican Valley. Similarly, Mary Mountain trail connecting the Hayden Valley and the Firehole was recorded as an historic migration pathway (Meagher 1973:25).

M. Meagher[10] inferred although there are passes through the Absaroka Mountains along the northern and eastern boundaries of YNP there was likely little bison migration through them historically. The high elevation passes are characterized by steep terrain with little or no habitat for bison. The only documented contemporary movements of bison through the Absarokas occurs through Sylvan Pass where a few bulls move east of YNP to low elevation range in the North Fork of the Shoshone River basin in late summer/fall through the winter, then return to YNP for the summer where they participate in the rut[11]. R. Wallen[12] referred to a conversation with a long time Wyoming Game and Fish Department game warden, who told him that adult male bison periodically end up in the Sunlight Creek Basin in the Shohone National Forest east of Cache Creek ridge. When found, the bulls were shot to eliminate the risk of transmission of brucellosis to cattle in Wyoming.

Meagher (1973: 24) did not report any evidence of bison moving through the Sylvan Pass when the YNP population was small. Similarly, there is little historical evidence that bison used Two Ocean Pass to move over the Continental Divide, which separates grasslands in Teton National Forest from extensive meadows in the Thorofare area of the Upper Yellowstone River. Meagher (1973) referred to a bison skull found on Two Ocean

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[9] *Supra* note 7.

[10] *Supra* note 7.

[11] Interview with R. Wallen, 23 July 2004.

[12] Email correspondence from R. Wallen, 29 March 2005.

Pass before 1925 (Fryxell 1926, cited by Meagher 1973). Snow is extremely deep in this high elevation pass of the Continental Divide.

The Bechler Meadows area in the southwest corner of the park (Figure 4.3) is characterized by very deep snow in winter (Meagher and Houston 1998:222) and high water in the meadows during the spring[13]. Meagher (1973:23, Fig. 11) illustrated the Bechler area as an historical migration corridor for bison spending summer in the interior of the park and returning to winter ranges on the Snake River Plains.

## Yellowstone Bison in the Historic Period

Beginning prior to the establishment of Yellowstone National Park, then throughout its history, park wildlife management has changed with prevailing scientific theory, shifting cultural expectations, competition between ambitious people and agencies, varying levels of public involvement, and economic interests in the park and surrounding communities (Pritchard 1999).

### *The Early Historic Era 1840 to 1902*

By 1840 intermountain bison populations were disappearing, a consequence of unregulated hunting. However, bison remained common in the Lamar and Yellowstone Valleys late into the 19th century. Meagher (1973) quotes an archival record (Potter 1962) of an observation made in 1867 for the Gardiner basin near Yankee Jim Canyon: “that whole flat would be covered with buffalo”. Schullery and Whittlesey (1992) also reviewed the interview with Lena Potter and did not think that the context was clear enough to assign a single year date to the report, inferring that the year could have been anytime between 1867 and 1878. In June of 1870 Bart Henderson recorded seeing “thousands of buffalo quietly grazing” on a flat near Hell Roaring Creek (Meagher 1973: 116). This quotation is controversial; Schullery and Whittlesey (1992: 1.38-1.51) inferred from a comment by Henderson’s travel partner, James A. Gourley, that hardly any bison survived in or near YNP.

Meagher (1973:118) cites the YNP Superintendent’s report of 1880 in which the distribution and abundance of bison in YNP was described for three areas of the park. About 200 bison summered in the Lamar Valley, described as “the valleys of the Crevice, Hellroaring, and Slough Creeks and the mountain spurs between them”. With the arrival of snow they moved to the “grassy valleys of the East Fork of the Yellowstone [Lamar] and Soda Butte”. A second herd of over 100 bison “summer in the elevated and abruptly broken, little known section of the Park, extending from the Hoodoo region to the Grand Canyon, and from Amethyst Mountain to Pelican Creek, near the foot of the Yellowstone Lake, and winter occasionally upon the East Fork [Lamar] of the Yellowstone and on Pelican Creek”. The Superintendent described a third herd numbering about 300 ranging in small groups on the Madison Plateau and along the “Little Madison River”. A further comment made by the Superintendent that this herd probably wintered on the Pacific side of the Continental Divide “and if so, they are not permanent occupants of the Park, and are therefore likely to be slaughtered by advancing settlers”. This comment reflected the pressure on large herbivore populations from

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[13] *Supra* note 11.

unrestricted hunting outside the park. Poaching was also a serious problem within the park boundaries.

Market hunters discovered abundant wildlife remained in the Yellowstone Valley Northern Range. Although the 1872 act establishing Yellowstone National Park outlawed hunting “for the purposes of merchandise or profit”, subsistence and sport hunting was still allowed. Hunters and poachers continued to kill bison and other big game in large numbers inside the park. Among them the Bottler brothers, who had settled about 50 km north of the park, participated in a profit-driven slaughter in 1874 - 1875 that Superintendent Norris claimed to have resulted in the taking of four thousand elk and large numbers of bighorn sheep, deer, antelope, moose, and bison, killed mostly for their tongues and hides. The kill was noted by George Bird Grinnell who accompanied the Colonel William Ludlow expedition to Yellowstone Park in 1875. His report expressed outrage against the slaughter. He initiated intense lobbying to protect wildlife remaining in the park and in so doing set the stage for public discourse on what a national park should represent. As editor (1876-1911) of the popular outdoors magazine *Forest and Stream*, he engaged in an editorial campaign to shape the purpose of Yellowstone National Park and to encourage a rational system of administration and management. George Bird Grinnell was also the founder of the Audubon Society and an organizer of the New York Zoological Society.

In 1880, the Secretary of the Interior (Carl Schurz) called for hunting to be outlawed in the park. General Philip H. Sheridan visited the park in the summer of 1882. He subsequently urged Congress to expand the park's northern boundary to prevent the slaughter of game (Haines 1997, Vol I: 252). In 1883, the new Secretary of the Interior (Henry Moore Teller) outlawed hunting for sport or subsistence, as well as continuing a ban on market hunting (Schullery 1997). Despite growing public concern over excessive hunting and declining numbers of bison, poachers based from Henry’s Lake and Cooke City continued to operate in YNP[14].

Public pressure finally caused Congress to act in 1886. It assigned the U.S. Army to establish a command in the park to protect wildlife and geothermal features. Although the presence of the army reduced poaching, penalties were weak and were an inadequate deterrent. A new regional market for bison heads (scalps) had developed. Poachers travelled on skis into the park to take bison remaining on the Madison Plateau, in the Firehole, and as far east as the Pelican Valley. It took a well publicized incident in 1894 to precipitate a more substantial congressional mandate to enforce anti-poaching laws. That year army troops caught poacher Edgar Howell after he shot five bison near Pelican Creek. This flagrant violation of the law added pressure to enact more substantial legislation to protect wildlife. As Scout Felix Burgess and Sergeant Troike escorted Edgar Howell to the guardhouse at Fort Yellowstone, they happened upon the "Yellowstone National Park Game Expedition." Emerson Hough, a member of the expedition, promptly wrote an article for *Forest and Stream* magazine about poaching in YNP. George Bird Grinnell, by then a prominent conservationist and editor of the magazine, persuaded members of Congress of the serious threat to wildlife in the park. On March 26, 1894, Representative John Lacey of Iowa introduced H.R. 6442, "An act to protect the birds and animals in Yellowstone National Park, and to punish crimes in said park". President Grover Cleveland signed the bill into law on May 7, 1894. The 1894

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[14] Interview with Mary Meagher, 15 July 2004

wildlife protection law gave sole jurisdiction over wildlife in Yellowstone to the federal government and prescribed fines of up to $1,000. Lacey introduced more general legislation to the House of Representatives in the spring of 1900. The Lacey Act, passed into law by President William McKinley on May 25 that year, prohibited trade in wildlife, fish and plants that have been illegally taken, possessed, transported or sold.

Despite increased protection, the park bison herd continued to dwindle in the closing years of the 19th century. In 1894, Edgar Hough, representing the publisher of *Field and Stream* Magazine, estimated that only 150 remained in the park. According to Albright (1925:3), Hough saw “85 to 100 wild bison in Hayden Valley and on Mary Mountain”. In 1902 the Superintendent estimated only 22 bison remained in remote Pelican Valley (Albright 1925).

Concerned about saving some of the few animals remaining in the park, in 1895 the Smithsonian Institution recommended construction of an enclosure in the interior for native park bison (Schullery 1976, Haines 1977 Vol II). A fenced pasture was constructed on Alum Creek in the Hayden Valley to capture bison. Baiting failed to attract any into the enclosure and the effort was abandoned. Subsequently, in 1901, Acting Superintendent Captain John Pitcher asked Congress for money to buy bison that would be kept in a fenced enclosure in the park. Fifteen thousand dollars was appropriated for the purpose. C. J. Jones, also known as "Buffalo Jones," had developed a reputation as an expert on buffalo by capturing calves from a remnant herd in Colorado. He offered his services to the Secretary of the Interior, arriving in the park in 1902. Jones established a captive herd near Mammoth Hot Springs that included three bulls from the Goodnight herd of Texas and eighteen cows from Conrad Allard's herd in western Montana. Jones ended up at odds with Superintendent Pitcher and resigned in September 1905. The captive bison herd grew and the operation was moved to Rose Creek in the central Lamar Valley. This site became known as the ‘Buffalo Ranch’, where Lamar herd was managed until 1952.

The 21 bison imported from Montana and Texas and an indigenous population of approximately 22 animals in the Pelican Valley represented the founders of today’s Yellowstone bison population.

### *The Bison Protection, Ranching, and Range Management Eras: 1902-1968*

Between 1907 and 1912, the imported captive herd was maintained in fenced pastures in the Rose Creek facility in the Lamar Valley. Activities at the ranch included irrigation, growing and feeding hay, roundups, culling, castration, and predator control. In 1913, the bison were released to graze freely in the surrounding areas during the day and brought back in at night. By 1915, the herd had increased to 259. Starting in 1915, bison were herded up the Lamar Valley to high elevation summer pastures then back again in the fall. This was done to reduce grazing pressure on the ranch during the summer. Seasonal herding was practiced until about 1930. In the early 1920s, a substantial log fence was built across the upper Lamar Valley to keep bison from returning prematurely to the hay fields. As the Lamar herd expanded its summer range, it mingled with the wild herd moving into the high country of the upper Lamar Valley from Pelican Valley. After 1932, there was no attempt to keep the two herds separate. They mixed with the wild herd in the high country summer range. In an internal report dated January 17, 1934, Chief Ranger G. F. Baggley commented:

> "The buffalo range during the grazing season from Junction Butte to Cache, Calfee, and Miller Creeks on the east to the head of the Lamar River on the south and Cold Creek on the west, also to some extent over the east part of the Mirror Plateau. In short, they occupy a considerable part of the Lamar River drainage, with a few getting over into Pelican Creek."

Early herding practices may explain much of the seasonal migration patterns observed in the Lamar bison population at the present time. The historical herding of bison into and out of seasonal habitats (winter and summer) was conducted to manage the distribution of bison in the park[15]. Although the Lamar herd was essentially wild by 1930, it was still fed hay during the winter months, a practice continued until 1952. Albright (1944:8) offered the following reason for winter feeding:

> "... the Lamar River herd if not fed in periods of deep snow or under blizzard storm conditions will move down the valley and out of the park into towns and farms and in such drifts there is always the possibility of excessive losses of bison as well as great property damage by the restless hungry animals".

Cahalane (1944*a*) explained that when the park was established the boundary in the Gardiner basin was set to protect geophysical resources, hot springs and high mountain scenery. Lowlands in the Gardiner basin with agricultural potential had been excluded from the park, and with them, low elevation grasslands lying in a snow shadow that would otherwise serve as critical winter range for bison. Cahalane (1944*a*) argued for expanding the boundary to take in the Gardiner basin north to Yankee Jim Canyon. This was was done.

Neither subject to winter deprivation nor to predation the Lamar herd grew rapidly, reaching approximately 1100 by 1930 (Meagher 1973). The mean rate of population increase (r) between 1902 and 1930 (adjusted for removals) was 0.19 ± 0.09 (s.d.) (data source Meagher 1973: Appendix IV). The Park Service began culling to limit the size of the Lamar herd in 1919, but population objectives were not defined until the early 1930s. Authority for the sale or disposition of surplus bison was granted in the Appropriation Act of 1923. 737 bison were removed from the northern herd between 1919 and 1931 at an average rate of 56/yr. A policy developed in 1932 stipulated that ungulate populations in the park would be managed within the carrying capacity of the range by limiting their numbers[16]. The "average winter carrying capacity" on the northern range was calculated as 7,059 elk and 245 bison (Grimm 1939). Reductions increased during 1932 to 1936 during which time 979 bison were removed at an annual rate of 196/yr. In 1937, 488 bison remained on the northern range.

In 1942, the Director of the Park Service, Newton Drury, ordered a reduction of the Lamar herd; 193 bison were culled and 17 shipped from the park. The winter of 1943 was

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[15] Interview with Keith Aune, 22 July 2004.

[16] Wayne B. Alcorn, "History of the bison in Yellowstone National Park", Supp. 1942-1951, cited by Franke *in press*.

harsh and despite reduction in the previous year, 160 bison moved down the valley and exited the northern boundary of the park. Cahalane (1944*b*) recorded that some of them traveled 50 km north to Carbella Flats and another was reported on a ranch 80 km from the park. He also reported 150 bison were observed in summer 1943 at Lake Abundance near the northeast corner of the park. Despite subsequent reductions of the northern herd (Figure 4.4), 68 of 313 bison on the Northern Range moved north of the park boundary into the Gardiner basin during the mild winter of 1948. Bison also exited the park in 1953 when a group wandered across the northern boundary of the park (Franke *in press*). The State of Montana authorized a hunt that year; three bison were taken. A second hunt was held in Montana 1954.

Mixed groups of bison (cows and juveniles) had not been seen in the Hayden Valley after 1895. In 1936, 71 bison were rounded up on the Northern Range and trucked to the Hayden Valley and Fountain Flats in the Firehole (Figure 4.3); about half of them were released in each area. Park Superintendent Edmund Burrell Rogers explained "This was done in an attempt to scatter the herd over a wider range and provide more opportunity for park visitors to see buffalo running free and wild" (Superintendent E. B. Rogers cited by Franke *in press*).

Before the translocation of bison to central YNP, there were two wintering populations, one in Lamar Valley and the other in the Pelican Valley (Meagher 1973: 31). While the Lamar herd originated from stock imported from captive herds in Montana and Texas (Chapter 4), the Pelican herd was indigenous. With effective protection, but no winter feeding and little management interference, the Pelican herd increased at an annual exponential rate of 0.056 between 1902 and 1954 reaching 461 that winter (Figure 4.5). The bison translocated to the Hayden Valley and the Firehole increased more rapidly than the Pelican herd ($r = 0.156$), reaching 858 by 1954 (Figure 4.6). Meagher (1971, 1974) explained that winter conditions in the Pelican Valley are the harshest in the park. The lower rate of increase in the Pelican Valley compared to the Mary Mountain population likely reflects the harsher conditions and the differences in resource availability between these ranges. As the Hayden Valley and the Firehole populations increased, movements were soon established between the Hayden Valley and the Firehole through the Mary Mountain corridor (Meagher 1973:31). During the 1950s and 1960s more animals were observed in the Hayden Valley than in the Firehole.

After the reintroduction to the interior ranges in 1936, bison were seen with increasing frequency in other areas of the park. Meagher (1973:33) cited ranger reports of bison on the Madison Plateau beginning in 1939. Bison had been absent from the Bechler Meadows for three decades after the early 1900s. Cahalane (1944*b*:138) saw a single bull in the Bechler Meadows in winter 1936. Meagher (1973) reported 3 bulls were there in February 1955 and a mixed herd was observed in winter 1962-63, then again during the next two winters. Forty to 50 bison wintered at the Cougar meadows in 1955-56 and bison were seen there again in 1959. Bison were occasionally reported in peripheral locations. Cahalane (1944*b*) reported a sighting in September 1943 of three bulls near Jackson Hole WY. Albright (1944:8) added the following comment on this sighting "...but they returned to the park or perished for they were not in sight this year [1944]", indicating he thought they were Yellowstone Park bison. Another unconfirmed sighting was relayed to the authors of a bull seen about 1945 near Two Ocean Pass outside the southeast corner of YNP[17]. Schullery et al. (1998) reported that bison were observed moving beyond the boundaries of the park in 16 of 25 years from the early 1940s to 1967. Most of these movements occurred on the northern range.

Although removals to limit the size the Lamar herd began in 1919 and continued until the mid 1960s, it was not until the 1940s that attention was paid to the condition of bison ranges in central YNP. In 1939, the Department of the Interior issued a wildlife policy developed six years earlier in which it was recognized that ungulate populations would be kept within the carrying capacity of the range by limiting their size[18]. In 1943, the Director of the Park Service accepted a recommendation to maintain the northern range bison herd at 350 and the central population at 300. This objective remained in place until the mid 1960s. Sizeable reductions were carried out on the northern winter range about every second year; 1748 bison were removed from the northern range between 1944 and 1965 (Figure 4.4). In 1966, only 66 bison were counted in the Lamar Valley (Meagher 1973: 147).

Reductions were not implemented in the central ranges until the mid 1950s. However, the first significant loss recorded for the Mary Mountain herd was accidental. In February 1946, 38 bison plunged through the ice of the Yellowstone River (Beal 1950). Concerned about trampling damage by bison to geothermal features in the central park, and in keeping with the range management objectives established in the 1940s, the park administration began removals to reduce the central bison population beginning in 1954 (Figure 4.4).

Like bison, Yellowstone's northern range elk population was intensively managed to control population size in relation to perceived carrying capacity. In 1962, confronted with a public outcry against elk reductions on the northern range, the Secretary of the Interior appointed a panel of scientists under the direction of Starker Leopold to review elk population management. Published in 1963, the Leopold Report (Leopold et al. 1963) provided the impetus for a profound change in Park Service management policy. The Committee concluded:

> "As a primary goal, we would recommend that the biotic associations within each park be maintained, or where necessary recreated, as nearly as possible in the condition that prevailed when the area was first visited by the white man. A national park should represent a vignette of primitive America."

However, the report continued to call for managing ungulate populations at levels "that the range will carry in good health and without impairment to the soil, the vegetation, or to habitats of other animals". Recommended methods included natural predation, trapping and transplanting, shooting migrants outside the parks, shooting within the parks. Between 1964 and 1968, 1673 bison were removed from the central herds. Reductions were carried out in the Pelican Valley on two occasions only: 118 were removed in 1956 and 38 in 1965 (Meagher 1973:146,147). The remaining removals were from the Mary Mountain population. At the end of the range management era in 1968,

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[17] Interview with Steve Cain, 11 August 2004.

[18] Wayne B. Alcorn, "History of the bison in Yellowstone National Park", Supp. 1942-1951, cited by Franke, M.A. *in press*. To save the wild bison, draft 10/15/04, University of Oklahoma Press to be published in Fall 2005.

160 bison were counted in the Pelican winter range and 188 in the Mary Mountain range (Meagher 1973: 147).

In 1964, the Secretary of the Interior instructed the Park Service to manage parks "toward maintaining, and where necessary reestablishing indigenous species" while "preserving the total environment"[19]. In the same year the "1964-65 Bison and Habitat Management Plan[20] ...", Yellowstone National Park prescribed removing 63 (34%) animals from the Lamar herd, 94 (34%) from the Pelican Valley herd, and 335 (67%) from the "Hayden-Valley-Nez Perce-Firehole Bison Herd". The plan was defined as a "reduction and brucellosis control program" whose intention was to allow for "range improvement" and reducing the prevalence of *B. abortus* infection.

A significant policy shift away from intensive management occurred in 1968 when the National Park Service issued a policy prescribing that national parks should be managed as ecological entities[21] providing for restoration, protection, and maintenance of native complexes "where practicable, at levels determined through historical and ecological research of plant-animal relationships". With the cessation of population management, elk and bison populations subsequently began to increase within the park.

### *Ecological Management Era: 1968 - present*

Bison populations in the northern and central ranges increased dramatically during the three and a half decades after the end of the intensive management era in 1967, (Figure 4.4). The main influences on population growth were removals at the boundaries in the Gardiner basin and near West Yellowstone beginning in the mid 1980s, and natural mortality during a few harsh winters (Cheville et al. 1998, DelGuidice et al. 2001). The populations grew rapidly until the early 1980s. During the 20 year period between 1984 and 2004 the northern herd fluctuated between 300 and >1200 and the central range population varied between 1400 and >3300 (Figure 4.4). Ecological mechanisms influencing bison populations, range expansion, and migration to boundary ranges were evaluated by a National Research Council committee tasked with examining the epidemiology of brucellosis in bison, elk and other species, the potential for a wild animal vaccination program, and key factors for reducing the risk of transmission from wildlife to cattle (Cheville et al. 1998). Mechanisms of population ecology, movements and range expansion are explored in further detail in the next chapter of this report.

Since 1968, bison management in the YNP area has been dominated by two major linked controversies: 1) the risk of transmission of brucellosis to cattle on surrounding lands from bison moving across the boundary (Cheville et al. 1998); and 2) criticism of the effects of winter road grooming on bison population dynamics, movements and range expansion (Meagher 1993, Meagher et al. 2002). The evolution of these issues is reviewed below.

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[19] Memorandum from Secretary of the Interior, Stewart Udall, on Management of the National Park System to National Park Service Director, July 10, 1964, cited by Franke *in press*.

[20] YNP Bison Management Office, document entitled "Yellowstone National Park, Wyoming, 1964-65 BISON AND HABITAT MANAGEMENT PLAN FOR YELL...", recommended by John.S. McLaughlin, Superintendent, Yellowstone National Park, approved by Fred J. Novak, Acting Regional Director, Midwest Region.

[21] Administrative Policies for Natural Areas, 1968. Reprinted in America's National Park System: The Critical Documents, Lary M. Dilsaver (ed.). Rowman & Littlefield Publishers, 1994.

### *Brucellosis Management*

Brucellosis is primarily a disease of the reproductive organs caused by bacteria in the genus *Brucella*; the causative agent in bovids and elk is *B. abortus*. Pathology in bison includes abortion, endometritus, retained placenta, orchitis and joint inflammation (Tessaro 1989, Rhyan et al. 2001). The primary route of transmission is contact with oropharyngeal tissues of susceptible individuals by touching, licking or ingestion of contaminated fluids and tissues associated with abortion or birth (Cheville et al. 1998). The organism is not native to North America and was likely introduced with infected European cattle (Meagher and Meyer 1994, Whittlesey 1994-95). Brucellosis was first diagnosed in Yellowstone's northern bison herd in 1917 (Mohler 1917, cited by Tunnicliff and Marsh 1935). The most likely source of infection of Yellowstone bison was domestic cattle. After 1915, bison were pastured with cattle near the Lamar Valley ranch providing the opportunity for transmission from infected cattle to bison. Bovine brucellosis is a zoonosis; it is a regulated disease because of its ability to infect humans. A national program to eradicate the disease from cattle was established by the U.S. Department of Agriculture in 1934. Since then, several billion dollars in federal, state and private funds have been spent on the program. The Animal Plant Health Inspection Service of USDA certifies states as brucellosis-free, class A, B, or C, depending on the frequency of occurrence of infected cattle herds in the state. The State of Montana worked aggressively to eradicate brucellosis from its cattle herds beginning in 1952. It attained brucellosis free status in 1985 after an expenditure of more than $30 million by the industry[22].

YNP was engaged with the U.S. Department of Agriculture on brucellosis testing and management in the bison herd since the early days of the national brucellosis eradication program[23]. Activities were limited to testing bison until the 1940s when it was expanded to include calfhood vaccination and slaughter of reactors in the Lamar herd. The program ceased when the ranching operation was abandoned in 1952. Testing was carried out again in 1961-62, when 143 were removed from the Lamar herd, then again in 1964-65 when some bison in the Mary Mountain herd were rounded up by helicopter. Brucellosis testing and herd reductions were not conducted in the park after the winter of 1965-66[24].

In 1967, State veterinarians from Montana, Idaho, and Wyoming expressed concern to the Department of the Interior about the potential for the YNP bison population to increase in the absence of reductions in the park, leading to greater numbers moving into surrounding areas where cattle were grazed[25]. YNP instituted a boundary control program the next year. Park personnel were authorized to shoot bison approaching the boundary in the Gardiner basin and near West Yellowstone. Only five bison were killed [by park personnel] under this program; park rangers shot three bulls in 1974 and one cow and one bull in 1978 (Meagher 1989*a*). Control actions were also undertaken by the State of Montana. The winter of 1975/1976 was harsh. Early winter storms interspersed with

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[22] Montana Department of Livestock web site: www.discoveringmontana.com/liv/animalhealth/bison/BRUCEINFO//bsnisu3.asp

[23] Barmore, W.J. 1968. Bison and brucellosis in Yellowstone Natonal Park: A problem analysis. Internal report. Yellowstone National Park Archives.

[24] Ibid.

[25] Montana Department of Livestock, *supra* note 21.

thaws locked up the northern range under a layer of ice. In January 1976, eight bison exited the park near Gardiner. They were killed by Montana State personnel[26]. A few weeks later, 84 bison were seen moving downstream along the Yellowstone River toward the northern boundary. The movement was viewed unlikely to be repeated, so managers decided to prevent the animals from leaving the park with drift fences and hazing rather than shooting such a large number (Meagher 1989*a*). In 1978, the Secretary of the Interior rescinded authorization for park personnel to shoot bison in the park.

Annual use of the Mammoth-Gardiner area by bison continued to increase after 1976. Mixed herds began to cross the boundary at Reese Creek in winter 1982-83 (Meagher 1989*b*). About 250 bison foraged in the Gardiner area in the winters of 1985-1986 and 1986-1987. Unable to use lethal methods to prevent bison from exiting the park, YNP managers decided to evaluate non-lethal techniques including ground-based (on foot or horseback) and aerial hazing, noise makers, tape-recorded wolf howls, barrier fences, cattle guards on roads, aversive conditioning (bird shot and rubber bullets), baiting with hay and scattering charcoal to increase snow melt (Meagher 1989*a*). Although some methods temporarily deterred bison, no method or combination proved effective in attenuating the drive by bison to use boundary areas with which they had recently become familiar. During the winter of 1984-1985 Montana State personnel removed 88 bison that wandered beyond the northern boundary. The Montana State legislature designated bison as a game animal and authorized a hunting season; 57 bison were taken in the Reese Creek area near the YNP north boundary in winter 1985-1986. In protest, the Fund for Animals sued the National Park Service for allowing bison to move into Montana where they could be killed; the Fund lost the suit (Cromley 2002). Authorized public hunting continued in Montana until 1991 when the Montana State legislature rescinded the authority for a hunting season in response to a strong national outcry against hunting bison exiting the park. Hunters had taken approximately 675 bison on lands adjacent to the park during the intervening six year period while hunting was permitted[27]. Thereafter, agency officials were tasked with removing bison wandering out of the park.

Interagency planning to address bison management in YNP and adjacent Montana began in 1985. This first effort failed because of conflicting agency mandates (Cromley 2002). By 1989, state and federal agencies recognized that conflicts could best be reconciled by coordinated development of a joint bison management plan. So began an eleven year effort among agencies at two levels of government that culminated with a Record of Decision dated December 20, 2000 (U.S. Department of the Interior and U.S. Department of Agriculture 2000). The cooperating agencies included the Department of the Interior (National Park Service), the U.S. Department of Agriculture (Forest Service and Animal and Plant Health Inspection Service), and the State of Montana (Department of Livestock and Department of Fish, Wildlife, and Parks).

In 1989, the State of Montana entered into an agreement with the NPS and the USDA Forest Service to develop a long term management plan and a requisite EIS for actions to manage bison migrating from the park into Montana. Montana required a plan that provided for protection of property, human safety, and the state’s brucellosis class-free

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[26] Franke, M.A. *in press*. To save the wild bison, draft 10/15/04. To be published by the University of Oklahoma Press in Fall 2005..

[27] Montana Department of Livestock, *supra* note 21.

status. NPS completed an environmental assessment in 1990 providing for limited actions in and near the park including hazing and monitoring bison. Park personnel were allowed to participate in shooting bison outside the park boundaries under the authority of the Montana Department of Fish, Wildlife and Parks. Another similar environmental assessment was completed in 1992. Activities described in the 1990 and 1992 EAs have continued to the present.

In 1995, the State of Montana legislature changed the primary authority for managing bison originating in YNP from the Department of Fish, Wildlife and Parks (DFWP) to the Department of Livestock (DOL), an agency without experience in wildlife management whose mandate is "to protect the health and well-being of the livestock industry and economic well-being of ranchers". The move was seen as ascendancy of commercial agriculture (brucellosis-free status) over the value of bison as free-ranging wildlife (Cromley 2002). It also reflected tensions among and between state and federal agencies caused by substantial differences in mandates and institutional cultures. Under pressure from veterinarians from other states, APHIS threatened to revoke Montana's brucellosis-free status. Out of frustration, the State of Montana filed a complaint in U.S. federal court in January 1995 against the federal government, claiming Department of the Interior policies caused diseased and disease-exposed bison to enter Montana, and U.S. Department of Agriculture policies might result in revocation of its brucellosis class-free status because of the presence of diseased wild bison in the state.

A settlement agreement was reached in November 1995 in which the NPS and State of Montana agreed to prepare an environmental assessment for actions prescribed in Interim Bison Management Operating Procedures. Actions described in the settlement were: capture and removal of bison moving north of the park boundary at Reese Creek; construction of capture facilities at Stephen Creek inside the park; all bison captured at the facility would be sent to slaughter; bison moving outside the park at West Yellowstone would be captured in facilities outside the park; all testing positive for exposure to *B. abortus* and pregnant females would be shipped to slaughter; test negative bison would be marked and released; Bison moving into the areas north of the park in Eagle Creek/Bear Creek, Hellroaring Creek and Slough Creek drainages and those moving into the Lee Metcalf Wilderness and Cabin Creek Recreation and Wildlife Management area west of the Park would be monitored. The settlement agreement also established that the long term bison management plan and draft EIS would be completed by late 1996 and a final EIS would be due by May 1997. APHIS agreed not to downgrade Montana's brucellosis class-free status if it complied with the Interim Bison Management Procedures.

The 2000 Joint Management Plan was the product of mediated negotiations between federal and state agencies following a decision of the federal court that the federal agencies could terminate a 1992 Memorandum of Understanding (MOU); the 1992 MOU formalized terms of reference for interagency negotiations on completion of a long-term bison management plan. The federal agencies wanted to issue a final EIS without Montana, citing the State's "unreasonable objections" to a federal proposal to increase tolerance for bison outside of the Park (Cromley 2002:140). At the request of Judge Charles Lovell, who had presided over the 1995 settlement agreement directing the agencies, the agencies agreed to mediated negotiations. The mediation was informed by the draft and final environmental impact statements, public comments submitted on both documents, other relevant documents in the administrative record, and negotiations with the State of Montana.

The Final EIS was a product of the Department of the Interior (National Park Service) and the U.S. Department of Agriculture (U.S. Forest Service and Animal and Plant Health Inspection Service). The State of Montana issued a separate Final EIS under Montana law that incorporated the federal agencies' final EIS by reference. The Records of Decision committed the National Park Service, U.S. Forest Service, and Animal and Plant Health Inspection Service to manage the risk of transmission of brucellosis from bison to cattle, to conserve free-ranging bison, and to work with agencies of the State of Montana in implementing the "Joint Management Plan". The following are highlights of the three step plan (the reader is referred to the original document for details):

- The plan provides for actions in Yellowstone National Park, the Gallatin National Forest, and private lands on the north and west boundaries of Yellowstone National Park.
- The primary tool is the spatial and temporal separation of cattle and bison.
- The number of bison will be limited in the boundary areas in the Gardiner basin and near West Yellowstone.
- The intensity of management will increase as bison move toward the edges of management Zone 2 (zone nearest the park in Montana in each boundary area).
- In the spring the agencies will haze bison back into the park when snow and weather typically allow bison to move back into the interior of the park.
- If hazing is unsuccessful, bison that do not return to the park will be captured or shot.
- Capture, test, and slaughter of seropositive bison in the Reese Creek and West Yellowstone areas in steps one and two,
- Hazing, capture, test and slaughter operations, or quarantine of bison that remain outside the park in these areas after specified haze-back dates.
- Vaccination of bison and cattle (including remote delivery) will be used to reduce risk and to work toward the eventual elimination of brucellosis in bison. The delivery system and development of a safe and effective vaccine require further research.
- Untested bison will be allowed to occupy the Eagle Creek/Bear Creek area, Cabin Creek Recreation and Wildlife Management Area, and the Monument Mountain Unit of the Lee Metcalf Wilderness year-round without agency interference because these areas do not have cattle grazing within them or nearby.

Given the difficult and lengthy negotiations that culminated in a judicially mediated agreement defined in the 2000 Record of Decision, it would be difficult to argue that there is a high level of satisfaction among the agencies in the outcome, or that their interests were served. In a critical review of the decision process for bison management, Cromley (2002) pointed to fractured governance structures and a low level of public involvement as the factors accounting for the failure to securely represent the common interest in a long-term management policy for bison. It was apparent from interviews and workshops conducted by us in July, August and October 2005 that agency personnel continue to protect their specialized mandates and policies from interference by competing agencies, and the affected publics feel disenfranchised from the decision process because of the low level of involvement provided for through the EIS review process under NEPA rules, i.e. limited term public comment on documents filed in the Federal Register. Requirements for public involvement associated with preparation of environmental impact statements or their equivalents cause agencies to ask “What are the legal requirements for public involvement?” rather than “What level of public participation is needed to achieve our objectives?” (Creighton 1999).

Optimism was expressed that working relationships between agency representatives on the Greater Yellowstone Interagency Brucellosis Committee (GYIBC) have gradually improved over the 14 year history of that committee[28]. However, the mission of the GYIBC is limited “to facilitate the development and implementation of brucellosis management plans for elk and bison in the GYA” and its main activities are focused on research on brucellosis epidemiology, pathobiology and on disease risk management, not on bison conservation. The GYIBC primarily serves the function of coordinating information on brucellosis research and keeping members agencies informed of the activities of other agencies[29]. Cromley (2002:146) claimed the GYIBC excludes representatives of the public from the committee because the Federal Advisory Committee Act prohibits public representation. The public may attend meetings but is restricted to providing comment during a designated time at the end of the agenda and is not allowed to participate in deliberations of the committee. In the absence of facilitated debate, there is limited potential for shared learning of values, interests and knowledge within the committee, for resolution of conflicts, or agreement on common interests.

The decision process followed by federal and state agencies to develop the Joint Management Plan appeared a divisive, deeply-rooted power-balancing struggle among agencies to protect fragmented and overlapping jurisdictions and avoid risk. Each interest committed resources to control the issue, which was blocked by competing interests, with little to show for the effort but increasing frustration. Outside (judicial) mediation was necessary to define a solution.

Despite the broad mission of the GYIBC “to facilitate the development and implementation of brucellosis management plans for elk and bison in the GYA”[30], the committee has no authority and its composition reflects a balance of power among the agencies. As one participant said:

> “The GYIBC was never designed as a decision making body; it has no enforcement or regulatory authority. The GYIBC was designed specifically not to usurp or abrogate any individual agency’s management authority or responsibility. The only incentive to buy into a GYIBC recommended action is through peer pressure or if the action is self-serving, that’s about it.”[31]

It is noteworthy to comment on bison management in Wyoming. A management plan was developed in 1994 for bison leaving Yellowstone National Park through Sylvan Pass into the North Fork of the Shoshone River west of Cody, Wyoming. The plan allows for

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[28] Interview with Keith Aune, August 10, 2004, Corwin Springs, MT.

[29] Interview with T. Roffe, 22 July, 2004, Bozeman, MT.

[30] www.nps.gov/gyibs/home.htm

[31] Interview with Tom Roffe, 22 July 2004, Bozeman, MT.

up to 15 bulls in the area, but cows are not tolerated to prevent establishment of a breeding population. When more bison move out of YNP than the target population, a hunt is authorized and hunters who have obtained a permit are notified. Twelve bull bison were harvested in winter 1995-96 and 14 bulls and a cow and calf were taken in 1996-97. Wyoming also established a regulated hunt in the Jackson area. The first hunt was in 1989. In 1990, the Legal Action for Animals sued over noncompliance with the NEPA; the hunt was being conducted on federal land. The hunt was shut down because of the complaint. Legal requirements were addressed and hunting resumed on private land, state land and in the Bridger-Teton National Forest. A regular hunting season has been in place every year since 1998. In 2005, the season ran September 1 to November 30; tags were issued for 25 bulls and 50 cows or calves[32]. Unlike the Montana/YNP bison management planning process, Wyoming "went to great lengths" to involve local conservation groups and local communities in direct dialogue on bison management, and unlike the YNP/Montana boundary bison control situation, there have been no disputes in the field in Wyoming[33].

The National Park Service (NPS) and the U.S. Fish and Wildlife Service (USFWS) are developing a plan for managing elk and bison in the National Elk Refuge (NER) and Grand Teton National Park (GTNP). Bison management is being addressed jointly by these agencies because the population has become habituated to the feed provided to elk on the National Elk Refuge in winter. There approximately 14,000 elk and 800 bison in the area in winter. The bison herd moves among several jurisdictions including the National Elk Range, Grand Teton National Park, Bridger-Teton National Forest, Bureau of Land Management resource areas, and Wyoming state and private lands. Inter-population movements are rare between the YNP and Jackson herds[34]. A management plan and environmental assessment was prepared in September 1996 (Grand Teton National Park et al. 1996). It called for hunting to limit the size of the Jackson herd to a range of 200 to 250 bison. A lawsuit filed in 1998 resulted in a court order dictating that bison could not be destroyed in the NER or in GTNP to control the population until the USFWS and NPS assessed bison management and the winter feeding program[35]. Before initiating a comprehensive management plan process for the Jackson bison and elk herds, the two federal agencies, with the support of the U.S. Forest Service and the Wyoming Game and Fish Department, invited the U.S. Institute for Environmental Conflict Resolution (U.S. IECR et al. 2000) to conduct a situation assessment to provide guidance on devising a public involvement strategy and an assessment of the range of interests and

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[32] Billings Gazette, January 27, 2005, Montana outdoors: Wyoming offers well-run bison hunt by Mark Henckel.

[33] Comment attributed to Mark Gocke, regional information specialist for Wyoming Game and Fish at Jackson, Woming, *supra* note 31.

[34] In winter 1995/96, 3 bulls from the Hayden Valley and wintered in the vicinity of Polecat Creek; they were captured and radio collared. For several years after that they returned each year to Hayden Valley during the rut then back to the Jackson Lake area to spend the winter. During the harsh winter of 1996-97 a mixed group of 3 cows and 3 juveniles followed the road from YNP through the south gate and spent winter in the same area as the 3 bulls. Then they moved south and joined the Jackson herd; this mixed group did not return to YNP. Source: Interview with Steven Cain, 11 August 2004.

[35] Homepage for the National Elk Refuge and Grand Teton National Park Bison and elk management plan/EIS, http://bisonandelkplan.fws.gov, February 2, 2005)

concerns about the management of the Jackson bison and elk herds (U.S. IECR et al. 2000). The issues included optimal herd size, disease management, artificial feeding, and other management tools such as hunting, increasing forage by irrigation, controlled burning, agency jurisdiction and perceptions of poor working relationships between and within the agencies.

The U.S. IECR et al. (2000) defined common interests among groups, including: "a shared vision of healthy herds of elk and bison, well-nourished, free of disease, and more in balance with their natural habitat; a general understanding of the importance of the herds to the Jackson area economy and way of life; a recognition of the national, perhaps international, significance of the herds; a desire for change, both in the way the agencies manage the herds and how the agencies work with each other; and finally, a strong desire for more and better information, especially scientific data, upon which to base management decisions". They recommended a three body planning structure comprised of an interagency planning team, a multistakeholder working group advising the planning team, and a science council.

### *Winter Use of YNP and Perceived Effects on Bison*

Grooming of snow covered roads and winter use of the park by large numbers of oversnow vehicles has been a significant and often controversial matter for Yellowstone National Park management since the 1940s (Table 4.1). The first published comment we discerned on the influence of roads on winter movements of bison was by Meagher (1989*b*). Reference was made to the influence of the plowed road through the northern range. The following statements are particularly relevant to understanding the beginning of concerns about the influence of roads on winter bison movements (Meagher 1989*b*:673,674):

- "After daily road plowing between Tower and Mammoth began in the 1940s (B. Hape, pers. comm.), a few males sometimes traveled this route, but mixed herds did not until 1975-76."
- "The bison used two major travel routes (Fig.1), the natural topographic route along the Yellowstone River from Tower to Gardiner was the primary route initially (Table 1). In 1982-1983, the plowed road became the primary route".
- "When human interference precluded use of the primary routes, the bison detoured across steep terrain, or traveled along tributary drainages"
- "Use of the plowed road for relatively easy and energy-efficient travel probably facilitated learning and a rapid increase in numbers."

The last statement in particular foreshadowed a more elaborate explanation of the influence of packed winter roads on population growth and range expansion by bison in the central ranges of the park. In 1993, Meagher (1993) published an internal report reviewing, in depth, the history of movement and distribution patterns and inferred the influence of groomed roads on winter movements of bison in the central ranges. The notions were put forth that grooming and high volumes of snowmobile traffic on roads in the central ranges created hard packed surfaces used by bison for "energy efficient travel that resulted in energy saving within traditional foraging areas, range expansion, major shifts among previously semi-isolated populations, and a mitigation of winterkill and enhancement of calf survival". In 2001, the Fund for Animals argued further that use of packed roads by bison facilitates emigration from the park where they are harassed and killed in the State of Montana[36]. We examine the ecological bases for these claims in the next two chapters. Here we wish to comment on the evolution of the issue surfacing during the extreme winter of 1996/97 when large numbers of bison were culled at the Park boundaries in Montana.

The winter of 1996-1997 was the most severe on record (Figure 3.9 and 3.10) with heavy snow and "snow crusting" that created a thick layer of ice early in the winter. Bison had great difficulty cratering through snow to obtain forage; > 1,000 left the park. Concern by the ranching community over spread of brucellosis from migrating bison to cattle resulted in APHIS, the State of Montana and Yellowstone Park culling about 1100 of them at the Park boundaries. This produced a great controversy (Peacock 1997*a*,*b*) and renewed the debate on brucellosis risk to the livestock industry. In 1997, the Fund for Animals and other groups sued the NPS for violating the Endangered Species Act and the National Environmental Policy Act (Yochim 1998*a*). The Fund for Animals requested NPS prepare an Environmental Impact Statement (EIS) concerning winter use, and evaluate the effects of road grooming on wildlife and other park resources (Yochim 1998*a*). The argument for an EIS under NEPA was based on the substantial and unpredicted increase in winter use visitation that had occurred since the first winter use management plan was released in 1990 (Figure 3.13) and that new information had come forward suggesting bison use of groomed roads during the winter had substantially changed their population dynamics and distribution. The NPS settled the lawsuit with the plaintiffs by agreeing to conduct an EIS to address a full range of alternatives for winter use and to conduct an EA on a proposal to close a road segment during the winter to study the effects of groomed roads on bison. Subsequent actions are noted in Table 4.1.

Protection of the park environment represents one set of interests in the debate over winter use; recreation and business interests are another. Since 1949, the public has had the opportunity visit the park with over snow vehicles. A substantial winter recreation industry has developed around OSV access to the park. Threatened by the proposed closure of the park to snowmobile access, the International Snowmobile Manufacturers Association (ISMA) and others filed a claim in federal court alleging that NPS violated the Administrative Procedure Act, NEPA, the NPS Organic Act and other laws in the 2000 NPS Record of Decision. ISMA agreed to settle with NPS when it committed to conduct a supplemental EIS considering new information and technology. Complaints by each side of the debate (environmental protection, and recreation and economics) have been addressed in federal courts in Washington D.C and Wyoming. Resolution of the battle between values and world views remains uncertain.

Like the bison/cattle/brucellosis issue, the winter use issue is a highly charged conflict with public interests having no mechanism for meaningful participation apart from the process prescribed by NEPA for public comment on EAs and EISs and that required by the Administrative Procedure Act for rulemaking. And, like the bison/cattle/brucellosis issue, the affected publics use the media or courts to be heard, or in some cases pursue more radical activism. The result is ongoing conflict, substantial

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[36] Statement of The Fund for Animals in Response to the Settlement Agreement in International Snowmobile Manufacturers Association et al. v. Norton 7/05/2001.

annual and incremental costs for the agencies in time and resources (Cromley 2002), and promoting the notion that more science, more information, will somehow result in a wiser outcomes.

## New Paradigm for Bison Management

The methods by which value conflicts have been dealt with by affected interests, including agencies and conservation advocacy groups, escalated to what Mary Meagher refers to as “the bison wars”[37]. Clearly, the governance systems and public involvement mechanisms in place for dealing with the complex issues described herein suffer from jurisdictional fragmentation and hierarchical decision-making. They appear grounded in the outdated precepts of “sufficiency of science” and “expert-authority” (Riley et al. 2002). The sufficiency of science precept is a belief that insights or reliable knowledge gained through science provides the exclusive keys to best management decisions (Decker et al. 1987). Expert-authority (Ludwig 2001) holds that experts (e.g. biologists and veterinarians), by virtue of their training, education and experience, are best qualified to make resource management decisions. Policy processes based on power and dominance are inefficient and incapable of defining the common interest. New foundations are being defined for resource management that are integrative, inclusive of diverse values and interests, more democratic, and more likely to define the common interest than command and control approaches to policy development. These emerging resource management approaches are also more likely to engage society in a better understanding of the real issues influencing decisions.

The Park was established in 1872 with the aspiration to manage its resources in the common interest, “for all people”; this has not changed (Cromley 2002). The challenge is to design a new way of dealing with complex issues that will reduce conflict, improve policy stability and achieve wise outcomes for society, conservation of ecosystem values, while respecting people who are a part of the Greater Yellowstone Ecosystem. Advancements in integrative approaches to management are being made under the rubrics of ecosystem management (Knight and Meffee 1997), collaborative resource management (Wondolleck and Yaffee 2000), coordinated resource management (Hicks et al. 1996), conservation biology (Meffee and Viederman 1995), conservation ecology (Shindler and Cheek 1999), citizen science (Light et al. 1998), integrated environmental management (Margerum 1999), and community-based natural resource management (Michaelidou et al. 2002, Virtanen 2003). Common aspects of these approaches as applied in successful resolution of environmental conflicts include: legitimacy (Mascarenhas and Scarce 2004); integrative problem solving and decision-making; shared learning (Schusler et al 2003); and value-based judgments informed by, but distinguished from, scientific judgments (Decker et al. 1991).

It is not the intent of this report to provide a full review of the natural resource policy literature. However, some key points are worth noting. We believe it would be beneficial to those engaged in the bison movements and brucellosis issues to redefine the structures and processes used to address them by taking an integrative policy-orientation approach (Clark 2002), which encourages integration of natural and social sciences to aid

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[37] Interview with Mary Meagher, July 15, 2005, Gardiner, MT.

managers, leaders, and the affected publics to make sound choices and effectively solve problems. Secondly, it is important to more clearly understand the nature of value dynamics underlying the conflicts. Base values are the things people desire, strive for, or demand (Lasswell 1971). Lasswell and McDougal (1992) provided a system of value analysis based on the belief that human dignity is the central goal of all people. Living with dignity means having adequate power, enlightenment, wealth, well-being, skill, affection and rectitude (Clark and Wallace 2002). Inadequate amounts of any of these values can generate conflict. In the current context, as lead agencies carry out federal or state ESA policy or work to satisfy specialized mandates, their personnel expect to wield a certain amount of power, use their knowledge (enlightenment) and skill to achieve the mission of their agency, and have the respect of other agencies and the public. Furthermore, they believe their service is justified by the legislated mandate of their agency, which in turn gives them the right to serve one or more public interests (rectitude). Those with more power, resources or knowledge may treat other stakeholders in ways that do not offer them dignity, leading to a loss of cooperation or more radical challenges, ineffective policies and inefficient programs.

The emphasis placed by stakeholders (agencies and conservation advocacy organizations) on technical knowledge and the natural sciences in the Yellowstone bison conflicts indicates how highly enlightenment is ranked. However, little attention has been paid to the importance of the social sciences, in particular policy process and organization theory in decision making. Formal assessments (Cheville et al. 1998, Klein et al. 2002) and environmental assessments (various EA and EIS) grounded in the natural sciences add information, address scientific information gaps and advance careers, but have not improved decision-making or cooperation (Cromley 2002). Indeed studies commissioned to date persist in focusing on technical details and call for further research to address scientific uncertainties; they have paid scant attention to improving the policy processes or organizational structures necessary for achieving wise and enduring solutions acceptable to the broadest possible range of stakeholders. Dery (1984; cited by Clark and Wallace 2002) commented that people’s behavior cannot be changed merely by bringing “new information” to their attention. Dispensing more or better knowledge without an effective policy process and organizational structures within which knowledge can be used to inform value-based decisions, is not an effective means to achieve lasting solutions. Win-win solutions are accomplished through a process that offers dignity to everyone involved (Clark and Wallace 1999). To be effective and successful, an integrative policy process requires appropriate structures for organizing people to work together (team work), acknowledgements of legal constraints and authorities, interdisciplinary skills and knowledge, pragmatism, and procedural rationality (Clark and Wallace 2002).

The 1998 National Parks Omnibus Management Act authorizes and directs the Secretary of the Interior “to assure that management of units of the National Park System is enhanced by the availability and utilization of a broad program of the highest quality science and information.” The role of science in supporting high quality decisions canot be overemphasized, but on its own scientific knowledge is insufficient for making effective decisions. Establishing the organizational structures and processes to link science to value-based decision-making is perhaps more challenging than conducting research.

There are significant research efforts being undertaken or supported by various institutions and individuals on bison ecology and brucellosis epidemiology. The US Geological Survey – Biological Research Division (USGS-BRD) website lists 16 projects funded by that organization. The GYIBC web site (www.nps.gov/gyibc/research.htm) lists 26 projects of which 11 are funded in whole or in part by the USGS-BRD. A group of three principal investigators (affiliations: Montana State University Department of Ecology, Yellowstone National Park, California State University Monteray Bay) has developed a research program focusing on detailed characterization of the landscape in the west central Yellowstone Park, the role of climatic variation in influencing ecological processes including plant productivity and phenology, snowpack dynamics, and linking climatic variation with both the spatial dynamics and population dynamics of the primary large mammals that inhabit the region: elk, bison, and wolves (www.homepage.montana.edu/~rgarrott/centralyellowstone/index.htm). The web site lists 22 separate projects: 6 projects on bison, 3 on wolf-ungulate dynamics, 6 on biophysical research, 2 on winter recreation impacts on bison and elk, 3 on spatial and population dynamics of elk, a project on geochemical cascades and another on plant productivity and phenology.

We could not find a current comprehensive list of projects on YNP bison or evidence of current comprehensive coordination of research efforts by NPS and other agencies. A recent effort to provide coordination was terminated in November 2003. Gogan et al. (2002) described the initiative by the USGS-BRD to coordinate research among various institutions, which began in the fall of 1995 when biologists from the park's Yellowstone Center for Resources contacted their counterparts in the USGS-BRD to discuss research needs on the ecology of bison in Yellowstone. The program was conceived as a joint cooperative effort between management and research biologists. It was intended to enhance the understanding of bison ecology, integrate past research and the results of new research into a predictive model of the role of bison in the GYA. Key elements of the program were extensive and continuous communication between management biologists and research biologists, and extensive planning and review of study designs to maximize the effectiveness of the research. Ecological studies supported under the initiative focused on forage availability, habitat use, and bison population dynamics. Brucellosis research included examining the risk of transmission of the disease from wildlife to cattle, identification of exposed animals in the field, and the safety of vaccines to wildlife species. We inferred from key informant interviews with some of the investigators involved in the program that competition has to a significant extent replaced the original intention of ongoing collaboration. Indeed, we found it difficult to obtain or get permission to use current data on bison ecology from several researchers and inferred that data were not shared to protect publication rights or to reduce competition for limited research funding.

Informed by key informant interviews and workshops held with various groups and individuals during July, August and October 2004, and by review of documents, we provide the following observations concerning the nature of the brucellosis and winter use conflicts and governance mechanisms being used to address them:

- There is strong competition and in some cases antagonism among some scientists and research groups which impedes data sharing, collaboration and coordination.

- There remains a strong sense of competition between agencies for influence over bison management based on individual agency mandates, disciplinary biases, and differences in institutional cultures.
- State and federal livestock agencies remain deeply committed to eradication of brucellosis from wildlife, and elimination of all risk to the livestock industry.
- The singular focus on bison as a vector of brucellosis is poorly understood by the public, which sees a much larger reservoir in elk associated with feed grounds in Wyoming and inconsistent policies by which the State of Montana deals with bison emigrating from the park.
- Many publics are frustrated with the low level of opportunity for involvement in decision processes and are willing to collaborate with government agencies.[38]
- There is a strong tension within some agencies over increasing public involvement in decision-making on bison management.
- The agency-based planning process used for these issues, and the low level of public involvement required under NEPA have generated conflict and reduced public trust in governance.

No organization yet exists to deal with the broad matter of regional bison conservation and management (including disease management at the boundary and winter use in YNP), or that provides for a level of public involvement higher than solicitation of individual commentary on agency plans or actions. We advise a thorough assessment is needed of the nature of the conflicts, including base values and biases, the potential for defining common interests, and the nature of current and historic decision processes and structures. The assessment should focus on designing new organizational structures and processes that can more effectively and efficiently deal with the ongoing and unresolved linked conflicts of bison/brucellosis/cattle and winter use/bison movements.

Finally, the definition (below) of wildlife management offered by Riley et al. (2002) represents recognition of the requirement for interdisciplinarity and the increasing demand for democratization of natural resource conservation now being experienced worldwide:

> Wildlife management is “the guidance of decision-making processes and the implementation of practices to purposefully influence interactions among and between people, wildlife, and habitats to achieve impacts valued by stakeholders”.

## Conclusions

The two major issues associated with Yellowstone National Park bison management are primarily a consequence of the successful recovery and expansion of bison as a wildlife species and value conflicts resulting from the arbitrary location of the park boundary within a large ecosystem in which people live and derive their livelihoods. In

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[38] 13 environmental non-government organizations attended a workshop hosted on October 29, 2005, at Livingston Montana. The systems model (Chapter 6) was reviewed. The overwhelming response we received was one of gratitude for being invited to be involved in dialogue and exploration of the issues in the formal context of the model. Participants invited and those attending are listed in the Appendix.

the early historical period, bison ranged widely in large numbers throughout the Great Plains, Snake River Plains, and intermountain regions, including the Yellowstone Plateau and valleys connected to it. Market and subsistence hunting during the mid 1800s reduced the bison population to a few hundred individuals at the time Yellowstone National Park was established in 1872. Subsistence hunting and poaching continued for three more decades, reducing the indigenous population to 23 survivors in the remote Pelican Valley. Concern about the persistence of bison in the park, and indeed in America, resulted in a captive breeding program being established on the northern range in 1902. It was managed by the military until 1916 when taken over by the newly formed National Park Service.

YNP Bison were managed through five decades under an agricultural paradigm necessitating periodic culling to keep them in balance with range ‘carrying capacity’. Throughout this period, egress from the park was frequent on the northern range in the Gardiner basin where a climatic gradient creates low snow cover and attractive winter range conditions relative to harsher environmental conditions in the higher elevation Lamar Valley. Park managers have long recognized the Gardiner basin as an integral part of the northern winter range for bison and elk. Movements out of the park increased following cessation of winter feeding in the Lamar Valley in 1952. Movement out of the park from central bison ranges was uncommon over the range of population sizes present between 1902 and 1967. Park policy then changed to one of minimum interference in ecological processes. The number of bison increased and, like the elk population, expanded their range, and pushed out from the central ranges to boundary areas. Initial concerns of the livestock sector about contact between migrating brucellosis-infected bison and susceptible cattle increased after 1967 with implementation of ecological management. Boundary culls increased after 1985, heightening conflict between bison conservation interests and livestock protection interests. Starting in the late 1980s, winter use management, specifically packing of snow on roads by grooming equipment and recreational over snow vehicles, was claimed to influence bison movements, range expansion, enhance reproduction and survival, leading to increasing egress from the park where animals were subject to culling.

Efforts to deal with the linked problems of bison/brucellosis/cattle and winter use/bison movements have suffered fractured government jurisdiction, inadequate policy process and low levels of public involvement, leading to intense conflict. Recent advancements in natural resource policy processes offer promise for dealing with complex problems such as bison management in the Greater Yellowstone Area. A pragmatic, procedurally rational integrative policy-oriented process is needed for organizing agencies and citizens to work together to use multidisciplinary knowledge for integrative decision-making.

Table 4.1. Chronology of winter use policy development in Yellowstone National Park.

| Year | Action | Outcome |
|---|---|---|
| 1940 | Senator Joseph O'Mahoney of Wyoming pressured the National Park Service (NPS) to plow Yellowstone National Park (YNP) roads in winter. | NPS denies request because of concerns about safety and costs. |
| 1949 | Yellowstone National Park (YNP) administrators allow first Over Snow Vehicle's (OSV) into the park. | OSV use increases steadily, but remains relatively low (<650 users in winter of 1954-55). |
| 1949 | Big Horn Basin Clubs (group of commercial clubs in Wyoming) renew pressure to plow YNP roads in winter. | U.S. Bureau of Public Roads winter use feasibility study determines that YNP roads are unsuited to plowing, buildings of park are not winterized and plowing would be too hazardous. |
| 1956 | MISSION 66 implemented; encourages and provides for infrastructure for winter use in National Parks. | Committee of representatives from NPS, regional highway departments, American Automobile Association and Yellowstone Park Committee recommend year round operation of YNP is feasible but not practical; park continues to allow OSV use. |
| 1967 | Congressional hearing held in Jackson, Wyoming to address public pressure to plow YNP roads in winter. | NPS concludes that roads will not be plowed; summer season will not be extended but YNP will remain open to OSV's. |
| 1967-1971 | Creation of first official NPS OSV policy and regulations. | Allow OSV use on roads only, road grooming began; Old Faithful snowlodge opened. |
| 1971-1983 | Promotion of winter use in YNP. | 1971 overnight accommodation available at Old Faithful; encouragement of tours in YNP; grooming program expanded to be more consistent and to include east entrance road; warming huts built and Mammoth Hot Springs Hotel opened in winter; gas become available at Canyon in 1977 and daily grooming of east entrance road began; by late 70s all roads were used in winter except Tower to Canyon across Mt. Washburn. |
| 1983-1990 | NPS recognizes growing winter use in YNP. | 1984 formal winter use planning begins; NPS develops winter use plans for YNP. Meagher (1989*b*) comments on the influence of plowed roads on bison movements on the northern range. |
| 1990 | Winter Use Plan completed for YNP, Grand Teton National Park and John D. Rockefeller Jr. Memorial Parkway. | First environmental compliance on winter use policy for YNP. |
| 1993 | NPS notes earlier than expected increase in winter use in YNP. | NPS agrees to evaluate winter use across the GYE in conjunction with the United States Forest Service (USFS). First published mention of winter |

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| | | recreation-induced changes in bison numbers and distribution Meagher (1993). |
| 1994 | Greater Yellowstone Coordinating Committee (GYCC; National Park Superintendents and National Forest Service Supervisors) evaluate increasing winter use. | Chartered interagency team to perform an analysis of winter use in the Greater Yellowstone Area (GYA). |
| 1996 | The Biodiversity Legal Foundation (BLF) send letter to NPS stating intent to sue for violating NEPA and the Endangered Species Act in YNP winter use policy | |
| Winter of 1996-1997 | Most severe winter on record (e.g. deep, hard snow) triggers migration of bison from the park. | Results in controversial culling of 1,084 bison at park boundaries to prevent brucellosis transmission from bison to cattle. |
| 1997 | Draft released - Winter Use Management: A Multi-Agency Assessment | |
| 1997 | Fund for animals et al. (including the BLF) sue NPS. | Alleged failure of winter use plan to consult United States Fish and Wildlife Service (USFWS) on impacts of winter use on threatened or endangered species, and adhere to the National Environmental Policy Act (NEPA). Request NPS prepare an Environmental Impact Statement (EIS) concerning winter use, and evaluate the effects of grooming on wildlife and other park resources. |
| 1997 | Fund for animals et al. agree to a settlement with NPS | NPS commits to write an EIS and new winter use plan; requests formal consultation with USFWS and evaluates possible road closure in YNP |
| 1998 | Environmental Assessment (EA) released on the possibility of closing road segments during the winter in YNP. | Alternative road closures proposed for EIS; YNP continues grooming until EIS completed. |
| 1999 | NPS releases final publication of Winter Use Management: A Multi-Agency Assessment. | Identifies desired conditions for the GYA, current areas of conflict, issues and concerns and possible ways to address them |
| 1999 | Draft winter use EIS released. | |
| 2000 | Final winter use EIS released. | Preferred alternative is phase out of snowmobiles by winter 2002-03, to be replaced by NPS managed snowcoach transportation system. |
| 2000 | Record of Decision (ROD) regarding winter use EIS is signed. | Preferred alternative from EIS implemented. |
| 2000 | International Snowmobile Manufacturers Association (ISMA) et al. file suit against the Secretary of the Interior et al. | Allege that NPS have violated the Administrative Procedure Act (APA), NEPA, NPS Organic Act and other laws in the 2000 ROD. |

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| 2001 | Final rule published in federal register implementing the ROD of 2000. | |
| 2001 | ISMA agrees to settlement with NPS. | NPS commits to conduct a supplemental EIS (SEIS) considering new information and technology and allowing for additional public participation. |
| 2001 | USFS, states of Montana, Idaho and Wyoming, Fremont county in Idaho, Gallatin and Park counties in Montana, Park and Teton counties in Wyoming, and Environmental Protection Agency (EPA) participate in SEIS. | Purpose of SEIS is to further the purposes of NEPA, solicit more public comment on earlier winter use decisions, consider additional information from ISMA and any other new or updated information not available at time of earlier decisions. |
| 2002 | NPS publish proposed rule in federal register to delay for one year the phase-out of snowmobiles. | Additional time needed to complete SEIS. |
| 2003 | NPS issue SEIS and supplemental ROD. | NPS chooses alternative that would allow 950 snowmobiles into YNP/day; subject to specific requirements to mitigate impacts to park resources. |
| 2003 | NPS issue regulations implementing the 2003 ROD. | |
| 2003 | Fund for animals et al. challenge the 2003 ROD in Washington, D.C. federal court. | Allege that NPS did not address trail grooming in manner required by NEPA, the 1997 Settlement and other federal laws.<br>Ask the court to enjoin NPS to close all roads to grooming except South Entrance to Old Faithful. |
| 2003 | US federal court, District of Columbia sets aside the 2003 ROD and regulations. | Concludes, in part, that NPS did not address the impacts of groomed roads on wildlife in YNP and that NPS violated NEPA's provision for addressing a full range of alternatives.<br>Concludes NPS in violation of the APA (i.e. concludes that a drastic change of policy requires documentation above & beyond the norm).<br>Concludes that prior ruling to phase out snowmobiles will remain in effect; NPS allows 493 snowmobiles/day into YNP. |
| 2003 | Wyoming and ISMA re-open their lawsuit challenging the 2000 EIS and 2001 regulations in Wyoming federal court | |
| 2004 | Federal court, Wyoming, issues preliminary injunction against original EIS. | Orders YNP to issue new rules that are "fair & equitable" to all parties.<br>Rules that 2000 EIS was inconsistent with NEPA and the APA.<br>Concludes that snowmobile limits should be increased for the remainder of the current winter season. NPS increases snowmobile limit to 780 snowmobiles per day midway through |

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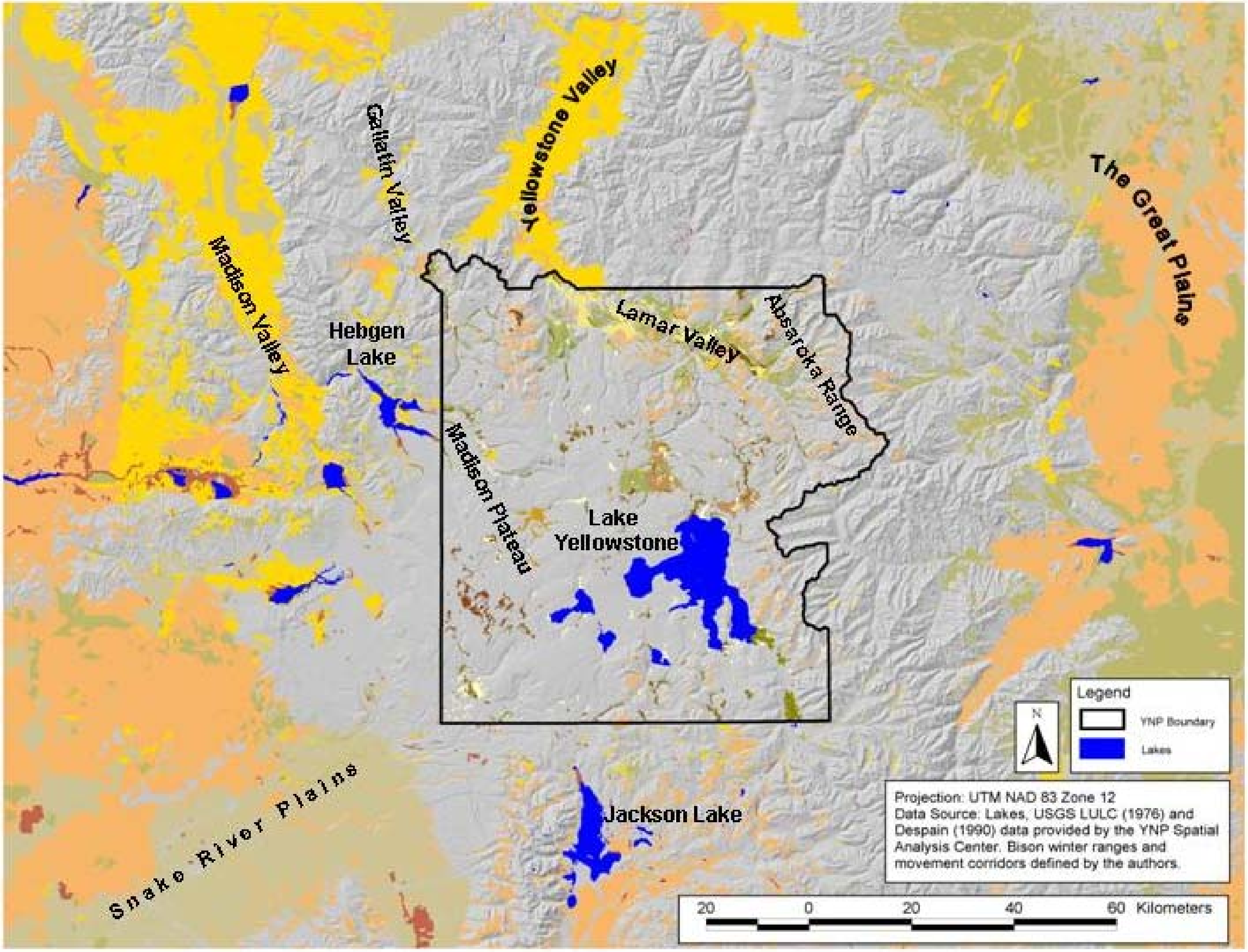
| | | winter 2003-2004. |
| 2004 | NPS issues a Draft Temporary Winter Use Plan EA that considers several winter use alternatives for next 3 years.<br>NPS issues a draft Finding of No Significant Impact (FONSI). | Preferred alternative allows 720 snowmobiles/day for next 3 winters. NPS contracts independent researcher to produce a report about what is known on road grooming and dispersal. |
| 2004 | NPS publishes proposed rule to implement preferred alternative from the draft EA and draft FONSI. | The Final Rule was published in the Federal Register on November 10, 2004. |
| 2004 | NPS issues final 2004 FONSI and Final Rule. | The Final Rule was published in the Federal Register on November 10, 2004. NPS decide to groom all roads for next 3 seasons and permit 720 snowmobiles/day. Announce will not be preparing an EIS on the temporary use plan for next 3 winters but will prepare an EIS for a long-term winter management plan. |
| 2004 | U.S. Congress passes an amendment to the Interior Appropriations Act requiring the temporary winter use plan be implemented during the 2004-2005 winter season. | |
| 2004 | Fund for Animals et al., State of Wyoming; Wyoming Lodging & Restaurant Association, and the GYC challenge NPS 2004 FONSI and final rule in federal court. | |

Sources: Meagher 1993; Yochim 1998*a*; 2003 YNP Winter Use Plans Record of Decision; Fund for Animals et al. Complaint 2004; M. Yochim (YNP planner, NPS) and K. Schneider (YNP planner, NPS), reviewed the table (Yochim's email response January 27, 2005; Schneider's email response January 29, 2005).



Projection: UTM NAD 83 Zone 12
Data Source: Lakes, USGS LULC (1976) and Despain (1990) data provided by the YNP Spatial Analysis Center. Bison winter ranges and movement corridors defined by the authors.

Figure 4.1. Potential bison habitat in the Greater Yellowstone Area (GYA). Habitat class color codes are described in Figure 4.2.

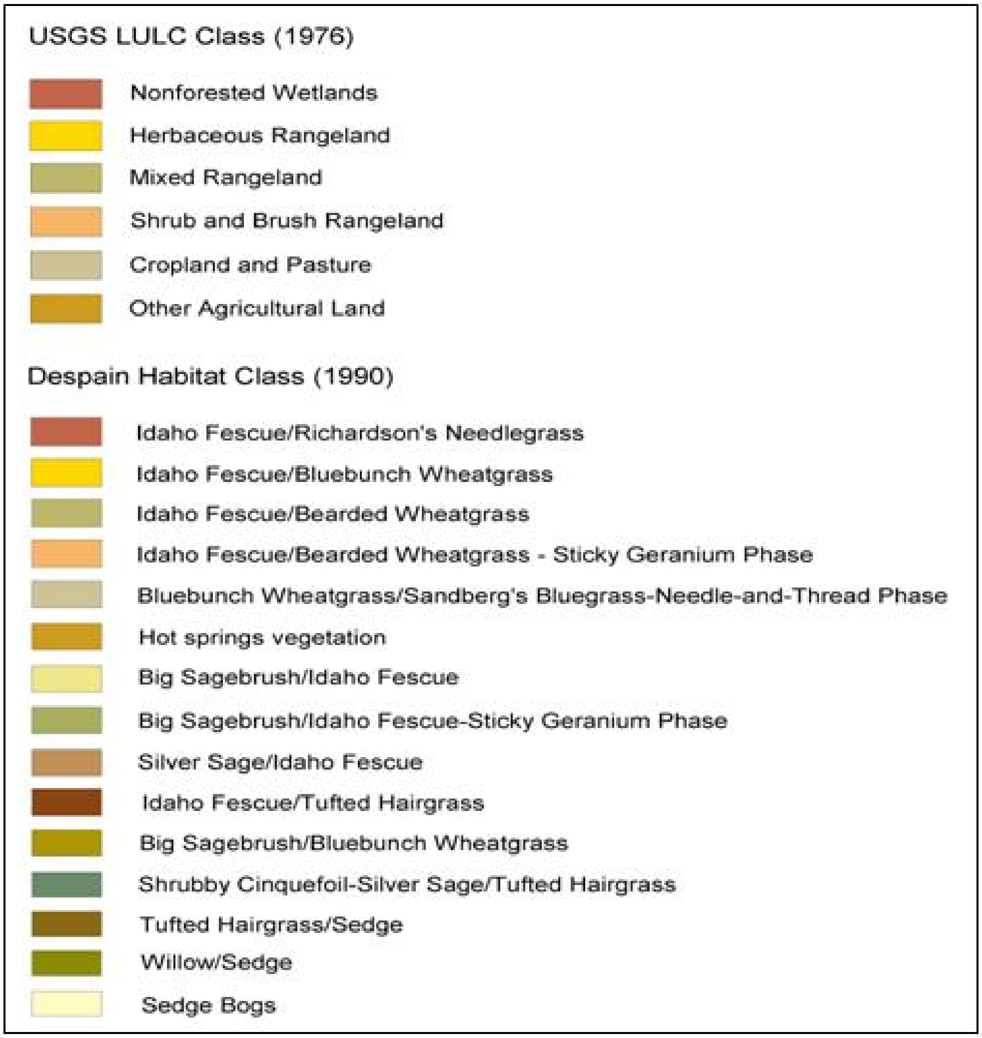


Figure 4.2. Habitat class color codes used in Figure 4.1 and Figure 4.3.

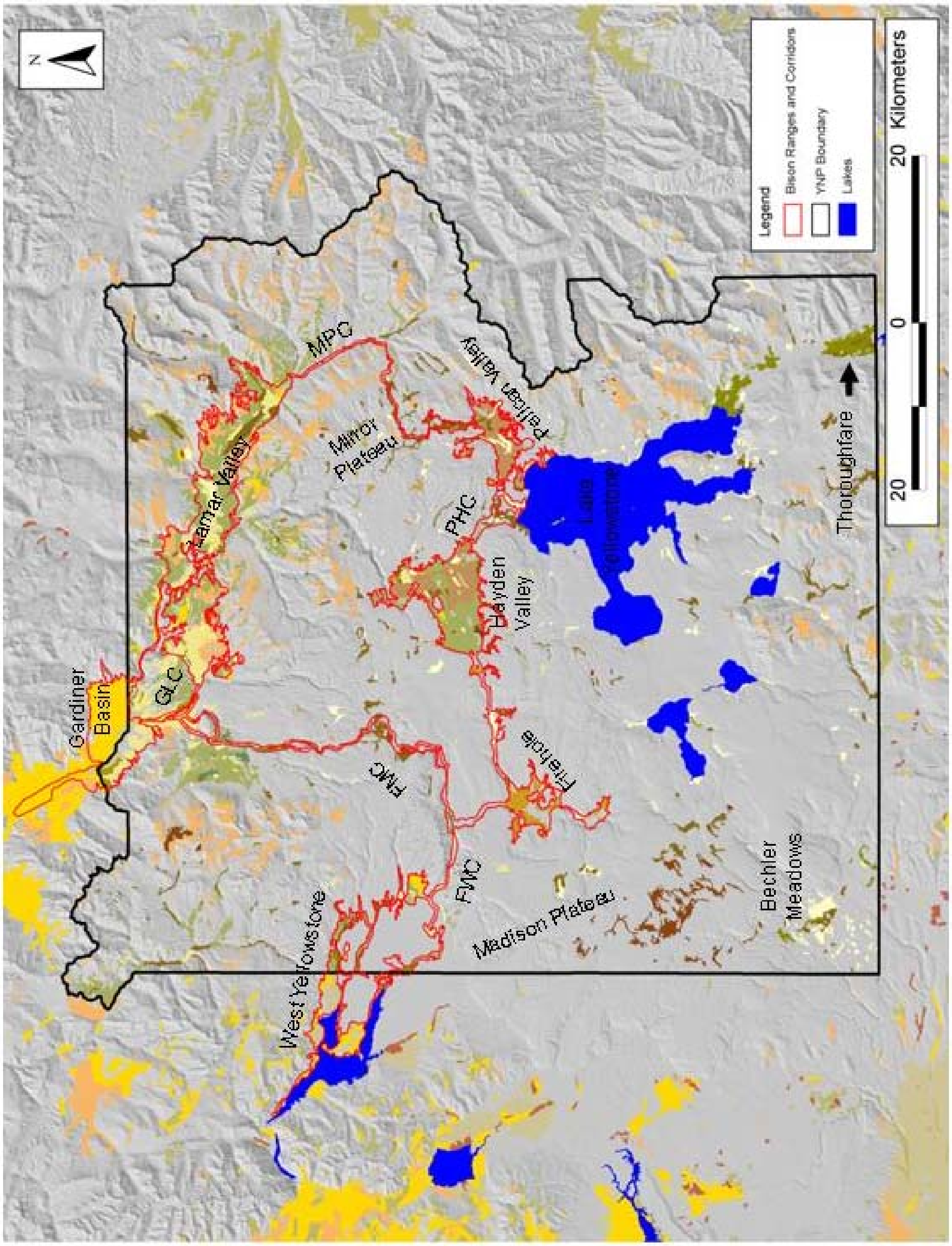


Figure 4.3. Location of bison winter ranges and winter movement corridors in Yellowstone National Park. Habitat class color codes are described in Figure 4.2. Ranges and corridors were mapped based on data from key informant interviews in July and August 2004.

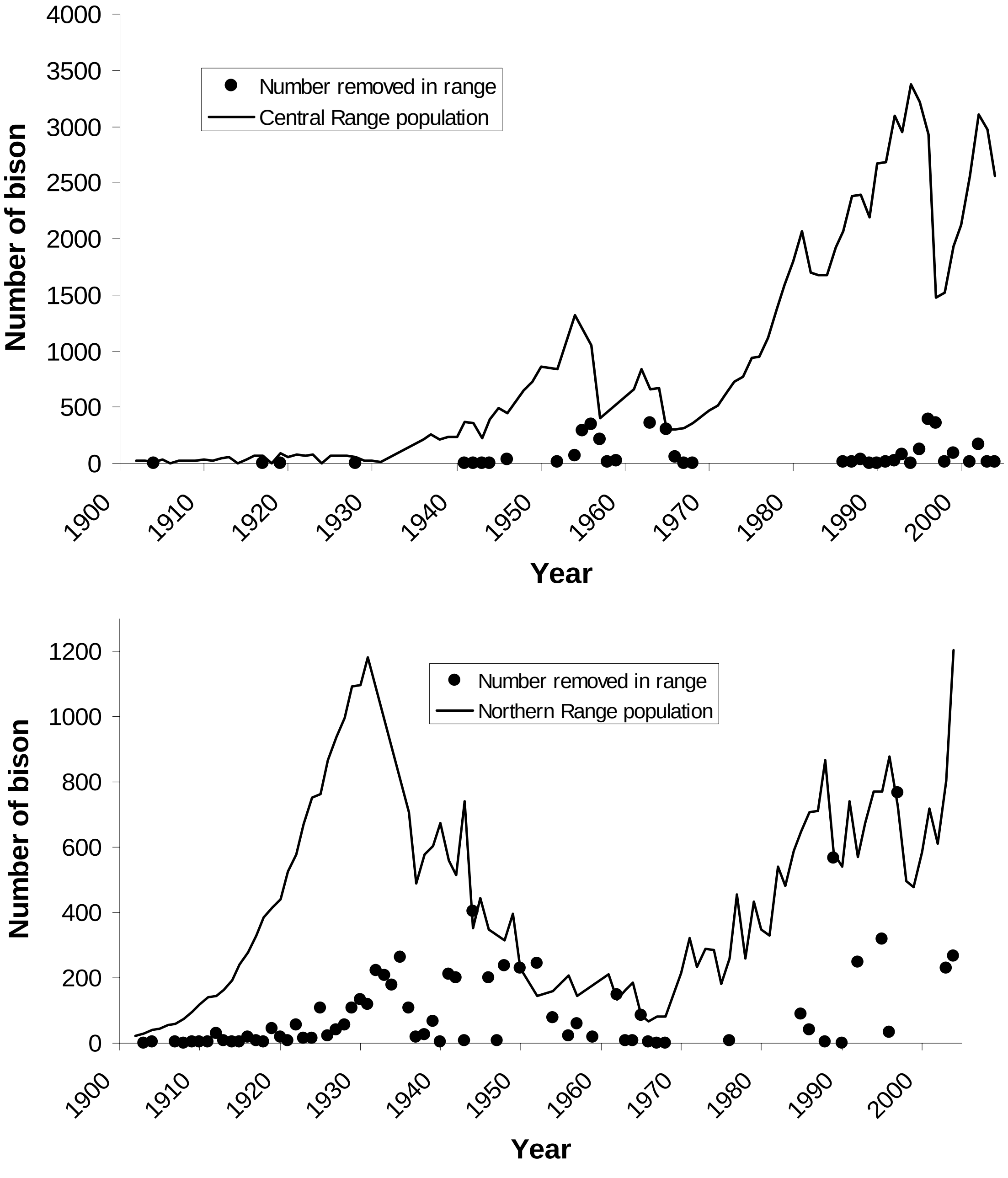


Figure 4.4. Population estimates and number of bison removed from the Central (top) and Northern (bottom) Yellowstone Bison Ranges between 1902 and 2004. Note: the Y-axis scales are different in each graph. Data sources: Meagher (1973) for 1902-1968, M. Meagher pers comm. for corrections to number of removals; M. Meagher, M. Taper, and C. Jerde for populations estimates 1970-1997; R. Wallen for population estimates 1998-2004.

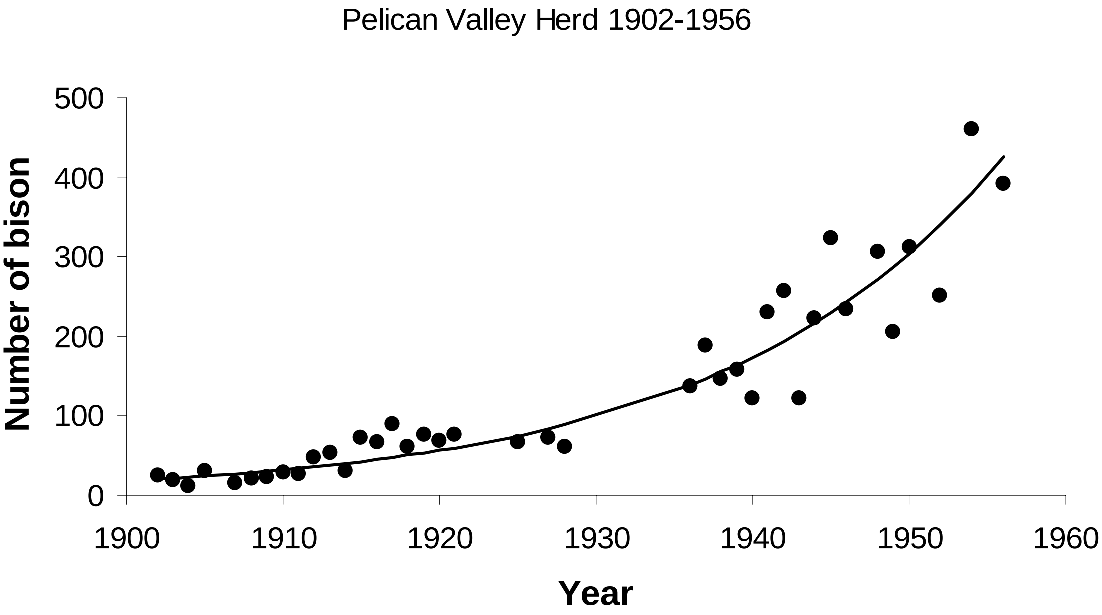


Figure 4.5. Growth of the Pelican Valley herd during 1902 – 1956 based on winter count data provided in Meagher (1973).

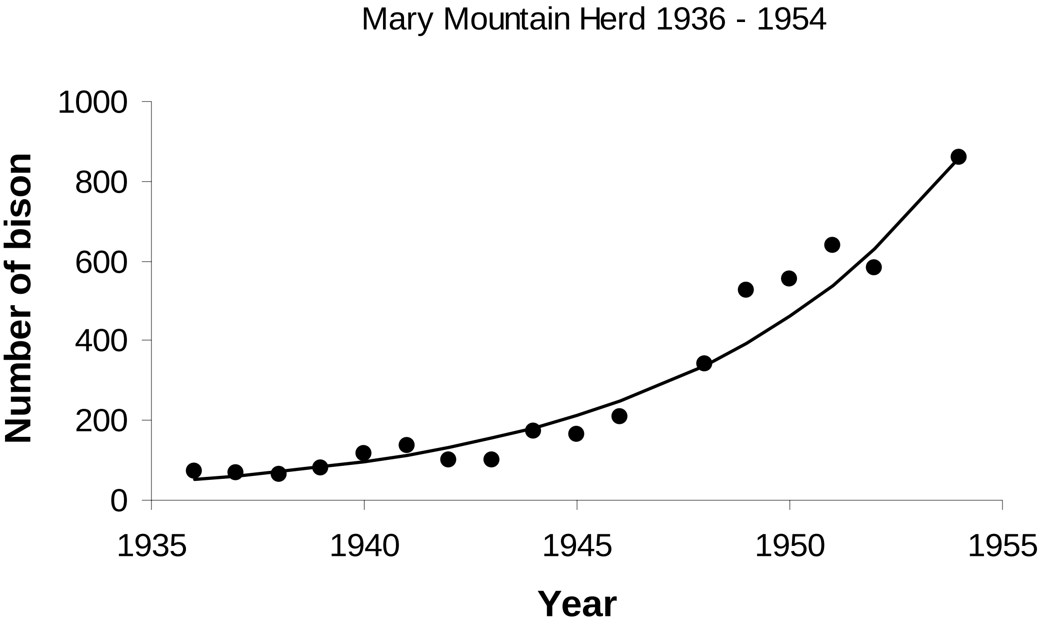


Figure 4.6. Growth of the Mary Mountain herd during 1902 – 1954 based on winter count data provided in Meagher (1973) with corrections by M. Meagher (pers. comm. October 2005).

## 5

# BISON POPULATION DYNAMICS AND SPATIAL ECOLOGY

Yellowstone National Park is not a self contained ecosystem. It covers 8,983 $km^2$ or slightly more than 10% of the Greater Yellowstone Ecosystem (> 80,503 $km^2$; Baden and Leal 1990, Clark et al. 1999). The movements and population dynamics of large mammal populations, including elk, grizzly bears, wolves, pronghorn, mule deer and bison, need to be viewed at spatial scales significantly larger than the park itself. In particular, herbivores can be expected to respond to regional environmental gradients in forage quality and availability, which are influenced by climate, seasonal weather, snow cover, elevation, vegetation cover, plant phenology, and herbivory. Understanding factors influencing bison movement and density distribution patterns is important for predicting range expansion and transboundary movements, and to form bison management decisions within and outside the park (Cheville et al. 1998). The influence of human activities and infrastructure in the park on bison movement and distribution patterns is also an important matter. The effects of road grooming in winter on bison movements and population dynamics is particularly controversial, and was the subject of several legal undertakings[1] and recent management decisions (National Park Service et al. 2000). Human infrastructure influences bison movements in other seasons as well.

The bison is the largest herbivore among ungulates occurring in the Greater Yellowstone Ecosystem. Typical of the species throughout its distributional range (Reynolds et al. 2003), the bison in Yellowstone National Park is an obligate grazer in winter (Meagher 1973). Its winter diet consists almost entirely of grasses and sedges (Delgiudice et al. 2001) and it is dependent on grasslands in the park and in areas where it is tolerated in surrounding jurisdictions. The ecological roles of bison include grazing, carbon and nitrogen cycling (Frank 2000), vegetation and soil disturbance (Coppedge and Shaw 2000), resource competition with elk (Delgiudice et al. 2001), prey for wolves (Smith et al. 2000), and food for bears, coyotes and other scavenging species (Green et al. 1997). The influence of bison on ecological processes and other species with which it interacts in an area can be expected to vary with abundance. During the past 100 years the number of bison in the park has ranged from > 23 to > 4,000. The population provides a valuable opportunity to study the dynamics of a recolonizing large herbivore population.

In 1968, Yellowstone National Park moved from a 33 year (1934-1967) period of controlling ungulate populations at predetermined stocking levels by culling to a regime of ecological management under which wildlife populations are allowed to fluctuate in the park without human intervention (Houston 1982). Subsequently, the bison population increased in size and area used (Taper et al. 2000), exhibiting characteristics of an erupting population (see Caughley 1970*a*). Spatial equilibria and regulation of colonizing

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[1] The legal history is summarized in a complaint filed against the Secretary of the Interior and Director, National Park Service by The Fund for Animals and other plaintiffs to the United States District Court for the District of Columbia, Case Number 1:04CV0193, 11/04/2004.

ungulate populations have been important topics in ecology since Riney (1964) and Caughley (1970*b*, 1977) established the theoretical foundations for understanding eruptive oscillations. An eruptive oscillation starts when there is a large surplus of resources available relative to resources required by animals present in a system. In established populations, such discrepancies can arise under three circumstances: by an environment becoming more favorable, e.g. following logging or fire; by a population being temporarily reduced by management interventions (hunting or culling) to well below per capita resource availability; or by a rare natural catastrophe, such as a flood or an exceptionally severe winter causing high adult female mortality. Once the source of perturbation is removed, a relatively low density population experiences high fecundity and survival, a high rate of increase, followed by increasing intraspecific competition for forage which serves as the stimulus for expansion into unoccupied range. This is followed by a new phase of population increase in the new range, and the pattern is repeated until available ranges are occupied. This pattern of pulsed expansion was first described by Caughley (1970*a,b*) for an exotic ungulate introduced to New Zealand. Pulsed expansion has also been demonstrated for recolonizing indigenous North American species: muskox in Alaska (Reynolds 1998), Northern Quebec (Le Henaff and Crete 1989) and Greenland (Oleson 1993); elk in Yellowstone (Lemke et al. 1998); and wood bison in Northern Canada (Gates and Larter 1990, Larter et al. 2000).

The substantial body of historical data available for bison in Yellowstone National Park provides a unique opportunity to examine long term spatial and demographic patterns in an expanding population subject to perturbations (management removals and variable winter severity). Historical observations predate establishment of the park (Meagher 1973). Population estimates varying in quality exist from 1902 to the present. Ecological studies have been carried out since 1963 (Meagher 1971, 1973, 1974, 1994, 1998, Meagher et al. 1997, Taper et al. 2000), creating a remarkable data set that has been only partially analyzed. Meagher (1993) reviewed changes in bison abundance, distribution and movements between 1970 and 1993. Long term data for the period 1970 to 1997 were recently analyzed and published by Taper et al. (2000, and *in press*). Cheville et al. (1998) and Klein et al. (2002) also reviewed population dynamics and factors influencing movements of bison within the park and movements to the boundaries of YNP in the Gardiner basin and West Yellowstone area.

Plowing and grooming of snow on roads in the Park for winter access management is claimed to influence bison ecology. In a paper reviewing the pattern of range expansion exhibited by the Northern YNP bison herd, Meagher (1989*b*:674) offered the first testimony concerning the effects of roads on winter range expansion: “Use of the plowed road for relatively easy and energy-efficient travel probably facilitated learning and a rapid increase in numbers.” The argument was further developed in a review of movements and range expansion in the Central Park in which Meagher (1993:2) claimed that groomed roads in YNP had the following effects on the YNP bison population:

- groomed roads provide movement corridors facilitating travel within traditional foraging areas;
- groomed roads induce major shifts among previously isolated population sub-units;
- groomed roads induce range expansion;

- groomed roads reduce the energy cost of displacing snow during movements within and between winter ranges;
- energy saved from the reduced cost of transport mitigates winter kill and enhances calf survival, resulting in a higher rate of population increase than would otherwise occur.

Meagher et al. (2000, 2002) further elaborated these notions in their "domino effect" hypothesis:

> "In the early 1980's, gradual but escalating changes in the bison population became apparent. Annual winter use of foraging areas by the Pelican bison expanded west from traditionally used, geothermally influenced places near the shore of Yellowstone Lake to sedge areas near the mouth of Pelican Creek, Lake area, and on the Hayden Valley. Because Hayden Valley (part of the Mary Mountain unit) was occupied already by wintering bison, as more shifted from Pelican Valley, more bison moved into the Firehole. They also moved earlier. The process of winter range expansion was coupled with a population increase, and more bison moved further west to Madison Junction and beyond, to spill over the park's west boundary into Montana. We term this cascading pattern of population increase the domino effect." (Meagher et al 2002:135).

However, the authors were ambiguous about the role of road grooming as the cause of the domino effect concluding, "The use of snow packed or plowed roads certainly represents some energy savings to the Central herd, and even provides access to areas that would otherwise be inaccessible to bison. It is unclear if these energy savings have merely facilitated a population and range expansion that would have occurred anyway, or if an apparently minor change has upset a delicately balanced demography and caused the expansion." (Meagher et al. 2002:145,146).

We reviewed these key sources and examined other available information, including key informant knowledge, on the spatial and demographic patterns of the Yellowstone bison population to address the following questions:

1. Does this erupting population experience density dependence?
2. Does the population follow a pattern of gradual or episodic/pulsed expansion?
3. Are boundary removals influenced by population size and winter conditions in the park?
4. Is there or has there been spatial independence of population sub-units?
5. Have patterns of movement and interchange among population subunits changed?
6. Has road grooming influenced spatial patterns and population dynamics in the ways described by Meagher (1993) and Meagher et al. (2002)?
7. Do bison management actions at the boundaries influence range expansion and demographic patterns differently on the northern and central ranges?

We address these questions by examining available information on the spatial patterns and population dynamics of the Yellowstone bison population over a century-long period during which management interventions and weather have perturbed the system. In the next chapter, we employ a population and distribution simulation model to test sensitivity of the system to assumptions presented in this chapter and ecological conditions described in Chapter 3.

## Population and Density Trends

Ecological conditions differ between the Northern and Central ranges in Yellowstone National Park (Chapter 3), making it necessary to consider population and distribution trends of Northern and Central bison subpopulations separately. Two previous analyses have considered YNP bison as if they were one population (Cheville et al. 1998, Klein et al. 2002). Lumping population subunits ignores important gradients in environmental conditions between YNP bison ranges that differentially influence reproduction and survival, and spatial ecology of bison, elk and their predators.

The Northern range provides a marked elevation gradient from the Upper Lamar Valley down to the Gardiner basin, where a precipitation shadow creates drier conditions in the summer (Chapter 3) and lower amounts of snow in the winter relative to the middle and upper Lamar Valley (Figure 5.1). The value of the Gardiner basin as refuge habitat for bison in harsh winters has long been understood (see Chapter 4; Albright 1944, Cahalane 1944*a*). Unlike the Central Range, there is an insignificant area of geothermally influenced bison habitat in the Northern range. The Central ranges experience a longer period of continuous snow cover and deeper snow than the Northern range (Despain 1987, 1990). Unlike the elevation gradient in snow depth on the Northern range, there is no significant gradient in mid winter snow cover (depth, density, SWE) between West Yellowstone and the Pelican Valley in areas not subject to geothermal influence (Chapter 3 and Figure 5.1). However, snow melt and spring greenup occur earlier in the West Yellowstone area than in the Hayden and Pelican Valleys (Despain 1990). Significant areas of geothermally influenced habitat are present in the Firehole, Gibbon and Norris Geyser Basins, Hayden Valley and in the Pelican Valley winter ranges (see Chapter 3 and note red polygons in Figure 5.1) in which diminished snow cover increases access to forage, and reduces the cost of thermoregulation and movements. In addition, Craighead et al. (1973:38) described thermal springs in the Duck Creek and Cougar Creek area used by elk in the winter during the 1960s and early 1970s. In addition to providing foraging opportunities, geothermal areas and streams in the Central range are used as movement corridors by bison and elk (Aune 1981, Bjornlie and Garrott 2001). Similar to the Northern Range where reduced snow cover in the grassland habitat of the Gardiner basin provides refuge habitat for bison, the geothermally influenced areas in the Central Range provides refuge for a significant part of the subpopulation in harsh winters. Meagher (1971, 1973, 1976) refers to geothermally influenced areas as the survival habitat for the Central Range bison.

There are major differences in the structure of ungulate assemblages on the Northern and Central ranges and differential intensity of seasonal grazing related to herbivore species abundance and composition (Singer and Norland 1994, Delguidice et al. 2001). Elk and bison are the dominant herbivores on these ranges. Since 1970, the Northern range elk population has varied from a low of < 5,000 to > 20,000 (Klein et al. 2002). In contrast, relatively few elk winter in the Central bison ranges, except in the Duck Creek-

Madison-Firehole area where 300 to 800 elk reside in winter (Craighead et al. 1973, Singer 1991, Garrott et al. 2002). Few elk winter in the Pelican Valley (Smith et al. 2000:1131, DelGuidice et al. 2001:8). The number of bison on the Northern range varied from > 100 in the late 1960s to >1200 in 2004. On the Central range the number of bison also varied 10 fold during this period, from >300 to >3,000. Elk and bison exhibit moderate habitat (Barmore 2003, Singer and Norland 1994) and dietary overlap (DelGuidice et al. 2001) in winter on both the Northern and Central ranges during the late 1980s. The mean dietary overlap between bison and elk during the winters of 1987-1990 was 0.59 for the Northern Range (DelGuidice et al. 2001). Dietary overlap was higher in the Madison-Firehole area (0.69) where elk and bison shared geothermally influenced habitat when snow was deep. Because bison are behaviorally dominant to elk (McHugh 1958) resource competition on geothermal habitat patches in winter may disadvantage elk, exacerbating the population effects of geochemically induced senescence (Garrott et al. 2002) of this species in the Central ranges of YNP.

By the early 1940s, a few years after the reintroduction of 71 bison into the Mary Mountain range (1936), the YNP bison population was considered structured into three wintering subunits, the Lamar herd, the Mary Mountain Herd (Hayden Valley and Madison-Firehole) and the Pelican Valley herd (Meagher 1973). Meagher (1993:2) reported interchange among subpopulations during the winter was minimal because of topography and deep snow between the wintering Valleys. However, the Lamar and Pelican herds shared common high elevation summer range in the Upper Lamar Valley and east slopes of the Absaroka Mountains, and late fall interchanges between the Lamar and Pelican herds were inferred from unexpected variations in the number of bison on either winter range (Meagher 1973: 87). Movement between the Pelican and Hayden Valleys was known in the summer and fall (Figure 5.2). Therefore, Pelican Valley bison were familiar with both the Hayden and Lamar areas.

There were long periods of relatively constant growth of the bison population within each range when management interventions and weather had little influence on population growth. These periods can be considered to represent the inherent capacity of each range to support population growth below levels where density dependence is exerted. At low densities, bison should have access to adequate forage, except during severe winters, and growth rate should be relatively stable and high. At high densities, productivity can be expected to decrease and juvenile mortality increase, lowering recruitment and population growth. Growth of the Northern population between 1902 and 1952 was excluded from consideration because the herd was subsidized by winter feeding to some extent throughout this period and it was intensively managed (Chapter 4). The only period during which growth of the Northern population was relatively unaffected by management interventions was between 1967 and 1988[2]. During 1970 to 1988 the Northern range population increased at an exponential rate of 0.072 (Figure 5.3). The period ended with the harsh winter of 1989 when a large proportion of the population moved into the Gardiner basin and 581 were removed near the Northern boundary (Meagher 1989*b*).

There were two periods in the history of the Pelican Valley herd without major perturbations to population growth, 1902-1954 and 1968-1995 (Figure 5.4). Rates of increase were not significantly different between these periods; r = 0.056 and 0.051,

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[2] Bison were removed from the Northern range in 1976 (8), 1985 (88), 1986 (41), and in 1988 (2).

respectively. At the end of these periods, first in 1956 then again in 1996 and 1997, culling and harsh winter weather reduced the size of the population (Meagher 1973, Taper et al. 2000).

The Mary Mountain subpopulation experienced a period of relatively constant growth between 1936 and 1955 before managers intervened to reduce the herd in 1956; a severe winter that year further affected the population (Meagher 1973). The highest observed growth capacity of the Mary Mountain population was 0.156 during 1936-1954 (Figure 5.5). 1970 to 1981 was another period free of perturbations and the Mary Mountain bison herd increased at a slightly lower rate of 0.13 (Figure 5.5).

Taper et al. (2000) proposed range expansion as a mechanism explaining stable population growth; we refer to this as ‘the density-equalization effect’. As the Central (Mary Mountain and Pelican) and Northern range populations increased in size (prewinter maximum count), the area they occupied in mid winter expanded within available grassland and meadow habitat (Figures 5.6 and 5.7). The pattern of range expansion was gradual and linear, differing from the pulsed pattern described for the Mackenzie wood bison population in the Northwest Territories (Gates and Larter 1990, Larter et al. 2000), the only other documented bison population eruption. In that case, population growth rate declined as density approached a threshold of approximately 0.55 bison /km$^2$. Then bison spilled over into the next available habitat temporarily reducing density, increasing per capita resources, with renewal of the growth rate of the population (Larter et al. 2000); the cycle was repeated twice. This pattern of increase to high density followed by expansion into new range is similar to that described for exotic ungulates in New Zealand (Caughley, 1970*a*,*b*) and for muskox reinvading their historic native range (Reynolds, 1998).

Differences in landscape composition and configuration between the Mackenzie and YNP bison ranges explain the different patterns of range expansion. Bison foraging habitat in the Mackenzie range occurs in discrete, widely spaced patches representing <6% of the landscape within a boreal forest matrix (Larter et al. 1991*a*,*b*, Matthews 1992). In contrast, the Northern and Central bison ranges of YNP consist of large tracts of continuous grassland and meadows connected by corridors containing foraging habitat and relatively short distances of non-foraging habitat (Chapter 3). The connected landscape of YNP bison ranges permits gradual expansion whereas the fragmented landscape in northern Canada supported pulsed expansion. We found evidence of only one exception to this rule. In the harsh winter of 1996-1997 a cow/juvenile of six dispersed south of the park following the groomed road out the south entrance, joined the Jackson herd and never returned[3]. Of interest, three mature bulls from Mary Mountain moved to near Jackson Lake the previous year; they returned to the Hayden Valley for the rut and repeated the migration for several years[4]. Exploratory movements by some mature bulls is characteristic of bison populations (Gates and Larter 1990).

Temporal patterns of density and population growth also differed between bison in northern Canada and YNP. Larter et al. (2000) described a cyclical pattern when population density was plotted against instantaneous growth rate. Population growth rate and density increased until population density exceeded approximately 0.55 animals/km$^2$. Once this point was reached both rate of growth and density decreased and the cycle

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[3] Interviews with R. Wallen (23 July 2004) and Steven Cain (11 August 2004).

[4] *Supra* note 3.

began again. In YNP, growth rate (r values from Taper et al. 2000) showed an inverse relationship to prewinter population size and density as a function of habitat area for the Central range subpopulation (Figure 5.8 and 5.9) but not for the Northern range population (Figures 5.10 and 5.11).

After increasing through the first decade of the ecological management era, instantaneous winter densities, calculated as bison within 95% kernel areas (Taper et al. 2000), remained relatively steady in YNP bison ranges as the population subunits increased (Figure 5.12). The mean instantaneous density of bison on the northern range between 1971 and 1997 was 3.17 ± 0.19 (s.e.), and 4.20 ± 0.26 for the Central Range bison (data source: Taper et al. 2000); the means were significantly different, t = 3.21, 52 d.f., P = 0.002. However, density calculated as a function of available grassland and meadow habitat area within ranges necessarily increased with population size (Figure 5.13).

Based on these patterns we propose that YNP bison attempt to compensate for declining per capita food resources by increasing the area used, hence maintaining a relatively stable instantaneous density (Taper et al. 2000). However, compensation is not exact; r declines because high quality winter foraging patches (sedge meadows) are limited in overall area (0 to 9.4% of ranges, Chapter 3), they are patchily distributed and depleted first, forcing bison to shift to poorer quality patches as density increases, with the demographic consequences of decreased fecundity and increased juvenile mortality. There is limited evidence from YNP and other populations to test this hypothesis.

Several geographically disparate studies have demonstrated that given a choice, bison preferentially forage in high biomass lowland meadows dominated by sedges and grasses in the winter, including the Mackenzie bison range (Larter and Gates 1991*a*,*b*) and the Slave River Lowlands (Reynolds et al. 1978) in the Northwest Territories, Elk Island National Park in central Alberta (Cairns and Telfer, 1980, Telfer and Cairns, 1986), and in YNP (Barmore 2003, DelGuidice et al. 2001). In 1970, when spring greenup was delayed on the Northern range in YNP, bison continued to forage in areas with deep snow in lowland areas, despite the availability of relatively snow free uplands (Barmore 2003). It is important to consider that bison density in YNP in 1970 was the lowest it had been in many decades; winter grazing would not have depleted standing biomass in lowland meadows to the same extent as at higher densities.

In Elk Island National Park where density was high, foraging bison shifted to snow free upland grasslands in late winter before green up (Van Camp 1975). This may be attributable to reduction of forage biomass in meadows by winter grazing, which by the end of the winter reduced forage availability to a level lower than or similar to the upland meadows. Evidence from the Mackenzie Bison Range (Larter et al. 2000) indicated that the winter diet of a recently established bison population subunit in an expansion area was higher in quality than for the core population. Unpublished results from YNP[5] indicate an increase in use of upland habitats and decrease in use of sedge habitat after the mid 1980s, coincident with a high population size. Between 1968 and 1988 the Northern bison subpopulation in YNP increased from < 100 to > 800. Singer and Norland (1994) compared diet composition and habitat selection for 1967-1970 and 1986-1988 finding that bison consumed less sedge and more grasses at the higher population level,

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[5] Interview with Chris Jerde, 24 June 2004, Edmonton, Alberta. Analysis of survey data series 1970 to 1997 collected by M. Meagher.

increased their habitat breadth, and increased habitat and diet overlaps with other herbivores. In particular, there was moderate diet overlap but high habitat overlap between bison and elk.

Heavy use in summer and winter has been recorded on YNP grasslands. Dawes and Irby (2000) studied forage production and utilization during two years, 1996 and 1997, in the Madison, Gibbon and the Firehole drainages at a time when the Central bison population was close to a record maximum and severe winter conditions induced high losses from starvation and a record number of management removals from boundary ranges in Montana. They found plant biomass was 54% lower in exposed compared to exclosed plots in high use areas. This apparent high utilization was similar to winter forage removal by herbivores recorded during 1986-1990 on the Northern Range (55%) by Singer and Harter (1996). Working in grassland communities in the Hayden Valley in the late 1990s, Olenicki[6] recorded grassland forage summer offtake of approximately 35%. Meagher (1993) referred to "loss of functional winter range" in the Hayden Valley resulting from heavy grazing during the summer and fall. Taper et al. (2000) reiterated this explanation and in addition suggested that soil compaction by large numbers of bison was causing damage to geothermal areas on Fountain Flats.

The mechanisms underlying regulation of YNP bison subpopulations have received limited attention by researchers. Food mediated density dependent effects on calf survival were suggested in a review of available information by Cheville et al. (1998). DelGuidice et al. (2001) studied the nutritional status of bison on different ranges, concluding the Pelican Valley was the harshest environment based on metabolic indicators. Extreme winter severity has caused significant starvation mortality, primarily of calves (DelGuidice et al. 2001). In a study conducted between 1963 and 1969 when the YNP bison population was small, Meagher (1973) found pregnancy rates for cows 2.5 years and older was only 52% and most cows did not reach sexual maturity until 4 years. Taper et al. (2000) suggested delayed maturity and low fecundity in Yellowstone bison are likely responses to severe winter climate and sub-optimal forage availability. In contrast, 82% of 45 females culled at West Yellowstone in winter 2001-2002 were pregnant (Gogan et al. 2002). The different rates obtained at these two times may indicate a high degree of lability in pregnancy rates in response to variable nutrition, or differences in methods. The reader is referred to Reynolds et al. (2003) for a review of pregnancy rates in other bison populations.

Predation on bison by wolves can also be an important limiting factor for bison populations and is the subject of current research in the central and northern portions of the park and the Pelican Valley. Similar to the numerical response seen in other wolf–prey systems (Messier 1996), wolf populations in the Mackenzie Bison Range, Northwest Territories (Larter et al. 1994) and Wood Buffalo National Park (Joly and Messier 2000) were shown to respond numerically to increasing bison population size. In the Mackenzie bison range, wolf predation became a significant mortality factor, particularly for bison calves, about 20 years after bison were reintroduced to the area (Larter et al. 1994). Predation is a significant limiting factor for bison in Wood Buffalo National Park in the presence of tuberculosis and brucellosis (Joly and Messier 1998). Wolves attack bison calves preferentially over older age classes of this species (Larter et al. 1994, Carbyn and Trottier 1998, Smith et al. 2000, Jaffe and Garrott 2001).

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[6] Interview (July 22, 2004) with Tom Olenicki and unpublished data.

Elk are the dominant herbivore and the primary prey of wolves in YNP (Smith et al. 2004*b*). Elk represented 92% of 1582 wolf kills recorded from 1995 to 2001 (Smith et al. 2004*b*). Unlike bison, wolves are more readily able to kill adult elk; calves represented 43% of wolf-killed elk, cows 36% and bulls 21% while these classes represented 15%, 60% and 25% of the population (Smith et al. 2004*b*). Bison are rarely killed by wolves on the Northern Range; typically only when individuals are weakened by starvation or injury (Smith et al. 2000). Most bison killed by wolves have been recorded in Central YNP where elk are substantially less abundant during the winter months than on the Northern Range. A numerical response by wolves to bison is possible in the Central Range of the park where bison is becoming increasingly important in their diet. Wolves prey almost exclusively on bison in the Pelican Valley where elk are not available during the peak of winter (Smith et al. 2000, 2004a). Similarly, bison are a significant component of the winter diet of wolves in the Mary Mountain range and Cougar meadows area near West Yellowstone.

Wolves are more successful killing elk than bison; bison were killed in 7% of 57 interactions compared to 21% of 372 interactions between wolves and elk (Smith et al. 2000). Elk outnumbered bison in YNP 5.6:1, yet the ratio of elk:bison killed by wolves between 1995 and 1999 was 47.6:1 (Smith et al. 2000). In three years of study in the Madison-Firehole area, Jaffee and Garrot (2001) located 101 definite and 29 probable wolf kills, including 70 elk calves, 34 cow elk, nine bull elk, one unknown adult elk, 13 bison calves, one cow bison, and one unknown bison.

Future effects of predation on bison population dynamics in YNP is an important research focus. We suggest that wolf predation on bison will continue to increase in the Central ranges, but not on the northern range as long as elk are relatively more abundant there. In systems where wolves show a numerical response to an abundant prey species that is difficult to kill, predation rate on easier prey can be inversely proportional to their density (Dale et al. 1994; Messier 1996), which could lead to extirpation of easier prey species. Examples of this phenomenon include woodland caribou (*Rangifer tarandus*) in a wolf–moose system (Seip 1992) and moose in a wolf-bison system (Larter et al. 1994). To critically evaluate if wolf predation on elk is acting or will act in an inverse density-dependent fashion in the Central YNP bison ranges will require measurement of both the numerical response of wolves and the killing rate per predator, i.e. the functional response. It is important to emphasize that, as with plant-herbivore dynamics, predator prey relationships are different on the Northern and Central YNP ranges.

## Distribution and Movement Patterns

With cessation of management interventions to control population size after 1967, bison began to increase in each subpopulation unit in YNP. Winter distribution and movement patterns changed over time as the population increased in size (Figure 5.14). Meagher et al. (2002) provided a thorough description of changes in distribution and movement patterns and suggested winter road grooming may have “...upset a delicately balanced demography and caused the expansion” (Meagher et al. 2002:146). Considering the evidence, we suggest the plausible mechanism underlying changes in winter distribution was the density-equalizing effect of range expansion described above, whereby density remained relatively constant as the population increased owing to an increase in area occupied (Taper et al. 2000). Although groomed roads facilitate movements within and among winter habitat patches, range expansion would have occurred regardless as bison responded to intraspecific exploitative competition. In only one instance (Firehole to Mammoth corridor) might a road have been the factor underlying range expansion into areas that would not otherwise have been used. The evidence for this is presented below.

Patterns of range expansion during 1970 to 1997 were analyzed by Taper et al. (2000). They mapped changes in the mid winter utilization distribution of bison using kernel home range analysis (Seaman and Powell 1996) and kindly shared the distribution maps with us. The key temporal changes in the pattern of winter distribution evident in Figure 5.14 were:

- the instantaneous area occupied increased with population size as previously noted;
- when population subunits were small, there were four primary wintering areas: the Pelican Valley, Hayden Valley, the Firehole, and the Lamar Valley;
- range use west of Tower Junction on the Northern range was first evident in the 1975 distribution, then increased thereafter;
- range expansion into the Mammoth-Gardiner area by the Northern population subunit was first evident in the 1983 distribution and increased thereafter;
- the entire Northern Range subpopulation may move to the Gardiner basin under harsh winter conditions (e.g. February distributions 1992 and 1997) where it may be subject to significant management actions;
- when Central subpopulations were small, the distance between Pelican Valley and Hayden Valley winter distributions was shorter than the distance between the Hayden Valley and the Firehole distributions;
- The areas used by bison in the Pelican and Hayden Valleys increased with population size and gradually coalesced;
- expansion of the Lamar subpopulation to Madison Junction was first evident in the mid 1970s;
- range expansion in the Madison River drainage towards the park boundary north of West Yellowstone progressed gradually thereafter, encompassing the park boundary by 1987 and every winter thereafter;
- the distribution maps illustrate the first measurable use of the Norris Geyser Basin occurred in 1986 and at Swan Lake Flats in 1991;
- bison used the Norris to Swan Lake area every winter after 1991;
- geothermal habitat in the Central Ranges is always used by a significant portion of the Central subpopulation.

The combined area from Madison Junction to the western boundary and north from Madison Junction is referred to as the West Side[7]. Forty to 50 bison had been reported wintering in the Cougar meadows (located in the West Side area) in 1956 and some were seen again in 1959 (Meagher 1973:36), but were not recorded again until 1974; there were no records indicating surveys during the intervening years. Two were observed in

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[7] Definition provided by M. Meagher.

1974 and again in 1978 (data source: M. Meagher survey data series). Six were counted in 1980; numbers increased thereafter. The number of bison using the West Side increased linearly (natural log transformed) with the number of bison in the Central subpopulation between 1978 and 1997 (Figure 5.15; data series provided by M. Meagher, M. Taper and C. Jerde), consistent with the pattern of range expansion by which density was equalized. The threshold Central Range population above which expansion into the West Side occurred was approximately 1,000 bison (converted x axis intercept, Figure 5.15). There was no detectable effect of mid February snow cover (SWE) on the number of bison occurring on the West Side. In contrast, Bjornlie and Garrott (2001) found a positive correlation between SWE at the Canyon SNOTEL site and the number of bison in the Madison-Gibbon-Firehole area during the winters of 1997-1998 and 1998-1999, with peaks in the number of bison in April both years.

Cheville et al. (1998) found that movements to the boundary of YNP (represented as removals) were influenced by total population size above 3,000 and snow conditions (SWE). We argue (see above) that winter ecology of bison on the Northern and Central Ranges is different and separate examination of bison trophic ecology and population dynamics is warranted. Accordingly, removals at the western boundary occurred at Central Range prewinter populations above 1500 (Figure 5.16). Consistent with Cheville et al. (1998), we found snow conditions and population size contributed significant effects in the Central Range. Similarly, on the Northern Range we found at populations above 550, population size and snow had significant effects on removals at the northern boundary (Figure 5.17).

Movements of bison between the Central Range and the Northern Range have been reported historically via the Mirror Plateau corridor (Chapter 4; Meagher 1973). The exchanges occurred in the late fall to early winter period before deep snow precluded movement in the high country. Since the 1990s, bison have migrated along the road allowance and adjacent habitat between the Firehole (Taper et al. 2000, Meagher et al. 2002) and the West Yellowstone area[8] and to the Northern Range near Gardiner Montana. In some recent winters, large numbers of bison have used this migration pathway (Meagher et al. 2002). Bison from the Central Range may reach and be subject to management actions at both the western and northern boundaries. To date there is no evidence that Northern Range bison have moved to the western boundary. Because of inter-range movements, it is important to look at the overall relationship between bison population size and total removals (Figure 5.18). Similar to Cheville et al. (1998), we found significant effects for total prewinter population size and average snow conditions in February on total removals; the model explained 73% of overall variance in boundary removals (Figure 5.18).

Until recently, when radio transmitters were used to monitor the movements of individuals[9], inferences about subpopulation interchange and movement patterns were based on anecdotal observations, limited records of neck banded bison, observations

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[8] Interview with Peter Gogan and Ed Oelexa, USGS, 21 July 2004: commented that radio collared bison captured and released in November 1996 13 km north of West Yellowstone were later captured 3 km from Gardiner, Montana.

[9] Keith Aune (Montana Fish Wildlife and Parks) and Tom Roffe (U.S. Fish and Wildlife Service, Bozeman, MT) deployed 52 VHF radio collars and 11 GPS collars on bison in YNP during 1995-1998. Pete Gogan and Ed Olexa radio collared (VHF collars) approximately 100 bison in YNP during late 1997 and March 1998. Rick Wallen, NPS, Yellowstone NP) deployed 13 GPS collars on bison in late 2003.

made during periodic aerial surveys (Meagher 1973, 1993, Taper et al. 2000, Meagher et al. 2002), and one specific study that examined winter movements in the Firehole-Madison-Norris area (Bjornlie and Garrott 2001). Meagher (1973) summarized historical information on distribution and movement patterns of Lamar and Pelican bison prior to 1936. Bison wintered in separate areas in the central Lamar Valley and in the Pelican Valley. Some time between 1915 and 1920, the summer ranges of Lamar and Pelican bison overlapped on the Mirror Plateau and Upper Lamar drainage. The pattern was one of mixing on the summer range followed by return to the respective winter ranges in the fall or early winter. There was little evidence that Pelican Valley bison ranged into the Hayden Valley before bison were reintroduced there in 1936. Meagher (1973:31) refers to one file report containing a penciled notation about "some bison in the Hayden Valley in 1930-31".

Within a decade of the reintroduction of 35 bison into the Lower Geyser Basin at Fountain Flats and 36 into the Hayden Valley in 1936, winter movements between the Hayden Valley and the Firehole were noted. McHugh (1958) reported 54 bison moved 10 km over the Mary Mountain Trail through 107 cm of snow in March 1945. As the number of bison in the Hayden Valley and the Firehole increased the areas they occupied increased and movements between ranges occurred during all seasons including the rut. The herds were considered merged into one population first given the cumbersome name of the Hayden Valley-Nez Perce-Firehole herd (Franke in press). It was later dubbed the Mary Mountain herd, referring to the height of land between the two ranges over which bison maintain a trail (Meagher 1973: 86).

Frequent interchanges between the Lamar and Pelican populations were evident from survey data. Meagher (1973: 87) noted significant shifts between these populations during 6 of 15 years between 1935 and 1950 when decreases in the number of bison on Lamar winter range coincided with increases in Pelican Valley or vice versa. Meagher (1973) explained that such shifts occurred less frequently (2/15 years: 1941 and 1946) between the Pelican and Hayden Valleys during the same period. In the harsh winter of 1956 a mixed herd of about 24 bison broke a trail from the Pelican Valley to the Hayden Valley through deep snow along the east side of the Yellowstone River (Meagher et al. 2002:140). Notably, the number of bison counted in the Pelican Valley that year was approximately the same as the number present in the early 1980s when bison from the Pelican Valley were again observed to move in winter to the Hayden Valley (Meagher 1993). Movement of a significant number of bison into the Pelican Valley was suspected in 1964-65 (Meagher 1973: 88).

As the Mary Mountain and Pelican Valley populations increased after 1970, the area they occupied gradually increased, eventually coalesced (Figure 5.14), and movements between ranges became fluid throughout the year, including the winter. Consistent with the high rate of bi-directional movement observed in winter over the Mary Mountain Trail connecting Hayden Valley and the Firehole (Bjornlie and Garrott 2001), VHF radio collared bison were documented moving between the Pelican and Hayden valleys continuously in most seasons during 1997-1998 and 1998-1999 including the winter months[10]. The movements of radio collared bison during mid summer 1998 and 1999 were consistent with the observation by Meagher et al. (2002) that Pelican Valley bison

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[10] P. Gogan and E. Olexa of the U.S. Geological Survey monitored the movements of 103 radio collared bison during 1997 - 1999

no longer moved up into the Mirror Plateau and slopes of the Absaroka Mountains where they previously had shared summer range with the Lamar herd for > 60 years. However, in 1998 and 1999 some radio collared bison moved to the Mirror Plateau from the Pelican Valley in the fall, after the rut[11]. The Central Range subpopulation, including the Pelican Valley herd, has developed a pattern of nearly exclusive aggregation in the Hayden Valley during the rutting season (Figure 5.19).

The scale of movements dramatically changed with population size. Although Central Range bison return to the Hayden Valley for the rut, the scale of movements in other seasons is extensive. Individual radio collared bison may move from the Hayden Valley to the western and the northern boundaries within the same year. Examples from recently GPS collected collar data[12] illustrate some of the variety of individual movements occurring in the Central Range (Figure 5.20 – 5.24). One cow remained entirely within the Mary Mountain range (Figure 5.20). Another included the Madison Valley and habitat in the western boundary area (Figure 5.21). Three others included parts of the Northern Range (Figure 5.22 – 5.24). The last two movement patterns (Figures 5.23 and 5.24) illustrate novel movements between Canyon Junction and Norris Junction and from Norris Junction north to Blacktail Deer Plateau following routes not identified by key informants in this study.

The data now being obtained from GPS collars will allow key questions about movement ecology to be addressed, including the timing and extent of movements in relation to plant phenology, snow conditions, forage production and utilization. In addition, with this technology research is now possible to address questions about the effects of roads and other anthropogenic or natural features on movements about which some uncertainty remains.

The influence of roads on movements has been questioned since the early 1990s (Meagher 1993; Meagher et al. 2002). Evidence presented above for the Northern Range indicates that population size above a threshold of about 550 is a driver of movement to lower elevation range in the Gardiner basin and egress is positively correlated with snow pack (SWE). A large proportion of the population has been documented to move to the Gardiner basin in harsh winters when the population exceeds 550. Roads were plowed in the Northern Range starting in the late 1940s. Bison follow either the plowed road or a natural corridor along the Yellowstone River (Figure 5.1). Stress induced movement to the Gardiner basin along the Yellowstone River corridor was documented before road plowing began (Cahalane 1944*b*); at 750 head in winter 1942-1943. It is evident that closure of the road in winter will not prevent movements of bison to the Gardiner basin. Indeed, 12 years of attempting to control and contain bison movements failed, e.g. bison detoured around obstacles placed along the corridors (Meagher 1989*a*). The Gardiner basin is at the lower end of an ecological gradient. It can be considered refuge habitat in harsh winters much the same as geothermal habitat serves this ecological role for bison in the Central Range. Bison are familiar with the Gardiner basin (Meagher 1989*b*) and there are no evident biophysical barriers to movement. Under current management, a large proportion of the Northern herd could be subject to removal in a harsh winter, particularly if bison from the Central Range arrive early and defined thresholds for

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[11] *supra* note 11

[12] To illustrate types of movements currently occurring we selected GPS location data for 5 of 13 bison provided by R. Wallen of NPS/YCR on February 25, 2005.

holding and tolerance of free-ranging bison are reached before Northern Range bison arrive. The bison population on the Northern range has existed as a semi-independent subunit and exhibits biological traits distinctive from Central range bison[13], including genotypes (Halburt 2003), fetal growth rates (Gogan et al. accepted, revision submitted), and tooth wear patterns (Christainson et al. *in press*). Assessment of an objective minimum viable population for the Northern Range is an important outstanding task under the adaptive management intent of the current bison management plan.

Under current policies, range expansion beyond the boundaries is limited by management interventions, primarily culling or hazing. Tolerance for bison in the Gardiner basin and West Yellowstone areas outside the park is defined in the current management plan as the modified preferred alternative. The plan does not provide for unlimited range expansion, a density-related phenomenon. Management zones 2 and 3 outside the western boundary of YNP have 25 $km^2$ and 7.3 $km^2$ of bison habitat, which if available could support 100 and 29 bison respectively at the instantaneous density typical of Central Range bison. Management zones 2 and 3 outside the Northern boundary offer 17.6 $km^2$ and 83.3 $km^2$ of habitat and would support 56 and 266 bison respectively at the typical winter density of the Northern Range bison subpopulation. We consider the Gardiner basin to be refuge habitat and an important component of the Northern winter range.

In contrast, the Hebgen Lake area offers no unique ecological value as winter range; we consider it an expansion area for the Central subpopulation. Even if this area is used to capacity, at densities above 4 /$km^2$ bison would continue expanding into adjacent range to equalize density, if permitted to do so. In 2003, in an effort to create winter range opportunities for bison where there are no conflicts with livestock, the National Wildlife Federation paid two Idaho based ranchers for their grazing rights to an allotment in the Caribou-Targhee National Forest, thus providing an alternative for cattle grazed in the Horse Butte grazing area[14]. Even if additional habitat is acquired in this area and bison are permitted to occupy it, the question remains about the extent to which continued range expansion is desirable in this area of Montana; moving the boundary will simply delay the required debate, but not for long.

Under the Interagency Bison Management Plan, state and federal agency officials either haze bison that leave YNP back into the park, or bison are captured and tested for brucellosis and those testing positive are slaughtered. Removals at the boundary temporarily reduce the density of the park population, diminishing the magnitude of density dependent effects on survival and reproduction from resource limitation within the park bison ranges. Either range expansion or removals at the boundaries compensate for forage limitation effects within the park on fecundity and particularly juvenile survivorship. Hazing bison back into the park should result in maintaining density dependent effects caused by exploitative competition. The additional energetic cost induced by hazing should accentuate the negative effects of resource limitation for bison

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[13] Interview with Peter Gogan, USGS and John Gross, NPS, 21 July 2004.

[14] National Wildlife Federation and the Montana Wildlife Federation. 2003. Yellowstone Bison Given More Room to Roam. Outdoor News, http://www.huntingandfishingjournal.org/archives/issues/wcr_horsebutte_ens_4-2003.php, Copyright Environment News Service (ENS) 2003. Republished with permission from ENS online at: http://ens-news.com.

exposed to this action. The ethical question of increasing physiological stress by hazing is a matter for deliberation.

Biophysical conditions are more complex in the Central Range than the Northern Range (e.g. refuge geothermal habitat is embedded within the winter range; ranges are separated by linear corridors), making it challenging to readily distinguish between the alternative hypotheses proposed by Meagher et al. (2002)[15]. The central question to be addressed is: In the absence of road grooming would bison in the original winter ranges in the Central Range (Firehole, Hayden, Pelican) have remained spatially isolated and demographically independent owing to deep snow in the movement corridors separating them?

Snow cover is an important determinant of ungulate trophic ecology, energetics, population dynamics and spatial ecology (Turner et al. 1994). Systematic research has not been carried out on the ability of bison to move through snow under the variety of circumstances present in Yellowstone National Park. All available information for YNP is anecdotal or the opinion of experts. Meagher (1973:73) commented that cow/juvenile (mixed) herds travel in line through deep snow, plunging to create trenches several feet deep, "frequently for more than a mile". In Pelican Valley bison were observed foraging through snow 102-114 cm and moving to areas with lower snow cover when depths exceeded 127 cm (Meagher 1971). Snow depths in interior YNP exceed those recorded for bison ranges in Elk Island National Park (< 70 cm, Van Camp 1975) and the Slave River Lowlands (< 65 cm, Reynolds and Peden 1987), hence data from those studies provide little inference about maxima at which foraging or movements become severely restricted. Van Camp (1975) suggested impediment of movement by adult bison starts at snow depths < 65-70 cm. For their model, Turner et al. (1994) used a maximum depth of 180 cm at which foraging ceased, based on expert opinion.

We inferred from the available information, key informant interviews and technical workshops, that the factors influencing movements important for designing research include the following:

- snow depth, density, and hardness (crusting);
- terrain (slope, ruggedness);
- habitat, including forage attributes (species, biomass, quality), patch size and dispersion;
- geothermal influence on snow depth and dispersion of low snow patches or linear thermal features such as streams;
- class of bison (e.g. mixed groups vs. mature bulls);
- group size of moving bison, and their behaviour (dominance and changing lead);
- distance attributes, e.g. length of the corridor between origin and destination ranges;
- index of bison condition;
- familiarity with destination;
- quality of destination;

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[15] Meagher et al. (2002:145) proposed 1) winter road grooming facilitated range expansion that "would have occurred anyway", or 2) alternatively, "an apparently minor change [road grooming] has upset a delicately balanced demography and caused the expansion".

- trails broken previously by bison moving in the corridor;
- number of bison on either side of a corridor; and
- per capita forage availability in ranges on either side of a corridor.

Three studies on use of groomed roads by bison and interactions with Over Snow Vehicles (OSVs) have been conducted in Yellowstone National Park in recent years (summarized in Appendix III). There is sufficient evidence from these studies and other sources (e.g. Meagher 1993) to conclude that groomed roads facilitate travel within traditional foraging areas and between ranges, where they are present. However, bison appear to use sections of road in winter where they are convenient. As a testable hypothesis we suggest bison do not typically use roads where they are not aligned with pathways that can be predicted based on terrain and habitat features and bison behaviour. Consistent with this hypothesis, bison rarely use the following groomed road sections: Canyon to Norris; the east entrance road to Sylvan Pass; the south entrance road south of Old Faithful; or the western half of the groomed road between Seven-Mile Bridge (on the Madison River) and West Yellowstone. Friction modeling is one method that can be used to predict movement pathways for bison based on preliminary information or expert opinion (Gates et al. 2001). Such modeling would allow comparison of pathways predicted based on decision rules in the virtual absence of roads with actual pathways selected by bison under varying conditions (GPS locations) including groomed roads.

The Pelican to Hayden Valley corridor has been of particular interest to some stakeholders. At 8.3 km, this corridor is the shortest of the Central Range corridors (Figures 5.1, 5.25); by comparison, the Mary Mountain Trail is 19 km. There is slightly more habitat in the Pelican-Hayden corridor than the Mary Mountain Trail (51% vs. 44%), and less snow on average (SWE 13 vs. 20 cm). The west face of Mary Mountain represents a long, steep incline while there is little elevation gradient in the Pelican-Hayden corridor. Other than the greater amount of geothermally influenced terrain in the Mary Mountain Trail we see no reason to consider the Pelican-Hayden less permeable than the Mary Mountain Trail, indeed it appears more permeable. It is instructive to repeat that in winter 1956, long before roads were groomed, a mixed group of about 24 bison was observed to break trail in the deep snow through the Pelican-Hayden corridor (McHugh 1958). Meagher (1993:12) also observed a major trail in unconsolidated snow along the east side of the Yellowstone River in winter 1991-1992. In August 2005, we observed a well used bison trail on the power line located < 1km west of the Yellowstone River in the Pelican-Hayden corridor (Figure 5.25). Open linear features such as this have been observed to influence movements of other ungulate species. Their influence on bison movements in any season in YNP has not been examined.

Roads were used by snow coaches (heavy tracked vehicles) many years before road grooming began. The first permit for a snowcoach operator to bring tourists intoYNP (Yochim 1998*a*) was granted to a businessman in West Yellowstone in 1955 (Aune 1981, Bjornlie and Garrott 2001). The packed snow in the trails of these vehicles would have had snow hardness similar to groomed road surfaces and could have provided movement pathways for bison. Cheville et al. (1998) questioned why groomed roads were not used by bison for inter-range movements when first available in the Central Range. They suggested the delay may have been due to a threshold density effect above which expansion to new ranges occurred and population pressure induced bison to maintain pathways between ranges. They explicated that attributing population increase to road grooming rather than the use of groomed roads to population pressure reverses cause and effect. Given the evidence, we concur for the most part with their assessment. However, groomed roads may have induced range expansion and development of a migration corridor by the Central subpopulation into the Northern Range along the Madison Junction to Swan Lake Flats corridor section where in the absence of road grooming, snow and topography of the Gibbon Canyon could otherwise have been a barrier to movement.

There is however some uncertainty about the nature of the effect of the Gibbon Canyon section of the corridor that cannot be resolved without further study. Key informants expressed conflicting opinions about the effect that closing the road to grooming would have on bison migrating to the Northern Range. Some commented that despite the rugged terrain in Gibbon Canyon, the geothermally influenced drainage provides reduced snow depth and affords opportunity for bison to navigate through the canyon, a distance of approximately 6 km (Figure 5.26). Most suggested that in the absence of road grooming, bison would not be able to push through deep snow on the road allowance in the canyon. The areas surrounding the canyon are steep and heavily forested and appear to offer limited potential for winter movements. A power line located approximately 1 km east of the road could provide an alternative pathway (Figure 5.26). In August 2005, we walked the power line to determine if it was used by bison and found no evidence to suggest it is used in the winter; there were few droppings and all appeared to be loose stool typical of summer rather than well formed droppings characteristic of winter. We concluded the power line is not currently used by bison moving to and from the Gibbon and Norris Geyser Basins in winter and there is very limited use of the power line in other seasons at the present time.

Despite the absence of specific research on bison movements in snow, we consider there is sufficient anecdotal evidence to suggest that once bison are familiar with destination ranges within the Central Range, range expansion will occur as a function of population size. If numbers are sufficient, bison will maintain trails (trenches in the snow) in most corridors, except the Pelican-Lamar and Firehole-Northern Range corridors, in the absence of road grooming, and movements between Central ranges will be fluid. However, the ability of bison to move through the Gibbon Canyon and further north to the Mammoth area in the absence of road grooming is an important consideration. The Gibbon Canyon could serve as a topographic gate preventing Central Range bison from migrating to the Northern Range once snow accumulates. Given the large number of Central Range bison moving in some years to the north boundary and the potential consequence for inequitable culling of the Northern subpopulation, the role the Gibbon Canyon as a potential barrier to movement is an important research question.

Finally, it is necessary to comment on the hypothesis that groomed roads reduce the energy cost of displacing snow during movements within and between winter ranges and energy saved from the reduced cost of locomotion mitigates winter kill and enhances calf survival, resulting in a higher rate of population increase than would otherwise occur (Meagher 1993). The effect, if any, was not registered in a detectable difference in the rate of increase in the Pelican Valley population during long periods before and after road grooming occurred (Figure 5.4). Bjornlie and Garrott (2001:560 and 570) posited that any energy saved by not displacing snow during travel on roads may be countered by losses associated with stress induced by a high encounter rate with OSVs. The proposed mechanism for this hypothesis is complex and it would be difficult if not impossible to design an experiment(s) to test it. However, it is worthy of investigation through systems modeling, the subject of the next chapter.

## Conclusions

The long term data set on bison population size and distribution in an area as large as YNP spanning more than a century is unparalleled in large animal ecology. Mary Meagher is to be credited with compiling much of the available data, first in her seminal publication of 1973, then systematically collecting data annually for over 30 years. Her attention to detail generated a data set for the period 1970 to 1997 that is not yet fully explored. In particular, population rates of increase presented in Taper et al. (2000) should be recalculated based on annual changes in the adult population (> 1 year old), rather than on the maximum annual count, to account for variation in annual productivity (calves/100 cows) related to winter severity and previous summer forage production. Since 1997, population monitoring has been somewhat inconsistent and data do not provide the same opportunity for continued analysis. A population monitoring program is needed that will provide for: 1) annual estimates of adult population size (< 1 year); 2) fecundity (calf production); 3) winter density distribution, i.e. during the period when distribution is most responsive to forage limitation; 4) inter-annual population rate of increase; and 4) seasonal and annual calf and adult mortality.

Ecological conditions are markedly different on the Northern and Central bison ranges requiring separate consideration of population and trophic ecology. On the Northern Range, reduced snow cover in the grassland habitat of the Gardiner basin provides refuge habitat for bison during harsh winters. In contrast, there is no range-wide gradient in snow conditions on the Central Range. Rather, geothermally-influenced areas provide refuge for a significant part of the Central subpopulation in harsh winters.

The data compellingly support the interpretation that YNP is a forage-limited system, where bison density coupled with snow conditions are the key drivers of bison distribution and movements. The evidence indicates that the population experiences density dependent effects on population growth despite range expansion that equalizes instantaneous density as the population increases. With two exceptions, the pattern of range expansion is gradual rather than pulsed. On both ranges, the instantaneous area occupied in winter (aerial survey data) increased linearly as a function of population size. Removals at the western and northern boundaries to control egress of bison from the park were a direct function of population size, influenced by snow conditions. The relationships were strongest for populations above 1500 for the Central Range and 550 for the Northern Range.

The only period in the Park’s history when a subpopulation may have been completely isolated and spatially independent of others was in the early years (before 1920) when the Pelican Valley population was the only free-ranging population in the park. Apparent isolation of bison in separate winter ranges when populations were small likely reflected high per capita availability forage and the low pressure to move or expand. From the evidence, we infer that as populations grew, the area they used expanded, and distributions eventually coalesced. Anecdotal information on bison movements suggests they can break trail for considerable distances through deep snow, but in addition to forage limitation, knowledge of destination is likely an important motivation. At the present time, there remain two relatively separate subpopulations, one on the Northern Range and the other on the Central Range. Some exchange has occurred since the 1920s via the Mirror Plateau. In recent years, there have been major migrations from the Central Range to Gardiner basin via the road allowance between Madison Junction and Swan Lake Flats. The Gibbon Canyon may not be navigable by bison in the absence of snow grooming.

With the possible exception of the Madison Junction Mammoth road section, road grooming likely has not induced range expansion although roads facilitate bison movements within and between winter ranges where aligned with natural movement corridors. Given the evidence, we concur with the assessments made by Cheville et al. (1998): 1); there is a threshold density effect above which expansion to new ranges occurred and population pressure induced bison to maintain pathways between ranges; and, 2) attributing population increase to road grooming rather than the use of groomed roads to population pressure may reverse cause and effect (except for the Madison Junction to Mammoth road segment). There is no evidence to suggest that groomed roads have changed population growth rates relative to what may have happened in the absence of road grooming. Furthermore, the bison population of YNP is likely approaching or has recently reached a state of dynamic equilibrium possibly not seen since the early 1800s. Conclusions formed about spatial and population ecology of bison when the population was increasing or at low densities cannot be readily applied to the dynamics of a population in dynamic equilibrium around a higher range of densities. The system is dynamic and continues to evolve, thus requiring systematic monitoring of key state variables and continuation of basic research on system properties.

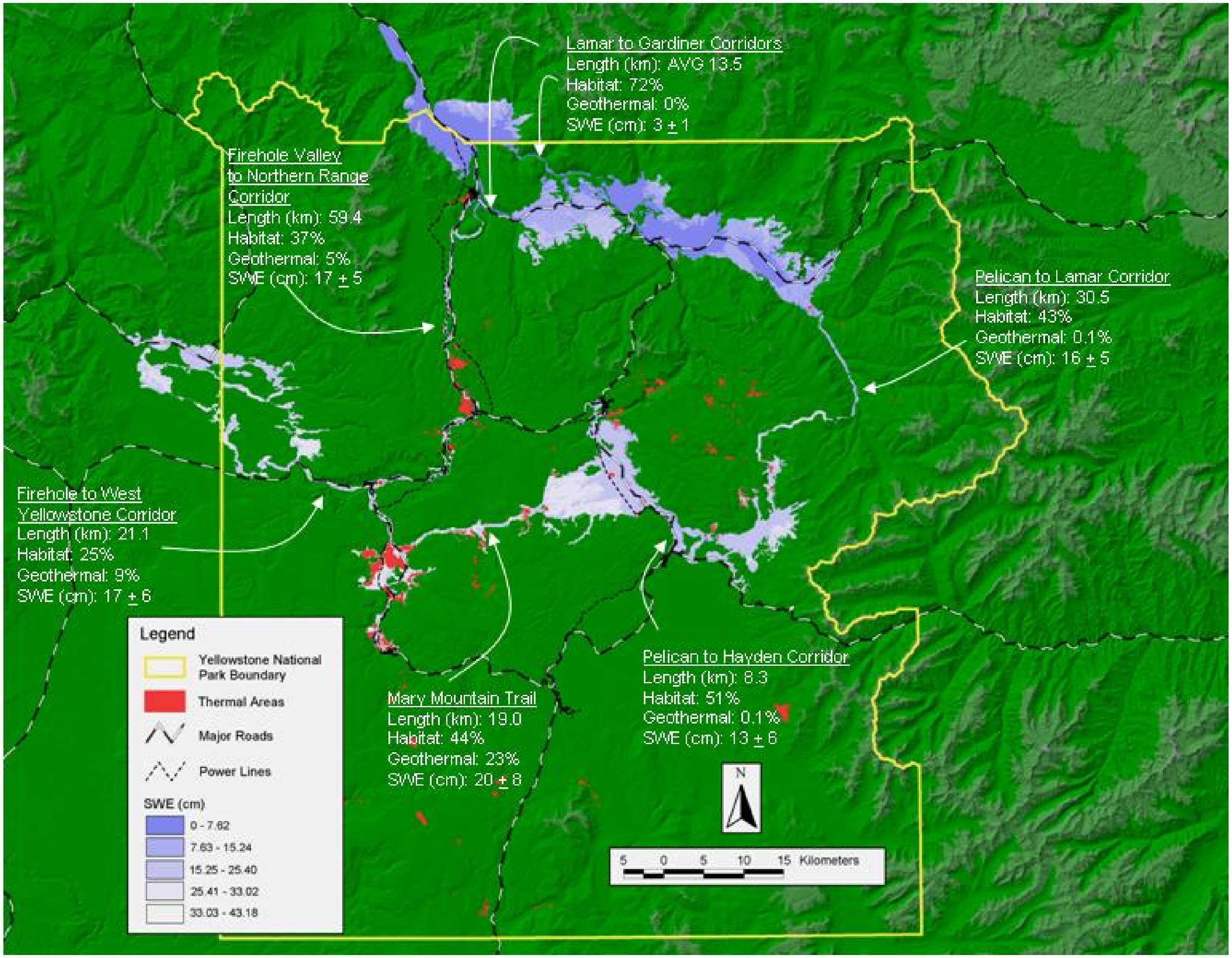
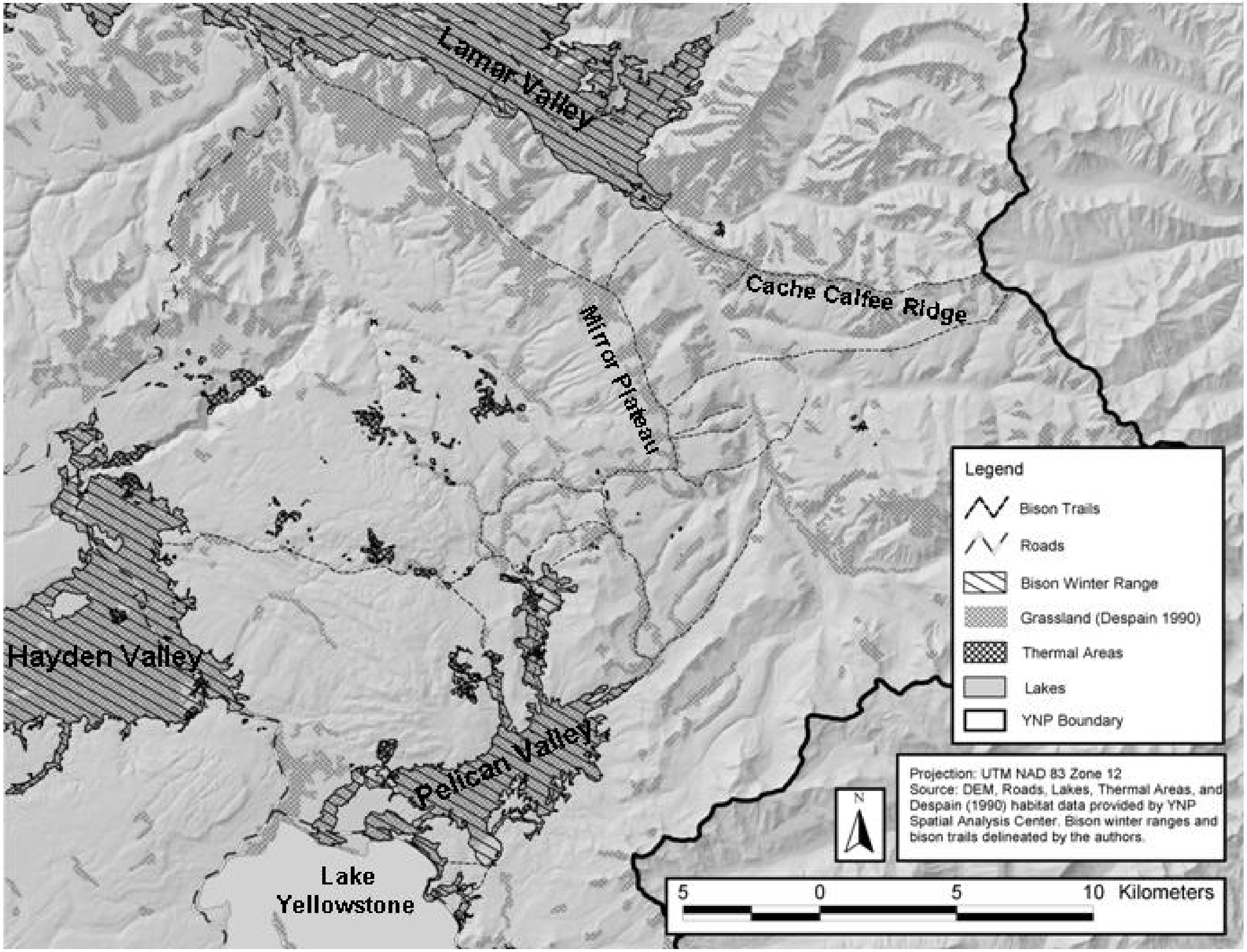


Figure 5.1 Bison winter ranges and movement corridors defined by key informants. Snow conditions (SWE in cm) are represented as shading for February 15th, 1995, an average to slightly above average winter. Corridor characteristics are indicated. SWE is the mean value of Snow Water Equivalence (SWE) on February 15th for the period 1982 to 1999 ± s.d.



Projection: UTM NAD 83 Zone 12
Source: DEM, Roads, Lakes, Thermal Areas, and Despain (1990) habitat data provided by YNP Spatial Analysis Center. Bison winter ranges and bison trails delineated by the authors.

Figure 5.2. Location of historic bison trails between, Hayden Valley, Pelican Valley and Lamar Valley mapped by Mary Meagher during an interview, July 15, 2004.

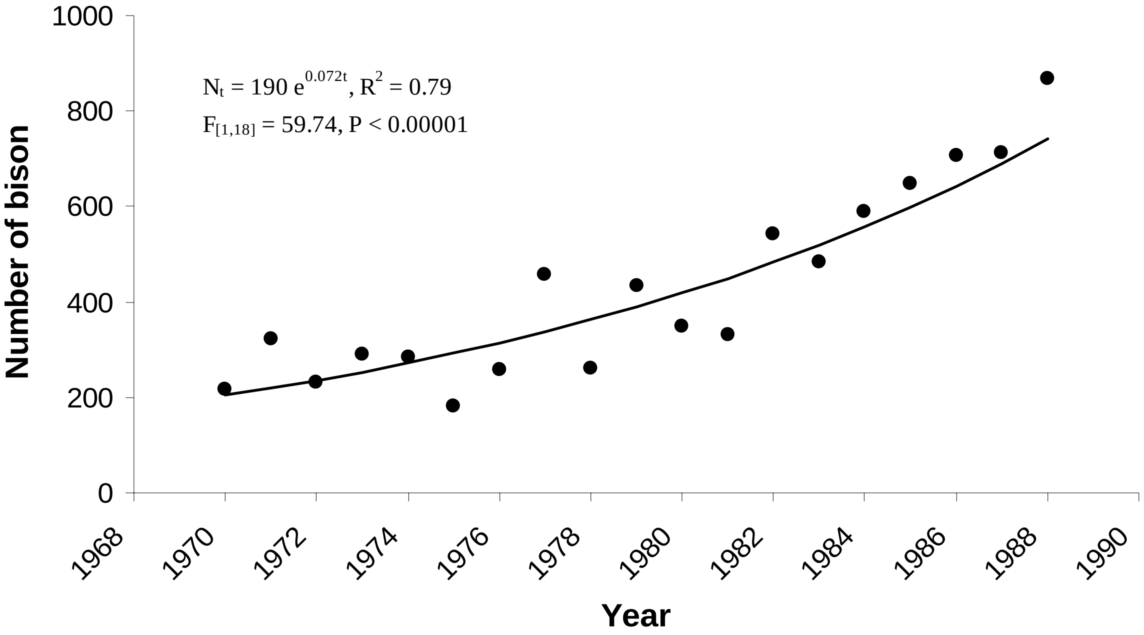


Figure 5.3. Increase in the YNP Northern Range bison subpopulation during 1970 – 1988. Data source: M. Meagher, M. Taper and C. Jerde pers. comm.

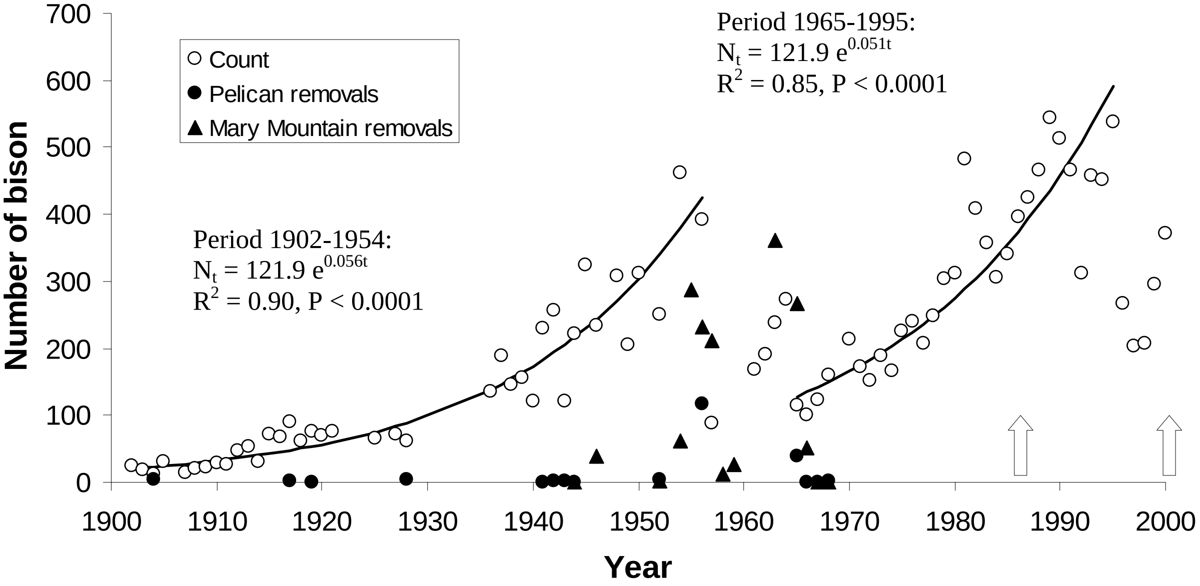
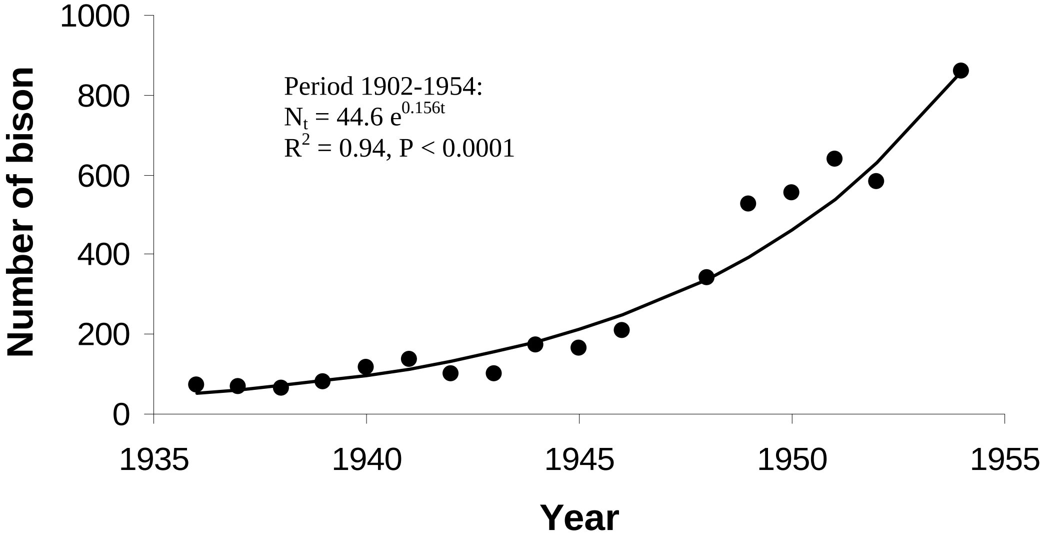


Figure 5.4. Growth of the Pelican Valley bison population during 1902 to 1997 based on mid-winter counts (data sources: Meagher 1973 for 1902 - 1968; M. Meagher, M. Taper and C. Jerde pers. comm. for 1970-1997; Hess 2002 for 1998-2000). Removals prior to the ecological management era (mostly culling and translocations) are indicated for the Pelican and other Central bison ranges. 38 bison removed in 1946 from Mary Mountain are likely those reported by Beal (1950) as falling through the ice on the Yellowstone River. The arrows indicate the harsh winters of 1981/82, 1995/96 and 1996/97. In the latter winter > 1,000 bison were removed at the boundaries of the park. Exponential rates of increase (r) of the Pelican Valley population (mid-winter counts) did not differ between the periods 1902-1954 and 1965-1995 (t = 1.762, 37 df).



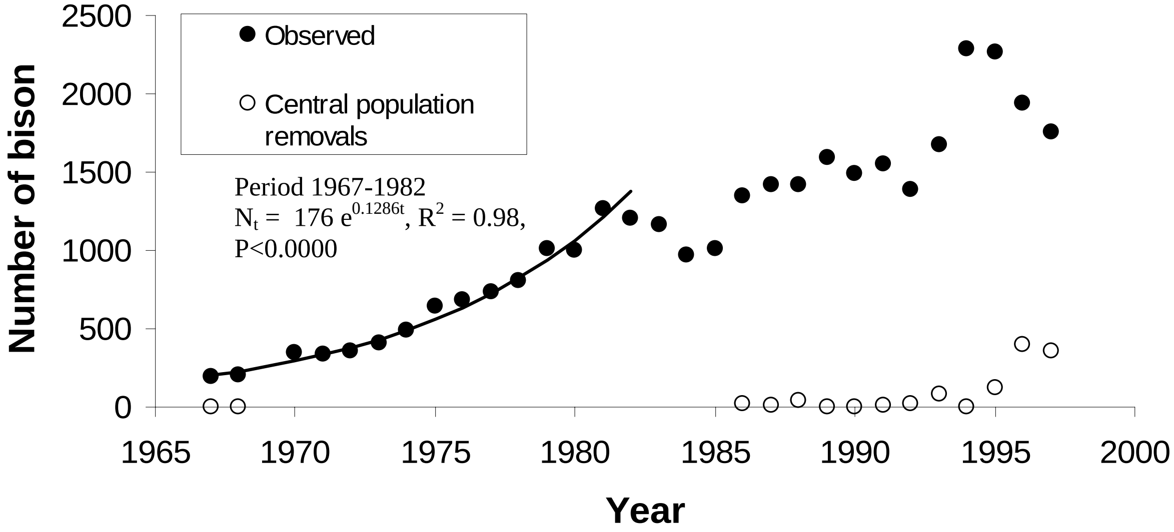


Figure 5.5. Growth of the central bison population excluding bison enumerated in the Pelican Valley during the periods 1935-1954 and 1967 to 1997. Equations represent growth of the population during the periods 1936-1954 (top graph) and 1967 to 1982 (bottom graph

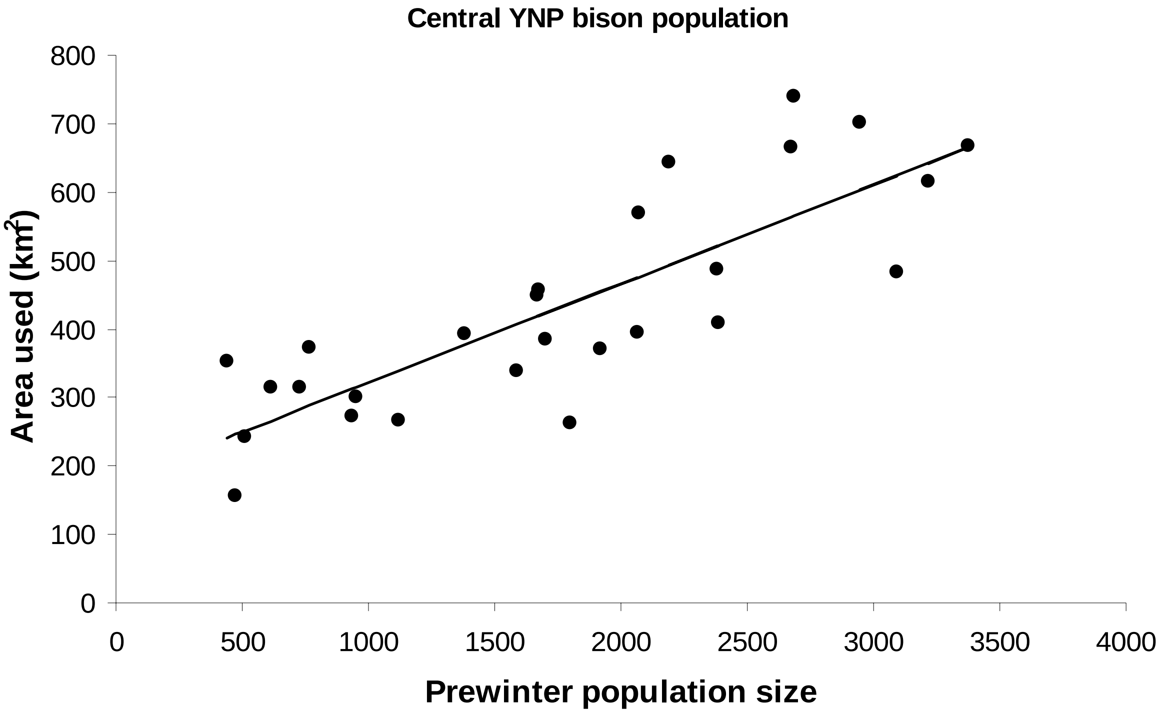


Figure 5.6. Relationship between the instantaneous area occupied (95% kernel; Taper et al. 2000) and prewinter population size for the Central YNP bison population. $Y = 177.2 + 0.140$ CPOP, $R^2 = 0.666$, $P < 0.0001$.

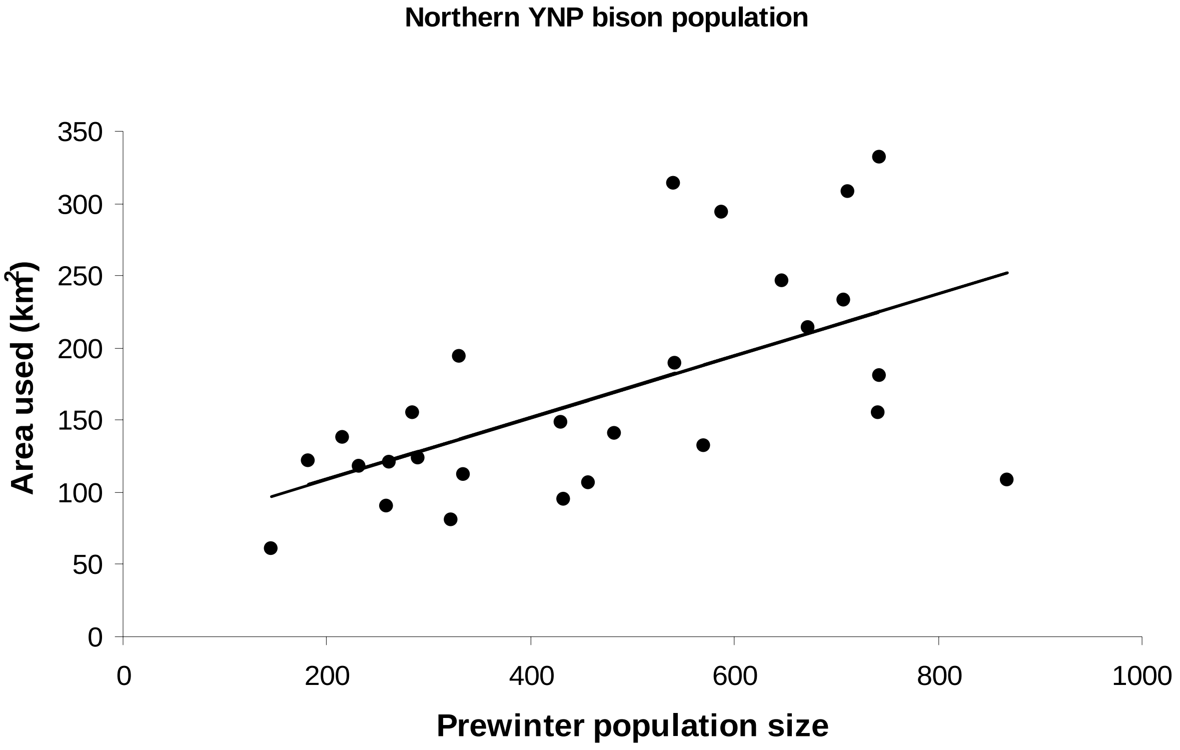


Figure 5.7. Relationship between the instantaneous area occupied (95% kernel; Taper et al. 2000) and prewinter population size for the Northern YNP bison population. Y = 66.9 + 0.316 NPOP, $R^2 = 0.316$, P = 0.0013.

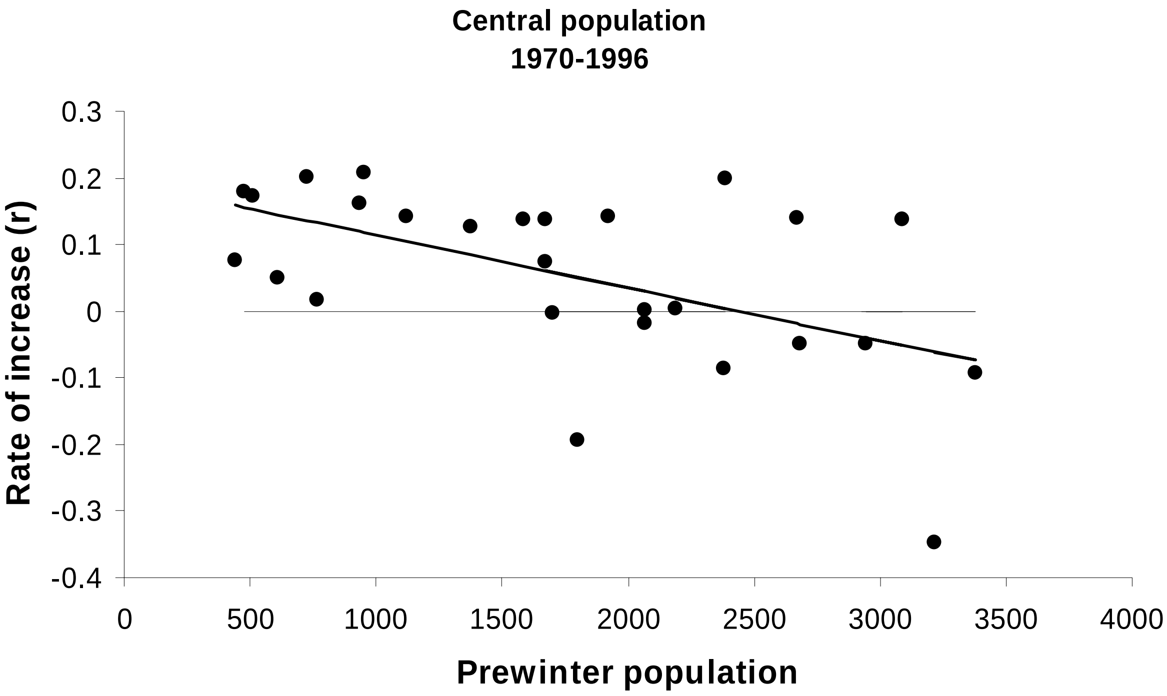


Figure 5.8. Relationship between the rate of increase (r) (Taper et al. 2000) and prewinter size of the central bison subpopulation: $Y = 0.193 – 0.000079\ CPOP_{max}$, $R^2 = 0.29$, $P = 0.0038$.

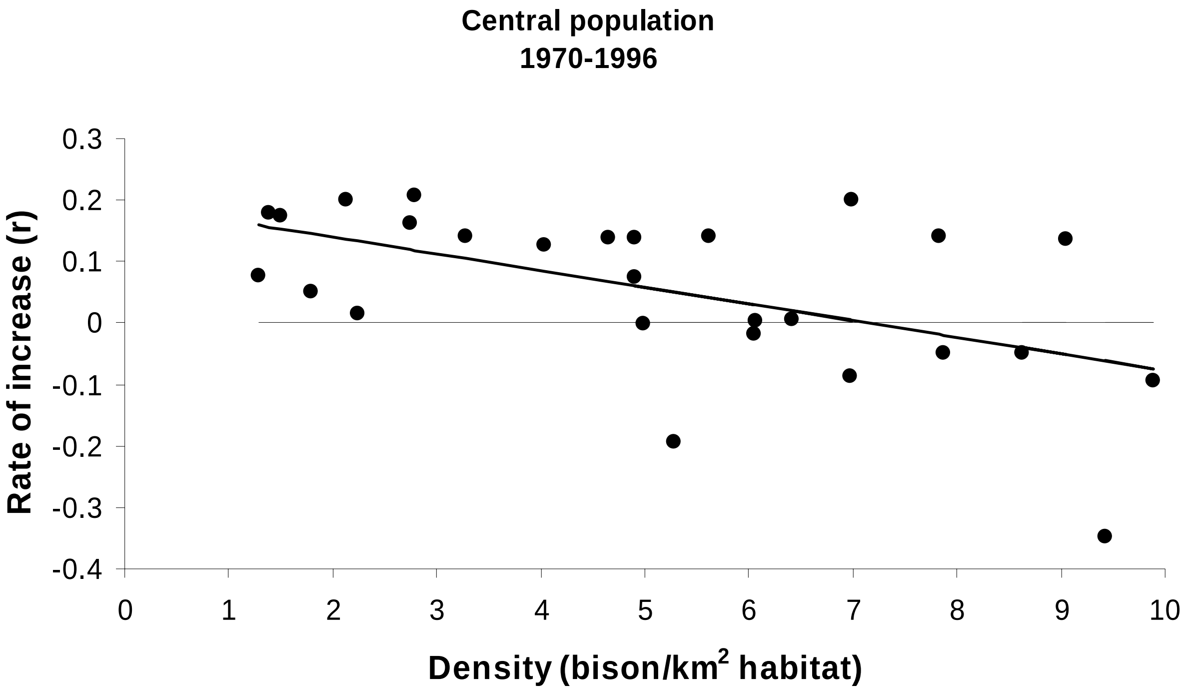


Figure 5.9. Relationship between rate of increase (r) (Taper et al. 2000) and density of the central bison subpopulation where density was calculated from the maximum number of bison counted in the central range prior to winter and the area of grassland habitat present in the maximum winter range area used by the population: Y = 0.193 – 0.0271 Density, $R^2$ = 0.25, P = 0.0038.

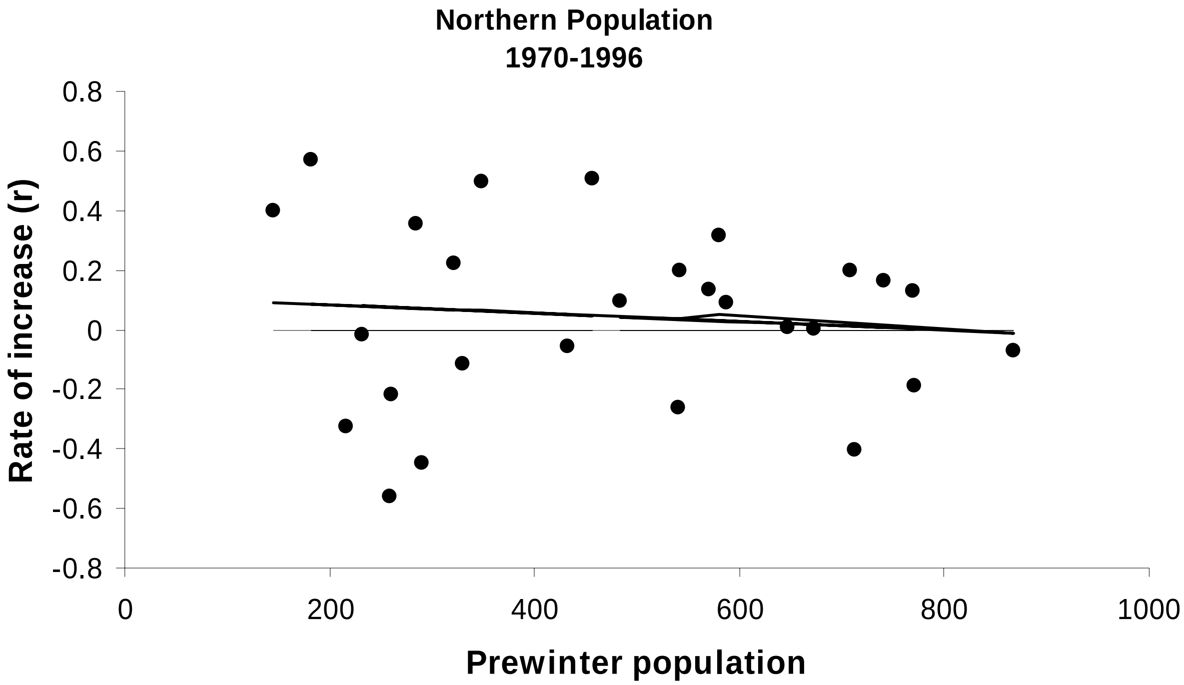


Figure 5.10. Relationship between the rate of increase (r) (Taper et al. 2000) and prewinter size of the northern bison subpopulation. The relationship was not significant ($F_{[1,25]} = 0.24$, $P = 0.63$).

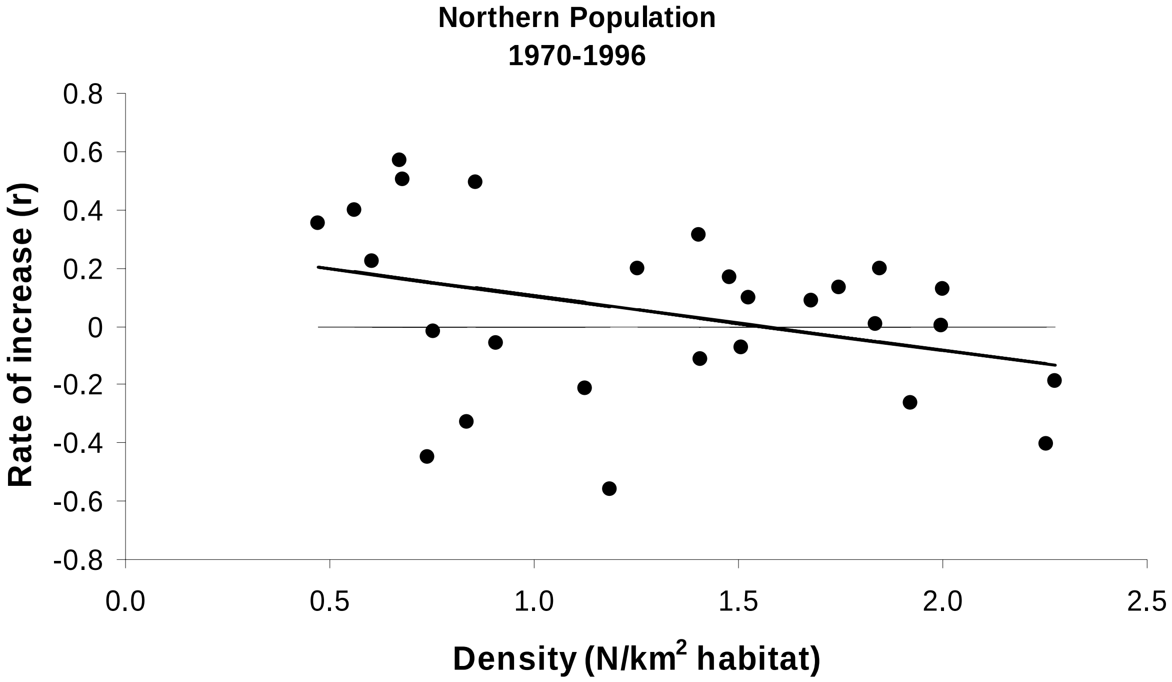


Figure 5.11. Relationship between rate of increase (r) (Taper et al. 2000) and density for the northern bison subpopulation where density was calculated from the maximum number of bison counted on the Northern Range prior to winter and the area of grassland habitat present in the winter range of the population. The relationship approached significance: $Y = 0.291 – 0.1869$ Density, $R^2 = 0.12$, $P = 0.0754$.

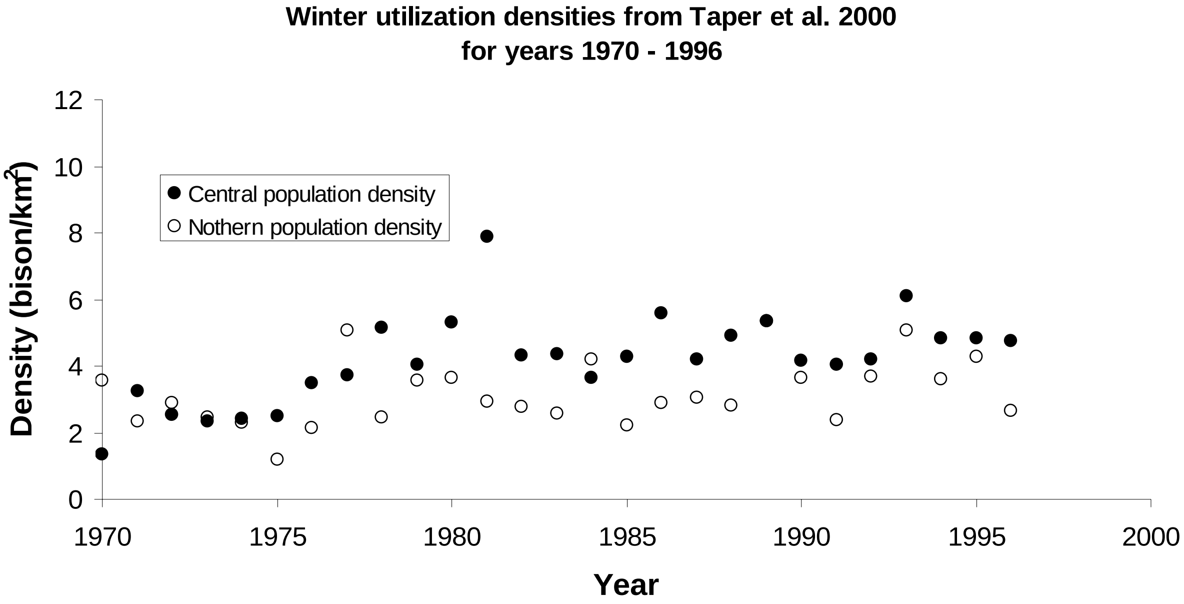


Figure 5.12. Trends in bison density (bison/km$^2$) calculated from the number counted within the observed 95% probability distribution in mid-winter in the Northern and Central Ranges of Yellowstone National Park between 1970 and 1996 based on Tables A2 and A3 presented in Taper et al. (2000).

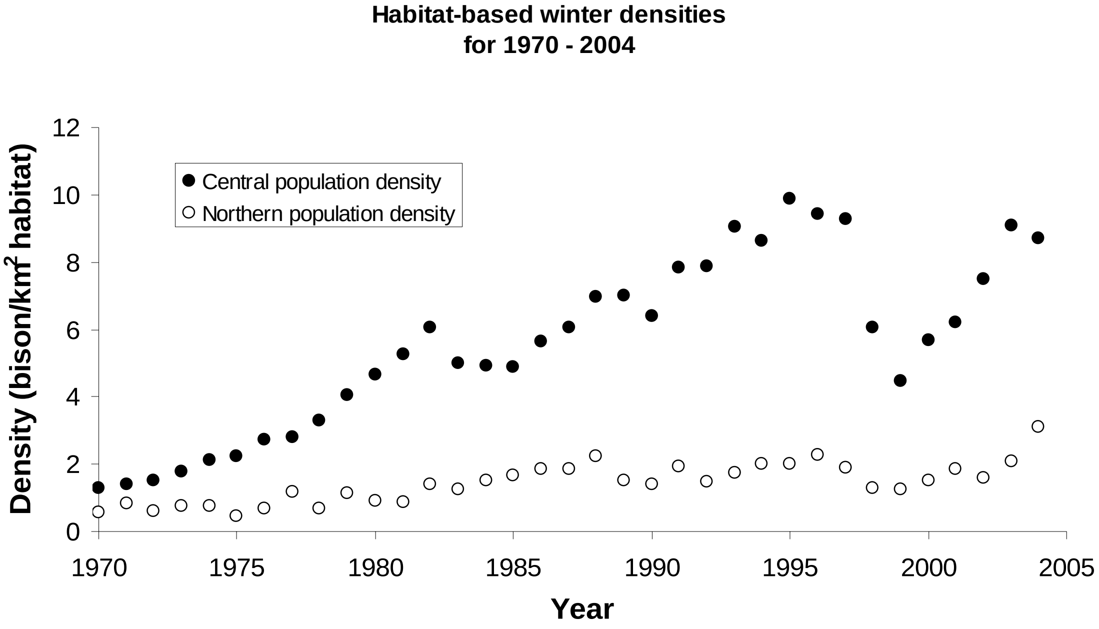
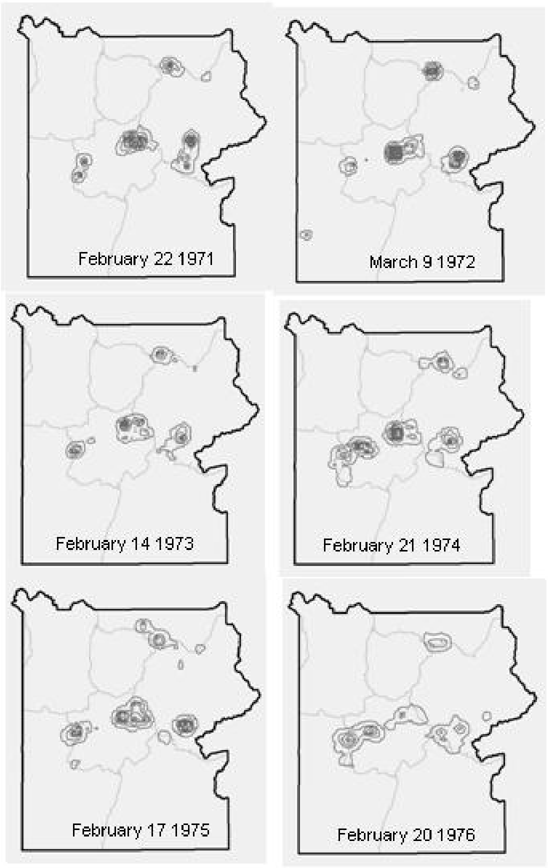


Figure 5.13. Density trends of the Central and Northern Range bison populations where density was calculated from the maximum number of bison counted in the range prior to winter and the area of grassland habitat present in the winter range of the population.



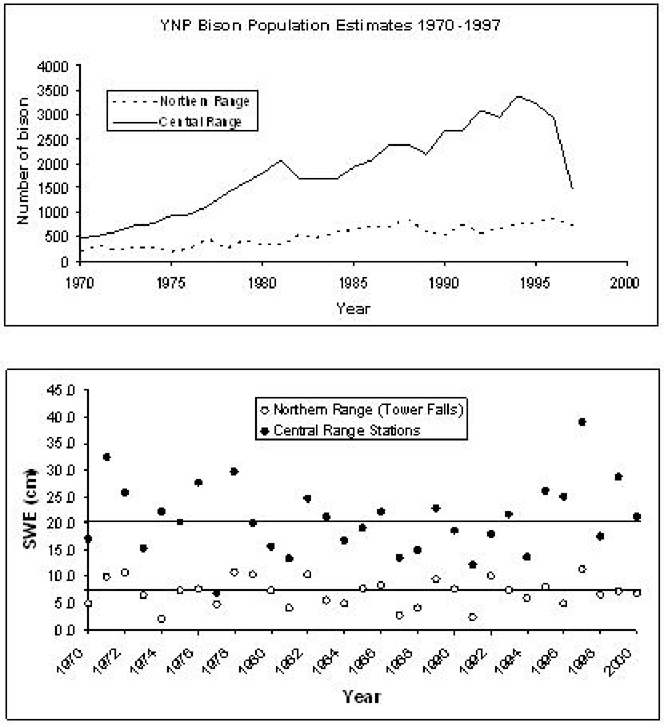
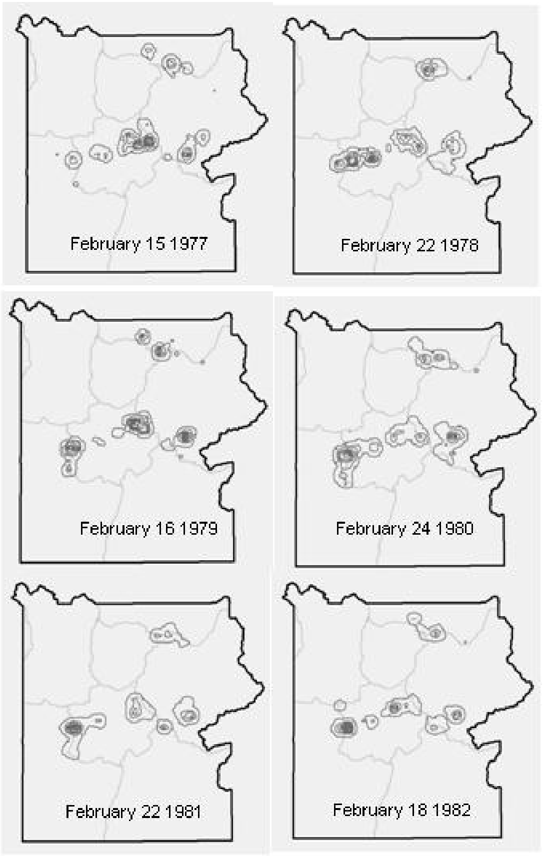


Figure 5.14. Winter distribution maps were created by C. Jerde with data from (Taper et al. 2000) using a fixed kernel density estimator (Seaman and Powell 1996). The isopleths are contours of probability distribution starting at the 95 % level. Each line represents the area used by the respective percent of the population. Jackknife cross validation was used to optimize the routine.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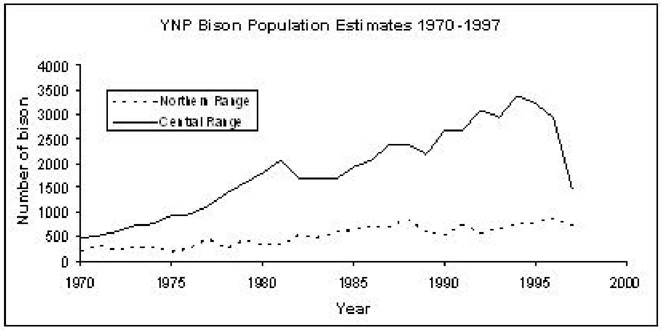
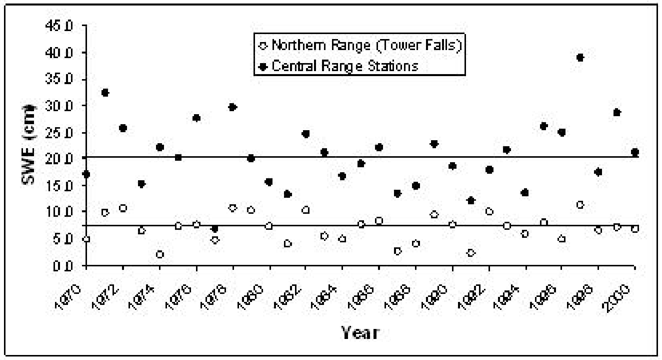
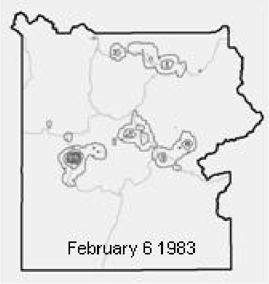
February 22 1978
February 16 1979
February 24 1980
February 22 1981
February 18 1982


YNP Bison Population Estimates 1970-1997
Number of bison
0
500
1000
1500
2000
2500
3000
3500
4000
Northern Range
Central Range
1970
1975
1980
1985
1990
1995
2000
Year


SWE (cm)
0.0
5.0
10.0
15.0
20.0
25.0
30.0
35.0
40.0
45.0
Northern Range (Tower Falls)
Central Range Stations
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year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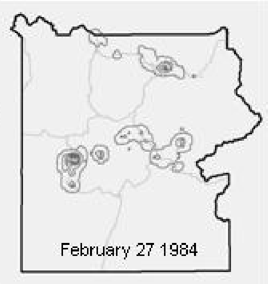
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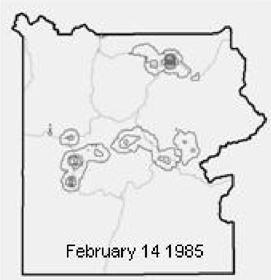
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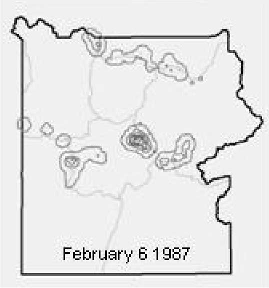
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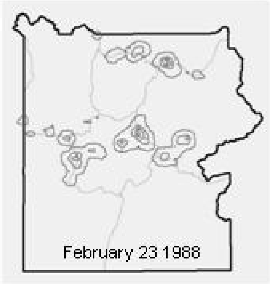
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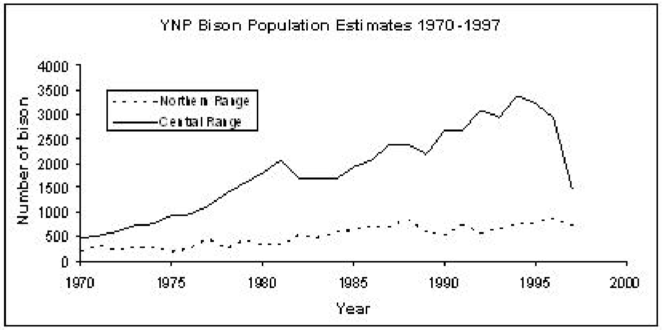
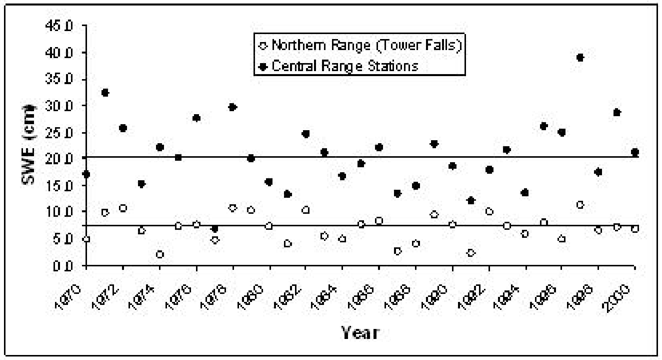
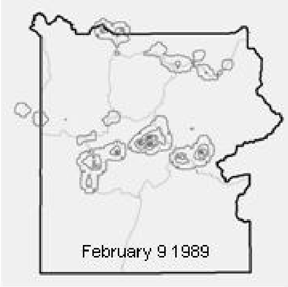

YNP Bison Population Estimates 1970-1997

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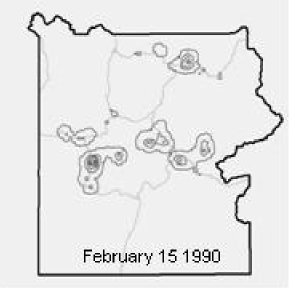
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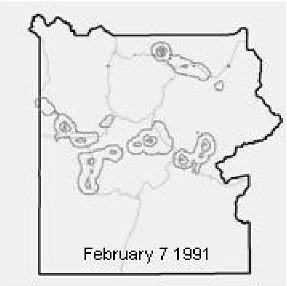
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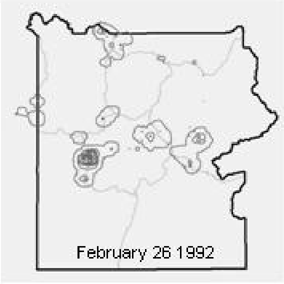
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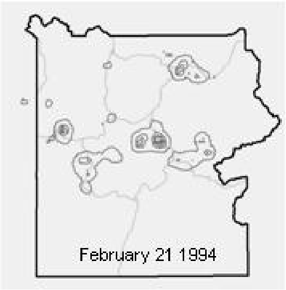
February 26 1993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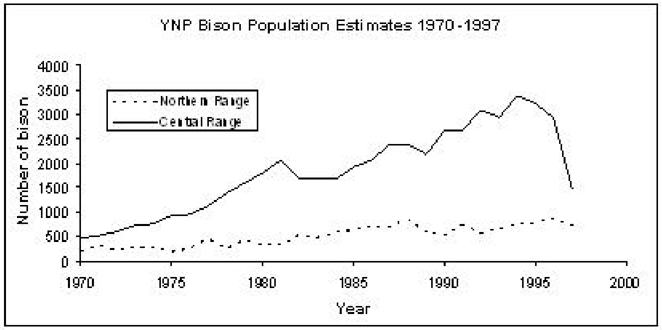
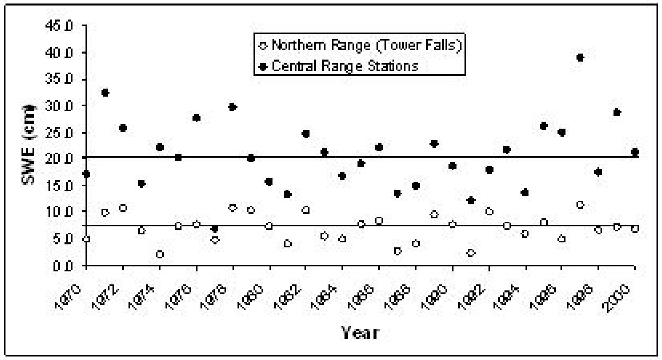
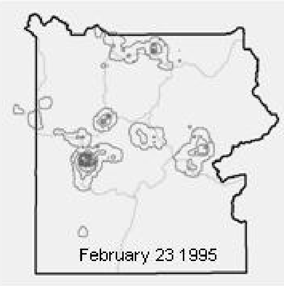

YNP Bison Population Estimates 1970-1997
Number of bison
4000
3500
3000
2500
2000
1500
1000
500
0
Northern Range
Central Range
1970
1975
1980
1985
1990
1995
2000
Year


SWE (cm)
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Northern Range (Tower Falls)
Central Range Stations
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year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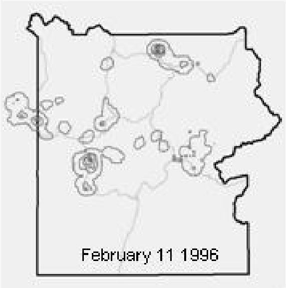
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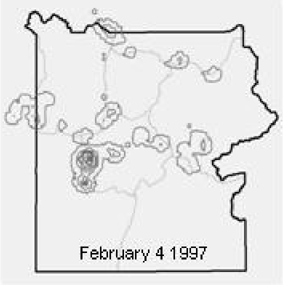
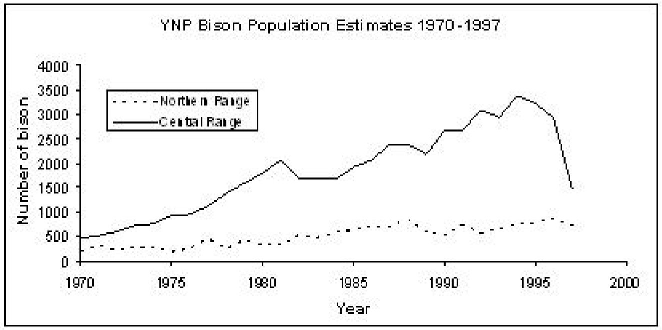
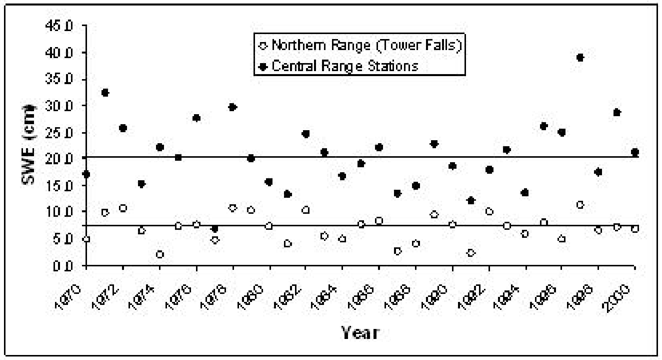

February 4 1997


YNP Bison Population Estimates 1970-1997
Northern Range
Central Range
Number of bison
4000
3500
3000
2500
2000
1500
1000
500
0
1970
1975
1980
1985
1990
1995
2000
Year


Northern Range (Tower Falls)
Central Range Stations
SWE (cm)
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year

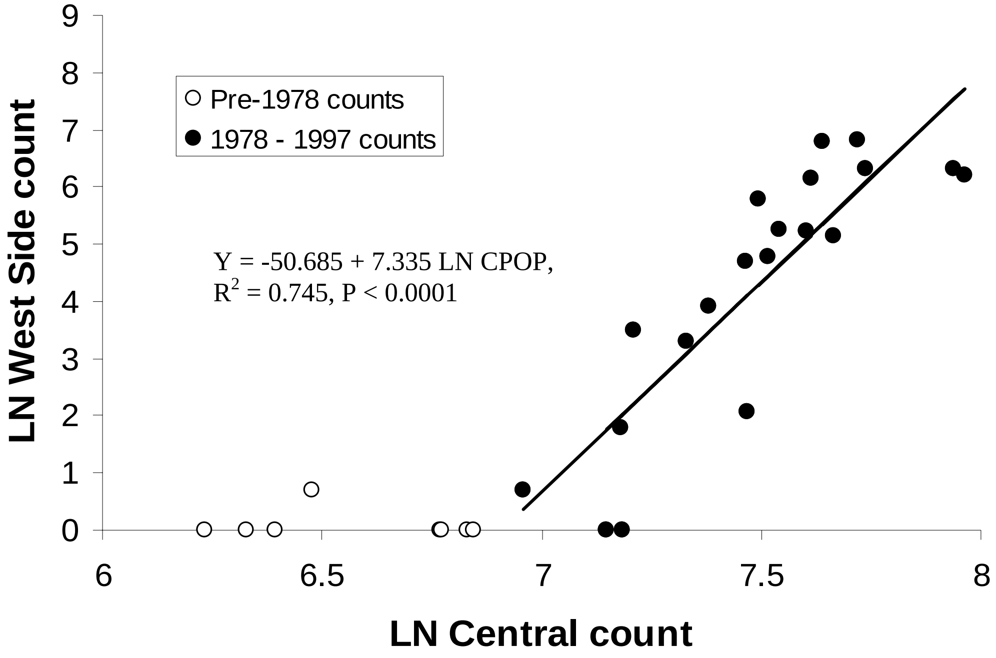


Figure 5.15. Relationship (natural log values) between the number of bison counted in the Central Range (includes West Side) and the number counted on the West Side of YNP for the years 1970 to 1997. Data source: M. Meagher, M. Taper and C. Jerde pers. comm.

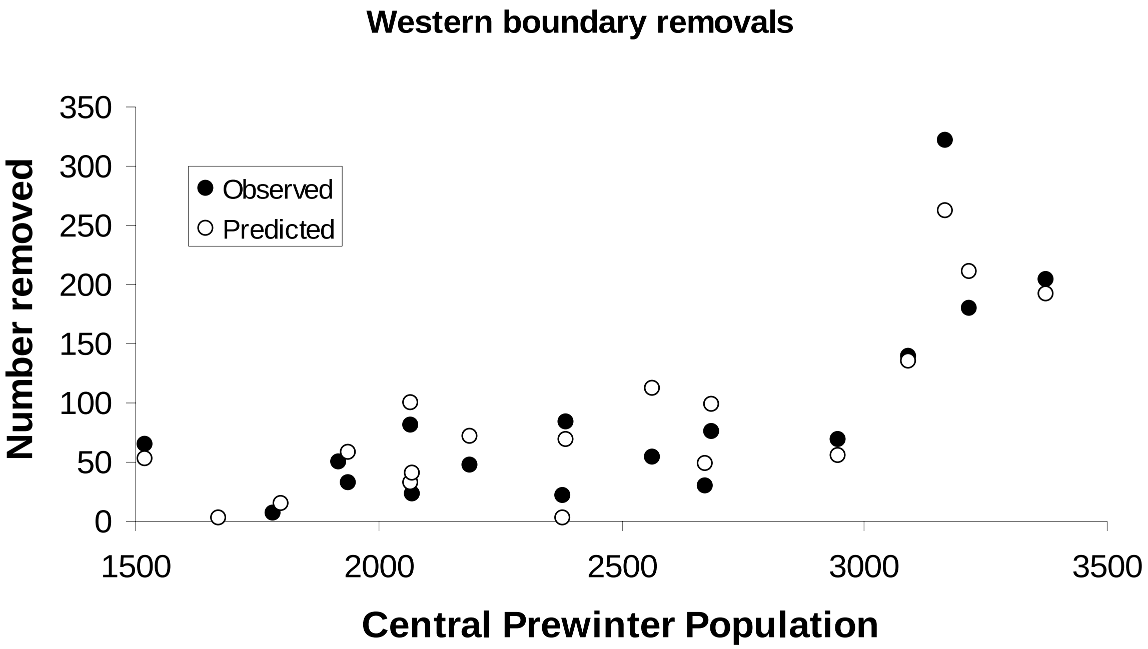


Figure 5.16. Bison removals at the western boundary of Yellowstone National Park in relation to the number of bison on Central Ranges prior to winter in years when the population exceeded 1500. Y = -312 + 0.91 CPOP + 9.58 SWE, $R^2 = 0.576$, $P < 0.001$, where SWE is average snow water equivalence (cm) at Central Range meteorological stations in mid-February, and NPOP is the number of bison on Central ranges prior to winter.

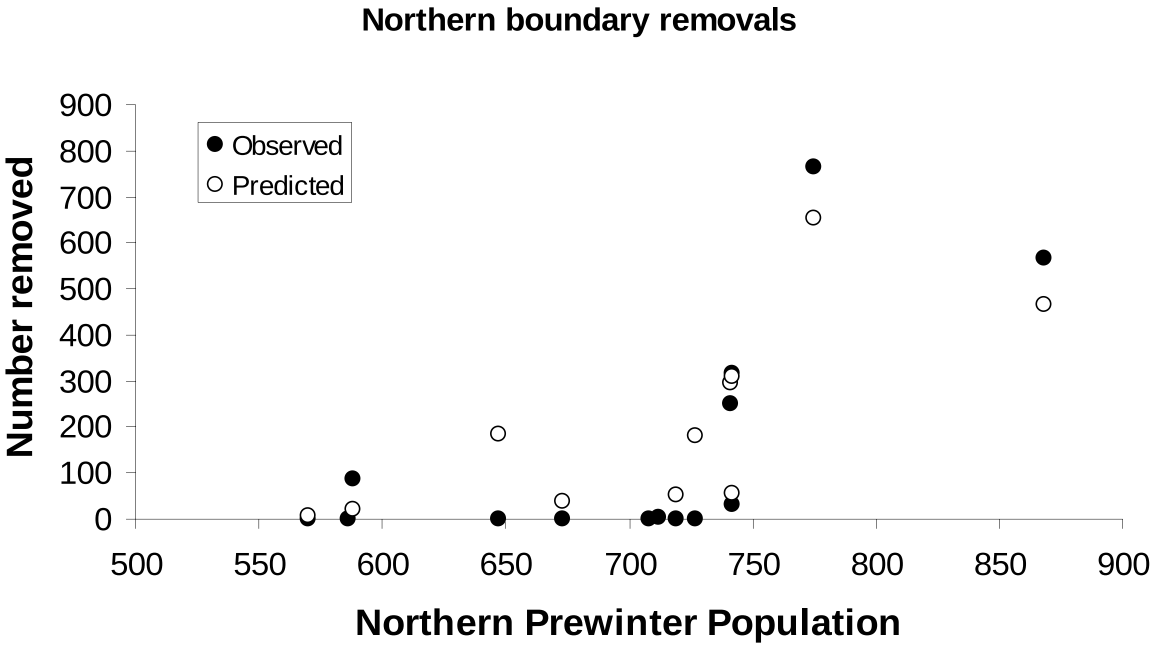


Figure 5.17. Bison removals at the northern boundary of Yellowstone National Park in relation to the number of bison on the Northern Range prior to winter in years when the population exceeded 550. Y = -1211 + 47.32 SWE + 1.337 NPOP, $R^2 = 0.793$, $P < 0.000$, where SWE is average snow water equivalence (cm) at Tower Falls meteorological stations in mid-February, and NPOP is the number of bison on the Northern Range prior to winter.

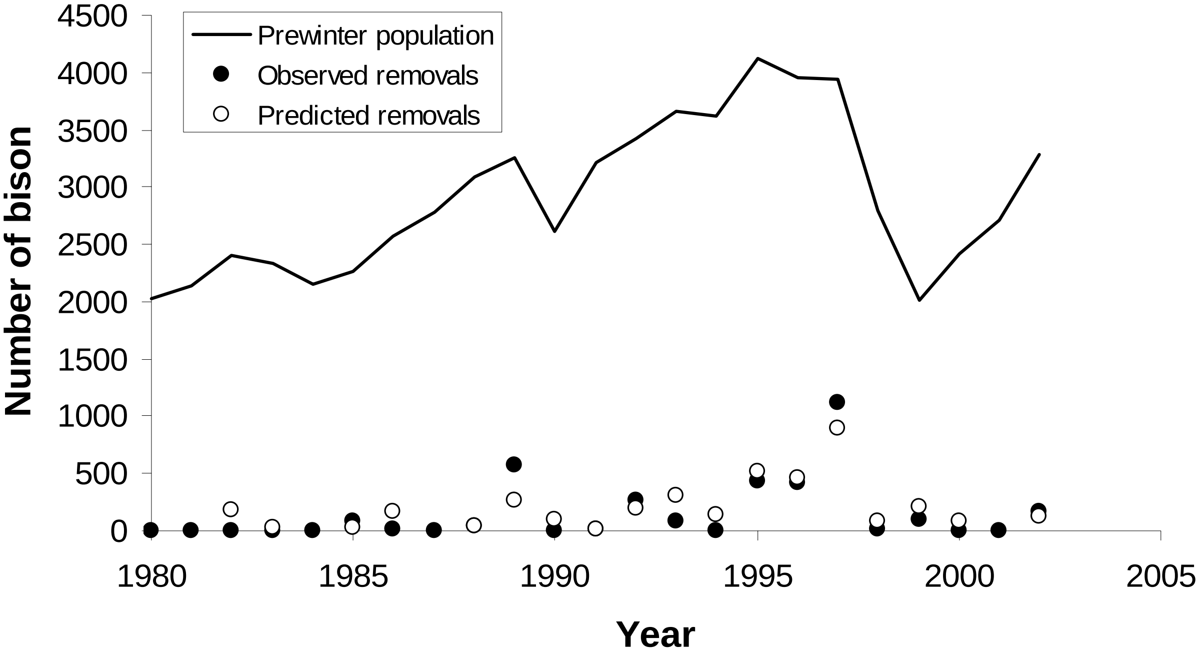


Figure 5.18. Total bison removals at the western and northern boundaries of Yellowstone National Park in relation to the number of bison present in the park prior to winter and snow. Y = -869 + 28.84 SWE + 0.183 TPOP, $R^2 = 0.734$, $P < 0.000$, where SWE is the average snow water equivalence (cm) in mid-February at Central Range meteorological stations and the Tower Falls station in the Northern Range.

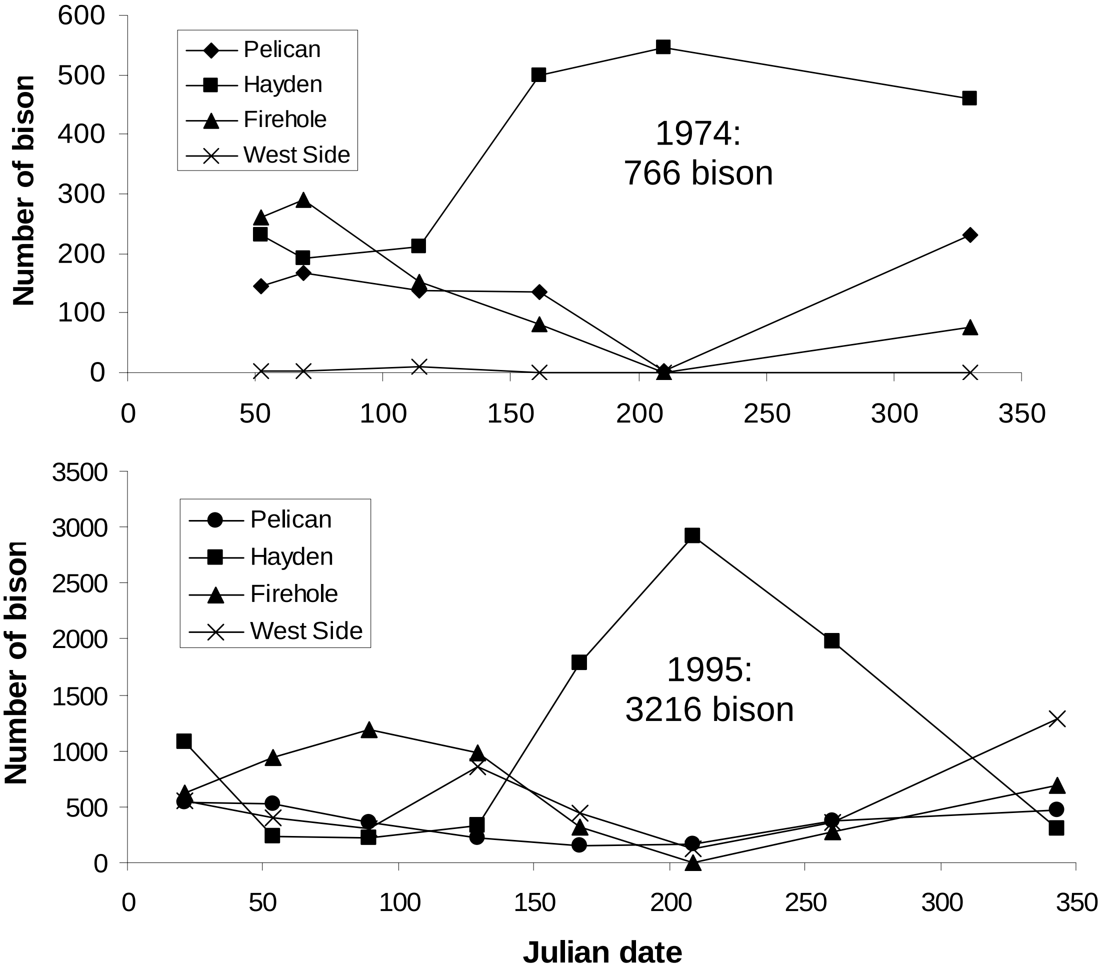


Figure 5.19. Distribution of bison in the Central Range during representative years 1974 and 1995. The maximum number of bison counted in the year in the Central Range is indicated. Data source: survey data of M. Meagher compiled by C. Jerde.

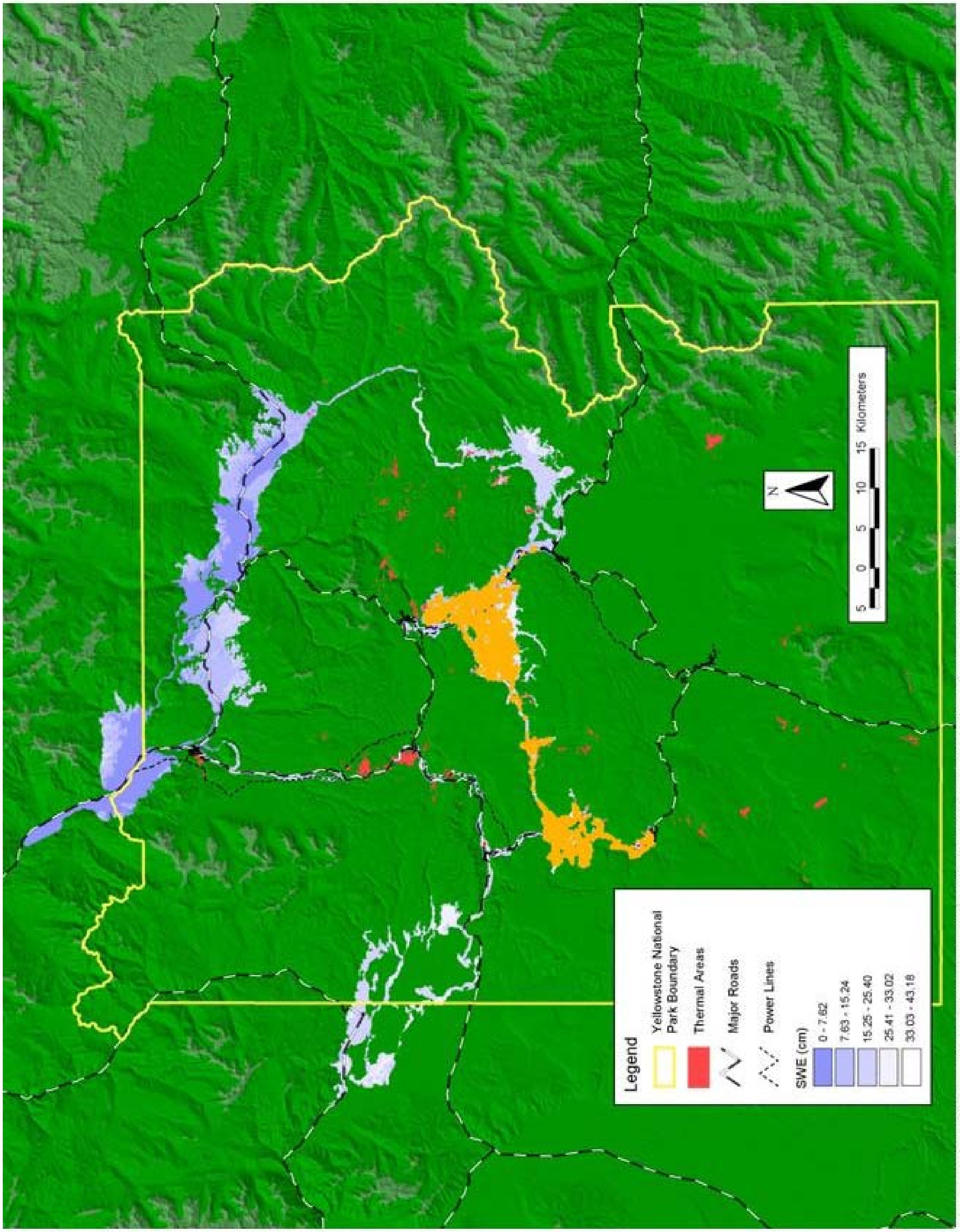


Figure 5.20. GPS locations (orange points) of bison YELL003 during the period November 2003 – December 2004.

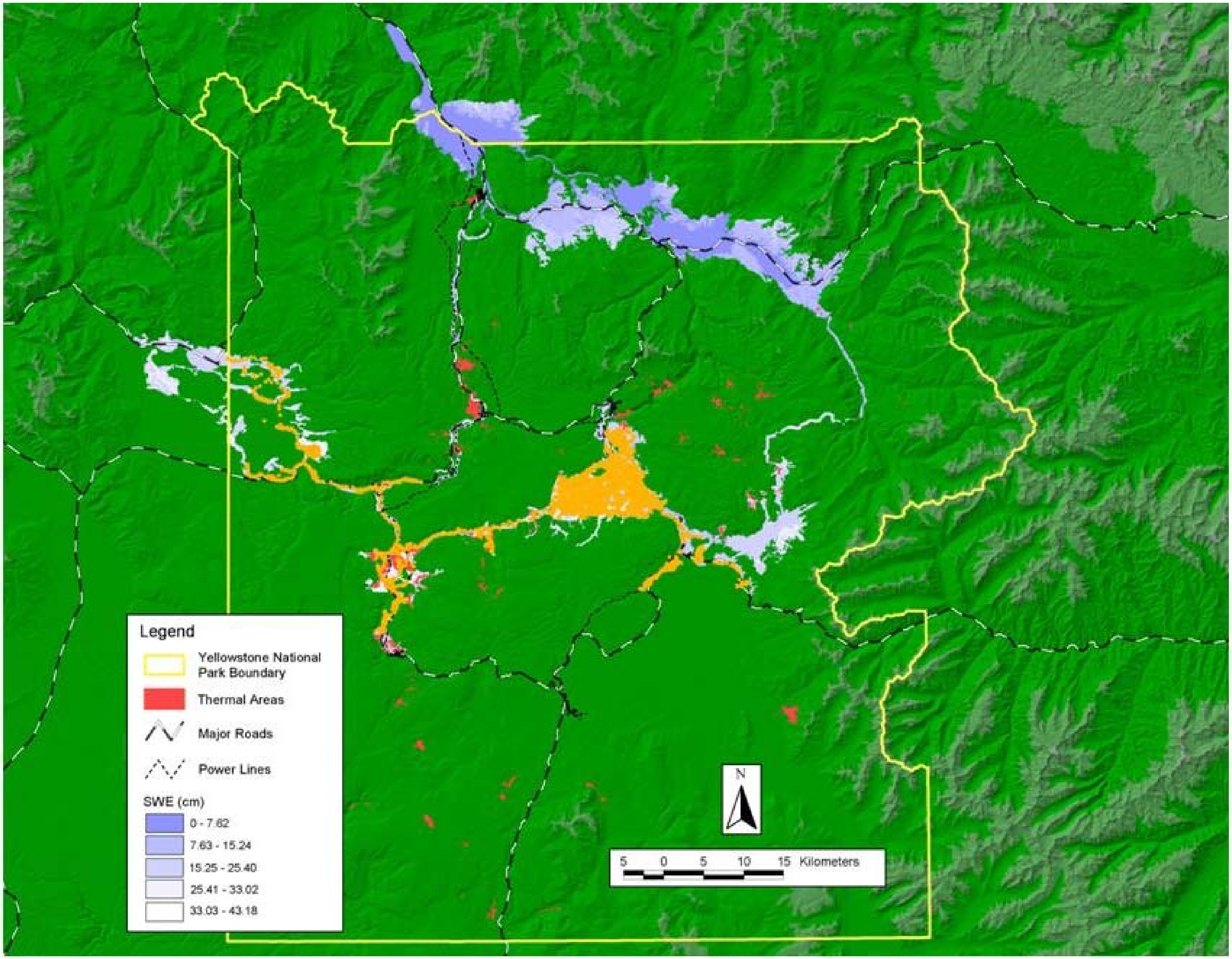


Figure 5.21. GPS locations (orange points) of bison YELL007 during the period November 2003 – December 2004.

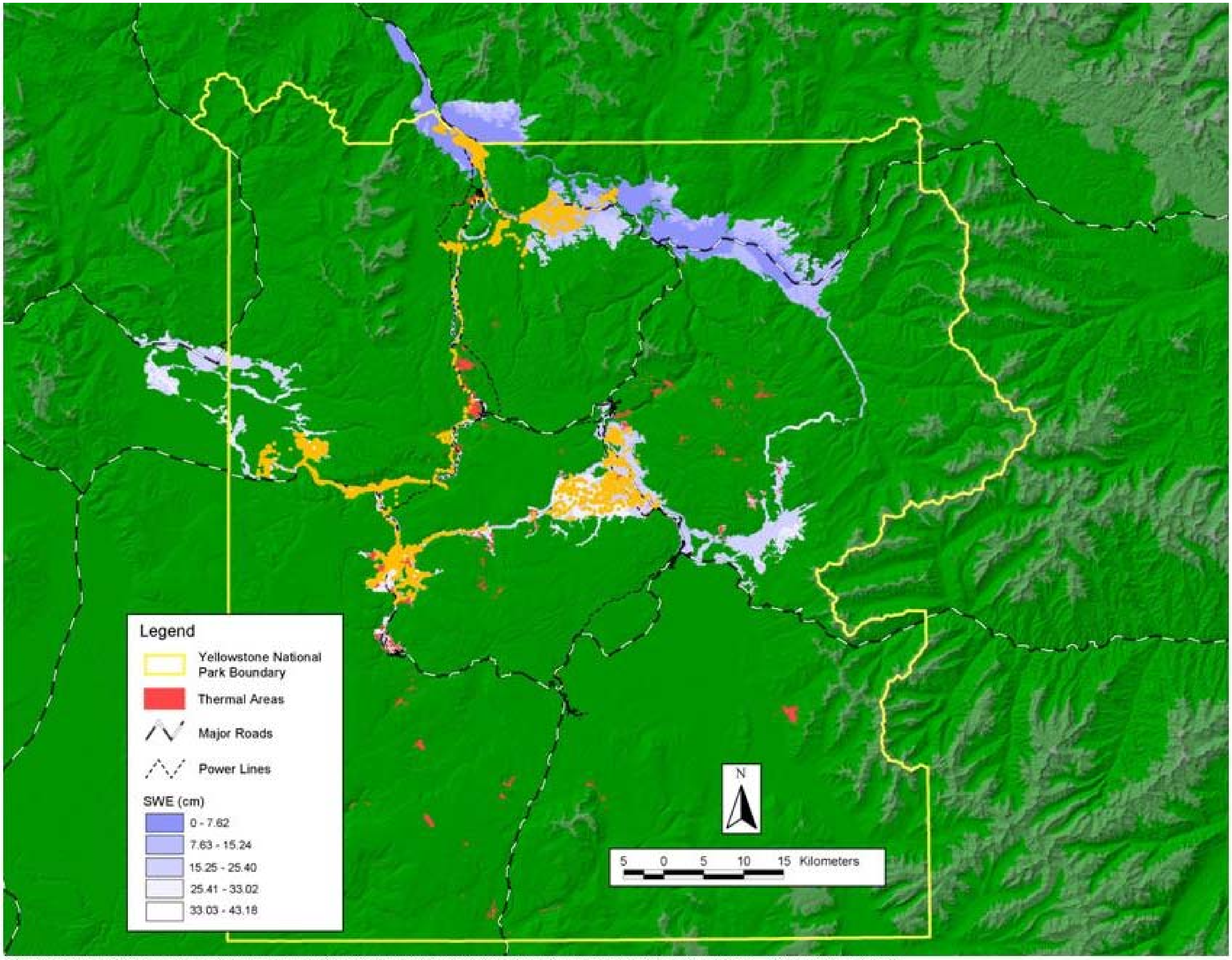


Figure 5.22. GPS locations (orange points) of bison YELL014 during the period November 2003 – December 2004.

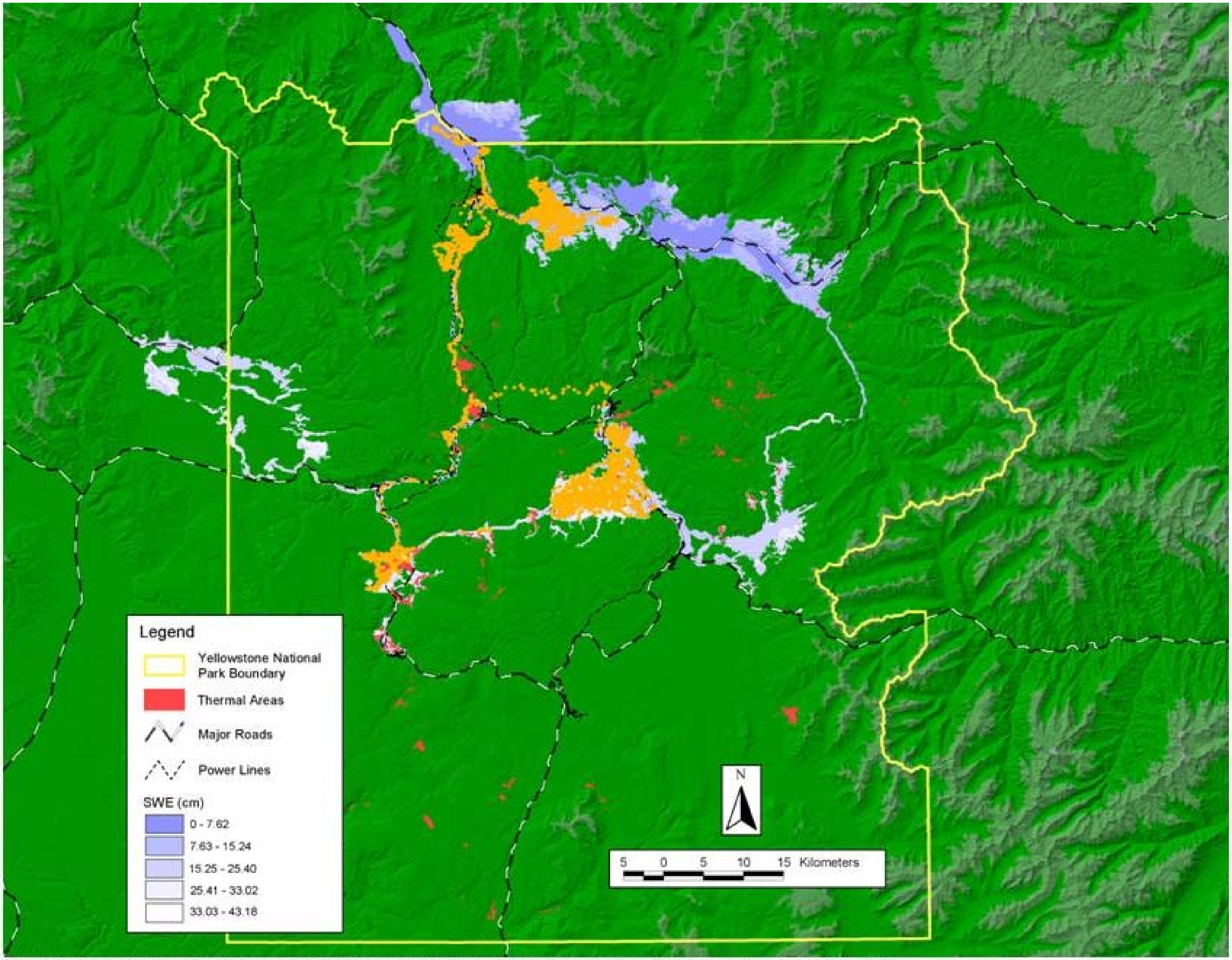


Figure 5.23. GPS locations (orange points) of bison YELL011 during the period November 2003 – December 2004.

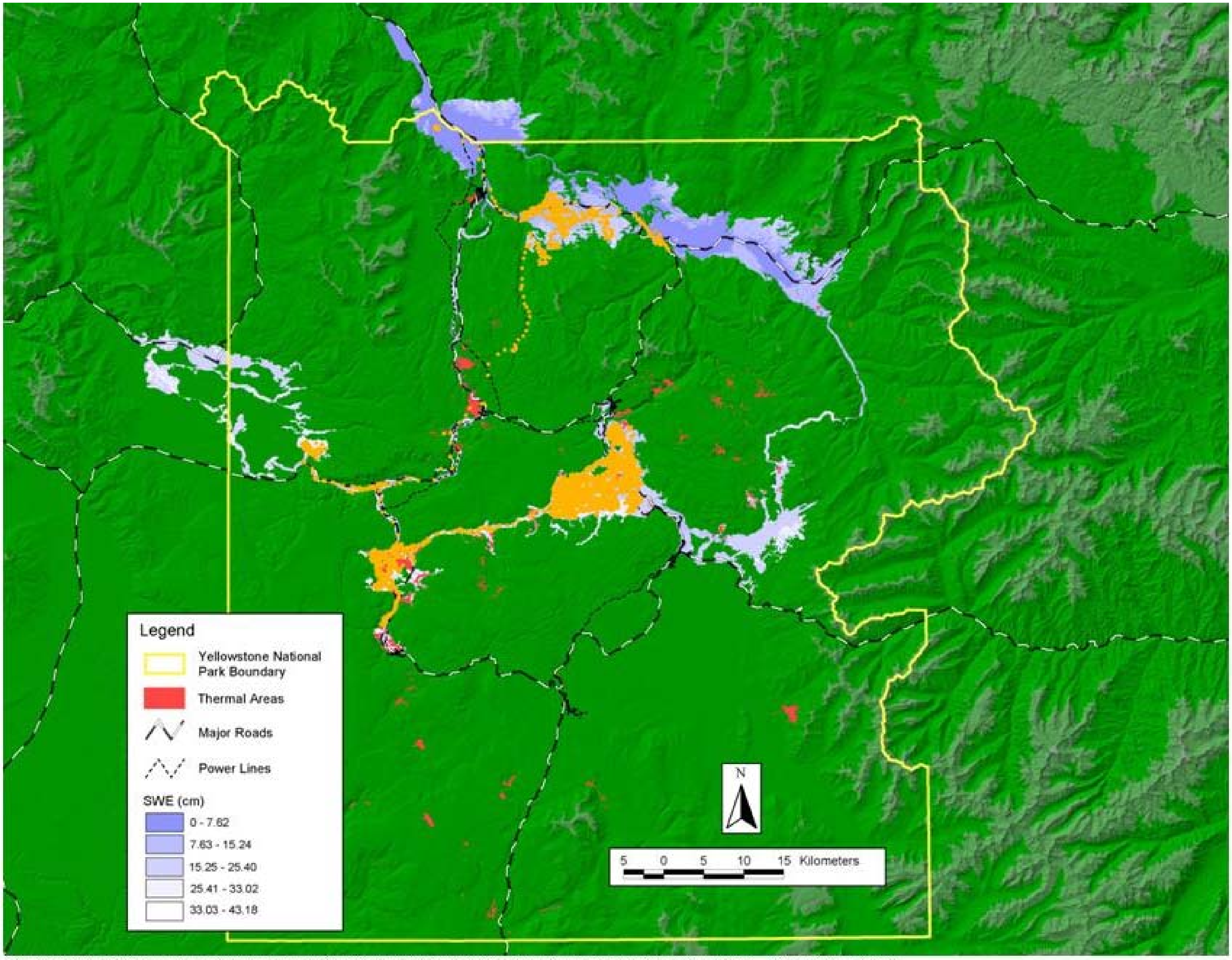


Figure 5.24. GPS locations (orange points) of bison YELL490 during the period November 2003 – December 2004.

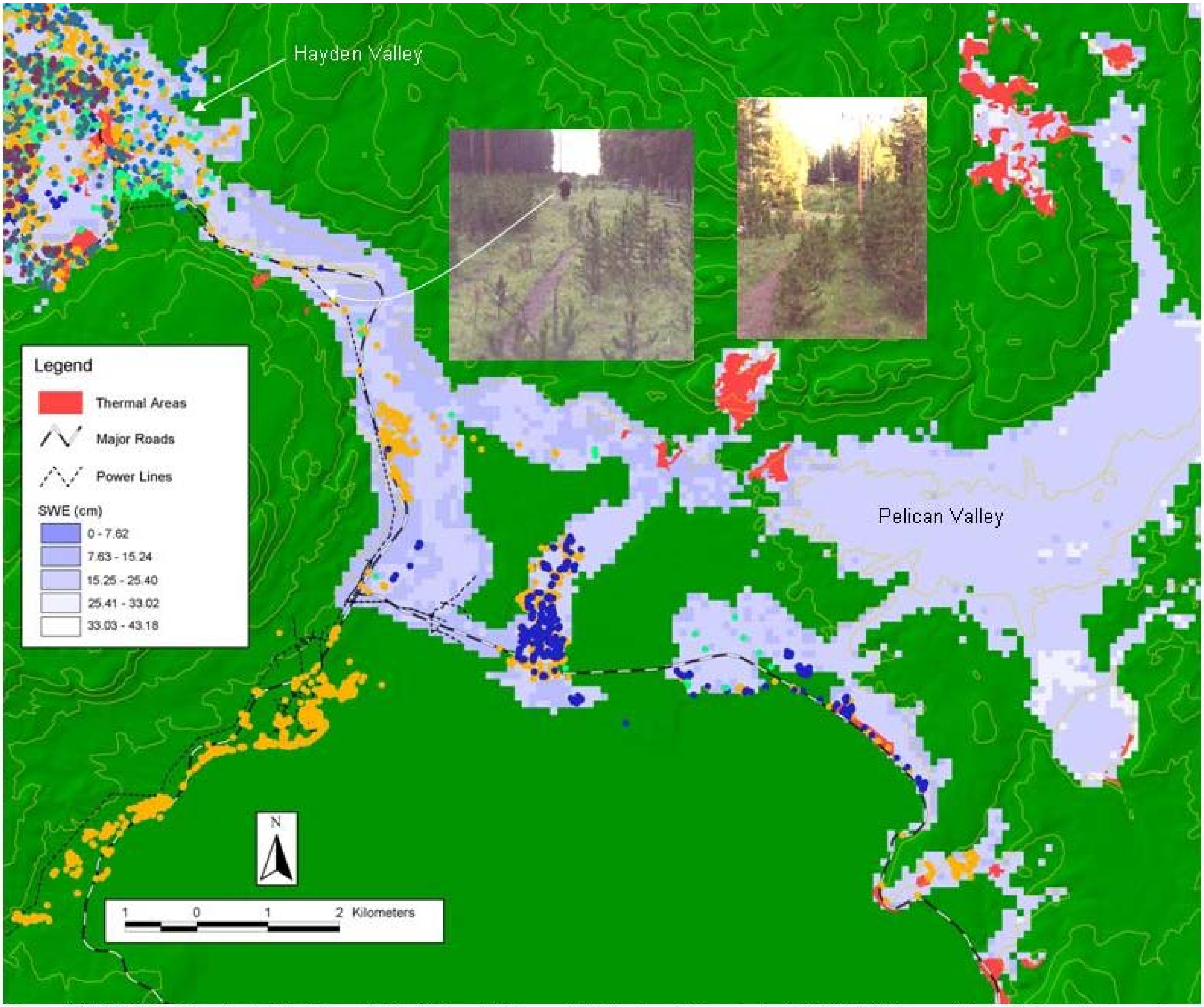


Figure 5.25. GPS locations (points) of bison in the Pelican Valley and SE Hayden Valley during 2003-2004. The corridor is 8.3 km. 50 m contour lines are indicated. Photographs of a bison trail deeply cut into power line were taken in August 2004; the location of the bison is indicated. Data source: R. Wallen, YCR.

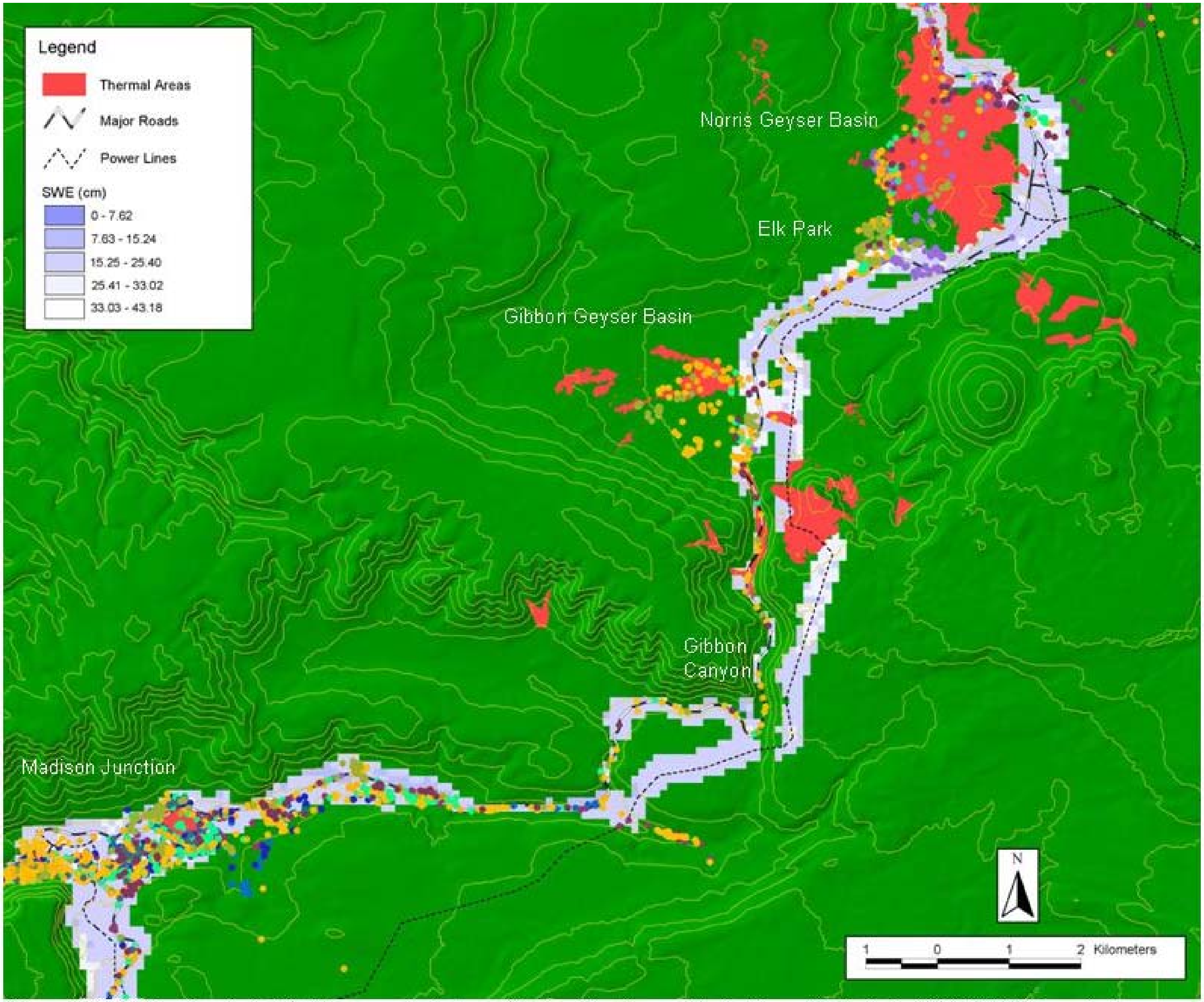


Figure 5.26. GPS locations (points) of bison moving between Madison Junction and Norris Geyser Basin during 2003-2004. Distance between Madison Junction and Norris Junction is 21.5 km. 50 m contour lines are indicated. Data source: R. Wallen, YCR.

# 6

# STRATEGIC-LEVEL BISON POPULATION AND DISTRIBUTION MODEL

Information compiled from regional data sources (Chapter 3), the literature, and key informants (Chapters 4, 5) were used to develop a systems dynamics model of population and spatial dynamics of bison in YNP. The model provides an interactive framework for exploring ideas and scenarios, building consensus and generally increasing collective understanding of the nature of the system. This chapter outlines the general structure of the model, projections illustrating its application, and specific "what-if" scenarios that informed recommendations in Chapter 7.

## Nature of Systems Models

A common belief among scientists is that ecological systems are sufficiently complex that full predictive understanding of their behavior is not easily or possibly achieved. The inability to comprehensively explain the behavior and underlying detailed mechanisms of an ecosystem does not however preclude comprehending important components, or how components interact in space and time. In recent decades, innovative computer-based systems models have become tools that assist in describing the architecture of natural systems, how system components interact, and how changes to individual components, combinations of components, or external perturbations, can affect system behavior (Ford, 1999). Much has been learned about the emergent properties of ecosystems through the application of models for a diversity of ecological systems, and many critical elements of systems have been identified that, although poorly understood, are found to be important to system function and thus deserving of more scientific inquiry.

A key challenge is to construct models that are no more complex than necessary, yet sufficiently complex to capture system behavior. Holling (2000) asserts there is a requisite level of simplicity/complexity behind complex, evolving systems that, if identified, can lead to rigorously developed understanding that can be lucidly communicated. Care must be taken to understand the types of questions/issues being addressed by managers and to adopt appropriate scale and resolution in building mathematical representations of natural systems. Once a mathematical model has been constructed about how system components interact, it is possible to use simulations to "project" the system into the future, allowing participants in a planning process to explore the consequences of various "what if" scenarios. Scenarios can explore natural variation in the system, the consequences of management actions, or both. By simulating the behavior of systems into the future, it is possible to gain insight into the sensitivity of the system to various internal or external variables.

A primary purpose of a system model is to inform stakeholders about the likely consequences of alternative management actions, thereby identifying actions most likely to achieve desired outcomes. Scenarios can help to build understanding of changing ecosystems and are an important tool both for making decisions about ecosystem management and for advancing science. Scenarios investigated with systems models can help people to rigorously define their assumptions and knowledge about how a system works, including responses difficult to quantify with current knowledge and worthy of more intensive study. Unlike empirical models, the most useful systems models should be easily understood as stories and can be used for communication and outreach to improve public appreciation of ecology and the challenges faced by ecosystem managers (Bennett et al. 2003).

A bison population and distribution model was developed for Yellowstone National Park for the above purpose. It was designed as a strategic-level model that provides a mathematical representation of key system elements and management levers. Information used to build the model included input emerging from key informants interviews (July and August 2004), technical group workshops (October 2004, February 2005), and empirical data on spatial and trophic ecology. Attention was given to building a model that can be used by stakeholders for assessing potential management outcomes and is sufficiently flexible to allow incorporation of new empirical data and relationships emerging from existing and future research.

## Impact Hypothesis Diagram (IHD)

Following the completion of key informant interviews, it was apparent they shared a general consensus on overall structure of the “system” that explained bison distribution and movement in YNP. Although agreement in model structure occurred, key informants differed in their assessment of the relative importance of components and response surfaces. During the interview process, an “Impact Hypothesis Diagram” (IHD) was employed to capture knowledge about system structure and function (Figure 6.1). An IHD is a graphic representation of the “system”. It illustrates how different components interact. Each arrow connecting variables in the IHD is described as a mathematical relationship derived with the key informants or based on empirical relationships taken from the literature.

The properties of the system defined by key informants revolved around a density-dependent forage-limitation model, whereby forage-limited bison emigrate from winter ranges with inadequate forage biomass. The three key variables determining winter forage availability are previous summer precipitation, snowpack characteristics, and herbivore density (i.e., forage demand). Emigrating bison depart winter ranges through corridors, the selection of which is based on relative permeability of available corridors leading from each winter range.

IHD variables are color-coded to indicate those that are treated as constants (blue) in the model, those that can be simulated as random variables (red), and those that represent management levers (yellow).

## The YNP Bison Distribution Model

The purpose of the YNP Bison Distribution Model is to simulate bison population sizes and movements under different “what-if” scenarios involving natural disturbance regimes and management actions. To accomplish this goal, the model must:

- spatially stratify the YNP study area into meaningful winter ranges and connecting corridors
- represent all major intrinsic or extrinsic variables identified by key informants in the Impact Hypothesis Diagram (IHD)
- allow precipitation and snowpack to occur as either constant (deterministic) or random (stochastic) variables
- simulate variation in primary production caused by inter-annual variation in summer precipitation and winter snowpack characteristics
- reflect phytomass removal by competing ungulate herbivores (elk)
- simulate inter-annual variation in availability of winter forage caused by stochastic snowpack events
- demonstrate how temporal changes in forage availability can affect over-winter survival and subsequent reproductive rates
- compute spatial and temporal variation in corridor permeability based on corridor length, topography, habitat characteristics, snowpack metrics, and road grooming decisions
- allow managers to explore the consequences of various management actions (i.e., levers) such as winter road grooming, vaccination initiatives, tolerance levels of boundary herd size, and predator population levels on population size and movement outcomes
- calculate the number of bison emigrants and immigrants for each winter range on an annual time step
- compare the input values and response surfaces of different Key Informant Groups on model output variables (bison movement, population dynamics, etc.)
- conduct sensitivity analyses of the system model, whereby managers systematically vary the values of input variables to assess their effects on movement-related output variables

The model is spatially stratified to represent winter ranges and corridors (tracked separately) defined by key informants:

Winter Ranges
- Gardiner basin (boundary range)
- Lamar Valley (internal range)
- Pelican Valley (internal range)
- Mary Mountain (internal range)
- West Yellowstone (boundary range )

Corridors
- Gardiner to Lamar Corridor (GLC)
- Mirror Plateau Corridor (MPC)
- Pelican to Hayden Corridor (PHC)
- Firehole to Mammoth Corridor (FMC)

- Firehole to West Yellowstone Corridor (FWC)

The model is comprised of the following sub-engines:

- meteorology
- rangeland dynamics
- population dynamics
- movement (emigration and immigration)
- mortality factors (starvation, predation, cull)

Management levers incorporated into the model include:

- road grooming
- boundary cull
- vaccination
- predation
- elk competition for forage
- repatriation of bison to ranges beyond YNP

The YNP Bison Distribution Model was built with Stella©, a stock and flow system dynamics modeling platform developed by ISEE Systems (www.iseesystems.com). The intent was to design a fast and flexible simulation model, scaled to address strategic level questions that can assist stakeholders in exploring the consequences of various "what-if" scenarios relevant to bison management (Figure 6.2). Meteorology, plant growth, forage demand, and herbivore movement were tracked using a 2-season time step. A two season approach ensures the model will run quickly and that users can efficiently explore multiple “what-if” scenarios.

This model is not intended as a replacement for spatially explicit, operational models, but rather as a complementary tool that can be informed by other modeling initiatives and results from ongoing or future research.

## *Major Indicators*

The major indicators reported by the Bison Distribution Model include:

- summer precipitation
- winter snowfall and snowpack depth (measured as snow water equivalence (SWE)
- forage production
- forage availability
- population (#, density) x winter range
- corridor permeability
- movement to boundary ranges
- winter starvation x range
- cull x winter range

## *Model Attribution*

The model was designed to provide for easy model attribution. All user-defined input variables and response surfaces are clearly displayed and can be easily modified. We recognized that improved empirical relationships will emerge as research proceeds in YNP, and that input values and response surface descriptions will be need to be modified by managers. Attribute data for winter ranges, meteorology, movement corridors, and forage production are described in Chapter 3.

### *Forage-Related Response Surfaces*

Response surfaces describing forage production, reproductive metrics, and bison movement were based on input from key informants and group workshops. At the time of preparation of this model, empirical relationships were not available for several key components of the model. The scale and shape of response curves generated at group workshops were similar, leading to a decision to build a single set of response surfaces (Figures 6.3, 6.4, 6.5, 6.6, 6.7, 6.8).

Forage production is computed from the area of a range, mean and variance of precipitation (current year rainfall, and previous winter snowpack), and the effect of previous (last year) herbivory on primary production. Total forage production available to herbivores is influenced by several factors, including the portion of total habitat used by herbivores (a function of herbivore density), the total herbivore population, the depth and crustiness of the snowpack, and phytomass lost to decomposition processes. Herbivores (bison, elk) consume forage based on a defined proportion of their body weight (daily dry weight intake of forage was set in the model to 2.5% of body weight).

### *Corridor Permeability*

One anthropogenic and four natural features were identified during workshops as important to defining permeability of corridors to migrating bison. These were presence/absence of road grooming, corridor length, corridor habitat composition, prevalence of thermal features, and snowpack water equivalence (SWE). The physical properties of each corridor are described in Chapter 3.

Importance values ascribed to each corridor metric group were derived from expert opinion using the AHP in each group workshop (Figure 6.9). The response surface describing the relationship between a corridor descriptor (i.e., length) and permeability were also constructed by each workshop group (Figure 6.10). Using a general additive model, permeability ratings were computed for each corridor based on rankings and response surfaces provided for each corridor feature (length, habitat composition, thermal features, and snowpack) by each workshop group (Figures 6.9, 6.10).

The model allows the user to identify “gates” in corridors in non-grooming scenarios, preventing bison movements because of physical impediments. There was a consensus among the key informant groups that the Firehole to Mammoth corridor would not be traversed by bison in non-road grooming scenarios. Some groups expressed doubt that the Mirror Plateau Corridor (connecting Pelican Valley and Lamar) is used by bison except in winters with an unusually low snowpack. Based on input from technical workshops the Firehole to Mammoth Corridor (FMC) was considered a barrier in non-road grooming scenarios, whereas the Mirror Plateau Corridor (MPC) was not considered a barrier to movements under some snowpack conditions. The authors suggest that YNP managers explore alternative outcomes to bison population and distribution dynamics by conducting “sensitivity” simulations using different combinations of corridor permeability values.

### *Population Dynamics Inputs*

Initial bison population sizes were set in the model for each range for two starting years: 1800 and 1970 (Table 6.1). The year 1800 represents the time before bison populations were depleted by commercial exploitation. 1970 was the approximate beginning of the ecological management era in YNP. It is important to understand that this model, when simulating populations beyond 1970, makes no effort to reflect actual "recorded" population levels in any given year. Population dynamics expressed by this simulation model are responding to the suite of internal and external variables (fecundity, mortality, movement, stochastic precipitation, variable snowpack) influencing the YNP system, and thereby ignore any historical data set of known population levels. The exception to this rule is when the user chooses to run the model under the "historical" simulation option, in which case the bison populations of each range are "generally" reduced to the recorded populations that occurred during the depopulation episodes of the 1800's through to 1970.

Estimates of range specific annual predation rates and incidental mortality rates for bison were provided by Rick Wallen (Bison Ecologist, YNP; pers. comm., Table 6.2). Maximum herd growth rates were computed from historical bison population data during decadal periods immediately following major depopulation events. Current levels of societal tolerance for bison in boundary ranges were provided by YNP personnel (Table 6.4).

Discussions with workshop groups identified the occurrence of some level of inter-range bison movement unrelated to either forage availability or bison density. This type of density-independent movement pattern, referred to as "random walk", was estimated to account for 10% of the total annual bison movement in YNP (Mary Meagher; pers. comm.; Table 6.5). To account for the observation that a minimum winter herd occurs in the Pelican Valley and Mary Mountain, even during harsh years, the model allows the user to define a minimum overwinter population that is not allowed to emigrate to alternate ranges.

The abundance and biomass of elk on several bison ranges requires that their effects on forage production and availability be considered when evaluating how forage influences bison. Using user-defined maximum winter elk populations in each winter range as a proxy of carrying capacity, the model incorporated a basic population model that allowed elk populations to fluctuate based on interactions of forage availability and demand. Elk populations experienced winter die-offs caused by low forage availability and responded numerically based on density-dependent fecundity.

### *Tolerance of Bison in Boundary Ranges*

Based on current tolerance levels specified for the two boundary ranges (Gardiner basin and West Yellowstone), the default tolerance values were set at 200 bison, beyond which the model will cull excess individuals. These two ranges are considered as non-permanent ranges in the model, and therefore surviving individuals return back to interior ranges during the spring. To improve our understanding of how bison population dynamics would respond to different levels of tolerance, boundary herds were subjected to tolerance ranges between 0 and 800 individuals.

*Vaccination*

A "what-if" scenario was run in the YNP Bison Distribution Model to explore plausible consequences of a bison brucellosis vaccination program given specific User-defined input relationships. The challenge posed by some key stakeholder groups was phrased as follows:

- If a vaccination program did occur, and all bison were vaccinated over a period of 30 years (Figure 6.11), and
- The vaccination program results in a reduction in prevalence of sero-positive bison from 50% to 30% (Figure 6.11), and
- Reduced prevalence of sero-positive bison resulted in increased tolerance of bison in boundary herds from 200 to 600 individuals (Figure 6.11), then
- What affect would the vaccination program have on the total number of culled bison?

*Exploring "Climate Change"*

Simulated dynamics of YNP bison presented in this report underscore the importance of forage availability to bison movement patterns. One of the key input variables to forage availability is forage production, which is in turn influenced significantly by inter-annual variation in precipitation. The YNP Bison Distribution model allows for exploration of anticipated changes to either averages or variances of precipitation.

To illustrate this capacity, two hypothetical "what-if" scenarios were run for the YNP landscape. In scenario #1, precipitation means remained constant, but variances were allowed to increase by 100% incrementally over a 100 year period. In scenario #2, precipitation means were again held constant, but variances were allowed to decline by 50% over a 100 year period. At a strategic level, these types of scenarios have merit to explore, as many climate change scientists believe that variances in precipitation (and temperature) are likely to increase under most 2 x $C0_2$ trajectories.

These scenarios are not intended to reflect the most meaningful climatic change trajectories to be explored by YNP managers, but to demonstrate the capacity of the model to evaluate climatic "what-if" scenarios.

## Simulation Results

### *Meteorology*

To illustrate inter-annual variation in precipitation (both rain and snow), and the effects of this stochastic variable on forage production, and ultimately on bison distributional patterns, two 100 year simulations were conducted, each based on a different set of random precipitation values drawn from user-defined means and variances. Based on an examination of historical meteorological records from various sites within YNP, random variation was synchronized between bison ranges. This ensures that dry and wet years occur simultaneously in each range of the study area.

Simulated variance in summer precipitation (Figures 6.12, 6.13) indicates that rainfall was lowest in the Gardiner basin, intermediate in Lamar Valley and Pelican Valley, and highest in West Yellowstone and Mary Mountain. These simulations indicate that proportional variance (actual/average) increases with increasing average annual precipitation (Figures 6.14, 6.15).

Simulated variance in winter range snow depth (measured as Snow Water Equivalence (SWE)) followed the same elevational pattern showed by summer precipitation, with the lowest snowfall in the Gardiner basin, low in Lamar Valley, moderate in Pelican Valley, and highest in West Yellowstone and Mary Mountain (Figures 6.16, 6.17). The proportional variance in SWE (actual/average) generally increased with average SWE (Figures 6.18, 6.19).

Differences in SWE of corridors occurred, with very low values occurring in the Gardiner Lamar Corridor. All other corridors had higher SWE values, with increasing order of depths occurring in the Pelican Hayden Corridor, Mirror Plateau Corridor, Firehole Mammoth Corridor, and Firehole West Yellowstone Corridor (Figure 6.20, 6.21).

### *Forage Production*

Inter-annual variation in forage production is determined by three variables in this model: winter snowpack during the previous winter, summer precipitation during the current growing season, and herbivory pressure (both bison and elk) during the previous growing season. The principle of grazing-induced changes to primary productivity was first described by McNaughton (1983). The relationship between herbivory pressure and primary production used in this model, developed through input by the workshop groups, is shown in Figure 6.6.

Highest forage production rates (tonne/hectare) occurred in the Pelican Valley, followed, in decreasing order, by West Yellowstone, Mary Mountain, and Lamar Valley and Gardiner basin (Figures 6.22, 6.23). Reflecting differences in total range area, forage production (total tonnes) was highest in the Lamar Valley, followed by Mary Mountain, West Yellowstone, Pelican Valley, and Gardiner basin (Figures 6.24, 6.25). The importance of summer precipitation and last year’s snowpack on forage production are shown in Figures 6.26 and 6.27. The high forage production levels attributed to the Pelican Valley have been questioned by Mary Meagher (pers. comm.), who has suggested that frequent late spring frosts, early summer flooding, and early fall frosts in this valley may require adjustments in the model to reflect an abbreviated growing season.

### *Forage Availability*

Winter forage available to bison exhibits significant inter-annual variation (Figure 6.28). Environmental variables included in this model that account for this variation include herbivore population density, forage production, and snowpack crustiness. The initial decline in per capita forage availability is attributed to a growing bison population following the initial 1970 levels (Figure 6.29). After this initial transformation period, forage availability (per capita) continued to express wide temporal variation. Of the explanatory variables, herbivore biomass density exhibited the strongest relationship to winter forage availability (Figures 6.30, 6.31), summer forage production showed a moderate to strong relationship (Figure 6.32), and current winter snowpack depth had little demonstrable effect on forage availability (Figure 6.33). These general relationships suggest that the magnitude of inter-annual variation of herbivore populations on any given winter range may exceed the variances observed in summer precipitation.

### *Corridor Permeability*

Each workshop group assessed the importance and response surface of different physical features (length, habitat composition, presence of thermal features, topographic relief, and snowpack depth) that defined bison movement corridors (Figure 6.9, 6.10). Using the coefficients from each knowledge group separately, the model computed corridor permeability values range from 0 (no permeability) to 1 (completely permeable) for each corridor, with and without road grooming, during a 100 year simulation characterized by stochastic precipitation.

Corridor permeability results for the ungroomed road scenario in models defined by Groups 1, 2, and 3 were generally similar and generated permeability values higher than those generated by Group 4 (Figures 6.34, 6.36, 6.36, 6.37). Lower permeability values of Group 4 were caused by the prescribed inability of bison to move through snowpack depth greater than 1 m (SWE = 10 cm; see Figure 6.10). With the exception of the GLC Corridor, results from the Group 4 model indicate that in many winters no bison movement can occur between any of the winter ranges. Because three of the Group models were similar, a fifth model was developed (Figure 6.38) representing the average inputs of Groups 1, 2, and 3. This “Majority Average” model was used to generate the results presented below.

In all simulations of the majority model in which roads were not groomed, the Firehole-Mammoth Corridor (FMC) was fully impermeable (value of 0) because it is considered to possess a topographic gate that prevents bison movement in situations where winter road grooming does not occur (Figure 6.38). In contrast, the Gardiner-Lamar Corridor was the most permeable corridor in all models, reflecting its low snowpack, modest length, and high bison habitat content. The permeability of the Pelican-Hayden corridor was generally high (0.6 to 0.9) with modest temporal variation caused by snowpack depth. The permeability of the Mirror Plateau and Firehole-West Yellowstone Corridors was highly variable (0 to 0.7), with deep snowpack depth preventing movement on average once each 5 years. The high inter-annual variance in snowpack depth is the key feature influencing the permeability of the MPC and FWC corridors.

Corridors that were groomed in the majority model included the Firehole-Mammoth (FMC), Pelican-Hayden (PHC), and Firehole-West Yellowstone (FWC) corridors. In comparison to the non-grooming scenario, all corridors receiving winter road grooming experienced higher corridor permeability for moving bison (Figure 6.38). As before, the non-groomed Gardiner-Lamar and Pelican-Hayden Corridors remained the most permeable (0.95) in all years, followed by the Firehole-West Yellowstone Corridor (0.85) and Fire-Mammoth (0.8) Corridors. The Mirror-Plateau Corridor maintained a highly variable permeability (0 to 0.75) based on inter-annual variation in snowpack on this non-groomed route.

### ***Bison Population Dynamics***

Simulated bison population dynamics (1970 to 2070) indicated that the population would be expected to expand from 1970 levels of ~630 individuals to ~5,000 individuals within 20-25 years (Figures 6.39 to 6.43). For scenarios where road grooming was excluded, 3 of the 4 group models (1, 2, and 3) generated temporal patterns with populations fluctuating generally between 2500 and 5,000 individuals (Figures 6.39, 6.41, 6.43). The Group #4 model exhibited far greater temporal variation, with populations fluctuating between 50 and 4,000 (Figure 6.45). The greater temporal variance associated with the Group 4 model can be attributed to the inability of bison to migrate through snow depths of 1 m or higher (SWE = 10 cm), and the attendant mortality that accompanies these sedentary bison during harsh forage-limited winters.

Based on similar input coefficients and output responses of Groups 1, 2, and 3, their input coefficients were averaged, and used to create a fifth group called the “Majority Average Group” (Figure 6.47). When road grooming occurred (for corridors FMC, PHC, and FWC), bison population responses based on all Groups were generally similar (Figures 6.40, 6.42, 6.44, 6.46, 6.48). With road grooming reducing functional snow depth to 0 along groomed corridors, the Group 4 model performed in a very similar fashion to the other Groups. Clearly the distinction between the Group 4 model and the other models focuses on the capacity of bison to move through winter snowpack.

To better appreciate the “range of natural variability” in temporal variation of population size, each range was simulated for a 300 year period in the absence of road grooming. These simulations were conducted separately for each Group model (Figures 6.49, 6.50, 6.51, 6.52, 6.53). As before, these graphs illustrate the magnitude of inter-annual and inter-decadal variation that is influenced, presumably, by forage availability caused by variation in herbivore populations and stochastic precipitation driving both forage production (through rainfall), per capita forage availability (proxy is herbivore density), and access to forage (through winter snow depth). Given the external input variables identified in these models, there is no evidence that populations should, or will, achieve any equilibrium. Rather, this system can better be described as a population of semi-discrete herds that continuously seek to expand toward maximum forage availability, but witness frequent depopulation events tied to either starvation or cull. In dynamic grazing systems where primary production is highly variable, it is reasonable to expect, in the absence of a suppressing predation effect, that herbivore populations will undergo similar variability. As before, the Group 4 model differs from the others in that it generates major episodic bison die-offs associated with deep snow winters.

The lower graphs (Figures 6.49, 6.50, 6.51, 6.52, 6.53) displayed in the “range of natural variability” set differ in that the herds were depopulated to recorded historical levels between 1820 and 1970. Bison population estimates of each range in 1800 were set in the model at values representing a projected longterm average and allowed to fluctuate around these values, only to be subsequently reduced through depopulation events. These graphs illustrate that population levels, and hence dynamics, during the period 1820 to 1970 were quite different from patterns observed in a “range of natural variability” scenario and are clearly an artifact of the intentional and unintentional depopulation events of that period. It follows, therefore, that descriptions of the “naturalness” of population dynamics observed in this period should be expressed with caution. Although we have learned much about low-density dynamics of bison populations responding to cull events, this knowledge may differ from patterns yet to be observed in YNP in coming decades and centuries if YNP maintains its ecological management.

In aggregating ranges into either northern or central herds, it was apparent that the northern herd experienced greater temporal variation than the central population (Figures 6.54, 6.55). Road grooming does not appear to cause any fundamental change in this temporal pattern (Figures 6.54, 6.55).

Since available winter forage is being influenced concurrently by the temporal dynamics of both bison and elk (Figures 6.56, 6.57, 6.58, 6.59) in YNP, any management action (or natural disturbance event) that influences one of these herbivore species is likely to have measurable effects on the other. To demonstrate this relationship, a hypothetical scenario in the YNP Bison Distribution Model was run where elk populations were intentionally maintained at 50% of their current population size (Figures 6.58, 6.59). The simulated outcome clearly illustrates the numerical response of the regional bison herd to a new landscape where competition is relaxed and forage availability increases.

### *Distribution and Movement Patterns*

Total bison movement between winter ranges was projected to have high inter-annual variation, with values ranging from 100 to 4,000 animals (Figure 6.60). Based on cumulative values, average movement of ~1,000 bison occurred in non-road grooming scenarios, and 1200 in road-grooming scenarios (Figure 6.61). Simulated results indicate that bison movement from interior (Lamar Valley, Mary Mountain, Pelican Valley) to boundary ranges (Gardiner basin, West Yellowstone) exhibited high inter-annual variation, with values ranging from 50 to 1300 animals (Figure 6.62). Using five 100 year stochastic simulations, total cumulative number of bison dispersing to boundary ranges indicated a long term average annual movement of 200-240 for non-road grooming scenario, and 290-340 in a road-grooming scenario (Figure 6.63). Bison movement from interior ranges to boundary ranges differed among models generated by different Groups (Figure 6.64). In all models except Group #4, bison emigrating to boundary ranges periodically exceeded 1,000 animals.

On average, 25-30% of the total number of bison emigrating from an existing winter range moved to boundary ranges for the winter months (Figures 6.65, 6.66), whereas the remaining 75% moved between interior ranges (for example, moved from Pelican Valley to Mary Mountain). Scattergrams between herbivore biomass density (tonne/km$^2$) and movement to boundary ranges showed that winter bison movement to West Yellowstone and Gardiner basin significantly increases when herbivore biomass densities exceed 4.5 tonne/km$^2$ (Figure 6.67). Whereas an average of 25-30% of all dispersing bison moved to boundary ranges in both road-grooming and non-grooming scenarios, the variance was much more pronounced in the non-road grooming scenario (Figure 6.68). Whereas winter road grooming clearly increased the permeability of all groomed corridors (Figures 6.69, 6.70), the increased permeability was more pronounced for the interior corridors than for boundary corridors. These results suggest that road grooming may have more of a facilitation effect on interior range bison movement than it does on interior-to-exterior range movement.

In simulation scenarios without road grooming, correlative patterns between numbers of bison immigrating and emigrating from each range offer evidence as to which ranges were responsible for inter-range movement (Figures 6.71, 6.72). Gardiner basin received its immigrating bison from the Lamar Range, West Yellowstone received its immigrating bison from Mary Mountain, and Mary Mountain and Pelican Valley exhibited significant exchange of individuals on an inter-annual basis. Interestingly, Lamar Valley and Pelican Valley ranges exchanged significant numbers of bison when snowpack conditions over the Mirror Plateau permitted.

When road grooming is employed, the pattern remains generally similar, with the exception that significant bi-directional movement of bison occurs between the Mary Mountain and Lamar Valley ranges (Figures 6.73, 6.74).

In summary, strong differences occurred between net immigration and emigration rates between ranges (Figure 6.75). The Mary Mountain range is clearly the central fecundity engine of the YNP bison system. Significantly lower net contributions of bison production occur in both Lamar Valley and Pelican Valley, and Gardiner basin and West Yellowstone ranges are clearly net sinks for bison.

The clear relationship between winter forage availability and the number of bison departing each range is presented in Figure 6.76.

### *Natural Mortality*

Simulated natural winter mortality is a common, though highly variable event for bison in YNP (Figure 6.78). Although average annual winter mortality in the absence of road grooming was simulated to be ~180 bison (5% of the population) and 225 with road-grooming (~6-7%) (Figure 6.77), mortality during specific winters may exceed 25% of the population (Figure 6.78). The extent of natural mortality appears to be much more closely related to forage availability than it is to forage production (Figure 6.79). As shown earlier, forage availability is influenced by two variables, primarily herbivore biomass, and secondarily, forage production. Road grooming appears to cause a increase (25%) in over-winter mortality (Figure 6.77), a difference that is explained by higher inter-range movement and increased probability that higher bison densities may occur on any given winter range. A comparison of winter mortality using each of the Group models indicated similar results (Figure 6.80).

### *Culling of Boundary Herds*

The “Majority Average” YNP Bison Distribution Model was used to explore the simulated extent of culling of excess bison from boundary ranges. Based on maximum acceptable tolerance levels of 200 for each of the Gardiner basin and West Yellowstone Ranges, required cull levels were highly variable and occurred in ~25% of the simulated years (Figures 6.81, 6.82). Maximum cull events periodically exceeded 500 animals, and rarely exceeded 750 animals. Cull events exceeded 10% of the total YNP herd in 15% of years in non-road grooming scenarios and 6% of the herd during road grooming scenarios. Cumulative required culls during ten 100-year stochastic runs varied considerably, and ranged between annual average culls of 50-90 bison during the non-grooming scenario, and 60-100 for road grooming scenarios. On average, 75 bison would be culled each year from boundary ranges with or without road grooming (Figure 6.83). In comparing bison cull numbers between the Key Informant Groups, all groups performed similarly in the road-grooming scenario, but no bison were culled in the Group

4 model in the non-road grooming scenario because of the inability of bison to disperse to boundary ranges (Figure 6.84).

Maximum tolerance levels were varied systematically from 0, 200, 400, 600, and 800 bison to evaluate the consequences of different tolerance levels for bison in exterior ranges. Unsurprisingly, the total number of culled bison declined significantly with each interval of increasing tolerance (Figure 6.85). A consequence of this management action, however, was an attendant increase in the level of natural (i.e., starvation) overwinter mortality that occurred between the tolerance ranges of 0 and 800 (Figure 6.86). Only at the highest tolerance level (800 animals in each of the boundary ranges) did cumulative starvation mortality not continue to increase, and this was because this “low-cull” scenario caused very high periodic winter die-offs and therefore reduced the total population size. When mortality attributed to cull and starvation is summed (Figure 6.87), it is clear that aggregate mortality remained similar at all levels of societal tolerance for bison in boundary ranges. These results demonstrate the clear underpinnings of most plant-herbivore systems - that herbivore populations chasing the inter-annual variation in primary productivity will overshoot carrying capacity, and that these animals will either die of starvation or elect to expand their ranges in search of additional forage. Although cull is a significant cause of mortality for bison in YNP, it is less than that caused by starvation (Figure 6.88).

### *Vaccination Initiative*

The ability of a vaccination program to reduce the incidence of brucellosis in YNP bison remains a controversial and poorly understood dynamic. Given this limitation, however, the YNP Bison Distribution model was used to explore various “what-if” scenarios involving vaccination. As better knowledge emerges about the efficacy of a brucellosis vaccination program, and how society might respond to changes in the prevalence of this pathogen in bison, it is intended that this model would be informed by this improved insight.

In this hypothetical scenario, the bison herd was fully vaccinated over a period of 30 years. During this period, sero-positive prevalence declined from 50% to 30% and tolerance levels for boundary bison was prescribed to increase from 200 to 600 animals. With these “user-defined” relationships entered into the model, the simulated cull results were generated (Figures 6.89, 6.90). These results suggest that no directional change in annual or cumulative cull would result from a vaccination program, but that the overall variance in the cull might increase. These results emerge from the following “assumed” or computed properties:

- Reduced sero-positive bison result in greater tolerance (assumption)
- Greater tolerance result in lower cull numbers during a given year (assumption)
- Lower cull numbers result in higher population levels (computed)
- Higher population levels result in greater numbers of bison emigrating to boundary ranges (computed)
- Greater numbers of bison in boundary herds (above the new tolerance levels) result in increased culls (computed)

## *The Great Plains Bison "Repatriation" Scenario*

To explore the consequences of allowing bison emigrating from the central ranges of YNP to repatriate grassland complexes outside the Park, a series of "what-if" scenarios were simulated. Five different simulations were conducted, with each varying the amounts of habitat (exterior to YNP) made available to an expanding bison herd (0, 2,500, 5,000, 7,500, and 10,000 $km^2$).

The results of these simulations revealed the following:

- An increase in bison habitat external to YNP will result in a proportional increase in exterior bison populations (Figure 6.89), (0 $km^2$ = 0 bison, 2,500 $km^2$ = 9,000 bison, 5,000 $km^2$ = 18,000 bison, 7,500 $km^2$ = 27,000 bison, 10,000 $km^2$ = 36,000 bison)
- An increase in bison habitat external to YNP will result in a proportional increase in the number of bison that will need to be culled annually at the margins of the expanded range (Figure 6.91), (0 $km^2$ = 0 bison, 2,500 $km^2$ = 1,250 bison, 5,000 $km^2$ = 2,500 bison, 7,500 $km^2$ = 3,750 bison, 10,000 $km^2$ = 5,000 bison)
- Increasing bison habitat exterior to YNP is an effective strategy to increase the total regional population, but is not a good strategy to minimize the number of bison that would need to be culled annually on the regional landscape. Although the number of bison to be culled on the direct border of YNP would be significantly reduced in a "repatriation" scenario, a greater number of bison would be required to be culled in more boundary locations.

## *Exploring "Climate Change"*

The outcome of two hypothetical "climate change" scenarios involving variance in precipitation reveal significant changes to the dynamics of forage production and bison populations in YNP. Relative to the base case (average precipitation and average variance metrics), incremental increases in rainfall variance lead to increasing variation in forage production, increasing variance in populations of elk and bison, and reduced movement of bison to boundary ranges (Figures 6.92, 6.93, 6.94, 6.95, 6.96). The reduction in movement to boundary ranges was caused by a general reduction in bison population size and hence frequency in forage limitation. Relative to the base case (average precipitation and average variance metrics), the climate change scenario involving reduced precipitation variance lead to reduced inter-annual variation in forage production, reduced variance in elk and bison populations, and similar levels of bison movement to boundary ranges.

These "what-if" climate change scenarios suggest that increased variation in precipitation, should it occur, will likely cause a de-stabilizing effect on primary production, and hence secondary herbivore production, and attendant distribution and movement patterns.

## System Sensitivity and Key Uncertainties

The authors recognize that many important numerical relationships in the YNP bison population and distribution model are not currently available from empirical knowledge published in the primary or secondary literature. In recognition that bison managers must make management decisions in the absence of complete knowledge, relationships generated from the AHP process were used where empirical data was lacking. The level of uncertainty of these relationships is important to evaluate. The model is designed to allow managers and other stakeholders to test the level of sensitivity of key indicators to changes in uncertain input variables and relationships.

Although not reported as graphics in this manuscript, the YNP Bison Distribution Model identified that key indicators (i.e., bison population levels and movement patterns) were highly sensitive to several input variables. It is important for YNP managers to evaluate the current level of certainty that accompanies these relationships. Where indicators are highly sensitive to input variables, and the "certainty" of these relationships is low, it is important to improve certainty by encouraging additional research or by conducting applied experimental manipulations. Examples of highly sensitive input variables and relationships in the YNP Bison Distribution Model include:

- Threshold depth/density of snow at which low and high density forage-limited bison cannot move through corridors in search of better foraging conditions. Systematic research has not been carried out on the ability of bison to move through snow under the variety of circumstances present in Yellowstone National Park.
- Terrain characteristics (slope, ruggedness) that affect the above snow depth/density threshold preventing movements.
- Snowpack characteristics in the Pelican Valley in relation to other ranges.
- The relationship (shape and scale of the curve) between winter forage availability, bison density and bison over-winter mortality.
- The relationship (shape and scale of the curve) between winter forage availability and probability of bison movement.
- There was contradictory opinion if the unroaded Mirror Plateau Corridor is a functional barrier to movements in winter between the Pelican Valley and the Lamar Valley when bison numbers are high and per capita forage is limited.
- Inter-range variability in forage productivity in response to precipitation and growing season length. In particular, one key informant suggested the growing season is shortest in the Pelican Valley range because of a long period of snow cover typically followed by spring flooding.
- Relationship between incidence of sero-positive bison and proportion of the herd that has been vaccinated.

## Conclusions

The model represents a grazing system dominated by two large herbivores (bison and elk) seeking to satisfy their forage requirements on a dynamic landscape comprised of multiple inter-connected ranges. The system is inherently dynamic reflecting significant year-to-year variation in forage production (driven by stochastic summer precipitation and winter snowpack), forage utilization (driven by bison and elk abundance), and variation in the influence of snowpack on access to forage. The bison population tends to a dynamic equilibrium around a mean of 4000, ranging between 2500 and 6000 with road grooming, and 2000 to 6000 without road grooming. The simulated bison population exhibited significant variation at regional and range levels and large numbers of individuals moved to boundary ranges during years when forage in the interior of the park was inadequate relative to threshold requirements.

Empirical evidence was used to construct the metrics of bison ranges, movement corridors, summer and winter precipitation, and forage production. Information from key informant interviews and group workshops was used to model bison distribution patterns. Four models were developed from workshops with five Key Informant Groups (two concordant group model were combined). Three models produced similar results and one was discordant. A new model was constructed based on average values from the three similar models. This ‘Majority Average Model’ was used to evaluate system behavior and management options and results were compared with the outlying model.

Information provided from key informant interviews and workshops suggested that inter-range movements of bison are not constrained by winter snowpack in three of five corridors (Pelican Valley to Hayden Valley, Firehole to West Yellowstone, and Gardiner to Lamar Valley), nor on the Mary Mountain Trail (not considered in the model). The unroaded Pelican Valley to Lamar Valley corridor (over the Mirror Plateau) was considered permeable during low snow winters. The Firehole to Mammoth corridor was considered a barrier in the absence of road grooming.

Simulation results indicate that road grooming is likely to have a greater influence on movement of bison between interior ranges (Lamar, Mary Mountain, Pelican) than between interior ranges and boundary ranges (West Yellowstone, Gardiner basin). Grooming of winter roads may provide a dampening effect reducing the number of bison departing for boundary ranges during winters with inadequate forage (below a threshold of 3 tonnes/bison).

Simulation results indicate that bison movements between interior winter ranges exhibited high inter-annual variation, ranging from 100 to 3700 animals. Average movements of ~750 bison occurred in non-road grooming scenarios, and 850 in road-grooming scenarios. Simulations indicated that bison movements from interior (Lamar Valley, Mary Mountain, Pelican Valley) to boundary ranges (Gardiner basin, West Yellowstone) also exhibited high inter-annual variation, ranging from 50 to 1500 animals. Five 100 year stochastic simulations indicated a long-term average annual movement of 150-220 bison dispersing to boundary ranges.

Per capita forage availability in winter was a key driver influencing inter-range movements. Although forage production was an important explanatory variable influencing forage availability, herbivore density (bison and elk) was more important. Although bison may move in response to diminished forage supply, they cannot be assured of the sufficiency of forage in destination ranges. Variation in winter forage supply among ranges and between years combined with the ability of bison to move between ranges results in unstable population dynamics particularly at high densities.

Without "controlling" populations at levels below the mean, the model suggests that natural winter mortality (i.e., starvation) would average 6% of the herd, varying between 0 and 21%. Cull mortality on boundary ranges (using current population tolerance levels) is predicted to average 2% of the herd, with values ranging between 0 and 10% of the population. Increasing the level of societal tolerance for bison on boundary ranges would reduce the number of bison culled, but would increase the number of bison dying from winter starvation; i.e. all bison must die from some cause. Predation was assumed invariant, which is unlikely to be the case particularly in the Central Range where bison are likely to become the dominant prey of wolves in time. This is an important factor to be considered in future simulations.

Simulation of vaccination of bison for brucellosis revealed that an increase of societal tolerance of sero-negative bison in boundary ranges did not result in fewer bison being culled over the simulation period. Simply put, short-term reduction in cull associated with reduced prevalence of sero-positive individuals only allowed more individuals to return to central ranges during the summer season. Reduced culls increased the number of bison departing interior ranges in forage-limited winters. This translated to larger numbers of bison subject to management actions in boundary ranges.

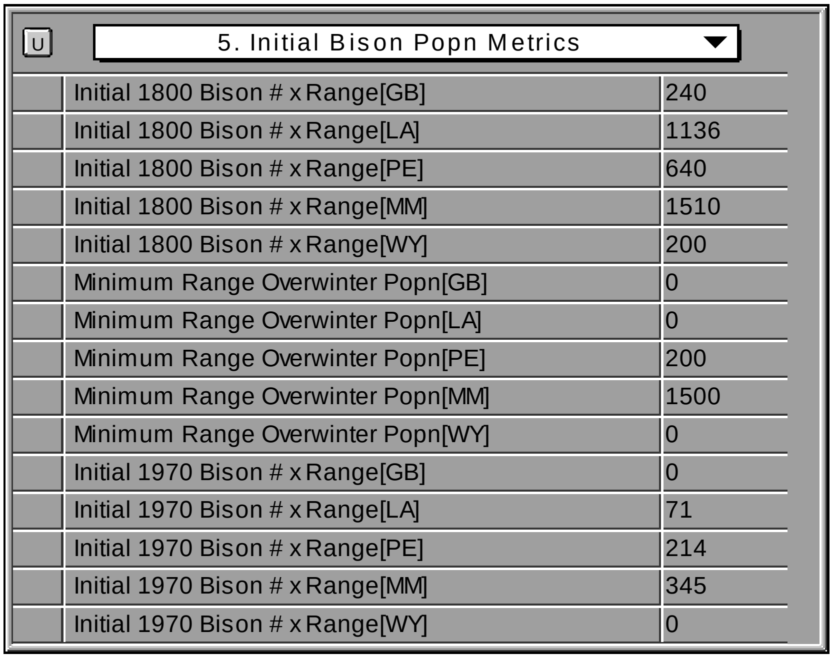
Increasing the area available to bison outside YNP would result in a larger regional population and would reduce mortality in the short-term because an increase in per capita resources. However, the population would rapidly increase to a level where density-dependency would increase pressure to expand range and reduce population growth through decreased fecundity and increased mortality. Increasing the area available to bison outside the park would result in a larger population and an increase in the number of bison dying from culls and/or winter starvation.

Changes in precipitation variance under a "hypothetical" climate change scenario suggested that primary productivity, herbivore populations and biomass, and movement to boundary ranges are all responsive to this externality. The potentially de-stabilizing influence of changed precipitation patterns on YNP grazing system dynamics represents an example of a "what-if" scenario that can be explored at a strategic level with the model.

The structure and attribution of the model were based on key informant knowledge and relationships provided in the literature. No attempt was made to adjust these values to "conform" to observed empirical patterns of bison movement, boundary cull, or over-winter mortality. The graphical user interface constructed for this model was designed to be user-friendly, allowing stakeholders test scenarios by varying key inputs without expert assistance. The model can also be readily adapted to include improved inputs, coefficients and relationships from empirical research.

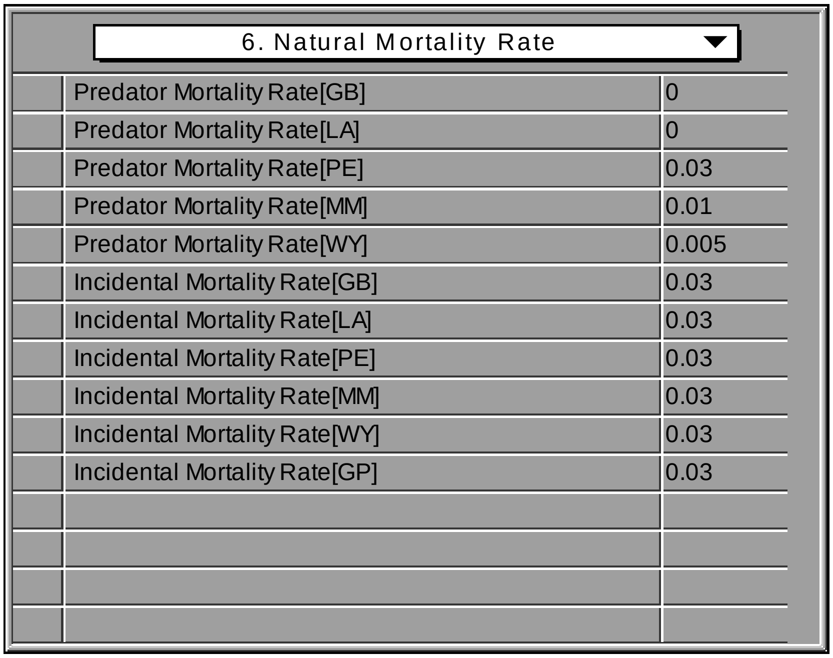
It is important for stakeholders to recognize that the greatest value of systems models is for exploring ecological and management scenarios, not to predict outcomes. Models can not be "right" in a predictive sense, but rather should strive to be "reasonable" in their structure, assumptions, and relationships. Simulation modeling allows users to gain better insight into the dynamics of a system Their greatest value lies in offering a "what-if" simulation tool for stakeholders to creatively explore alternative futures.

Table 6.1. Initial bison population size for pre-settlement era (1800), for post-settlement era (1970), and minimum over-wintering population.



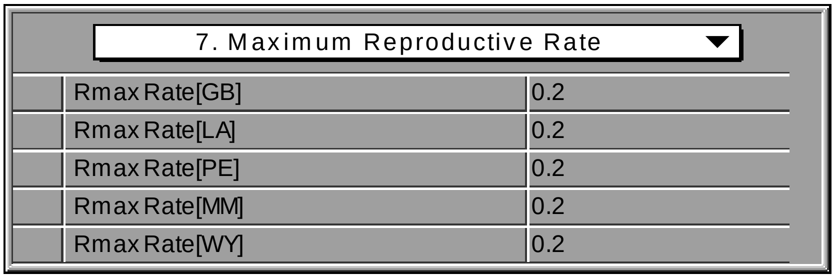
| | |
|---|---|
| Initial 1800 Bison # x Range[GB] | 240 |
| Initial 1800 Bison # x Range[LA] | 1136 |
| Initial 1800 Bison # x Range[PE] | 640 |
| Initial 1800 Bison # x Range[MM] | 1510 |
| Initial 1800 Bison # x Range[WY] | 200 |
| Minimum Range Overwinter Popn[GB] | 0 |
| Minimum Range Overwinter Popn[LA] | 0 |
| Minimum Range Overwinter Popn[PE] | 200 |
| Minimum Range Overwinter Popn[MM] | 1500 |
| Minimum Range Overwinter Popn[WY] | 0 |
| Initial 1970 Bison # x Range[GB] | 0 |
| Initial 1970 Bison # x Range[LA] | 71 |
| Initial 1970 Bison # x Range[PE] | 214 |
| Initial 1970 Bison # x Range[MM] | 345 |
| Initial 1970 Bison # x Range[WY] | 0 |

Table 6.2. Predator and incidental mortality rates applied to each winter range. Based on input from key informant workshops.



| | |
|---|---|
| Predator Mortality Rate[GB] | 0 |
| Predator Mortality Rate[LA] | 0 |
| Predator Mortality Rate[PE] | 0.03 |
| Predator Mortality Rate[MM] | 0.01 |
| Predator Mortality Rate[WY] | 0.005 |
| Incidental Mortality Rate[GB] | 0.03 |
| Incidental Mortality Rate[LA] | 0.03 |
| Incidental Mortality Rate[PE] | 0.03 |
| Incidental Mortality Rate[MM] | 0.03 |
| Incidental Mortality Rate[WY] | 0.03 |
| Incidental Mortality Rate[GP] | 0.03 |
| | |
| | |
| | |
| | |

Table 6.3. Maximum bison herd growth rate.



7. Maximum Reproductive Rate

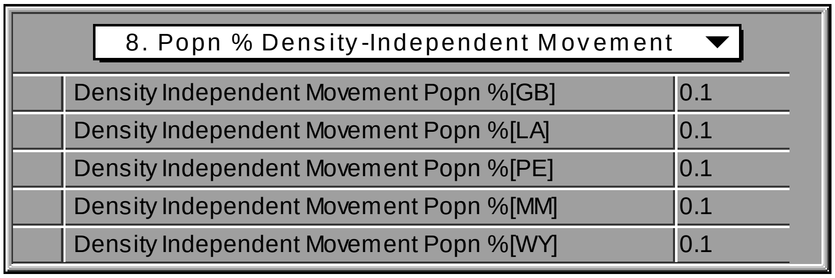
| | |
|---|---|
| Rmax Rate[GB] | 0.2 |
| Rmax Rate[LA] | 0.2 |
| Rmax Rate[PE] | 0.2 |
| Rmax Rate[MM] | 0.2 |
| Rmax Rate[WY] | 0.2 |

Table 6.4. Maximum tolerance for bison in boundary ranges.

11. User Defined Maximum Tolerance

| | |
|---|---|
| Maximum Tolerance[GB] | 200 |
| Maximum Tolerance[WY] | 200 |
| | |
| | |
| | |

Table 6.5. Portion of total movement attributed to random walk. Based on input from key informant workshops.



8. Popn % Density-Independent Movement

| | |
|---|---|
| Density Independent Movement Popn %[GB] | 0.1 |
| Density Independent Movement Popn %[LA] | 0.1 |
| Density Independent Movement Popn %[PE] | 0.1 |
| Density Independent Movement Popn %[MM] | 0.1 |
| Density Independent Movement Popn %[WY] | 0.1 |

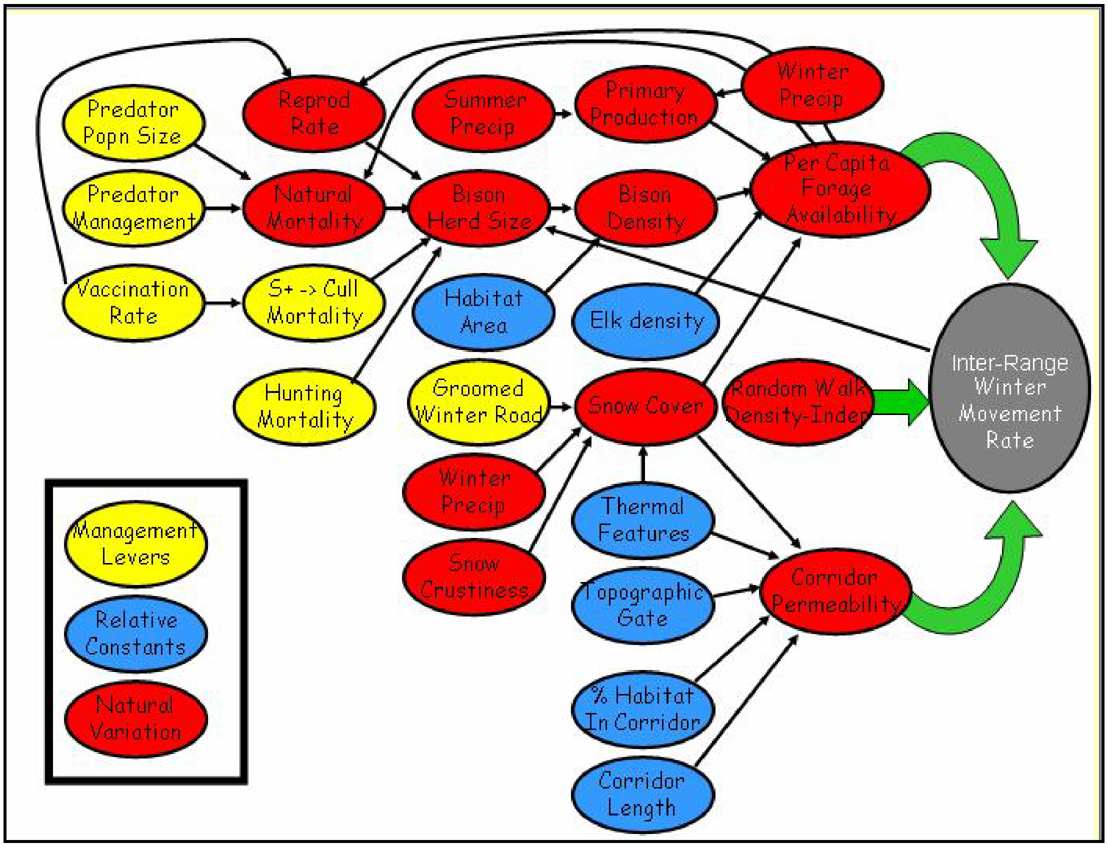
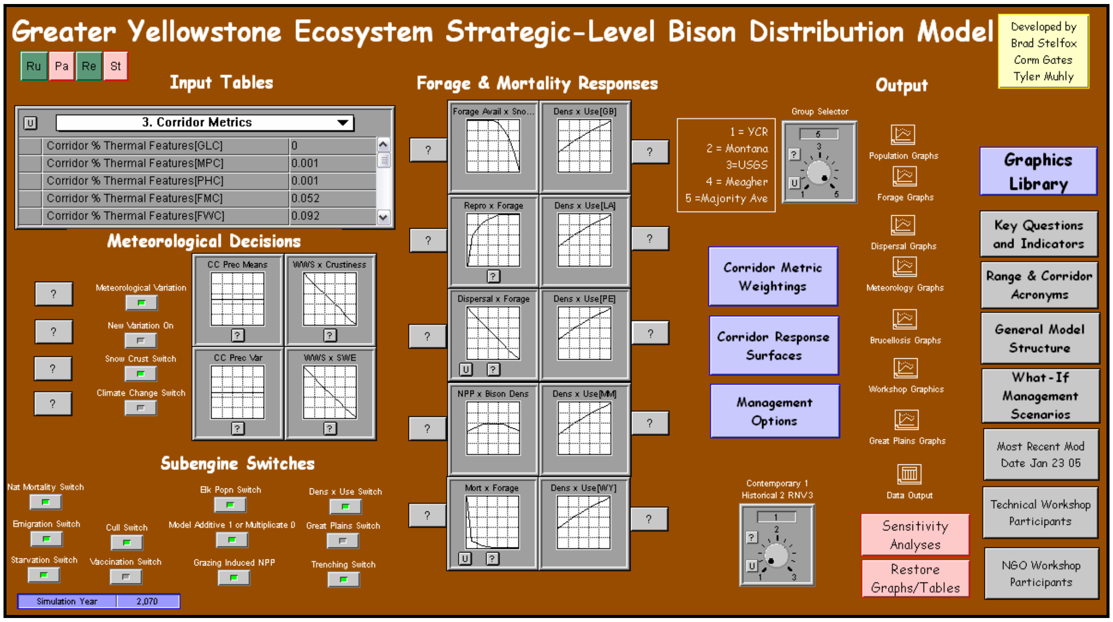


Figure 6.1. Impact Hypothesis Diagram (IHD) used as basis for YNP Bison Distribution Model. The structure of this diagram was based on information gathered at key informant workshops.



3. Corridor Metrics

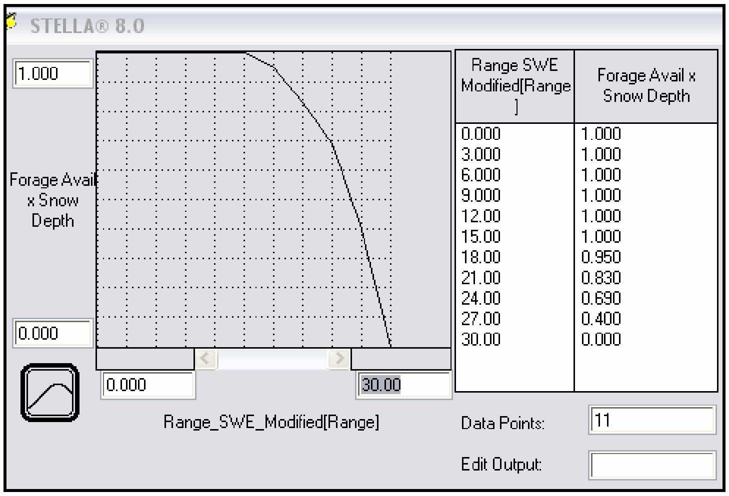
| | |
|---|---|
| Corridor % Thermal Features[GLC] | 0 |
| Corridor % Thermal Features[MPC] | 0.001 |
| Corridor % Thermal Features[PHC] | 0.001 |
| Corridor % Thermal Features[FMC] | 0.052 |
| Corridor % Thermal Features[FWC] | 0.092 |

Group Selector 5

Contemporary 1 Historical 2 RNV3: 1

Simulation Year 2,070

Figure 6.2. Master Panel of the YNP Bison Distribution Model.

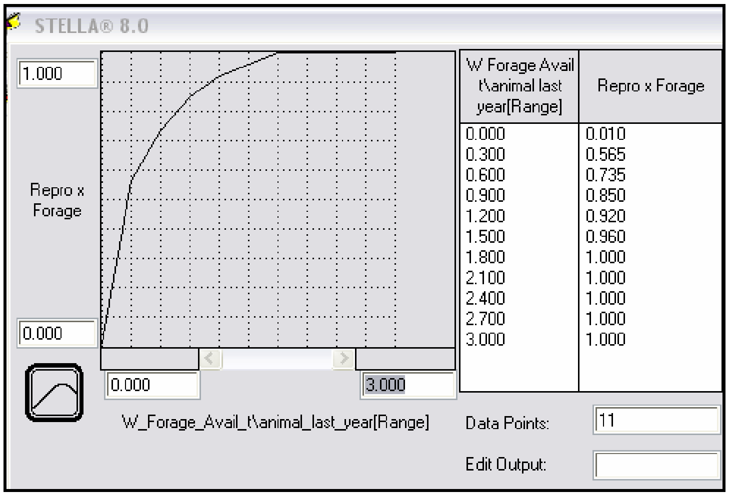


| Range SWE Modified[Range] | Forage Avail x Snow Depth |
|---|---|
| 0.000 | 1.000 |
| 3.000 | 1.000 |
| 6.000 | 1.000 |
| 9.000 | 1.000 |
| 12.00 | 1.000 |
| 15.00 | 1.000 |
| 18.00 | 0.950 |
| 21.00 | 0.830 |
| 24.00 | 0.690 |
| 27.00 | 0.400 |
| 30.00 | 0.000 |

Data Points: 11

Edit Output:

Figure 6.3. Relationship between bison winter forage availability and Snow Water Equivalence (cm).

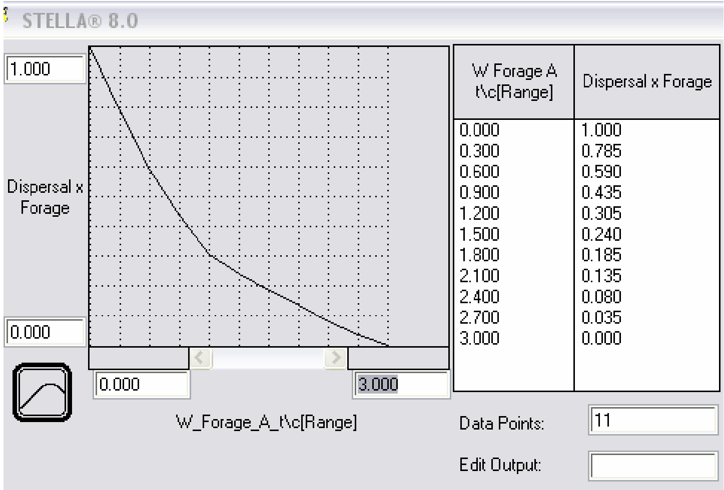


| W Forage Avail t\animal last year[Range] | Repro x Forage |
|---|---|
| 0.000 | 0.010 |
| 0.300 | 0.565 |
| 0.600 | 0.735 |
| 0.900 | 0.850 |
| 1.200 | 0.920 |
| 1.500 | 0.960 |
| 1.800 | 1.000 |
| 2.100 | 1.000 |
| 2.400 | 1.000 |
| 2.700 | 1.000 |
| 3.000 | 1.000 |

Data Points: 11

Edit Output:

Figure 6.4. Relationship between bison winter forage availability and index of reproductive performance. A value of 1 returns a maximum population growth rate of 0.2.

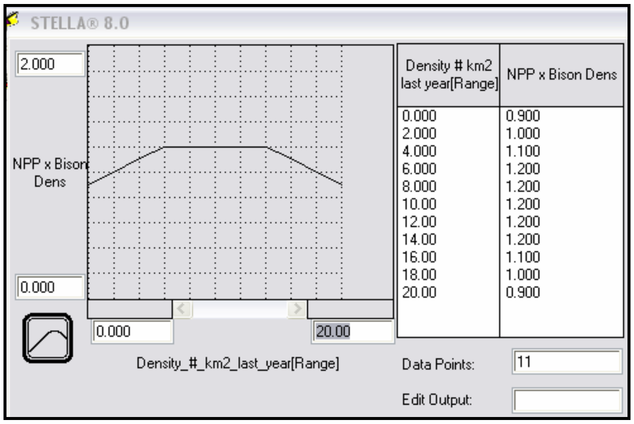


| W Forage A t\c[Range] | Dispersal x Forage |
|---|---|
| 0.000 | 1.000 |
| 0.300 | 0.785 |
| 0.600 | 0.590 |
| 0.900 | 0.435 |
| 1.200 | 0.305 |
| 1.500 | 0.240 |
| 1.800 | 0.185 |
| 2.100 | 0.135 |
| 2.400 | 0.080 |
| 2.700 | 0.035 |
| 3.000 | 0.000 |

Data Points: 11

Edit Output:

Figure 6.5. Relationship between winter forage availability (tonne/bison) and probability that bison move from current winter range to another winter range.

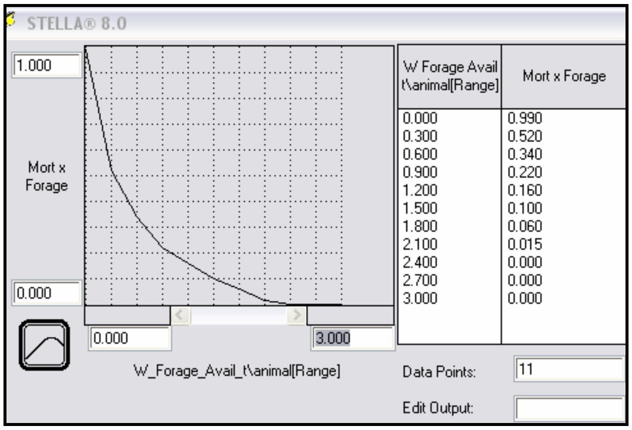


| Density # km2 last year[Range] | NPP x Bison Dens |
|---|---|
| 0.000 | 0.900 |
| 2.000 | 1.000 |
| 4.000 | 1.100 |
| 6.000 | 1.200 |
| 8.000 | 1.200 |
| 10.00 | 1.200 |
| 12.00 | 1.200 |
| 14.00 | 1.200 |
| 16.00 | 1.100 |
| 18.00 | 1.000 |
| 20.00 | 0.900 |

Data Points: 11

Edit Output:

Figure 6.6. Relationship between bison density and net primary productivity modifier. This relationship reflects the understanding that very low and very high levels of herbivory can reduce primary production below long term average values. Intermediate herbivory levels, in contrast, can lead to modest stimulation of primary production. Preliminary shape and magnitude of curve based on discussions with Mike Coughenhour (pers. comm.) at a key informant group workshop.

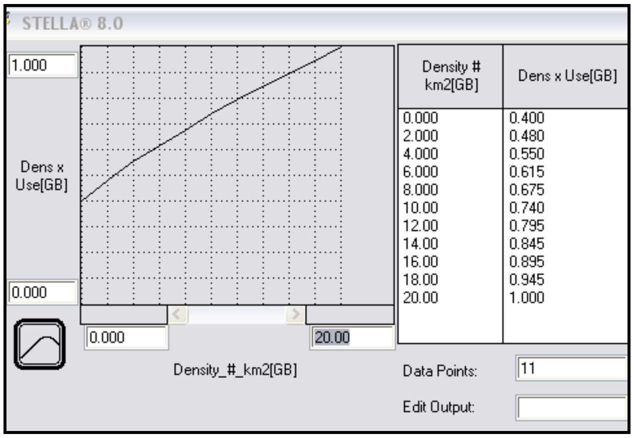


| W Forage Avail t\animal[Range] | Mort x Forage |
|---|---|
| 0.000 | 0.990 |
| 0.300 | 0.520 |
| 0.600 | 0.340 |
| 0.900 | 0.220 |
| 1.200 | 0.160 |
| 1.500 | 0.100 |
| 1.800 | 0.060 |
| 2.100 | 0.015 |
| 2.400 | 0.000 |
| 2.700 | 0.000 |
| 3.000 | 0.000 |

Data Points: 11

Edit Output:

Figure 6.7. Relationship between winter forage availability (tonne/bison) and overwinter bison mortality rate. In this model, no mortality effect occurred until forage availability declined below 2.2 tonne/bison. Rapidly increased levels of starvation mortality occur once forage availability declines below 0.5 tonne/bison.

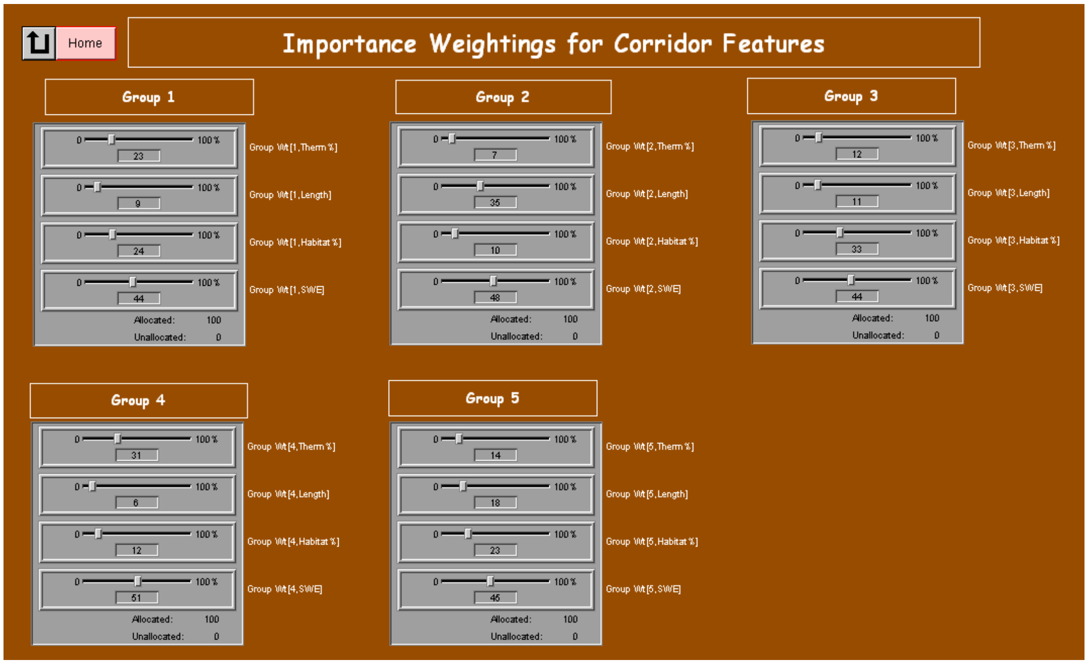


| Density # km2[GB] | Dens x Use[GB] |
|---|---|
| 0.000 | 0.400 |
| 2.000 | 0.480 |
| 4.000 | 0.550 |
| 6.000 | 0.615 |
| 8.000 | 0.675 |
| 10.00 | 0.740 |
| 12.00 | 0.795 |
| 14.00 | 0.845 |
| 16.00 | 0.895 |
| 18.00 | 0.945 |
| 20.00 | 1.000 |

Data Points: 11

Edit Output:

Figure 6.8. Relationship between bison density and proportion of winter range used. This relationship reflects the observation by several of the key informants that use of winter bison range is influenced by bison density. An identical relationship was used for all winter ranges.



Group 1
Group Wt[1,Therm %] 23
Group Wt[1,Length] 9
Group Wt[1,Habitat %] 24
Group Wt[1,SWE] 44
Allocated: 100
Unallocated: 0

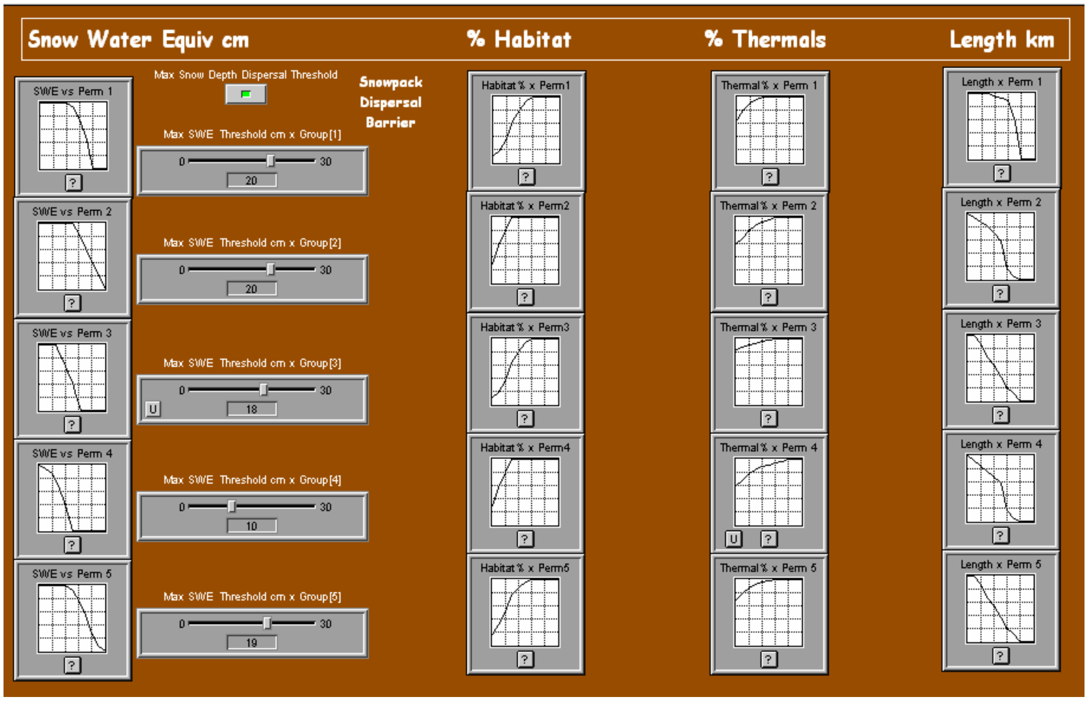
Group 2
Group Wt[2,Therm %] 7
Group Wt[2,Length] 35
Group Wt[2,Habitat %] 10
Group Wt[2,SWE] 48
Allocated: 100
Unallocated: 0

Group 3
Group Wt[3,Therm %] 12
Group Wt[3,Length] 11
Group Wt[3,Habitat %] 33
Group Wt[3,SWE] 44
Allocated: 100
Unallocated: 0

Group 4
Group Wt[4,Therm %] 31
Group Wt[4,Length] 6
Group Wt[4,Habitat %] 12
Group Wt[4,SWE] 51
Allocated: 100
Unallocated: 0

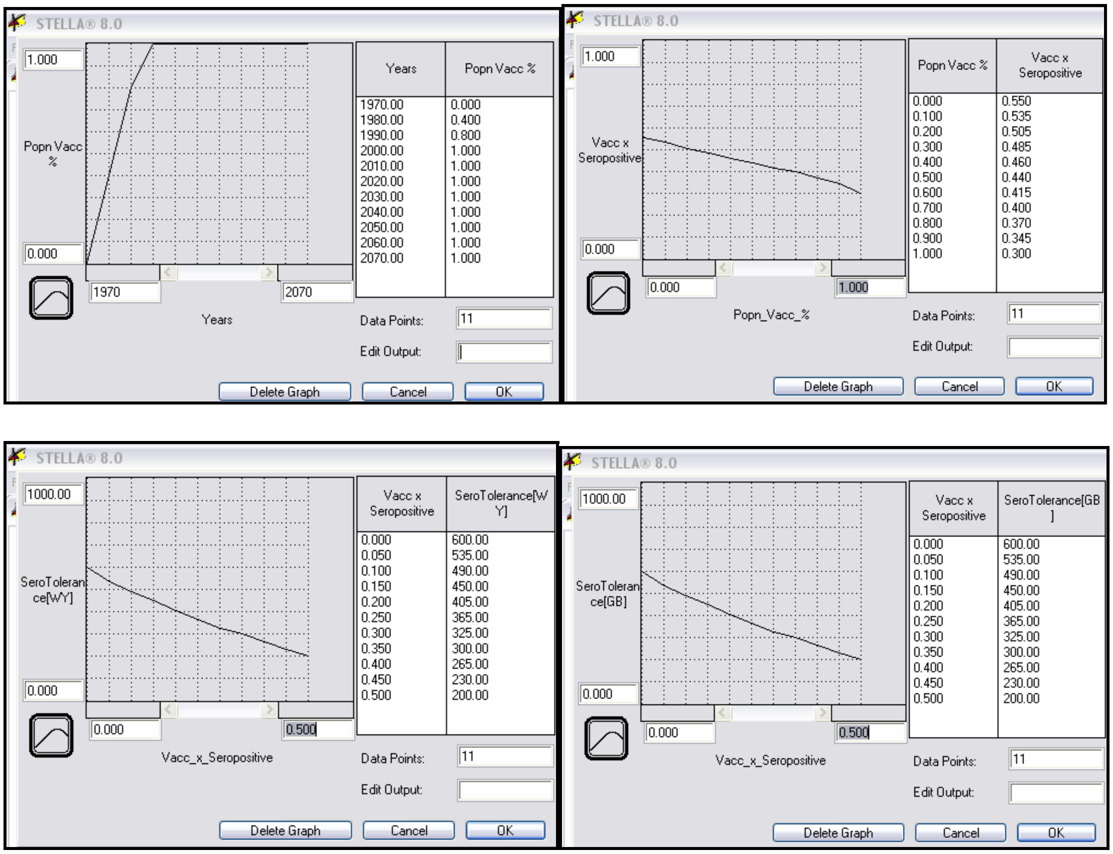
Group 5
Group Wt[5,Therm %] 14
Group Wt[5,Length] 18
Group Wt[5,Habitat %] 23
Group Wt[5,SWE] 45
Allocated: 100
Unallocated: 0

Figure 6.9. Importance weightings attributed to corridor metrics from each of the Key Informant Groups.



Max SWE Threshold cm x Group[1] 20
Max SWE Threshold cm x Group[2] 20
Max SWE Threshold cm x Group[3] 18
Max SWE Threshold cm x Group[4] 10
Max SWE Threshold cm x Group[5] 19

Figure 6.10. Corridor permeability response surfaces provided by each of the Key Informant Groups.



| Years | Popn Vacc % |
|---|---|
| 1970.00 | 0.000 |
| 1980.00 | 0.400 |
| 1990.00 | 0.800 |
| 2000.00 | 1.000 |
| 2010.00 | 1.000 |
| 2020.00 | 1.000 |
| 2030.00 | 1.000 |
| 2040.00 | 1.000 |
| 2050.00 | 1.000 |
| 2060.00 | 1.000 |
| 2070.00 | 1.000 |

Data Points: 11

Edit Output:

| Popn Vacc % | Vacc x Seropositive |
|---|---|
| 0.000 | 0.550 |
| 0.100 | 0.535 |
| 0.200 | 0.505 |
| 0.300 | 0.485 |
| 0.400 | 0.460 |
| 0.500 | 0.440 |
| 0.600 | 0.415 |
| 0.700 | 0.400 |
| 0.800 | 0.370 |
| 0.900 | 0.345 |
| 1.000 | 0.300 |

Data Points: 11

Edit Output:

| Vacc x Seropositive | SeroTolerance[WY] |
|---|---|
| 0.000 | 600.00 |
| 0.050 | 535.00 |
| 0.100 | 490.00 |
| 0.150 | 450.00 |
| 0.200 | 405.00 |
| 0.250 | 365.00 |
| 0.300 | 325.00 |
| 0.350 | 300.00 |
| 0.400 | 265.00 |
| 0.450 | 230.00 |
| 0.500 | 200.00 |

Data Points: 11

Edit Output:

| Vacc x Seropositive | SeroTolerance[GB] |
|---|---|
| 0.000 | 600.00 |
| 0.050 | 535.00 |
| 0.100 | 490.00 |
| 0.150 | 450.00 |
| 0.200 | 405.00 |
| 0.250 | 365.00 |
| 0.300 | 325.00 |
| 0.350 | 300.00 |
| 0.400 | 265.00 |
| 0.450 | 230.00 |
| 0.500 | 200.00 |

Data Points: 11

Edit Output:

Figure 6.11. Initial user-defined input relationships for a “hypothetical” bison brucellosis vaccination program. The graph in the upper left describes the number of years required to complete a full vaccination of the YNP herd. The graph in the upper right describes the relationship between the percent of the herd vaccinated and the anticipated change in sero-positive incidence. The two lower graphs describe relationships between anticipated changes in societal tolerance for bison in boundary herds (West Yellowstone – lower left graph; Gardiner basin – lower right graph) and incidence of sero-positive bison.

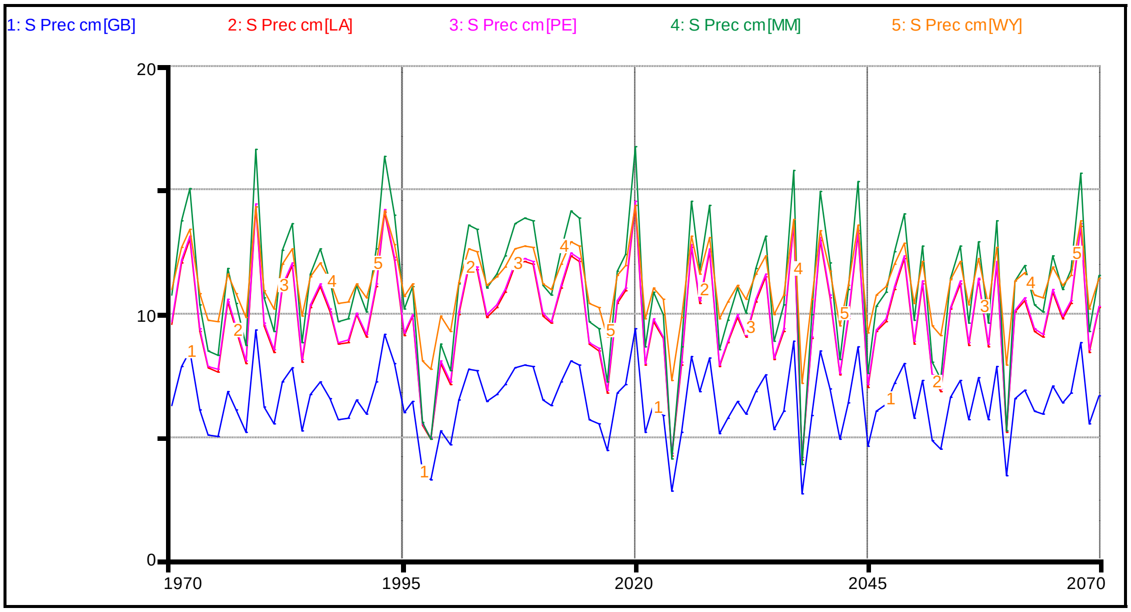


Figure 6.12. Simulated summer precipitation (cm) in each bison winter range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

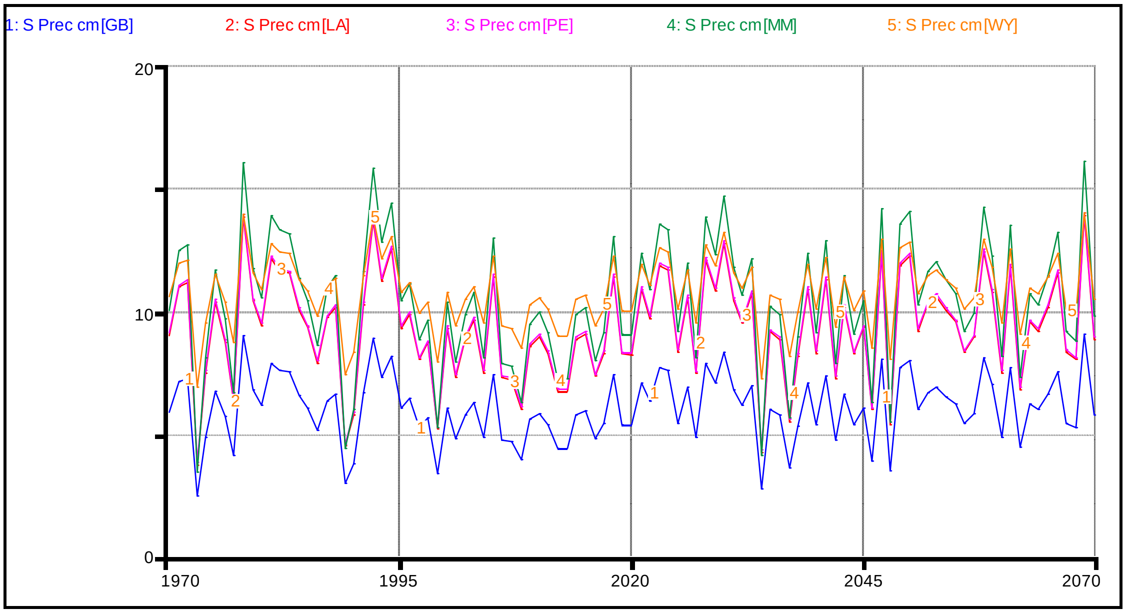


Figure 6.13. Simulated summer precipitation (cm) in each bison winter range. Simulation Run #2. Random precipitation sequence was synchronous among winter bison ranges.

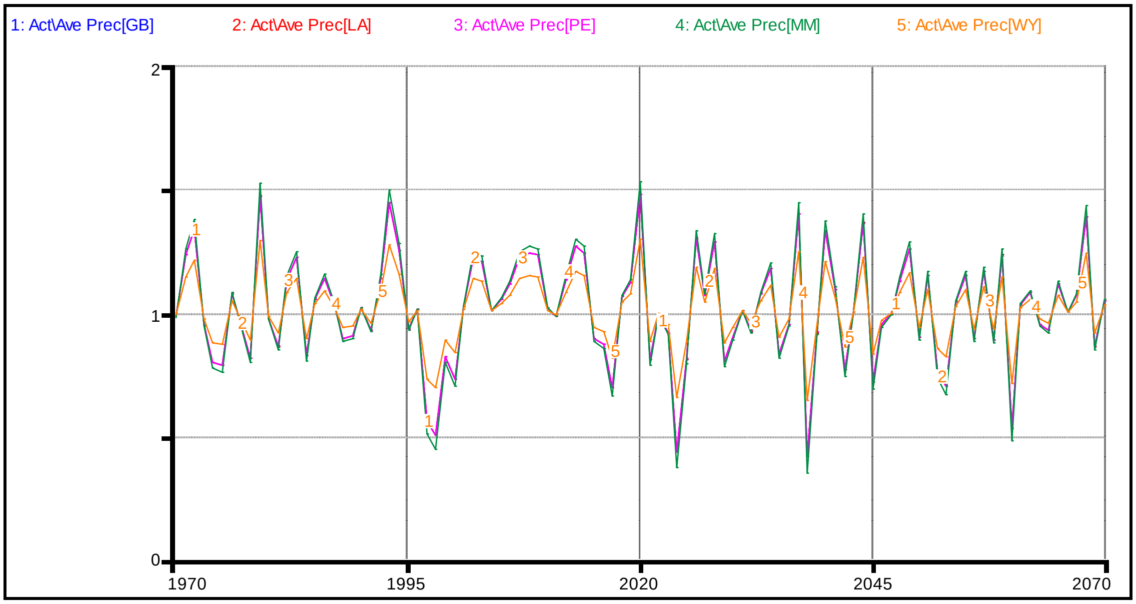


Figure 6.14. Simulated ratio of actual to average summer precipitation in each bison winter range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

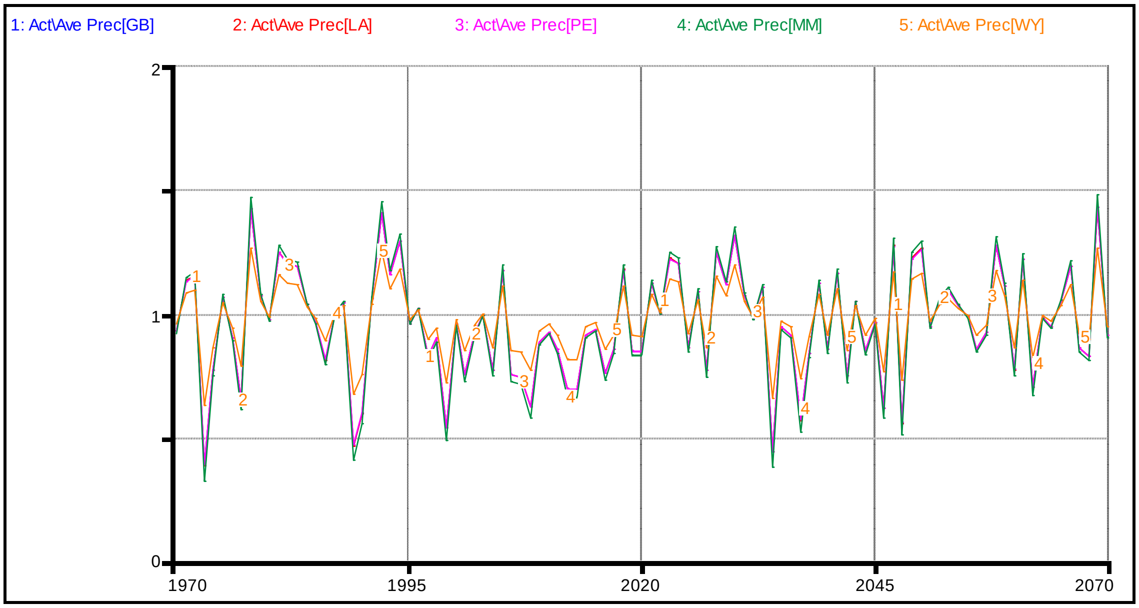


Figure 6.15. Simulated ratio of actual to average summer precipitation in each bison winter range. Simulation Run #2. Random precipitation sequence was synchronous among winter bison ranges.

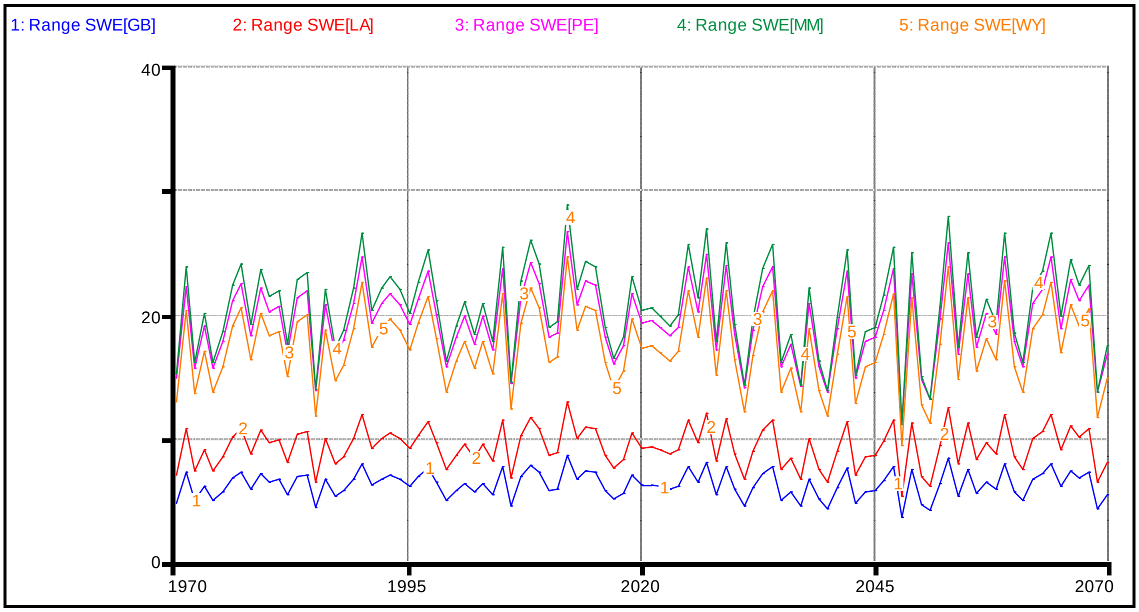


Figure 6.16. Simulated snow water equivalence (SWE) in each range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

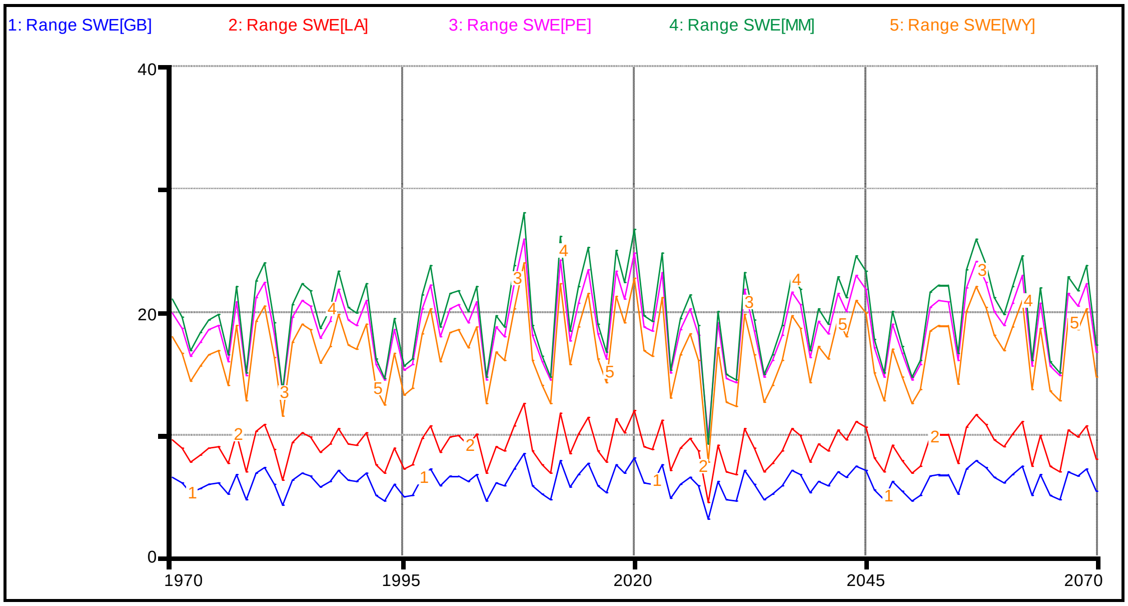


Figure 6.17. Simulated snow water equivalence (SWE) in each range. Simulation Run #2. Random precipitation sequence was synchronous among winter bison ranges.

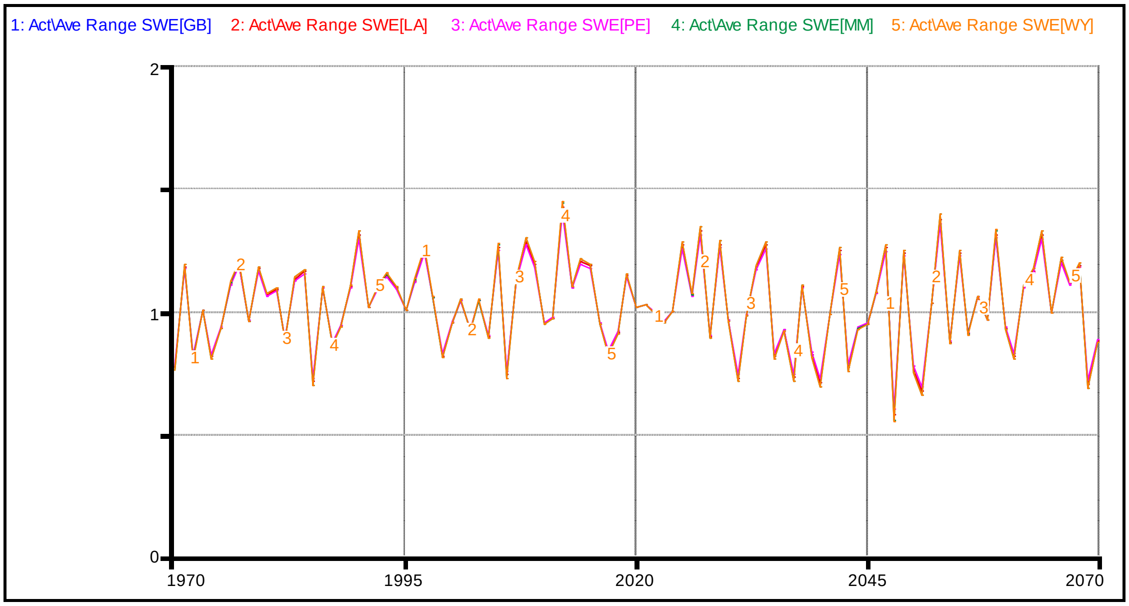


Figure 6.18. Simulated ratio of actual to average snow water equivalence in each range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

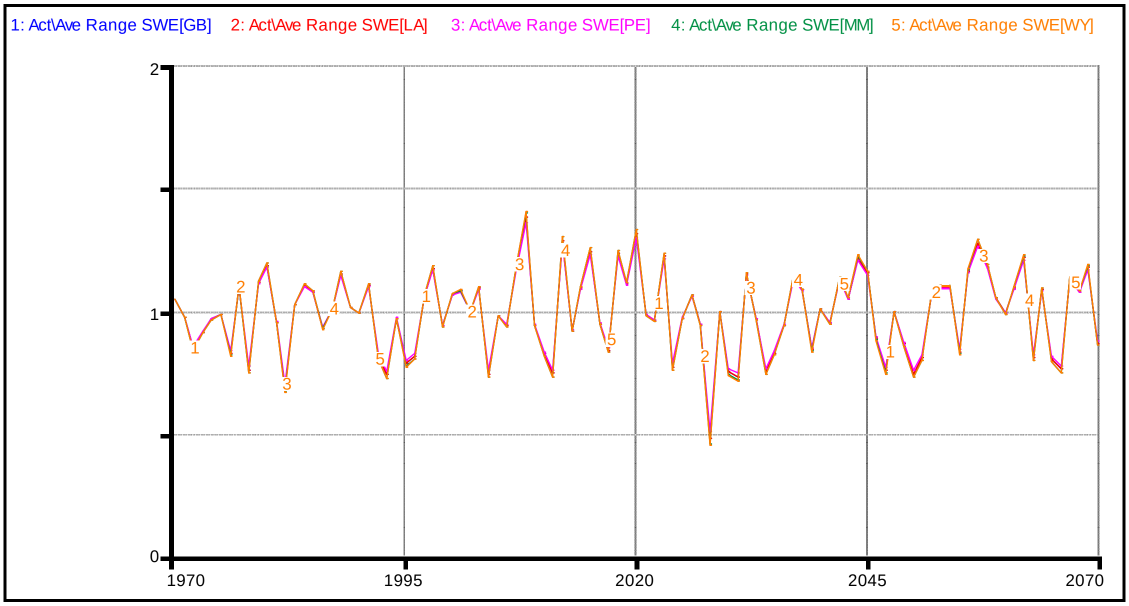


Figure 6.19. Simulated ratio of actual to average snow water equivalence in each winter range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

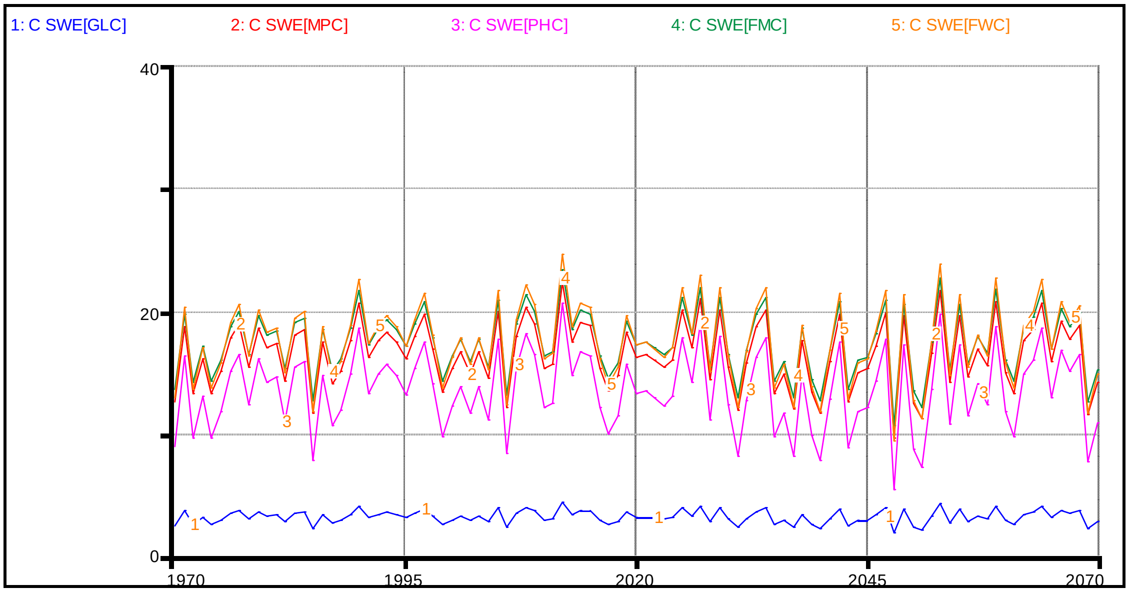


Figure 6.20. Simulated snow water equivalence (SWE) in each corridor. Simulation Run #1. Random precipitation sequence was synchronous among corridor routes.

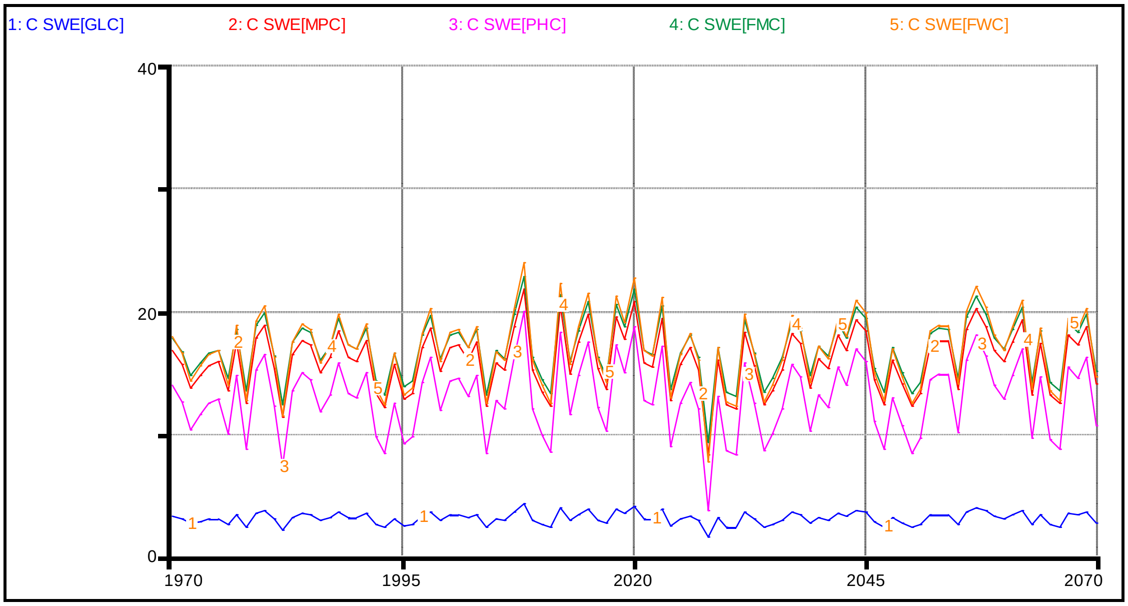


Figure 6.21. Simulated snow water equivalence (SWE) in each corridor. Simulation Run #2. Random precipitation sequence was synchronous among corridor routes.

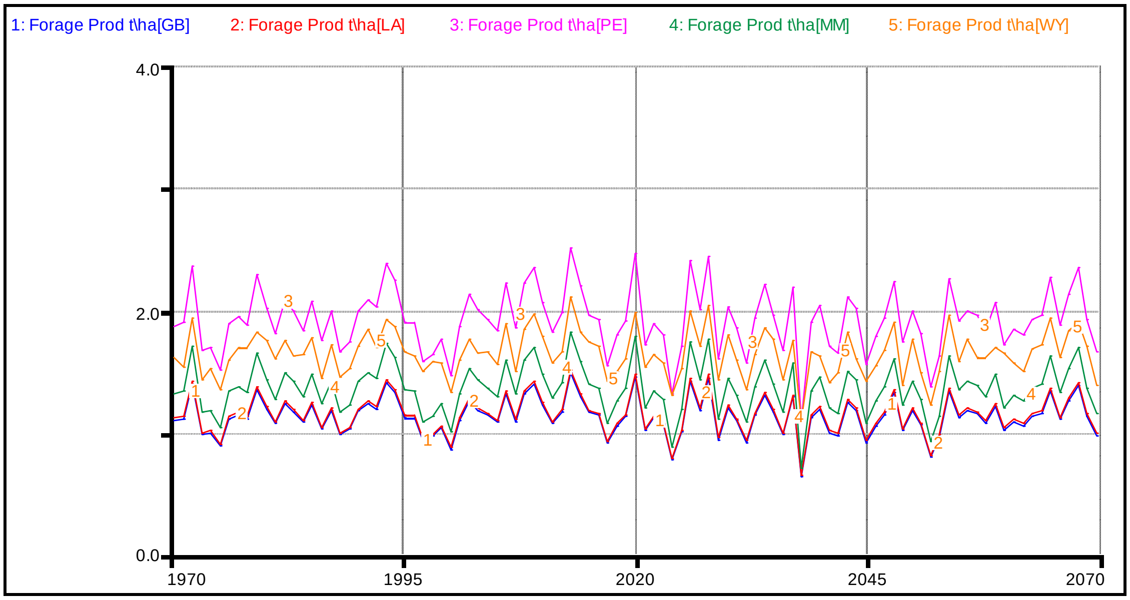


Figure 6.22. Simulated annual winter range forage production rate (tonne/hectare/year). Simulation Run #1. Random precipitation sequence was synchronous among corridor routes.

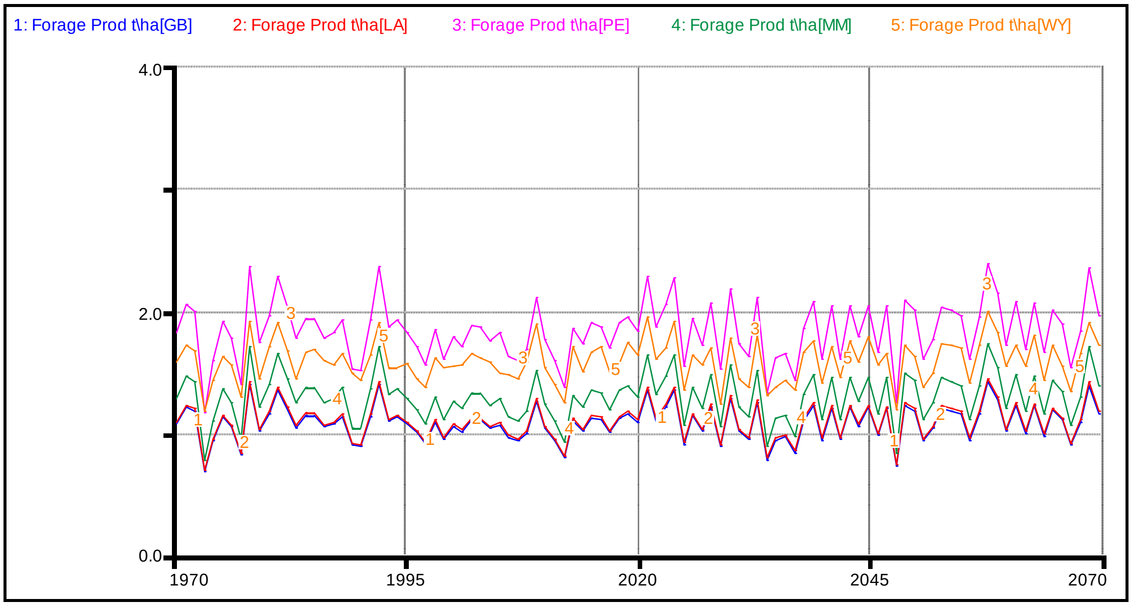


Figure 6.23. Simulated annual winter range forage production rate (tonne/hectare/year). Simulation Run #2. Random precipitation sequence was synchronous among corridor routes.

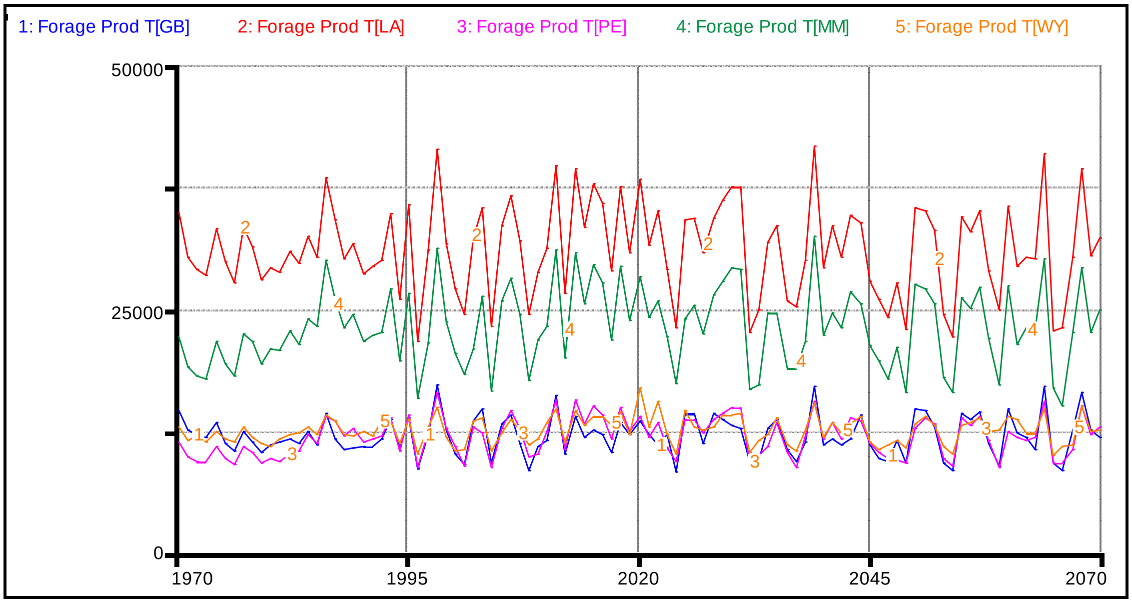


Figure 6.24. Simulated annual forage production (tonne) on winter ranges. Simulation Run #1 was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

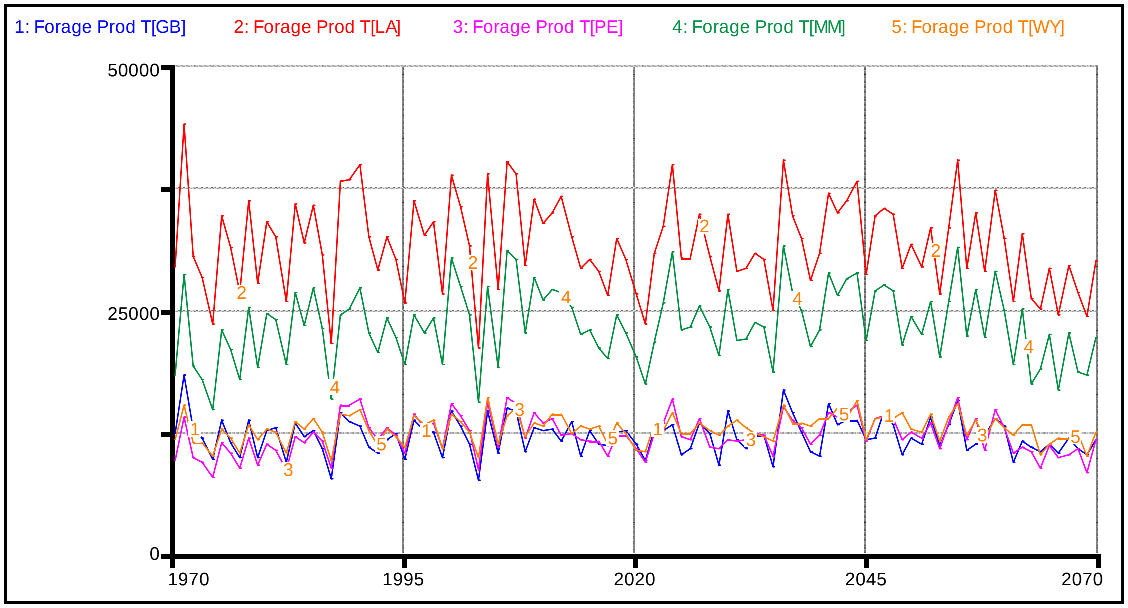


Figure 6.25. Simulated annual forage production (tonne) on winter ranges. Simulation Run #2 was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

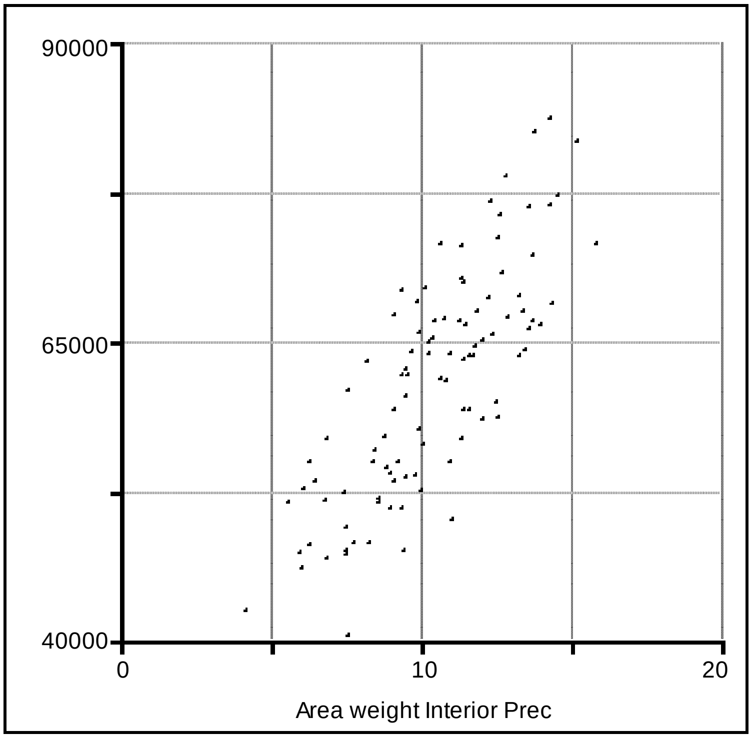


Figure 6.26. Simulated relationship between forage production (tonne; Y-axis) and area-weighted summer precipitation (cm) of interior winter ranges. Simulation was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

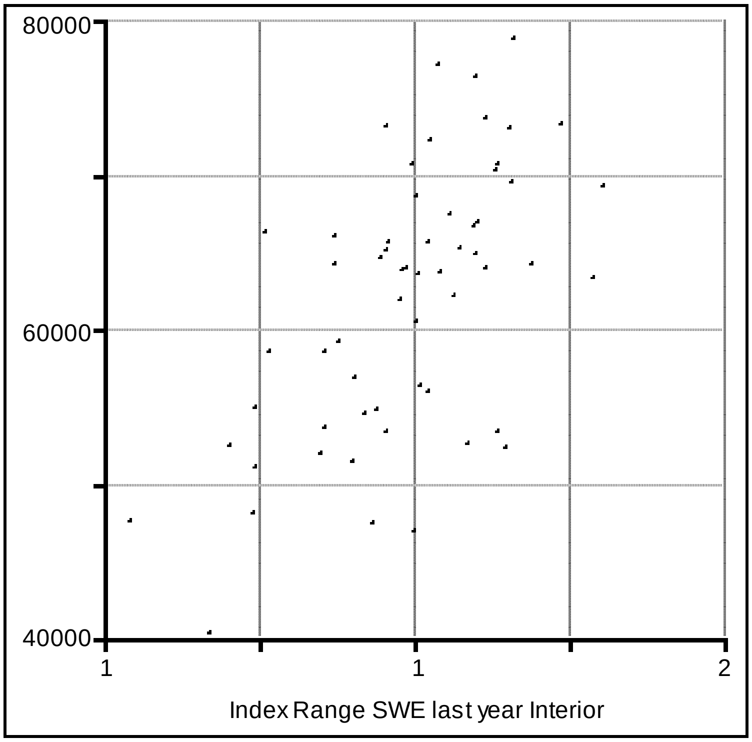


Figure 6.27. Simulated relationship between forage production (tonne; Y-axis) and previous winter snowpack (measured in SWE) of interior ranges. Simulation was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

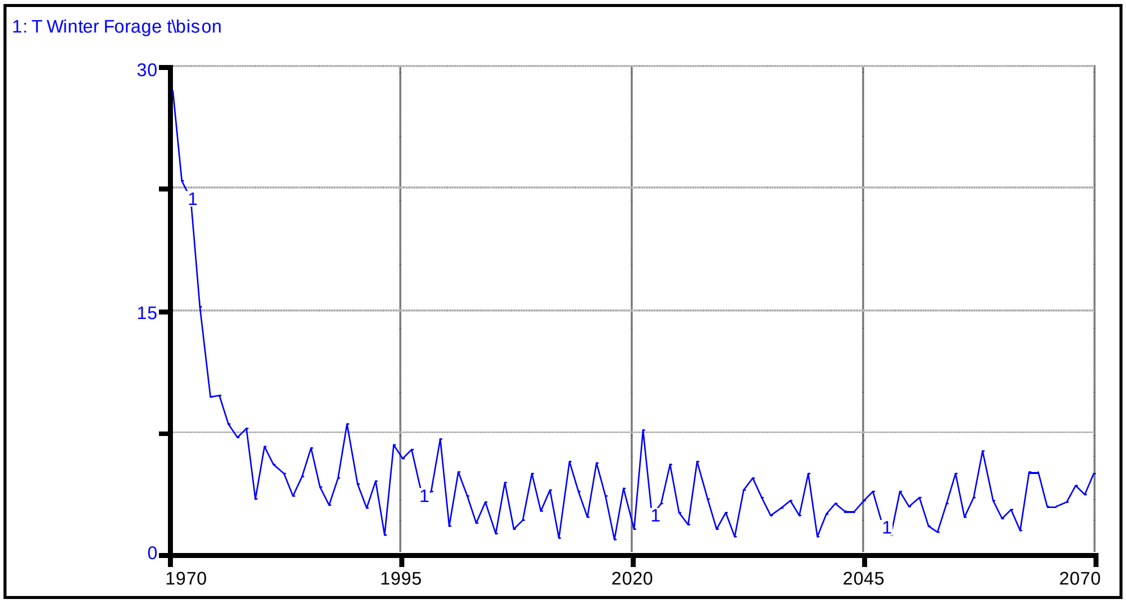


Figure 6.28. Simulated temporal pattern in winter forage availability (tonne forage (dry weight) per bison) using majority average model. The initial reduction in forage availability reflects the initialization of the model with the 1970 populations and their subsequent population growth.

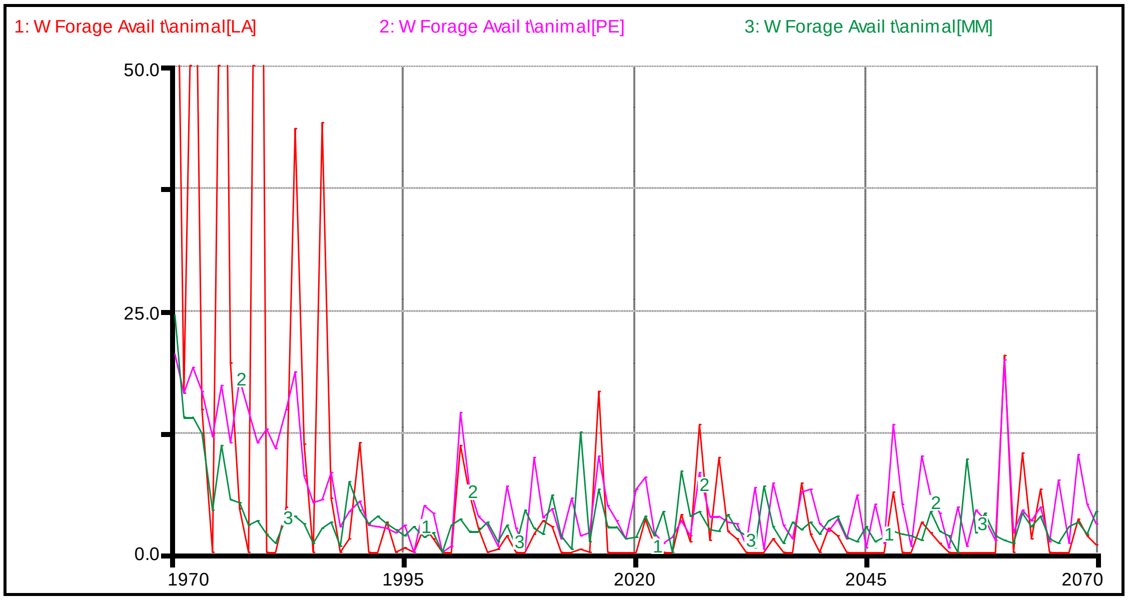


Figure 6.29. Simulated temporal pattern in winter forage availability (tonne forage (dry weight) per bison) using majority average model. The initial reduction in forage availability reflects the initialization of the model with the 1970 populations and their subsequent population growth. High inter-annual variation caused by inter-annual variation in summer precipitation, previous winter snowpack, winter snowpack crustiness, and herbivore biomass density.

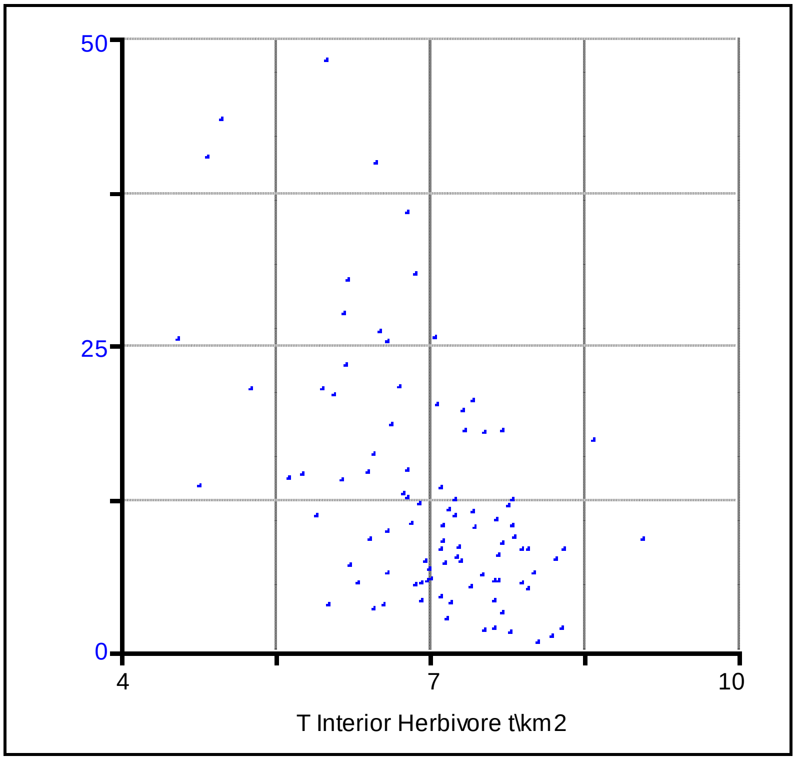


Figure 6.30. Simulated relationship between herbivore (bison and elk) biomass density (x axis; tonne/km$^2$) and availability of bison winter forage availability (tonne/bison; y-axis) for all of the interior ranges. Simulation based on majority average model.

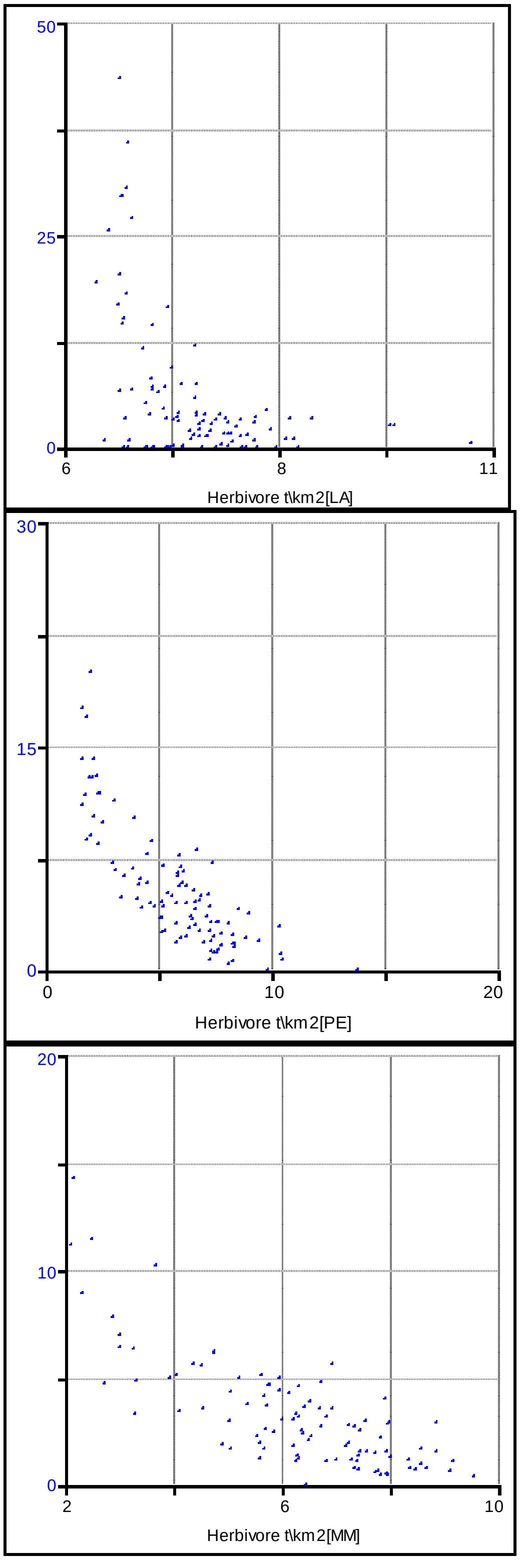


Figure 6.31. Simulated relationship between herbivore (bison and elk) biomass density (x axis; tonne/km$^2$) and availability of bison winter forage (tonne/bison; y-axis) for each of the interior ranges. Lamar (upper), Pelican (center), and Mary Mountain (lower). Simulation based on majority average model.

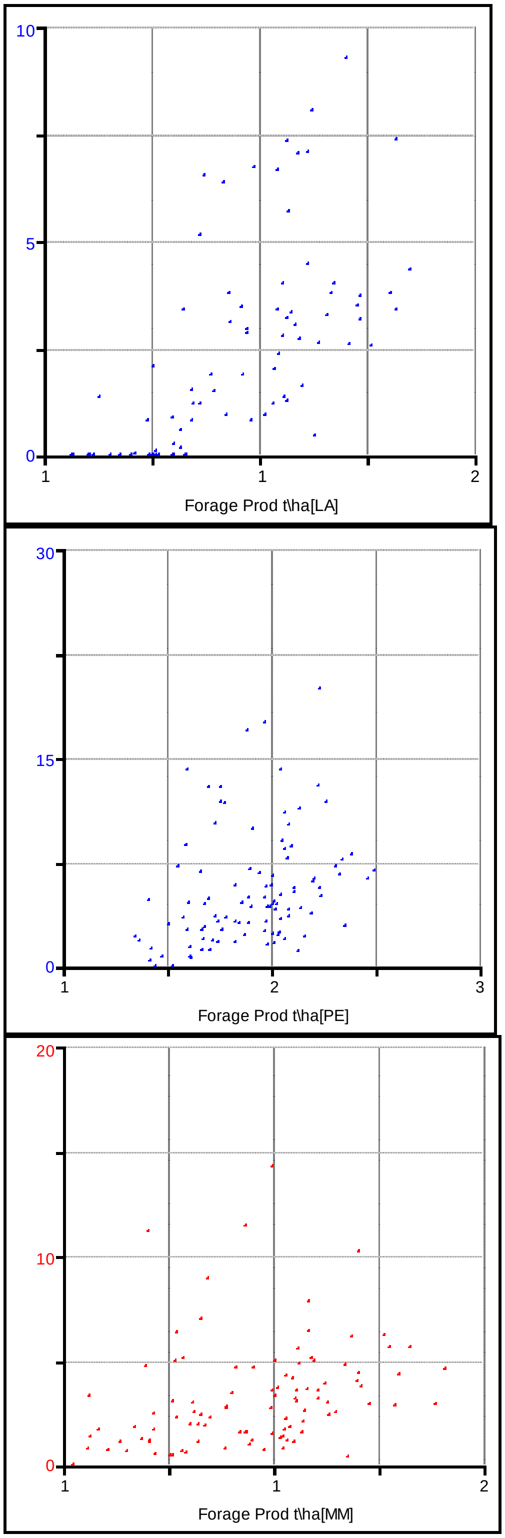


Figure 6.32. Simulated relationship between forage production (x axis; tonne/ha) and availability of bison winter forage availability (tonne/bison; y-axis) for each of the interior ranges. Lamar (upper), Pelican (center), and Mary Mountain (lower). Simulation based on majority average model.

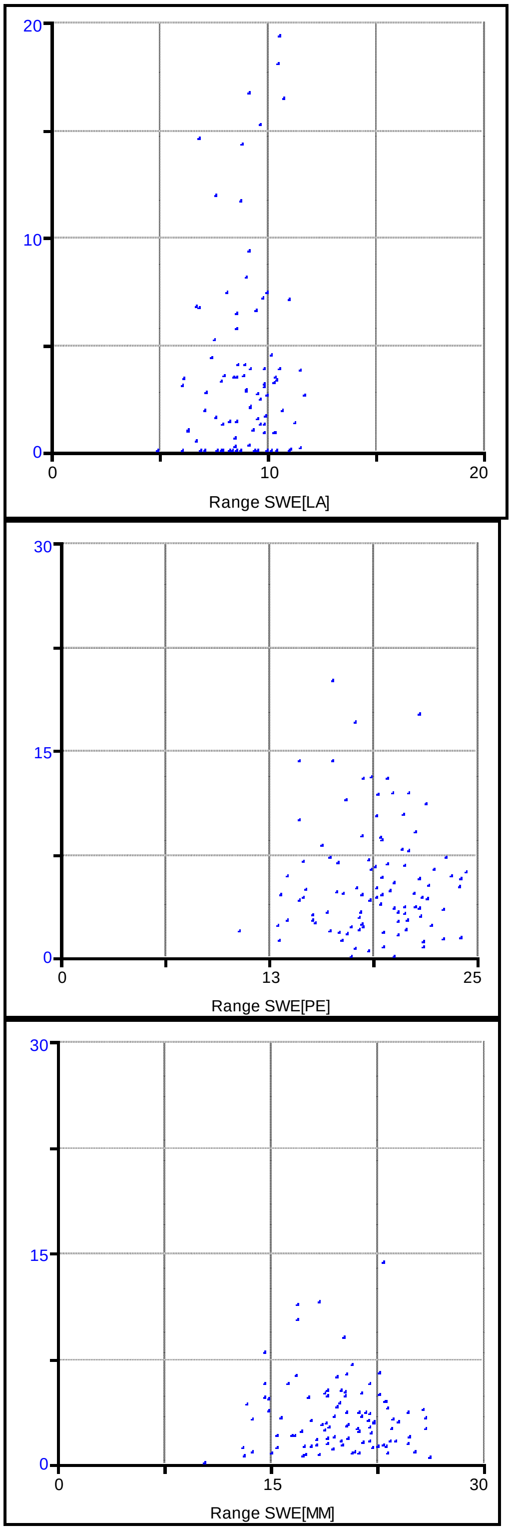
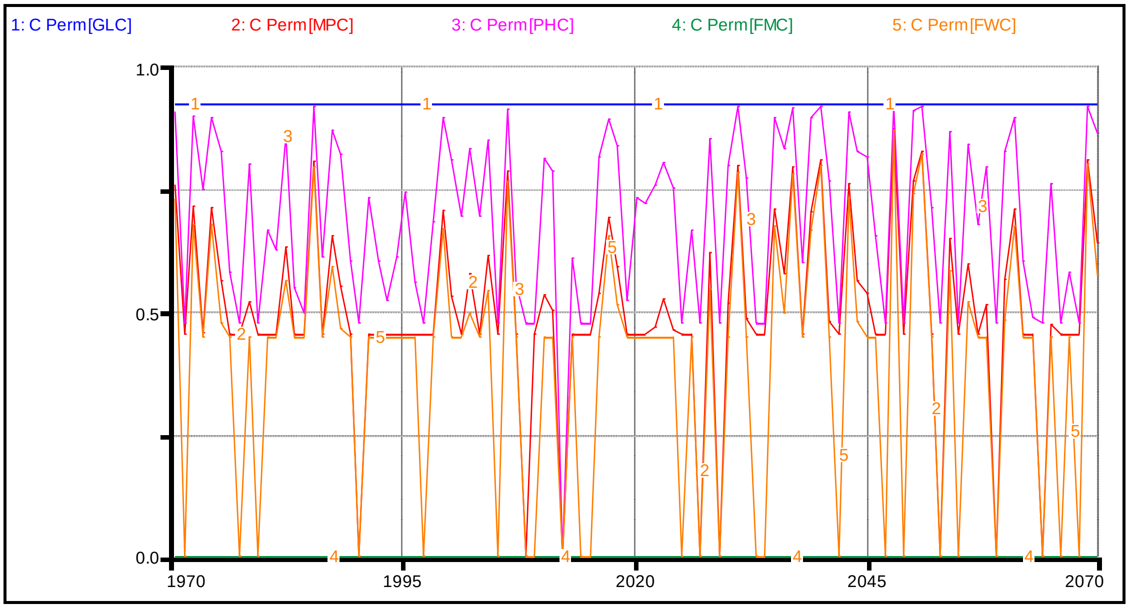


Figure 6.33. Simulated relationship snowpack water equivalent (x axis; cm) and availability of bison winter forage availability (tonne/bison; y-axis) for each of the interior ranges. Lamar (upper), Pelican (center), and Mary Mountain (lower). Simulation based on majority average model.



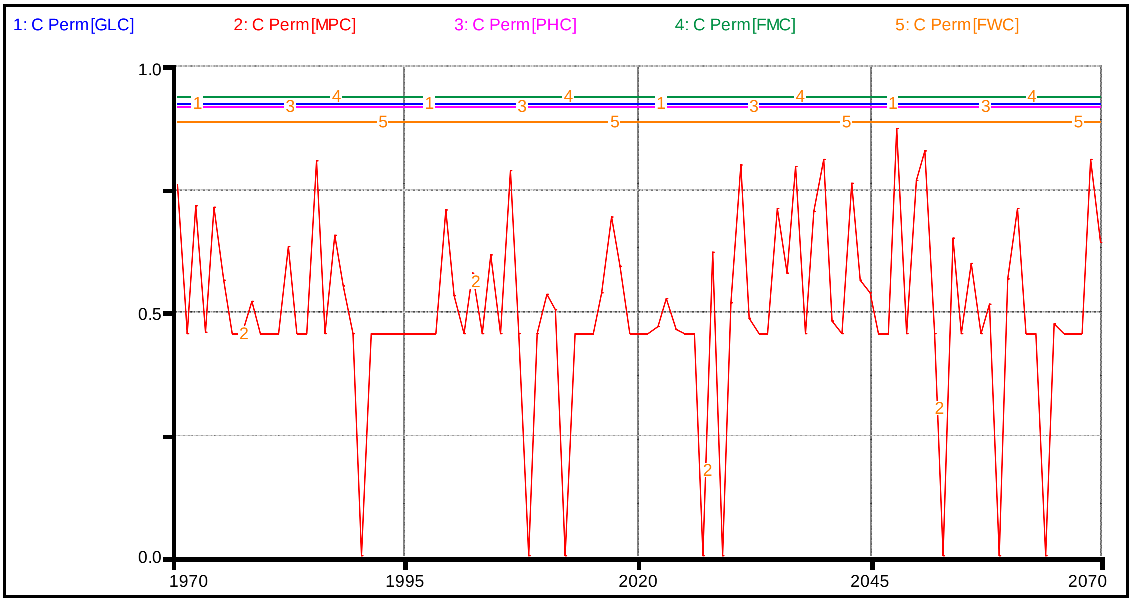
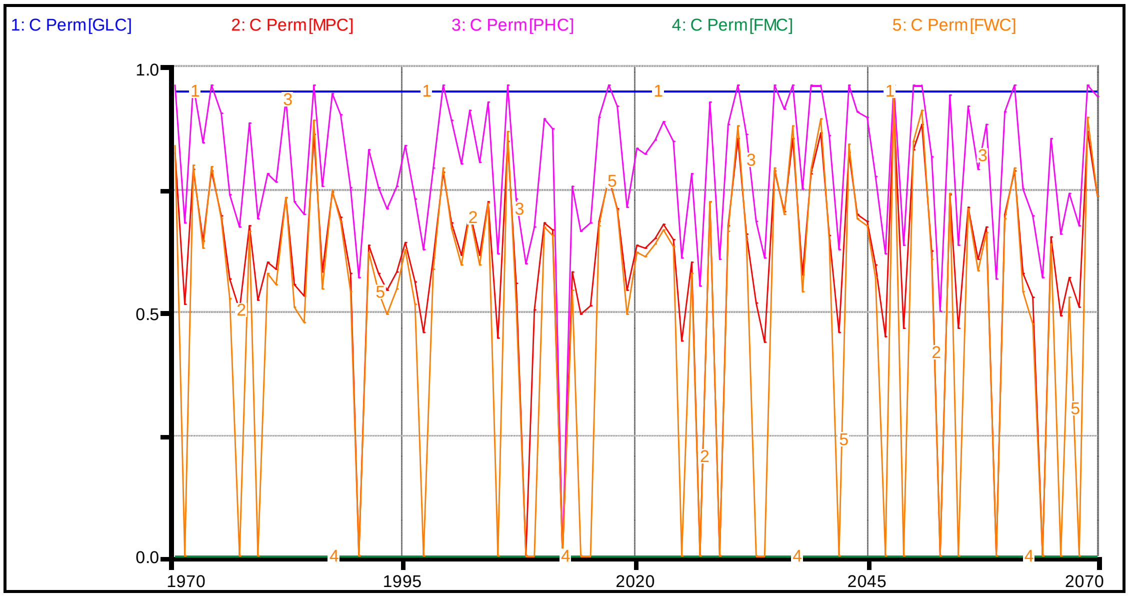


Figure 6.34. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided by Key Informant Group 1. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road grooming along corridors PHC, FMC, and FWC.



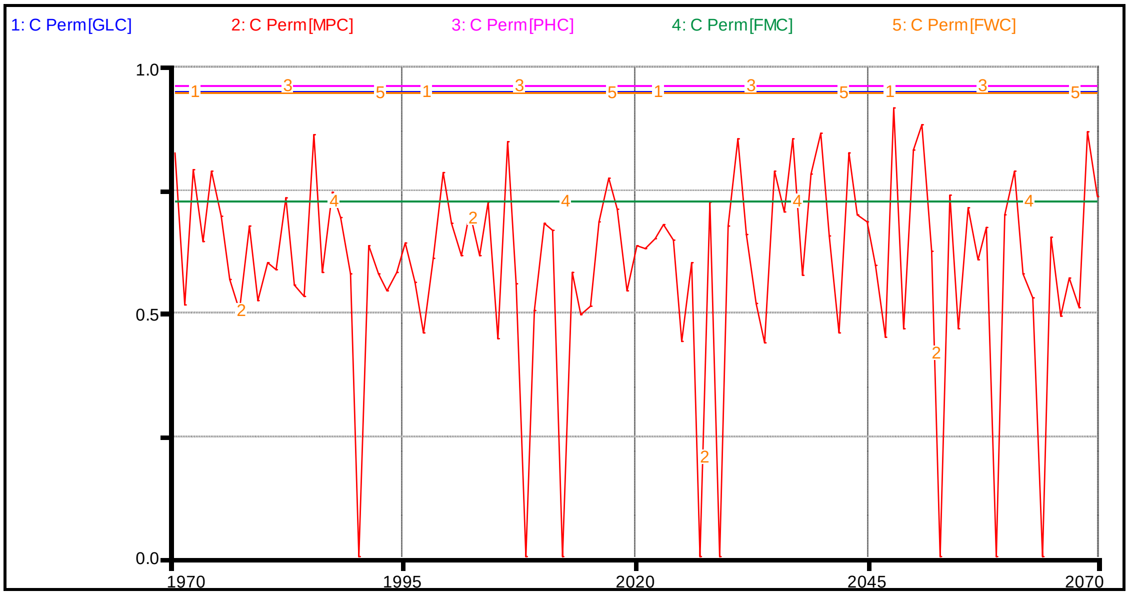
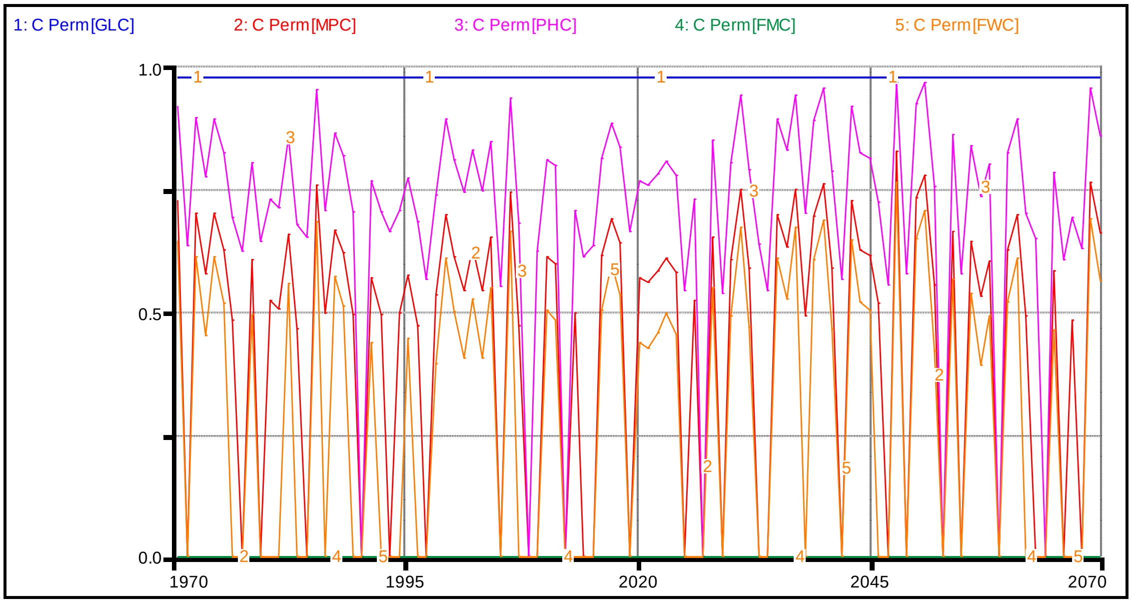


Figure 6.35. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided by Key Informant Group 2. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road grooming along corridors PHC, FMC, and FWC.



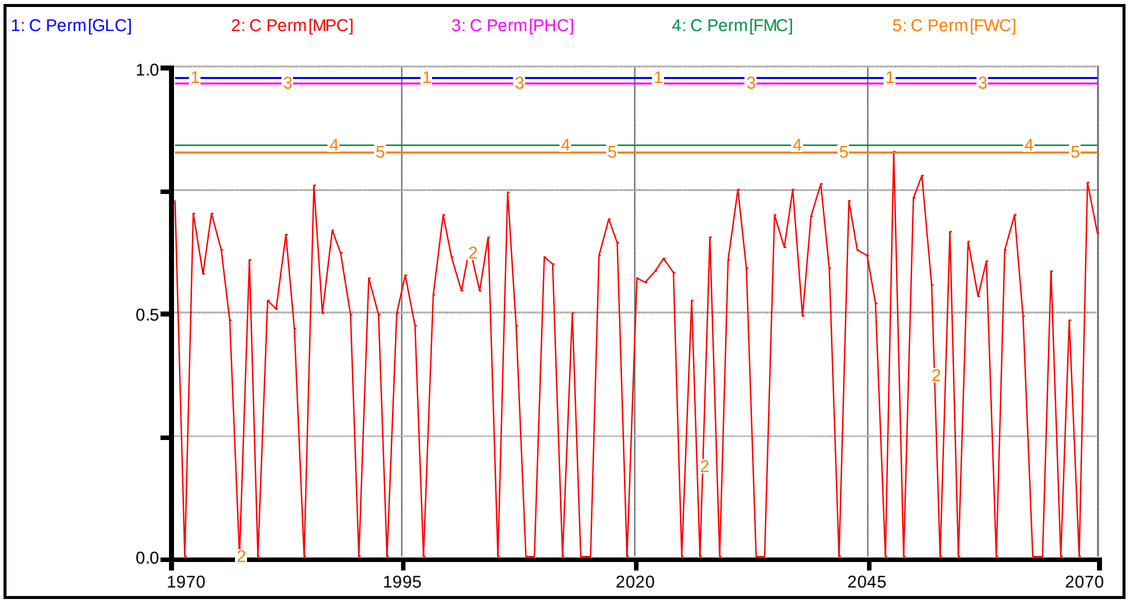
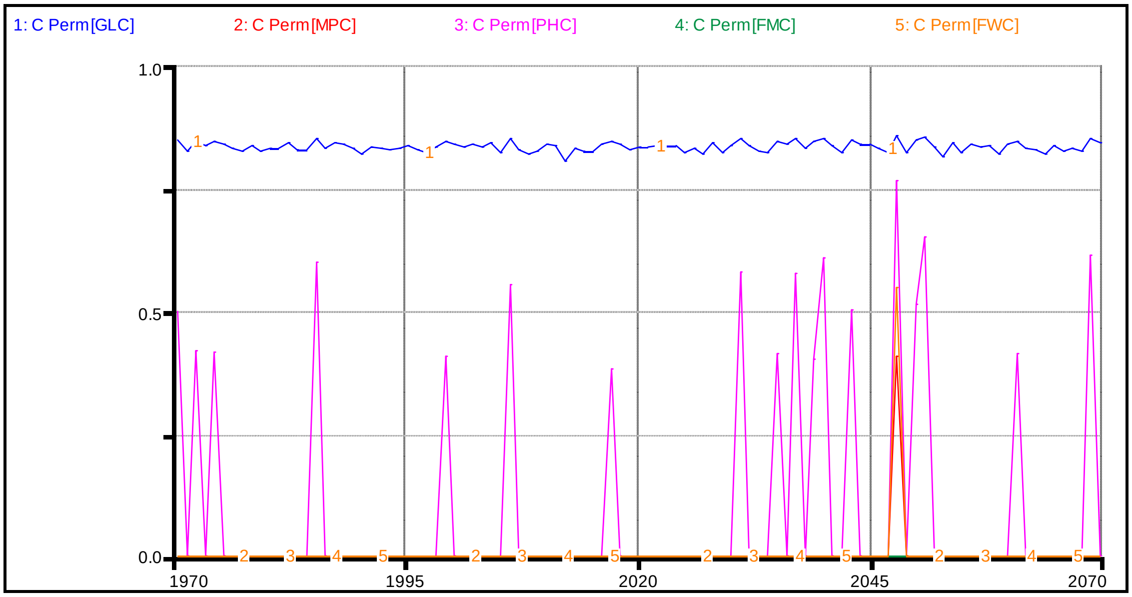


Figure 6.36. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided by Key Informant Group 3. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road grooming along corridors PHC, FMC, and FWC.



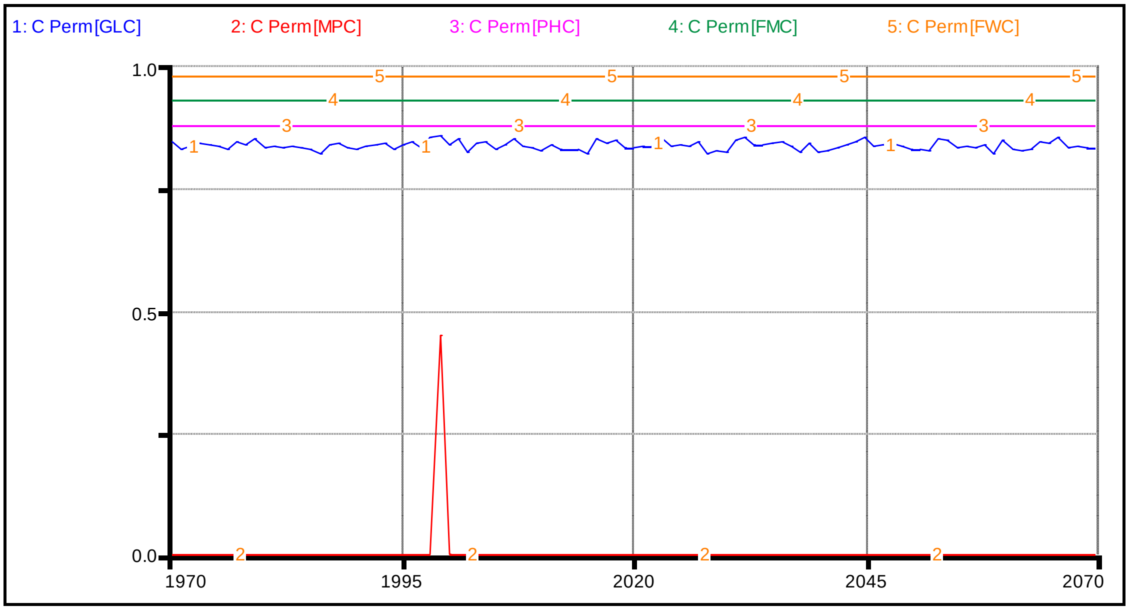


Figure 6.37. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided by Key Informant Group 4. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road grooming along corridors PHC, FMC, and FWC.

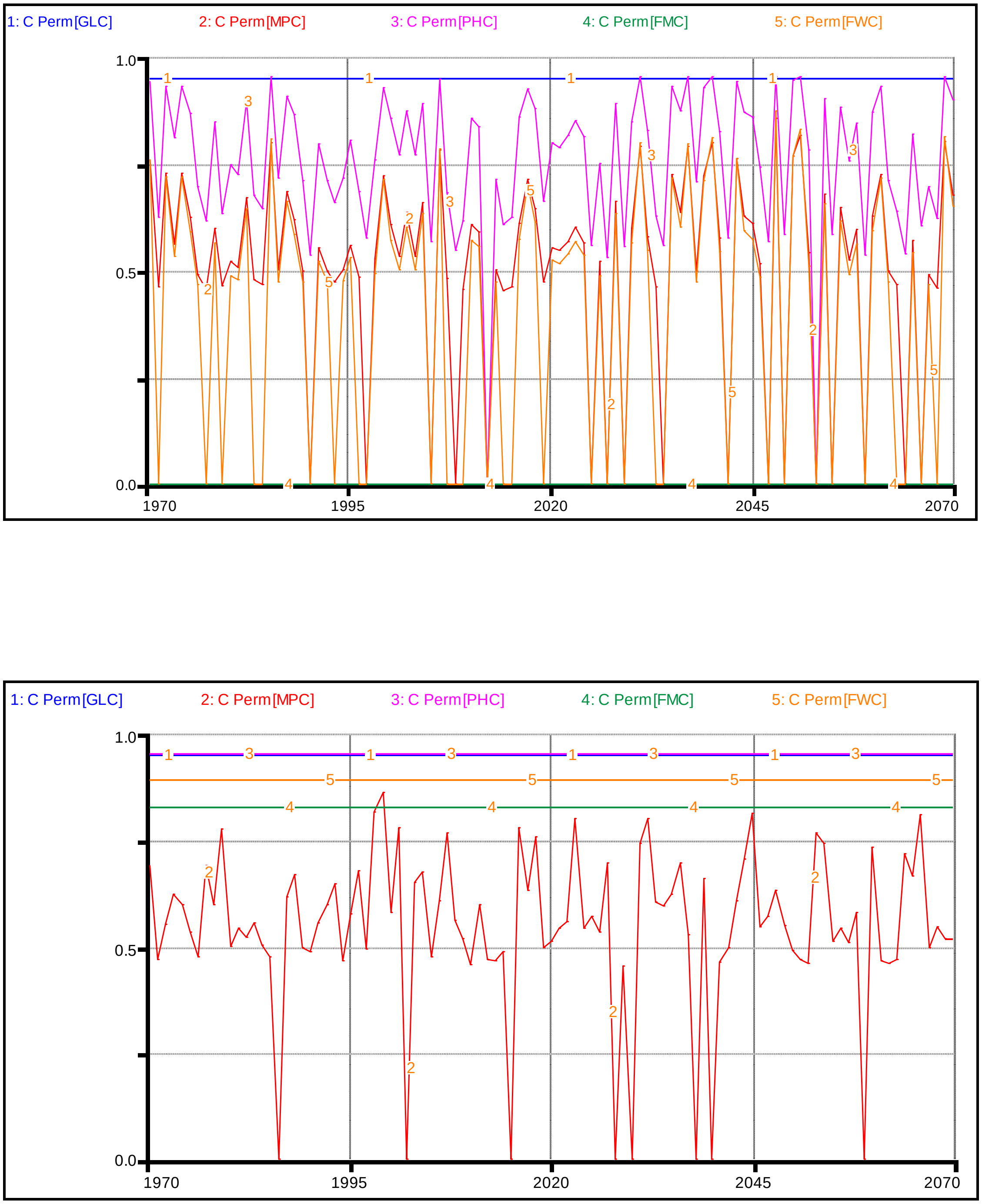


Figure 6.38. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided from Majority Average Group (average of Group 1, 2, and 3. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road grooming along corridors PHC, FMC, and FWC.

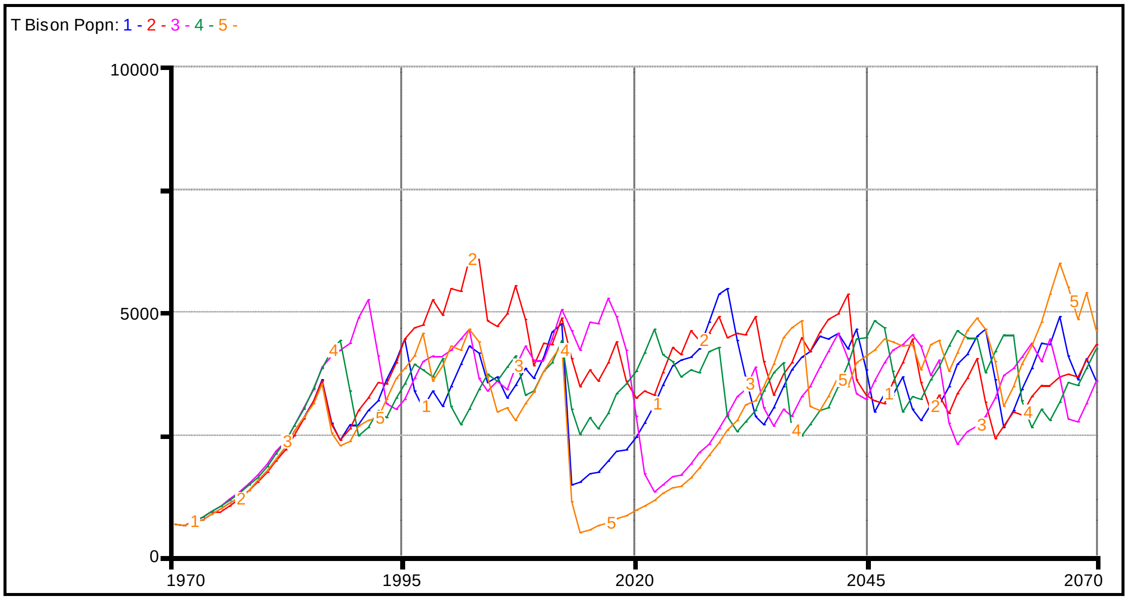


Figure 6.39. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #1. This scenario involves no winter road grooming.

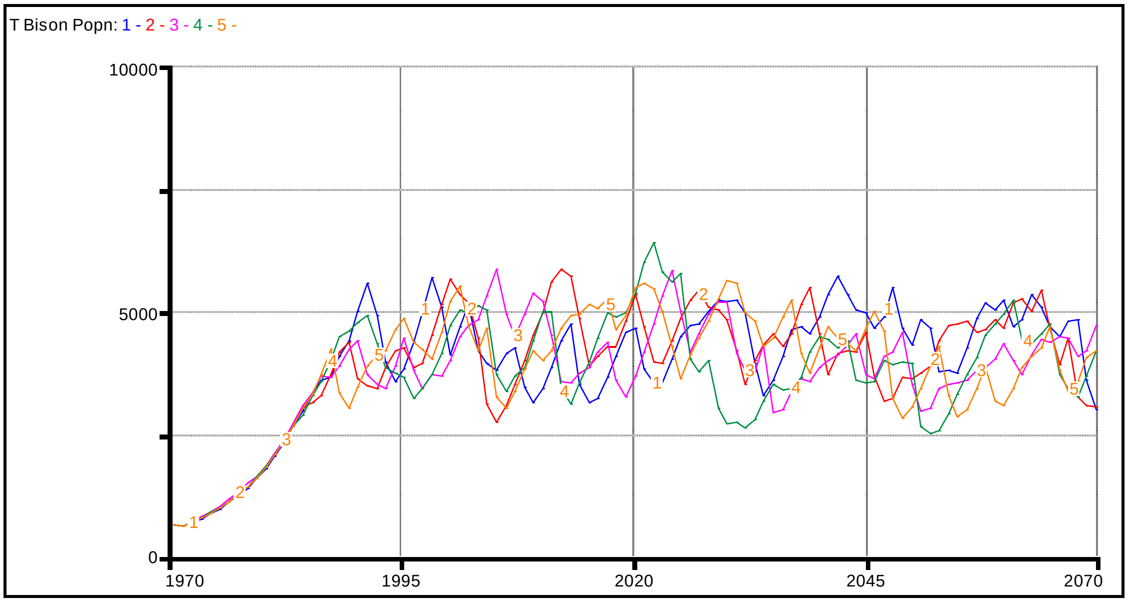


Figure 6.40. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #1. This scenario includes winter road grooming along corridors PHC, FMC, and FWC.

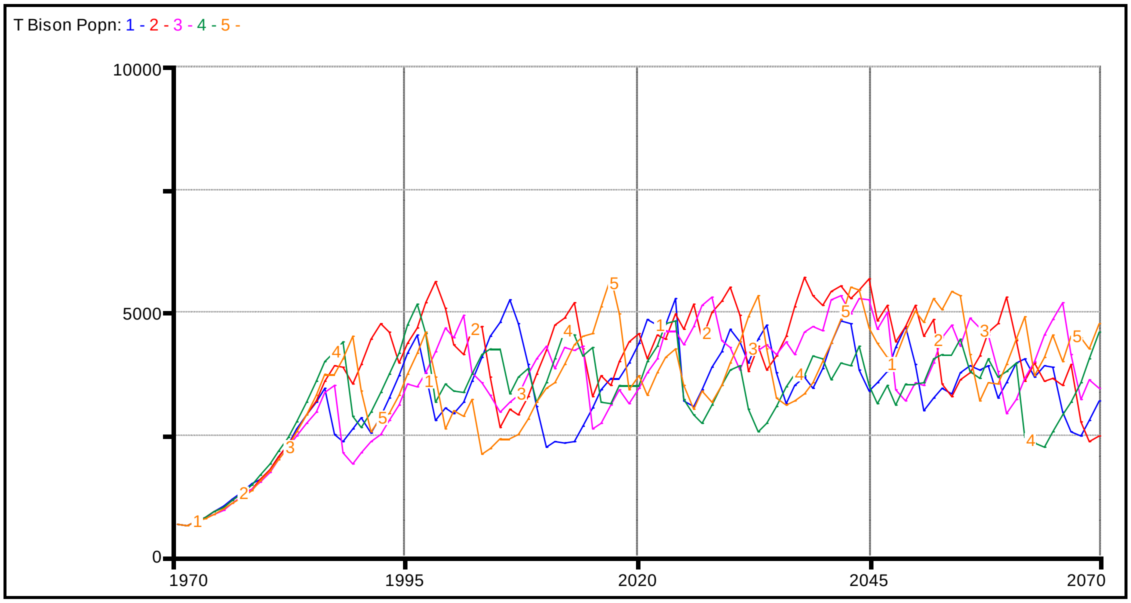


Figure 6.41. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #2. This scenario does not involve winter road grooming.

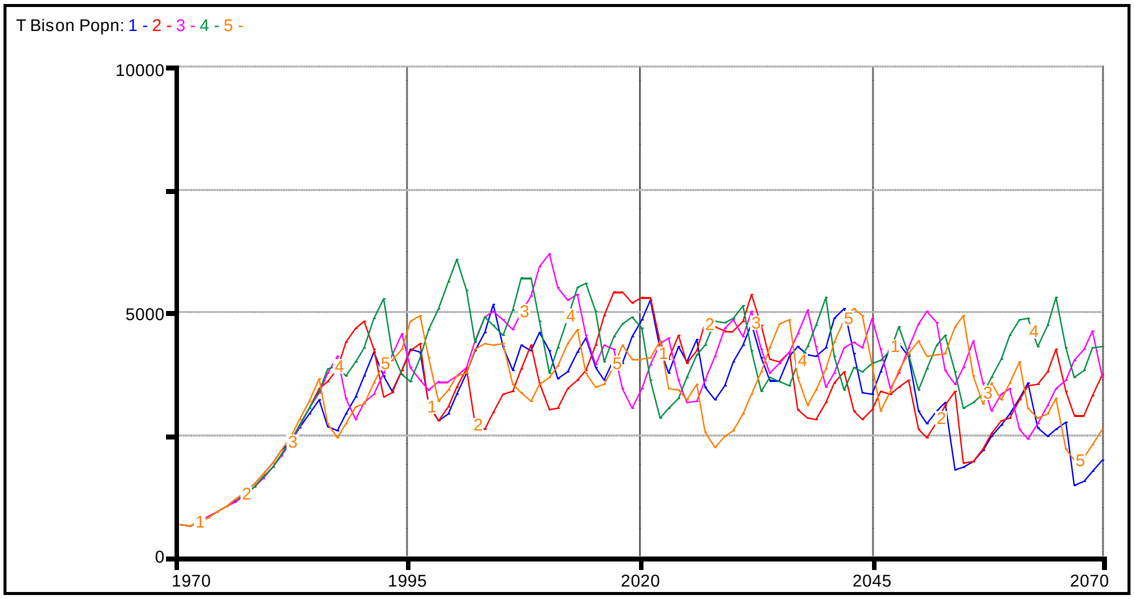


Figure 6.42. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #2. This scenario includes winter road grooming along corridors PHC, FMC, and FWC**.**

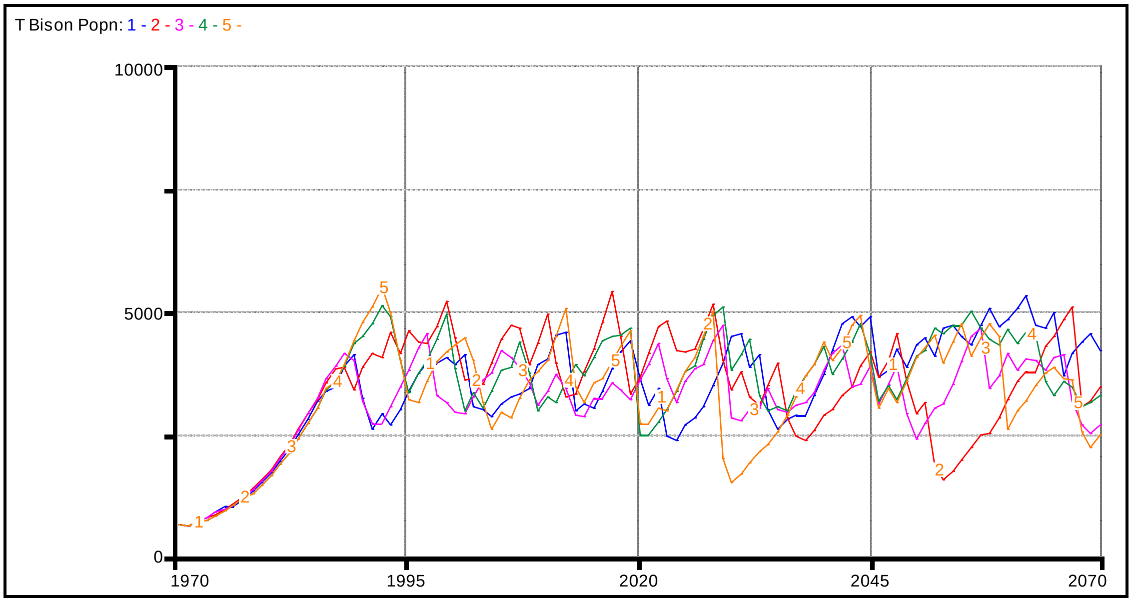


Figure 6.43. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #3. This scenario does not involve winter road grooming.

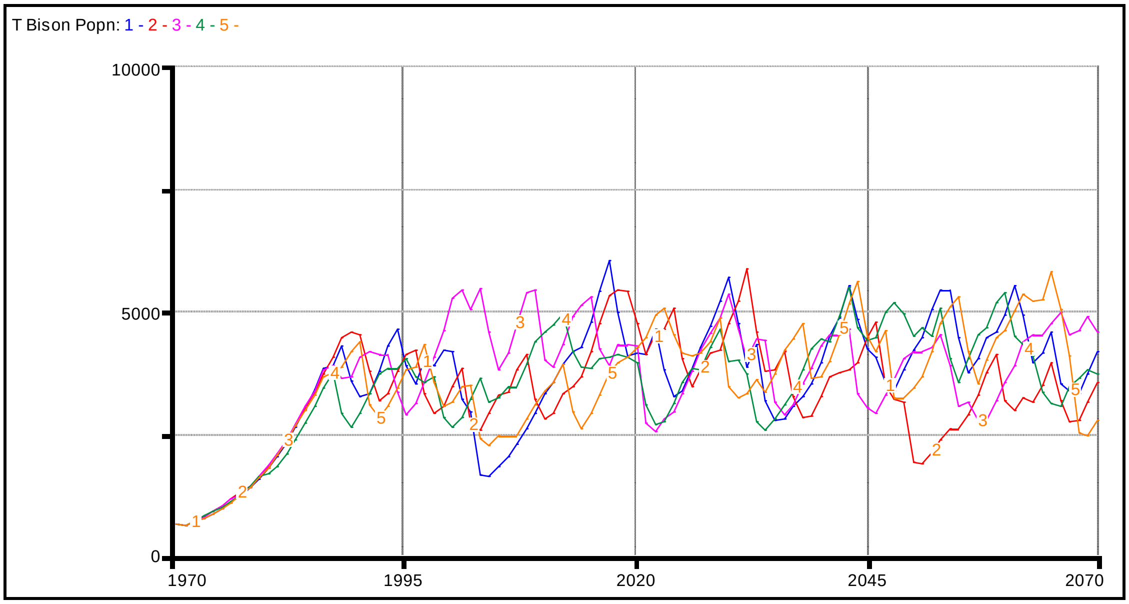


Figure 6.44. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #3. This scenario includes winter road grooming along corridors PHC, FMC, and FWC.

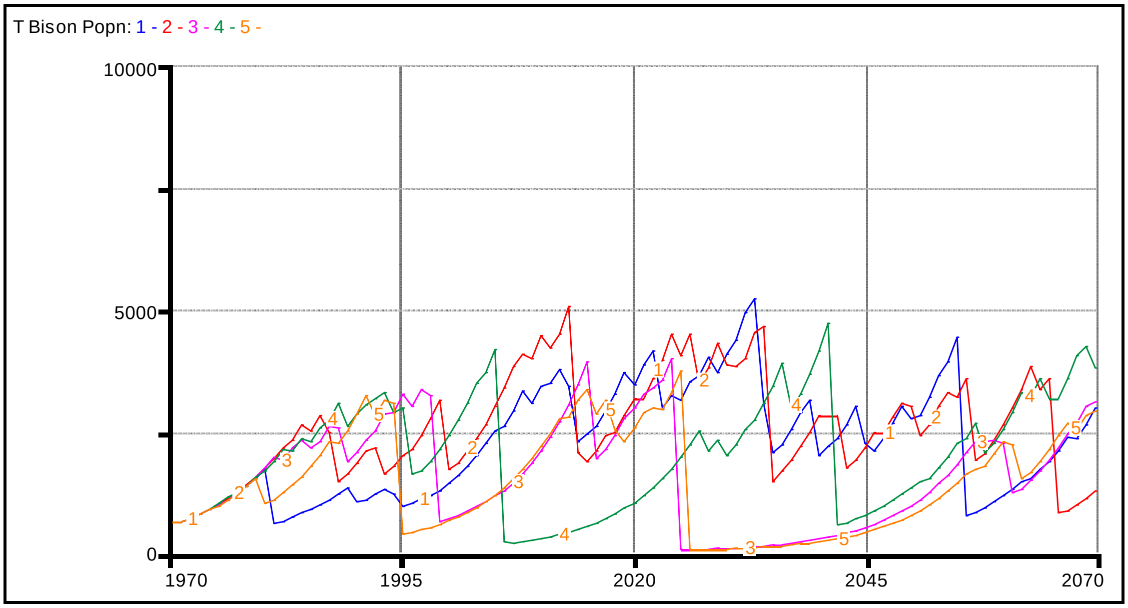


Figure 6.45. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #4. This scenario does not involve winter road grooming.

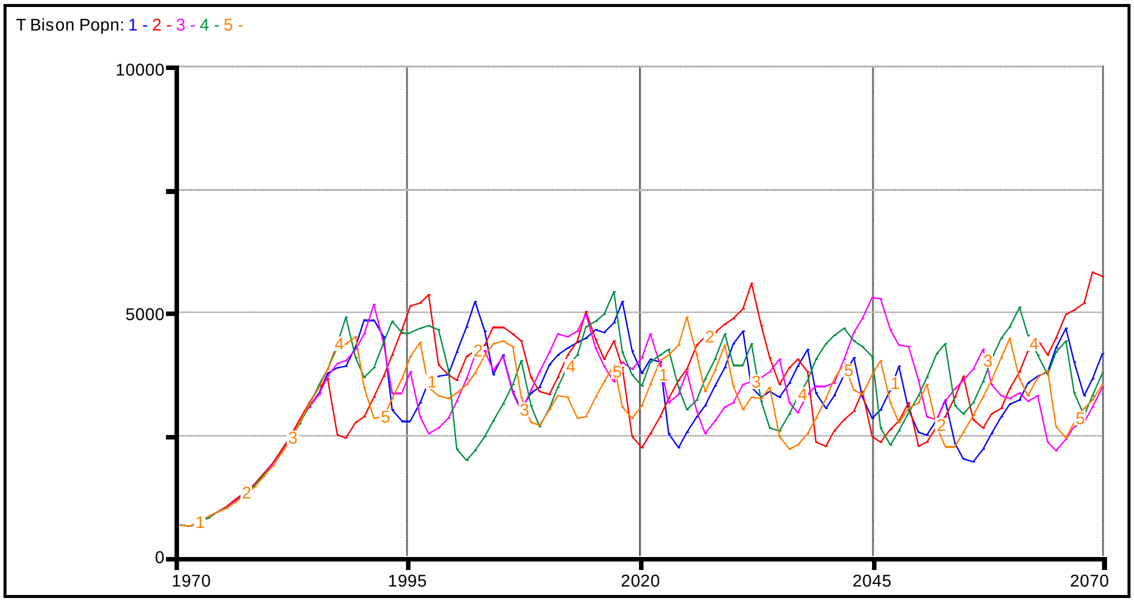


Figure 6.46. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #4. This scenario includes winter road grooming along corridors PHC, FMC, and FWC.

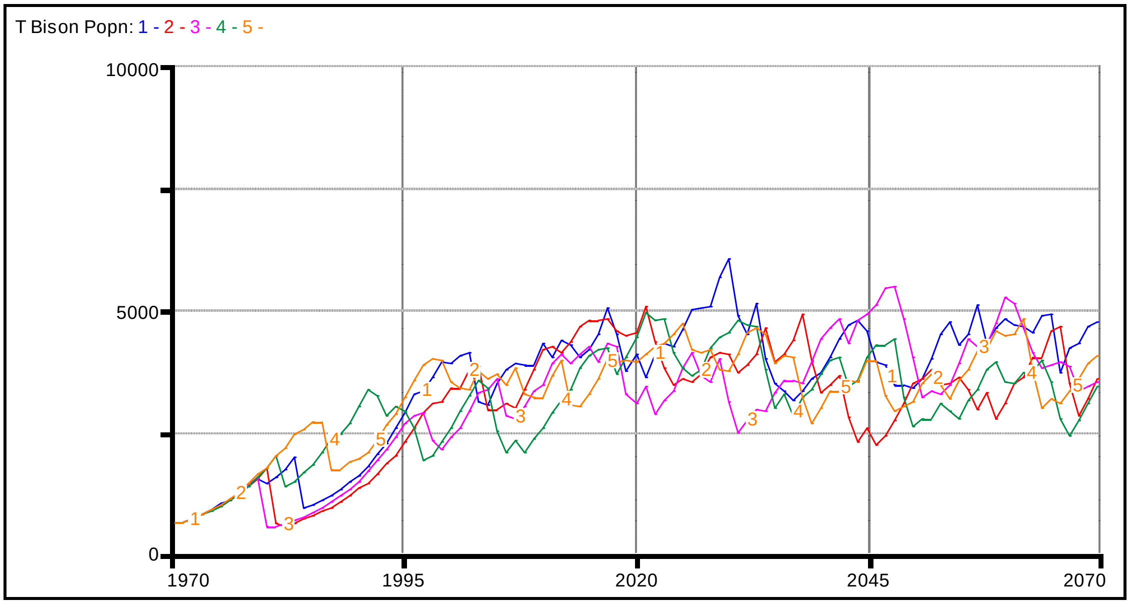


Figure 6.47. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Majority Average Model (average of Group 1, 2, and 3). This scenario does not involve winter road grooming.

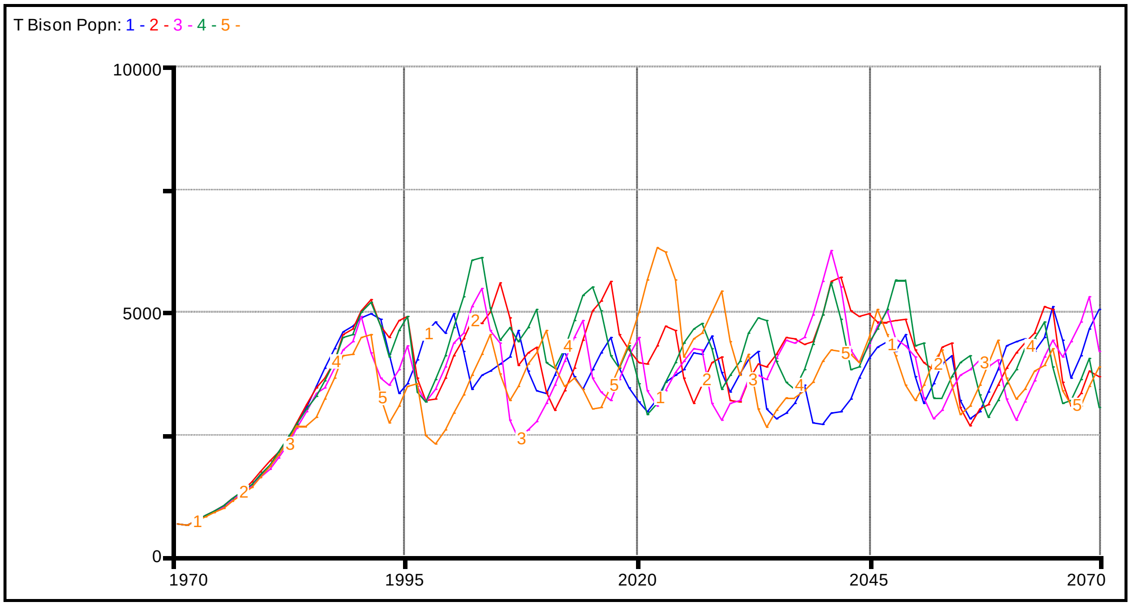
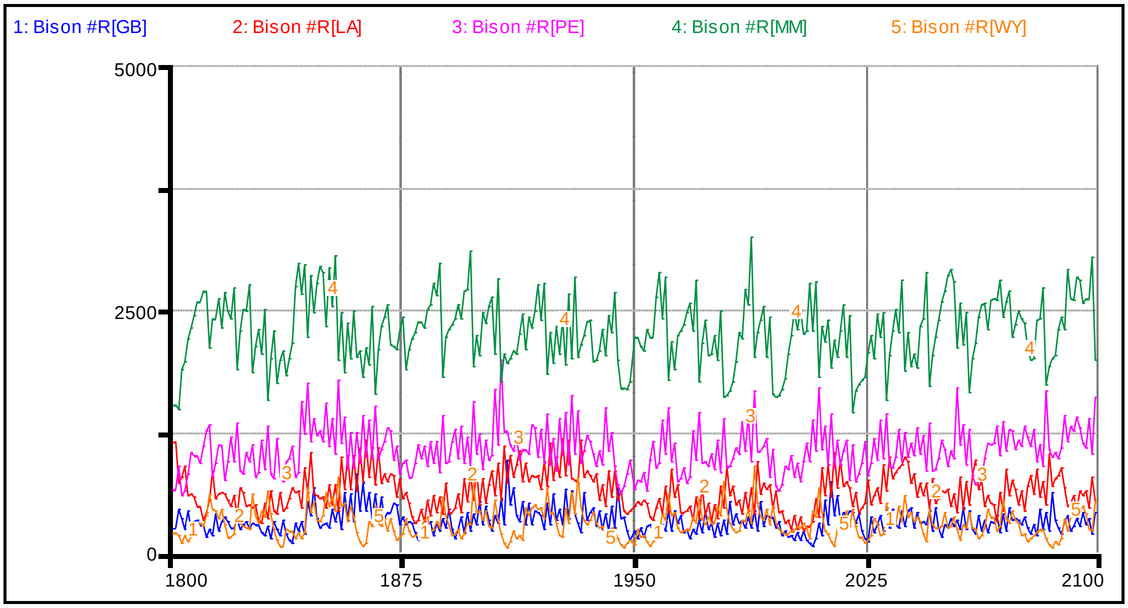


Figure 6.48. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Majority Average Model (average of Group 1, 2, and 3). This scenario includes winter road grooming along corridors PHC, FMC, and FWC.



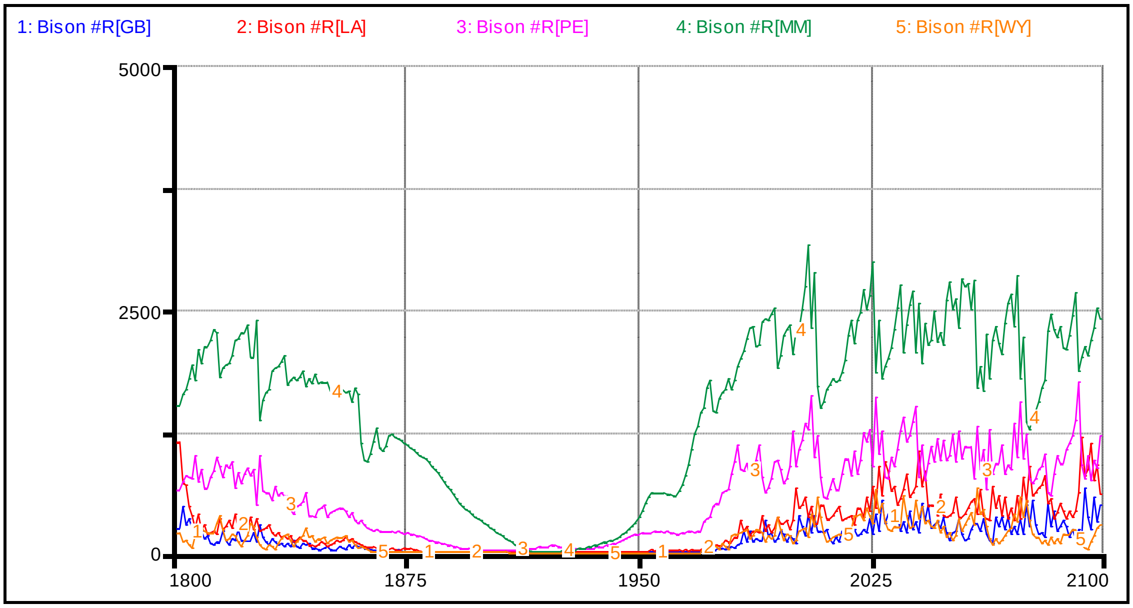


Figure 6.49. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #1. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.

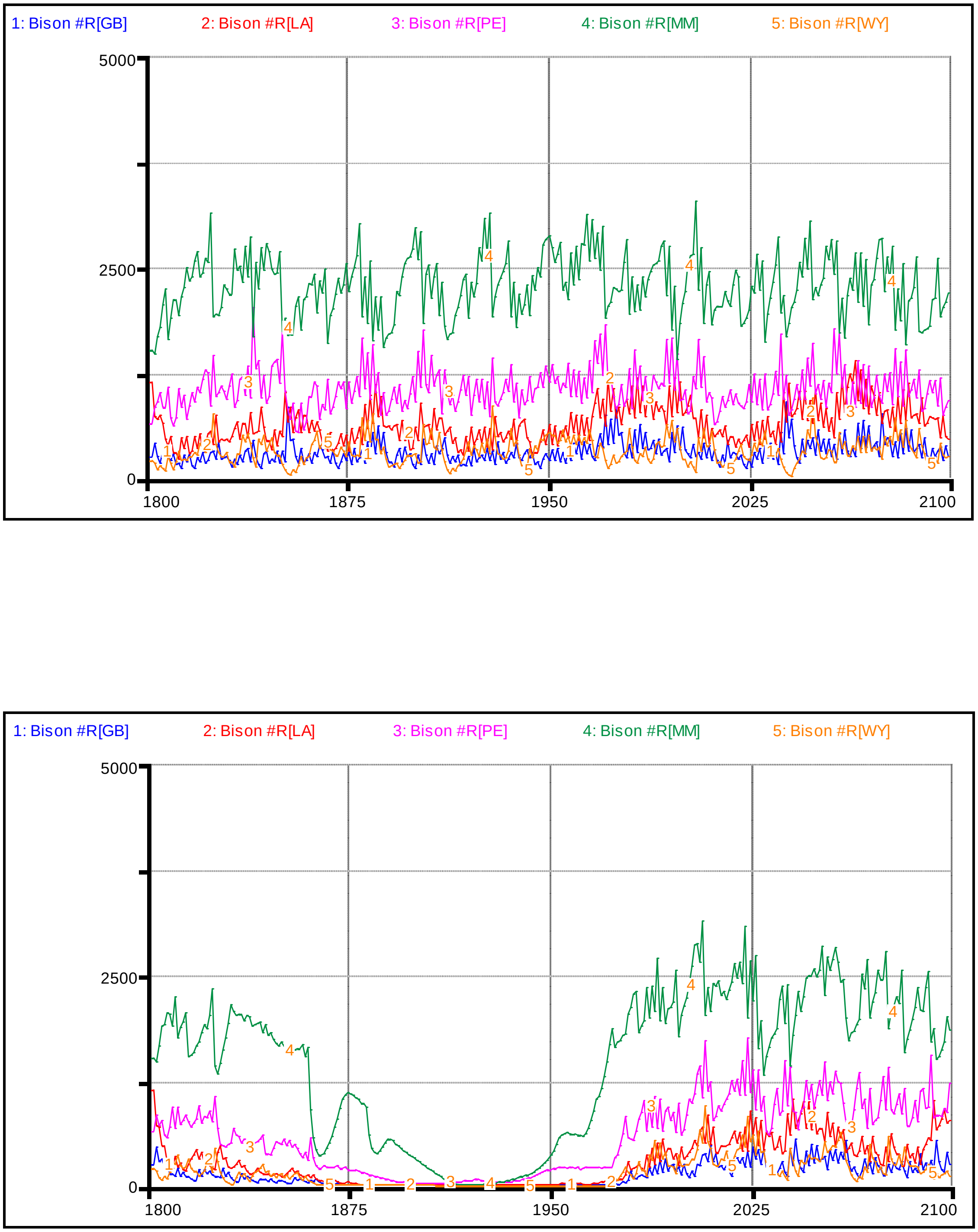
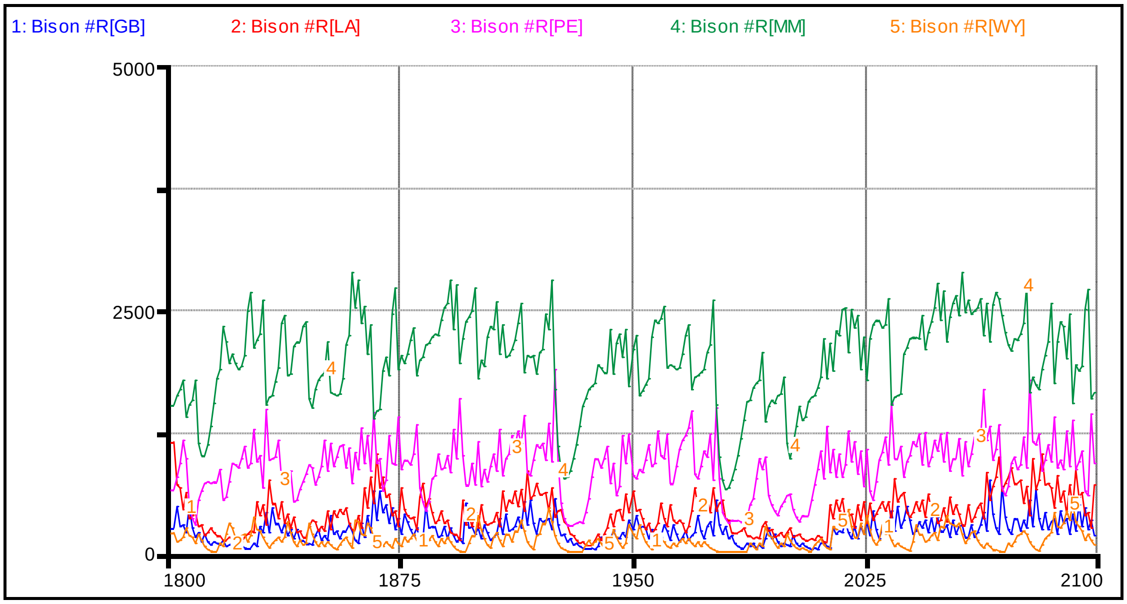


Figure 6.50. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #2. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



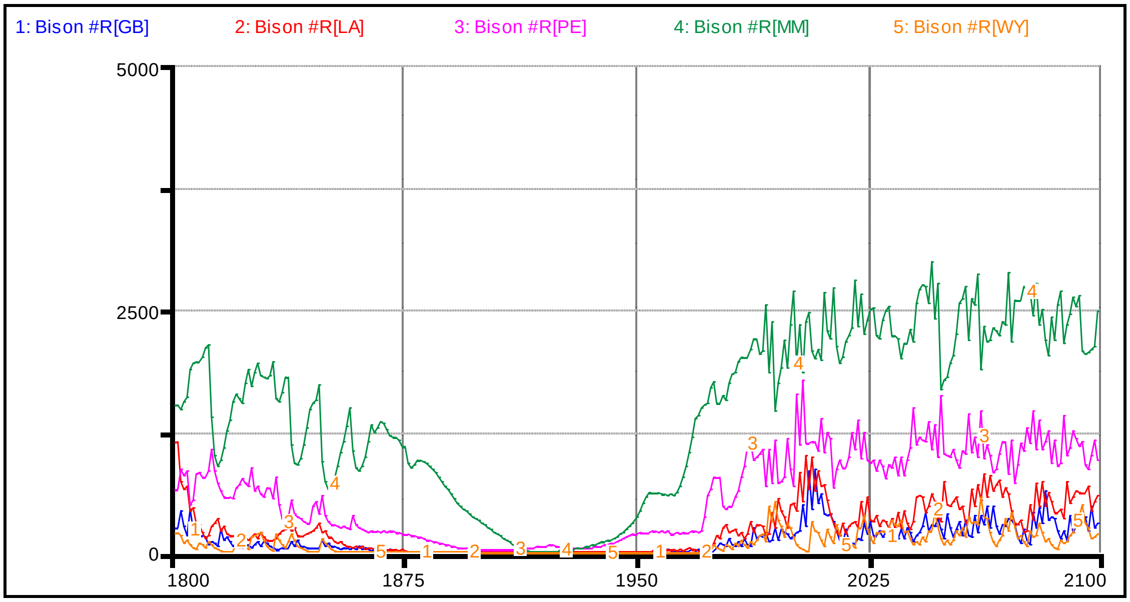
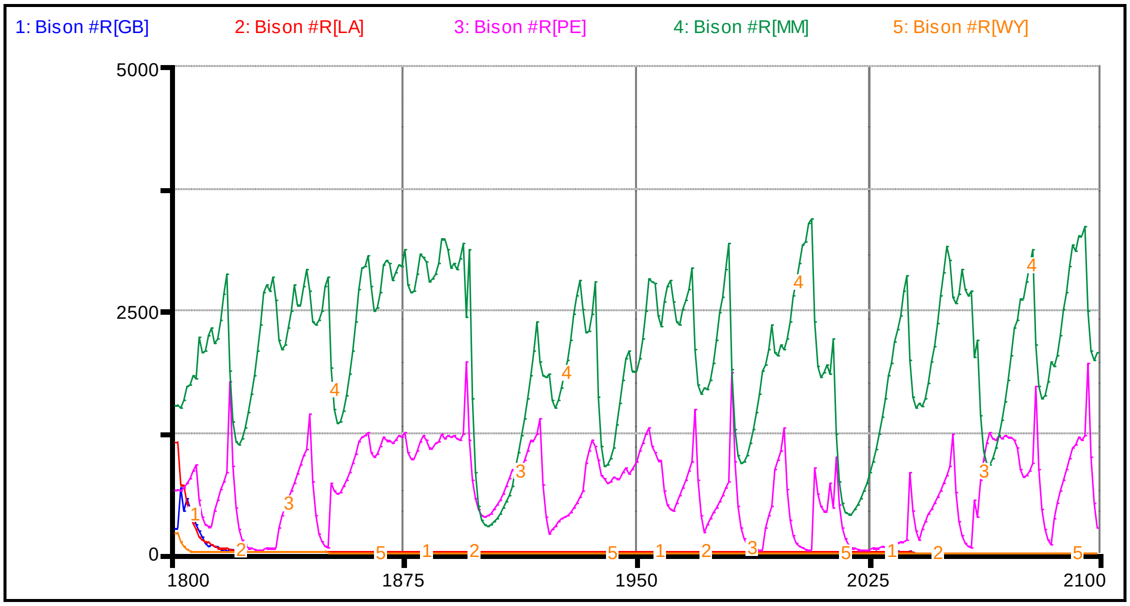


Figure 6.51. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #3. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



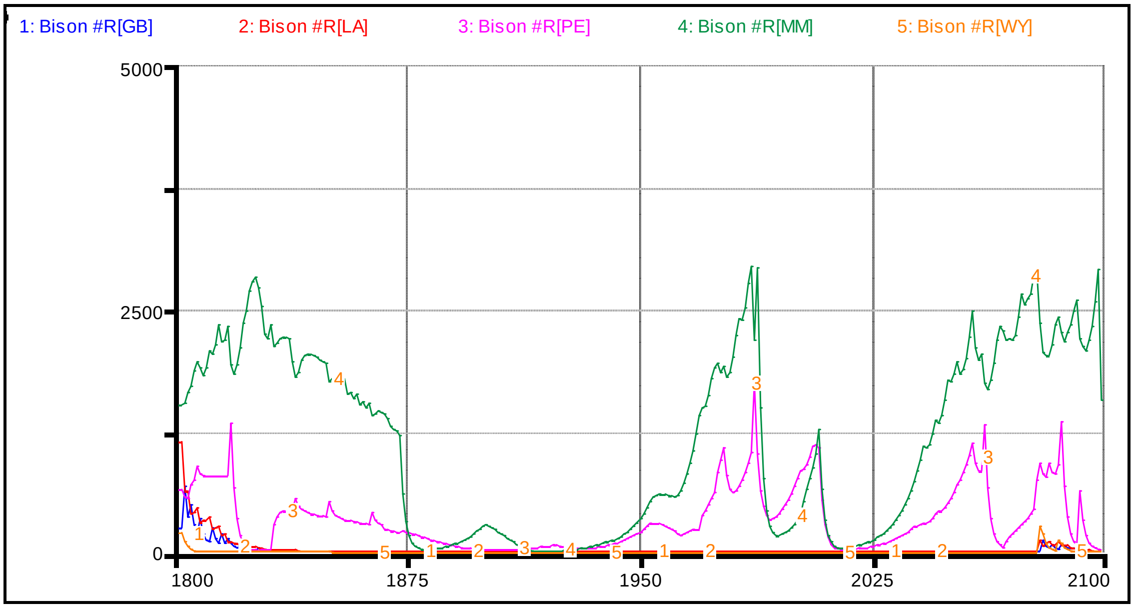
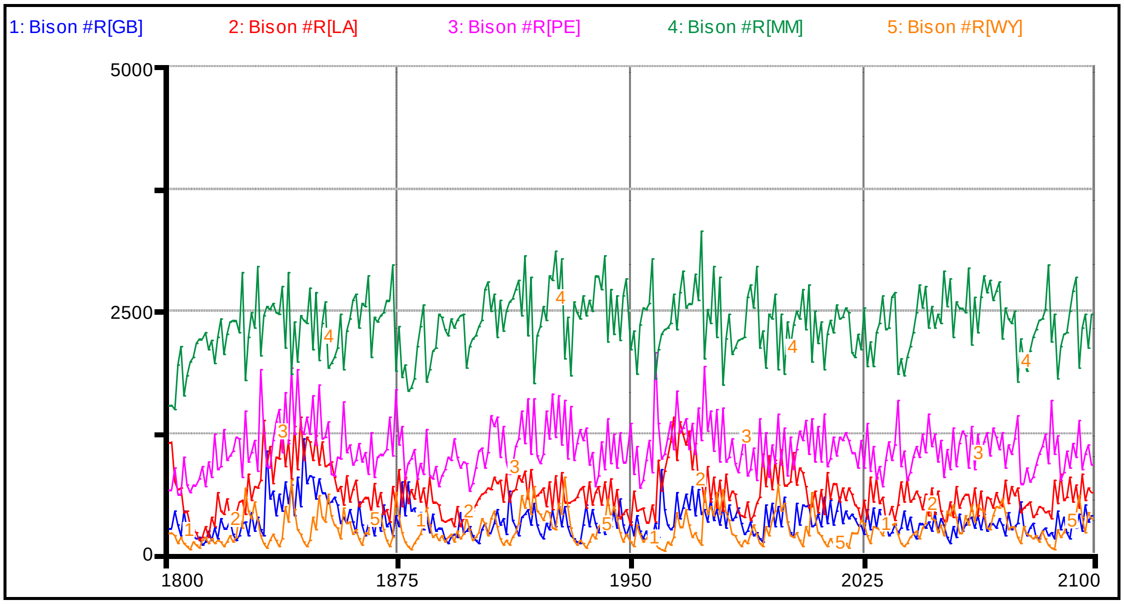


Figure 6.52. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #4. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



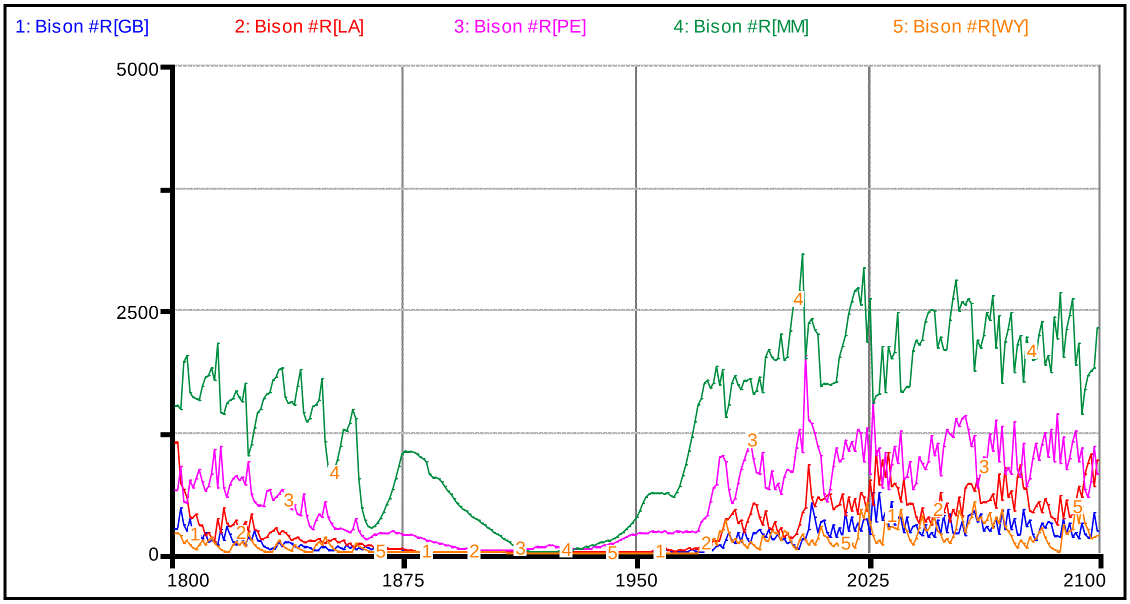
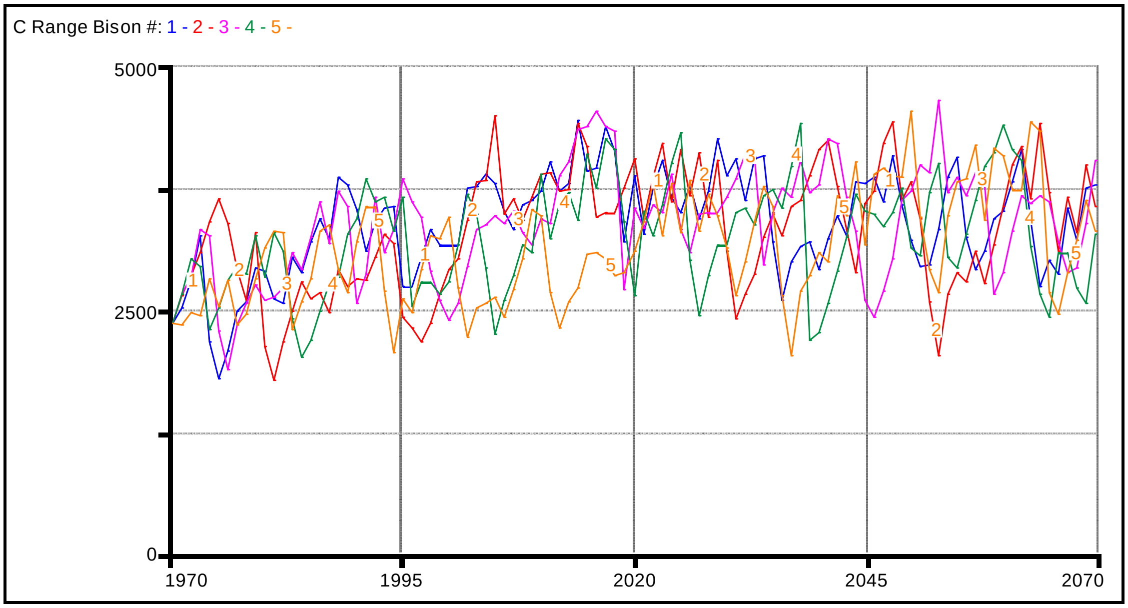


Figure 6.53. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Majority Average Model (average of Group 1, 2, and 3). The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



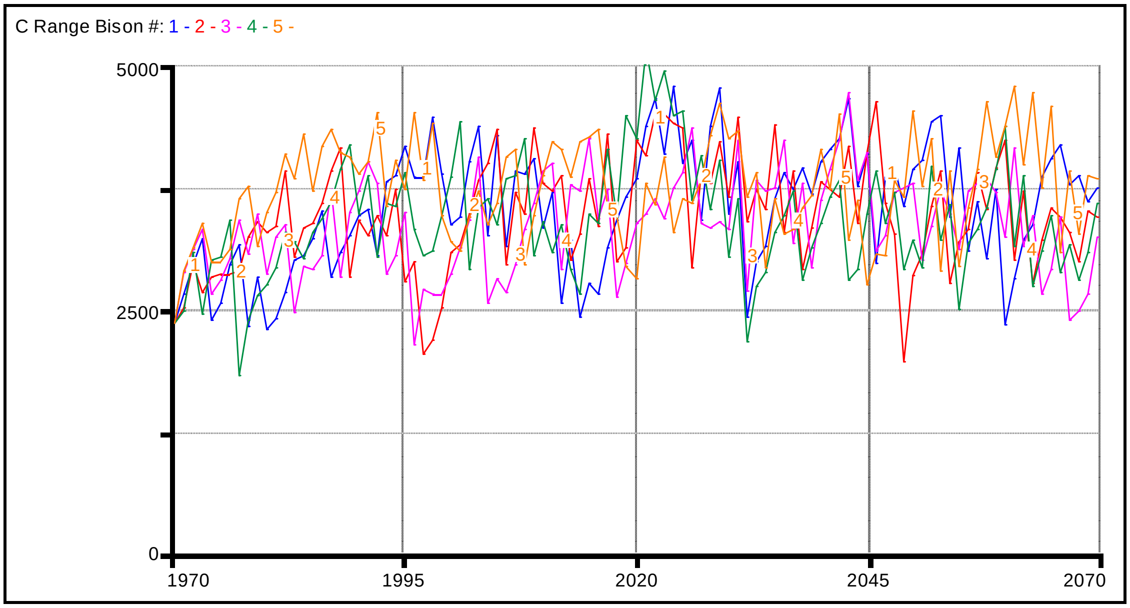


Figure 6.54. Simulated comparison of bison population in the Central Range without (upper) with (lower) road grooming. Simulations were 100 years and reflected stochastic precipitation patterns. Simulation based on Majority Average Model.

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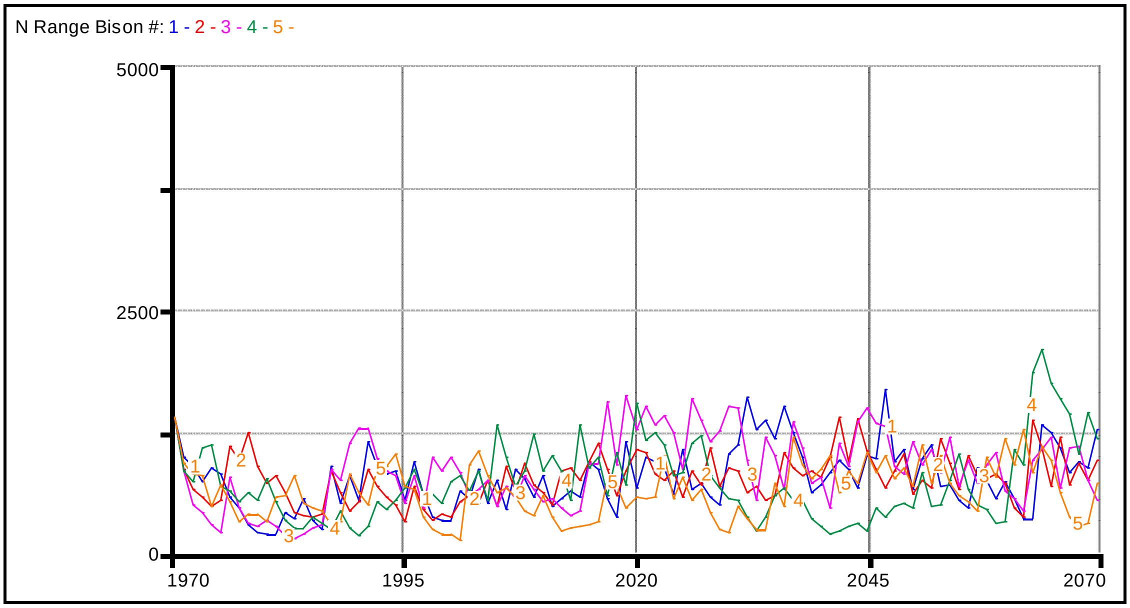

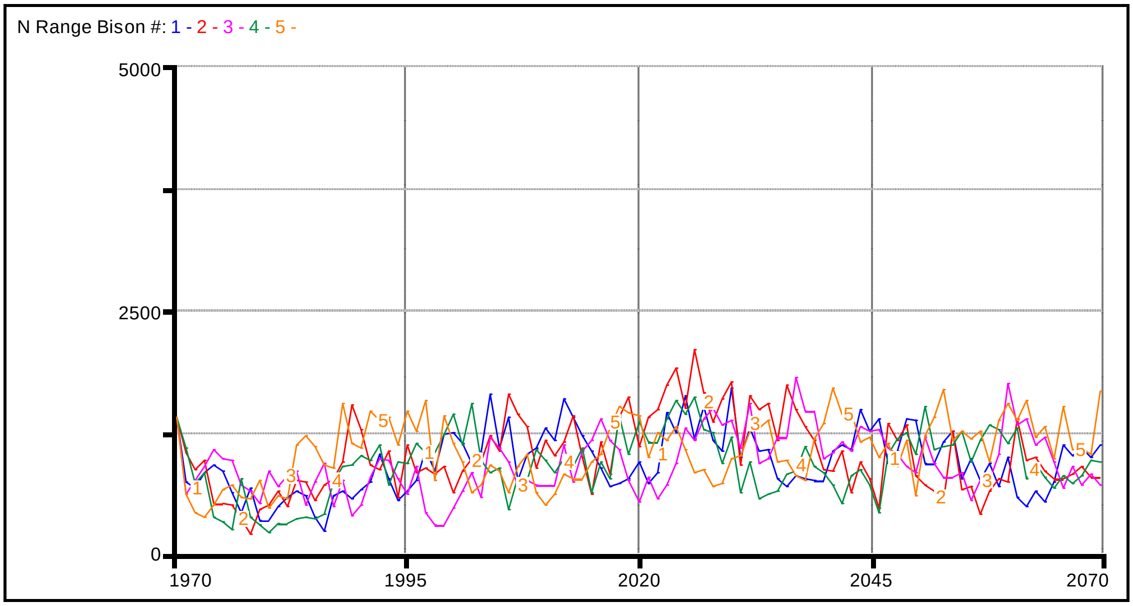

Figure 6.55**.** Simulated comparison of bison population in the Northern Range without (upper) with (lower) road grooming. Simulations were 100 years and reflected stochastic precipitation patterns. Simulation based on Majority Average Model.

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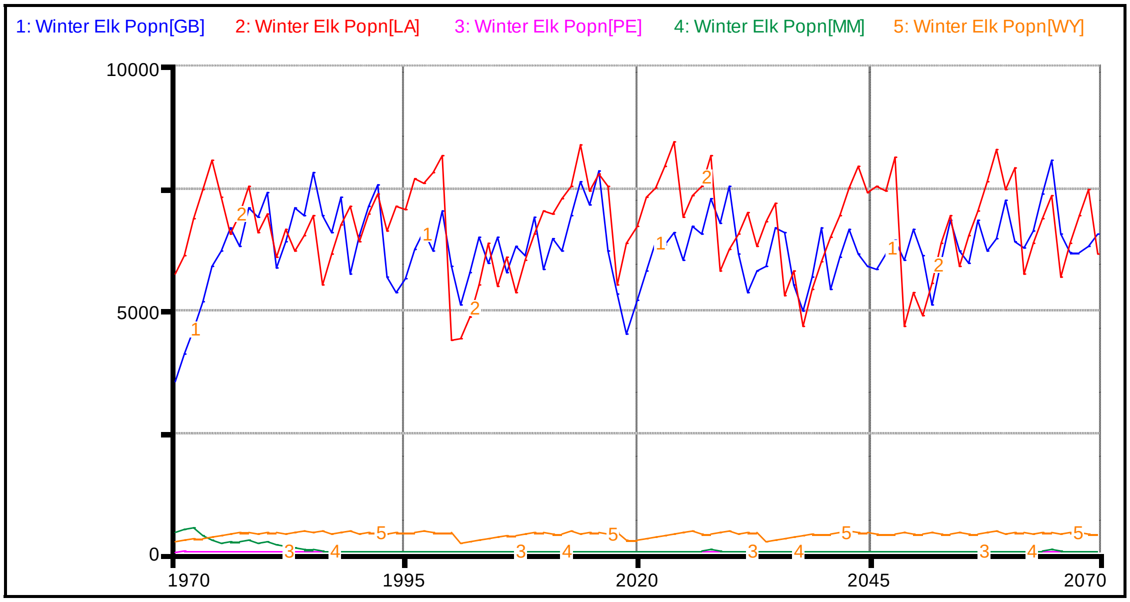


Figure 6.56. Simulated variance in elk populations on winter bison range based on simple population model where fecundity and mortality are influenced by forage availability relative to requirements. Simulation based on Majority Average Model.

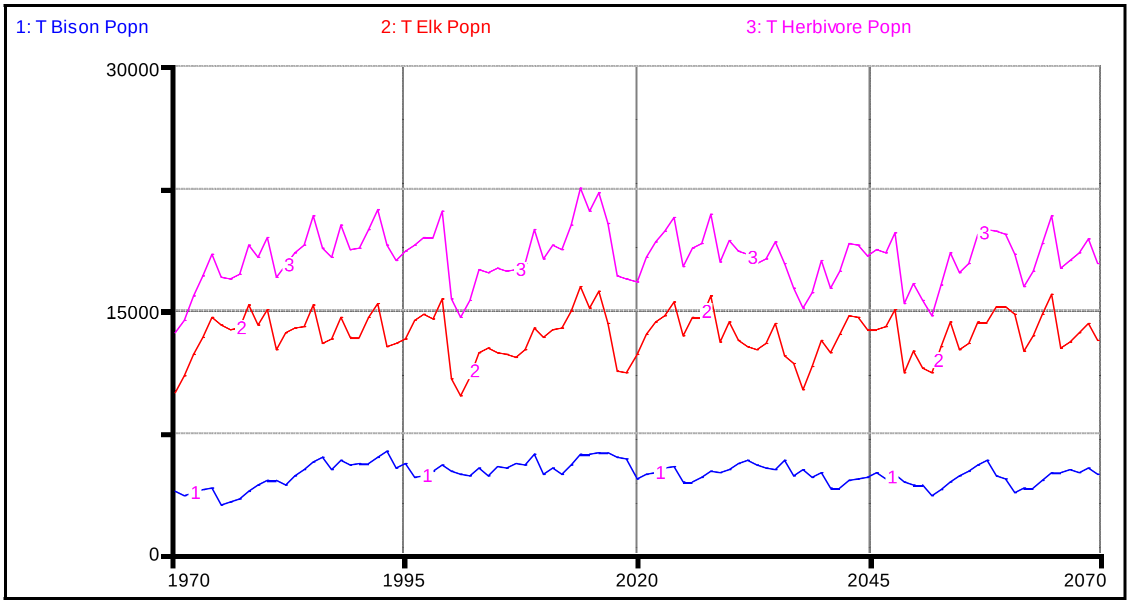
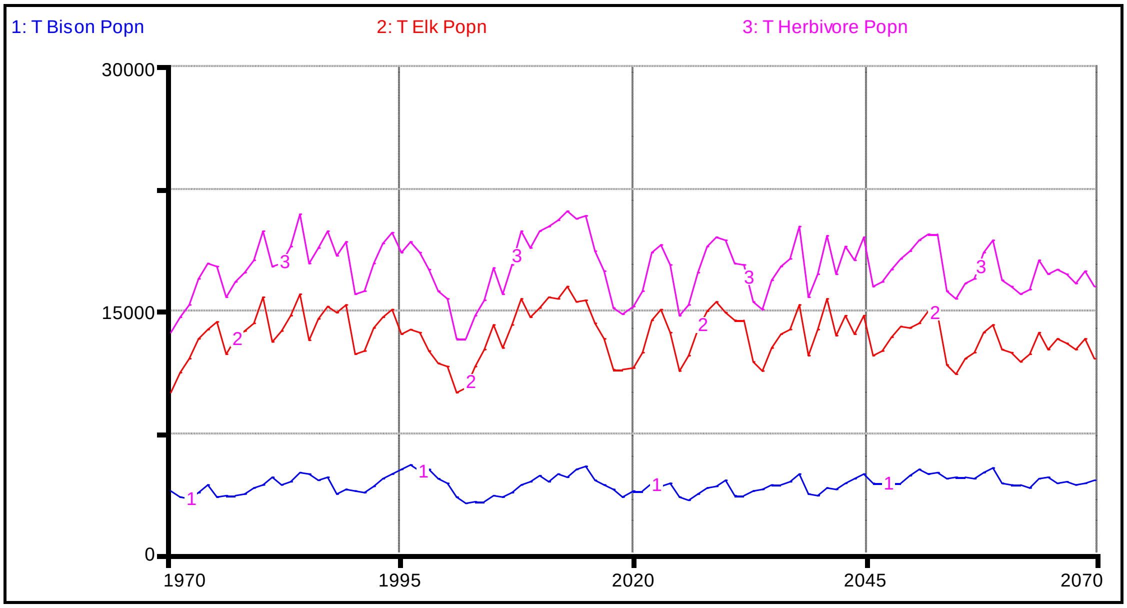


Figure 6.57. Simulated variance in bison, elk, and total herbivore populations on winter bison range to illustrate the relative temporal abundance of these two major herbivore species. Simulation based on Majority Average Model.



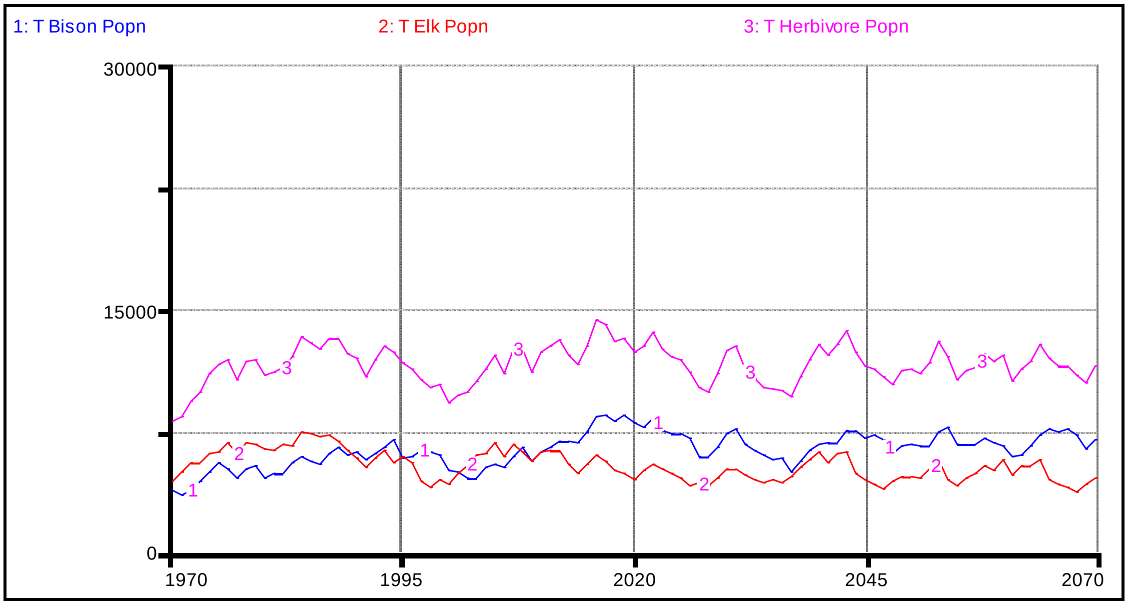
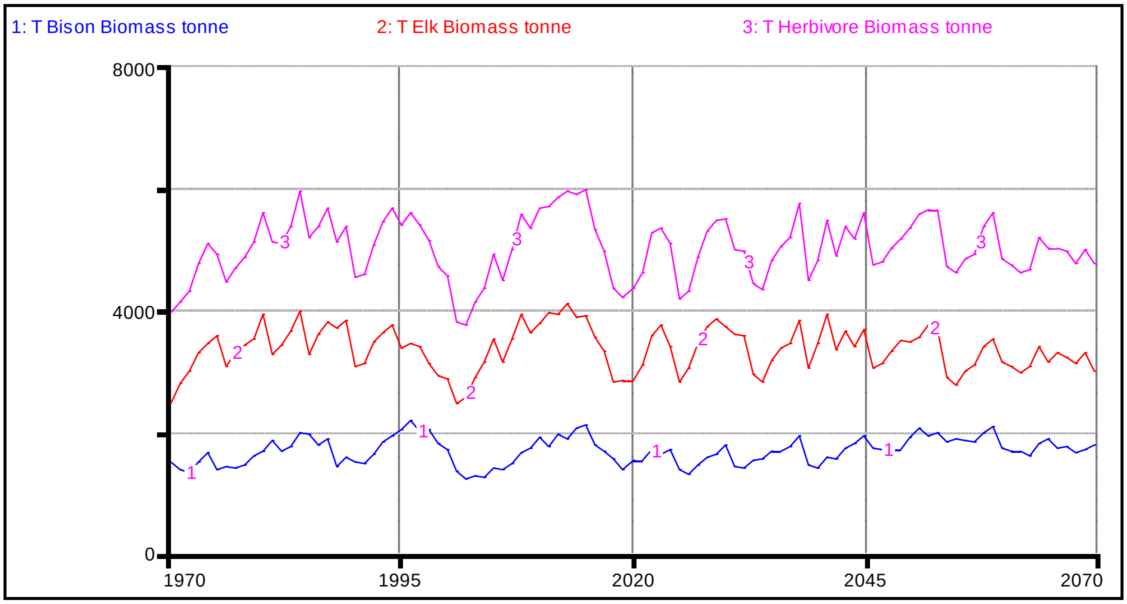


Figure 6.58. Simulated variance in bison and elk population on winter bison range to illustrate the relative temporal abundance of these two major herbivore species. Upper graph illustrates range of natural variability under current system, and lower graph illustrates a “what-if” scenario where elk populations are held at ~50% of current levels. Both scenarios involve grooming of winter roads. Simulation based on Majority Average Model.



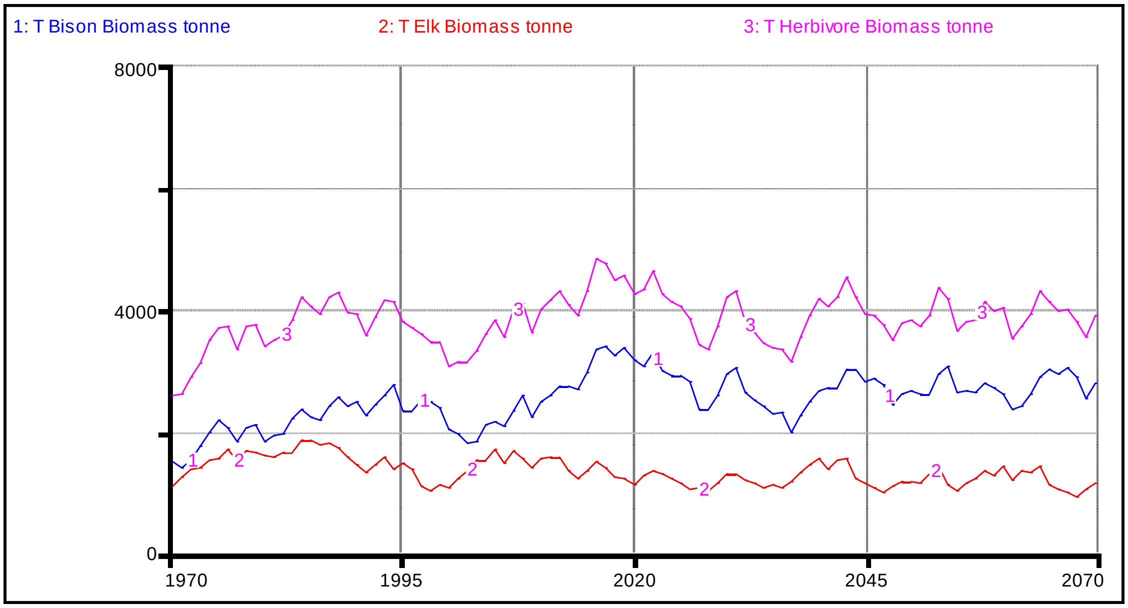
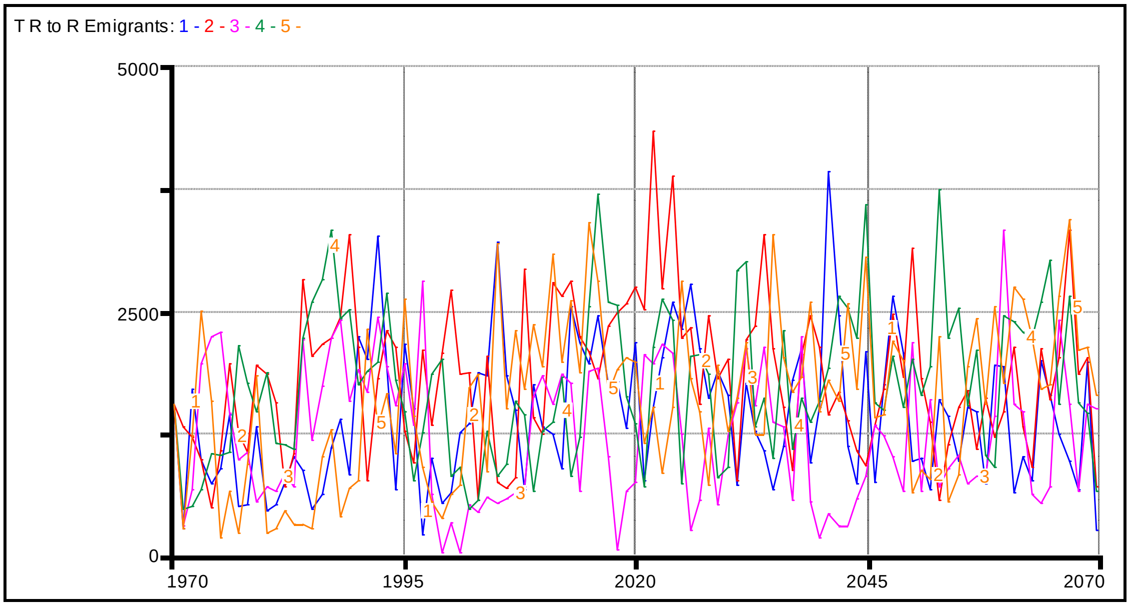


Figure 6.59. Simulated variance in bison and elk biomass (tonne) on winter bison range to illustrate the relative temporal abundance of these two major herbivore species. Upper graph illustrates range of natural variability under current system, and lower graph illustrates a “what-if” scenario where elk populations are held at ~50% of current levels. Both scenarios involve grooming of winter roads. Simulation based on Majority Average Model.



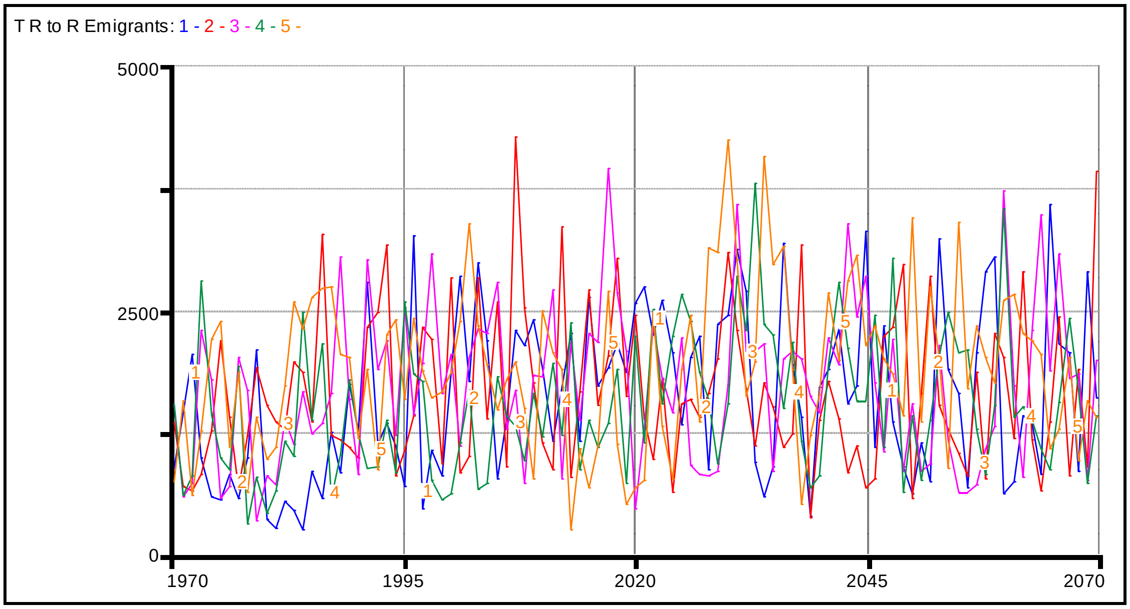
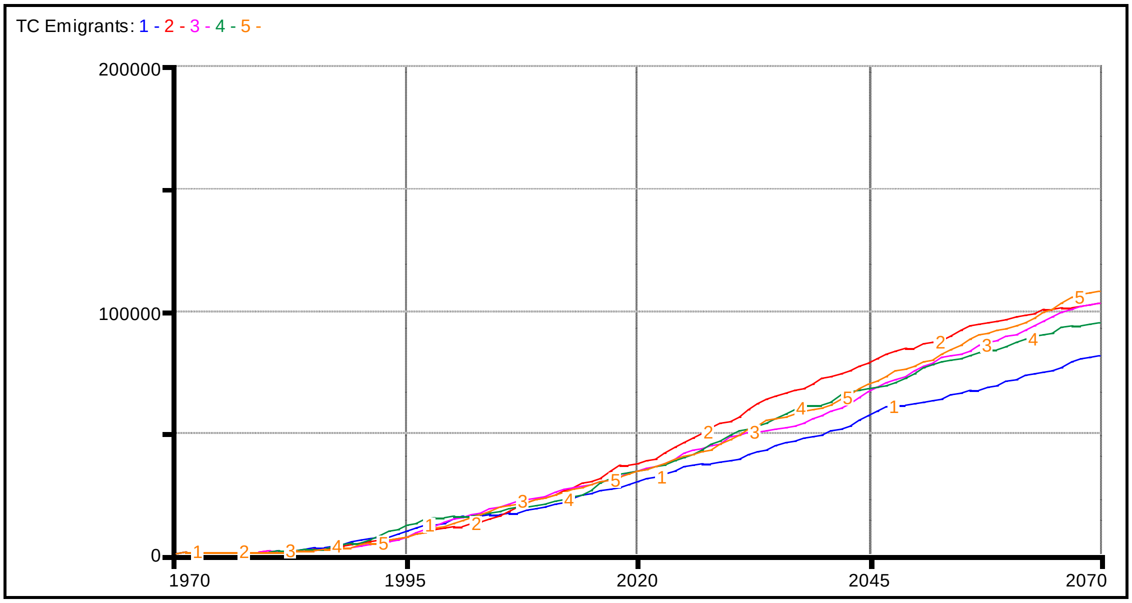


Figure 6.60. Simulated total annual movement of bison between winter ranges; graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario without any road grooming, and the lower graph indicates scenarios involving road grooming along corridors PHC, FMC, and FWC.



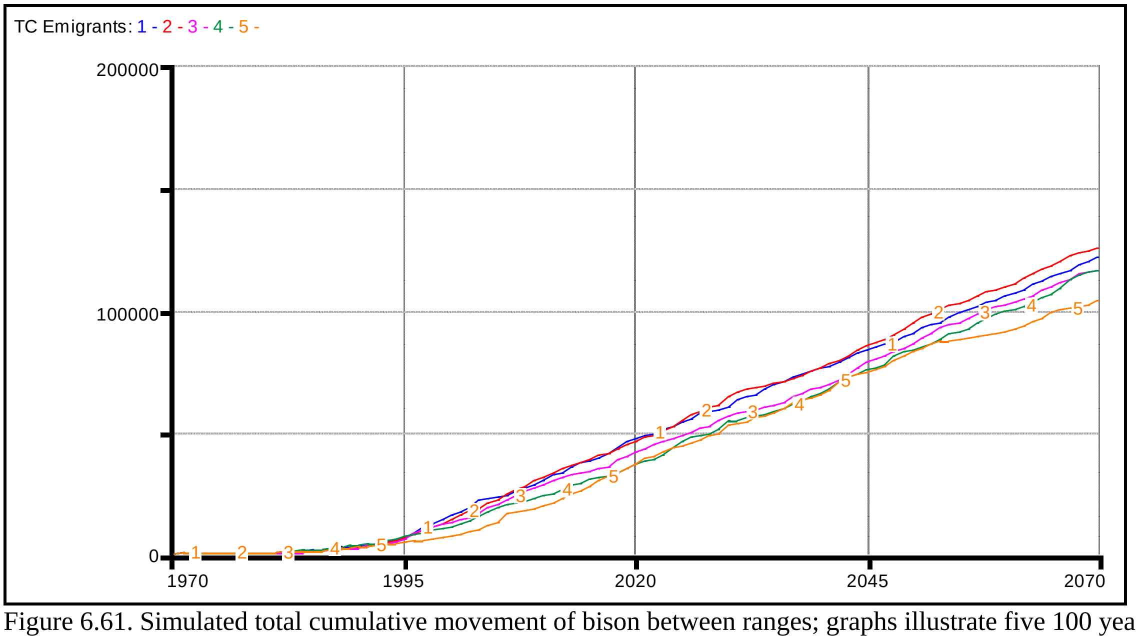
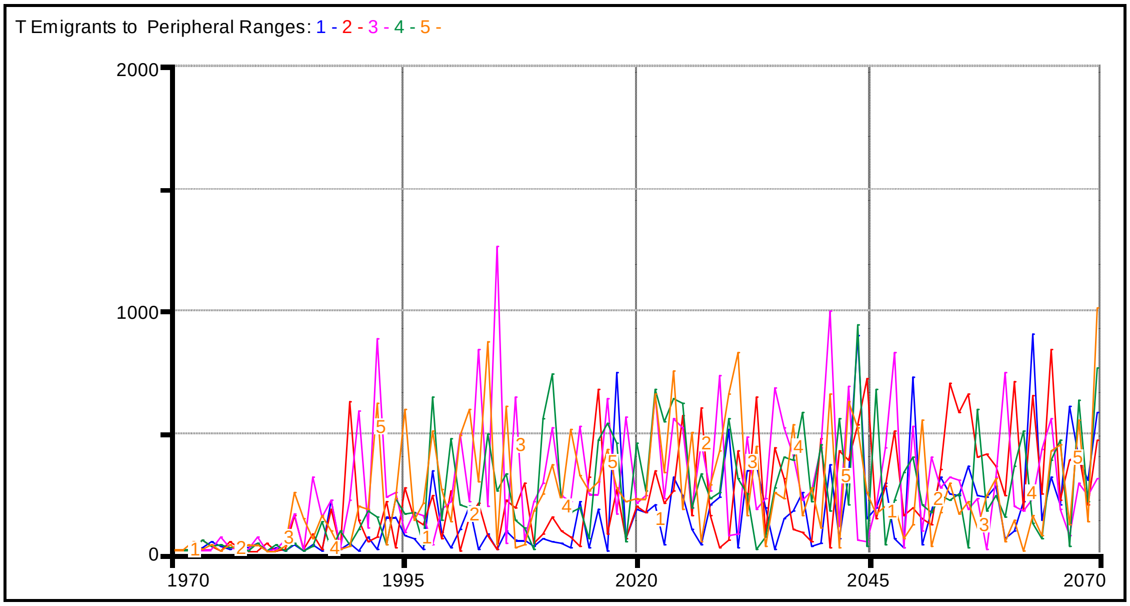


Figure 6.61. Simulated total cumulative movement of bison between ranges; graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario without any road grooming, and the lower graph indicates scenarios involving road grooming along corridors PHC, FMC, and FWC.



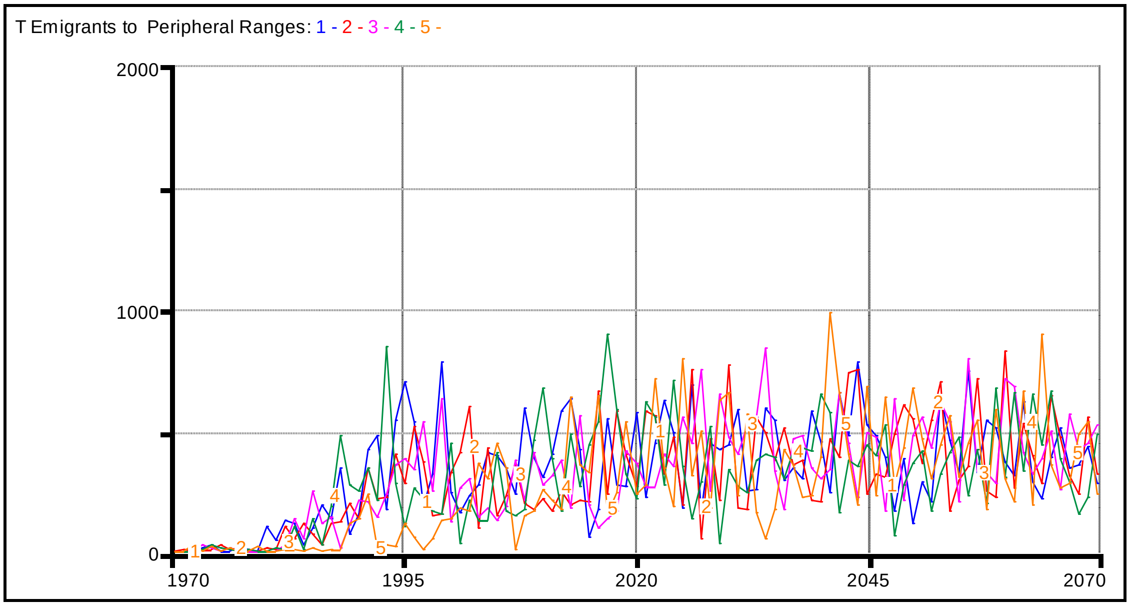
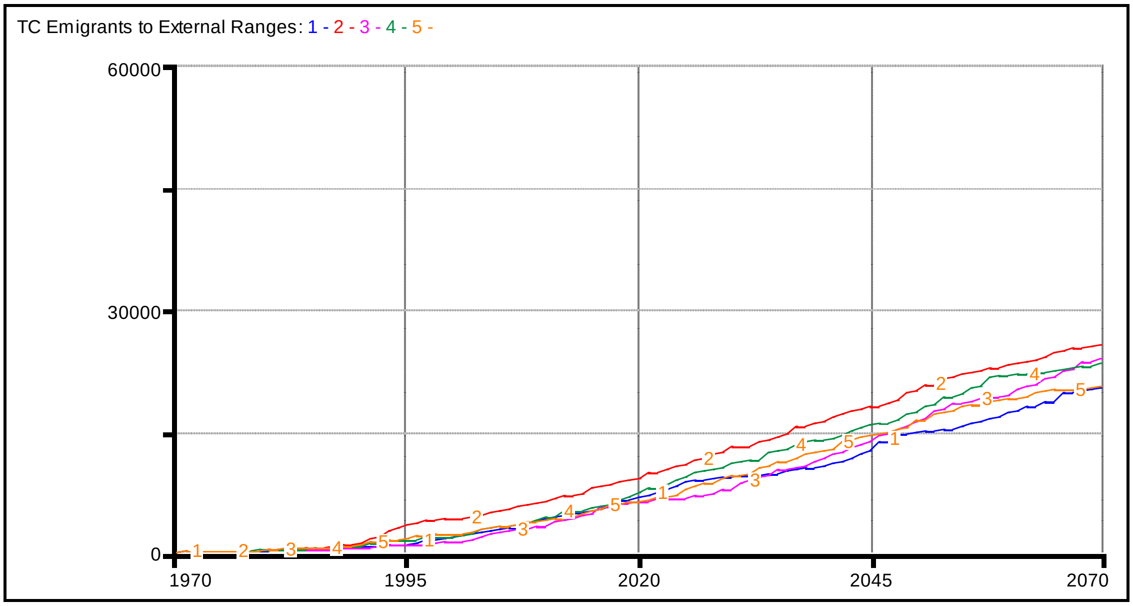


Figure 6.62. Simulated total annual movement of bison to boundary winter ranges (Gardiner basin and West Yellowstone); graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario without any road grooming, and the lower graph indicates scenarios involving road grooming along corridors PHC, FMC, and FWC.



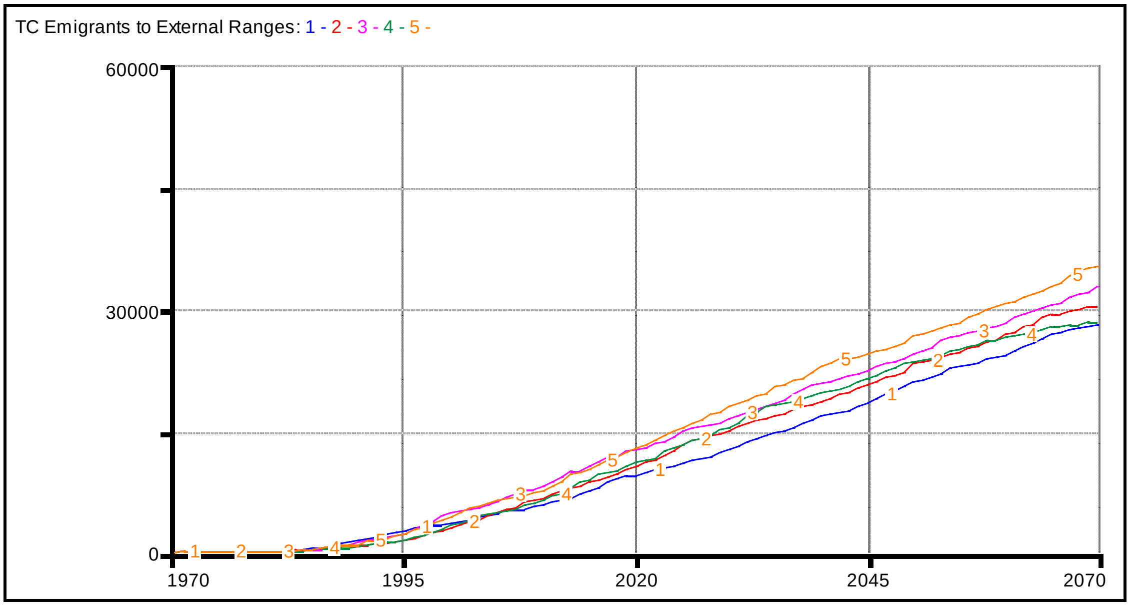


Figure 6.63. Simulated total cumulative movement to boundary winter ranges (Gardiner basin and West Yellowstone); graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario without any road grooming, and the lower graph indicates scenarios involving road grooming along corridors PHC, FMC, and FWC.

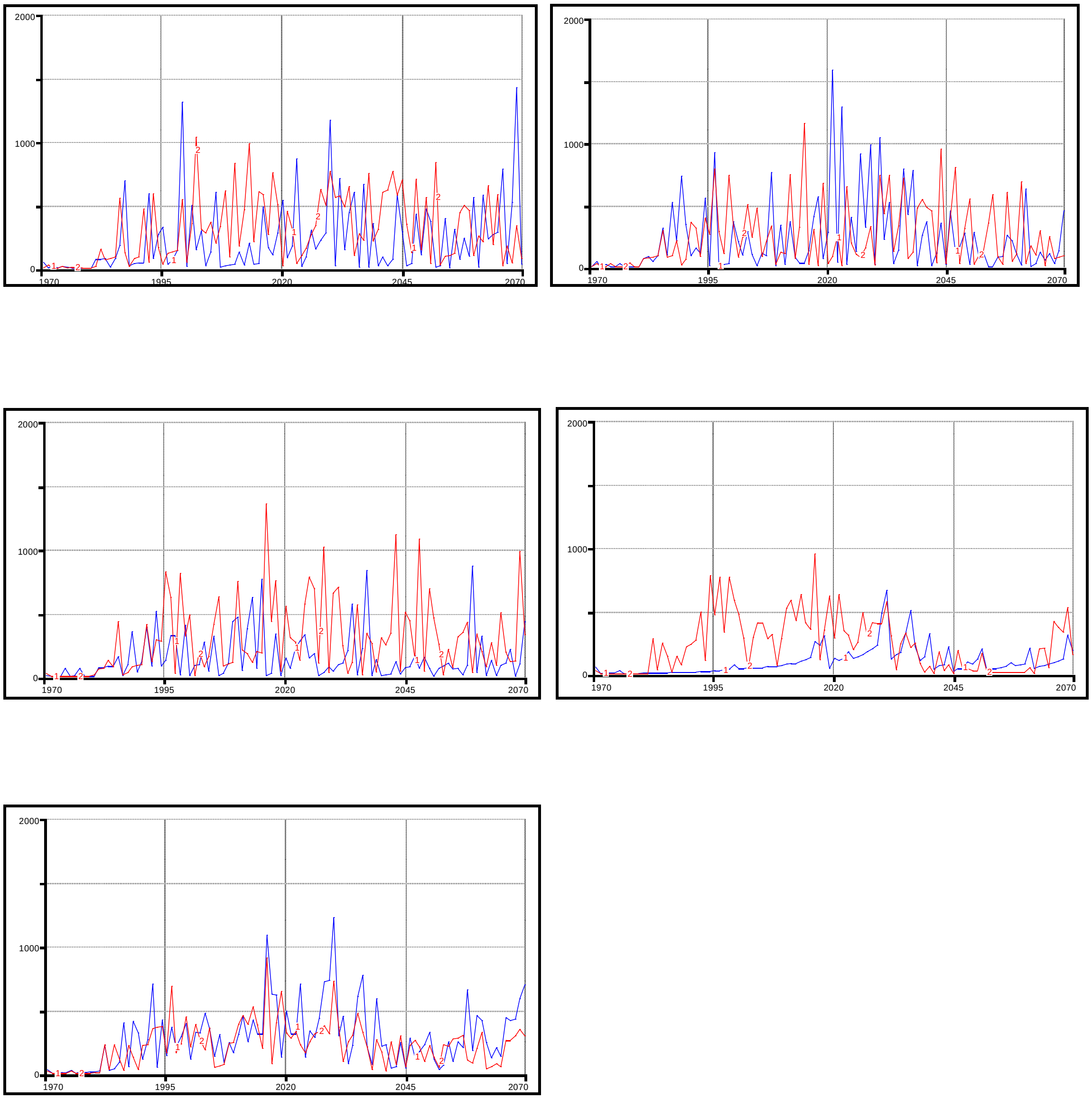


Figure 6.64. Simulated annual movement from interior to boundary winter ranges (Gardiner basin and West Yellowstone); graphs are based on input values from each Key Informant Group. Simulation #1 reflects a scenario without road grooming, and scenario #2 indicates a scenario involving road grooming along corridors PHC, FMC, and FWC. Order is Group 1 (upper left), Group 2, (upper right), Group 3 (middle left), Group 4 (middle right), and Group 5 (lower left).

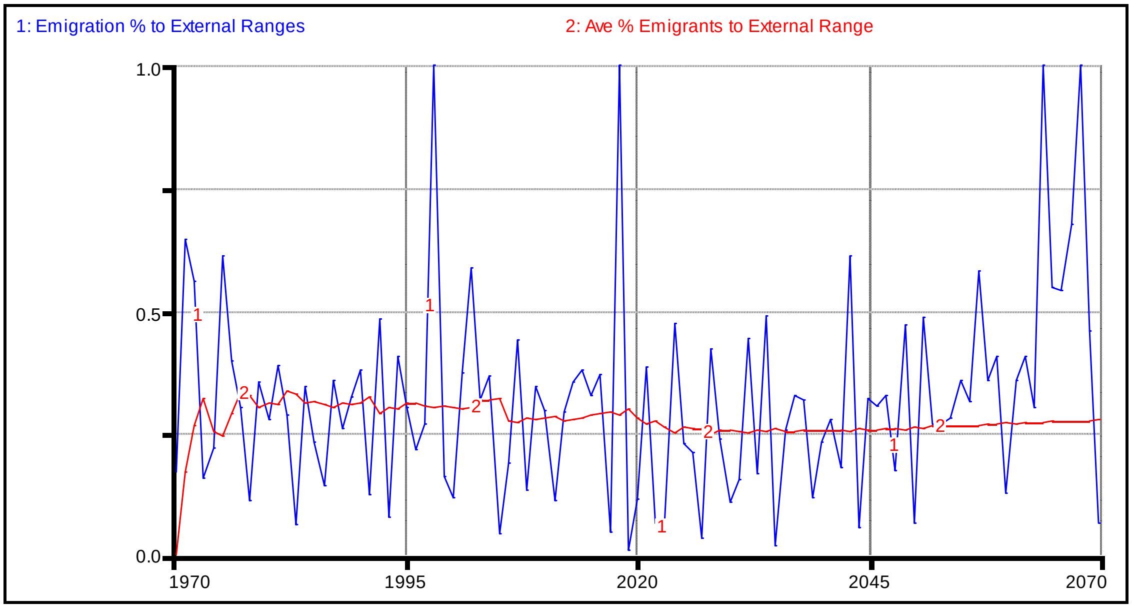


Figure 6.65. Simulated percent of annual bison movement that goes to boundary winter ranges (Gardiner basin and West Yellowstone); based on movement coefficients from Majority Average Model. Graph #1 reflects annual values and Graph #2 reflects a running average. No road grooming occurred during this scenario.

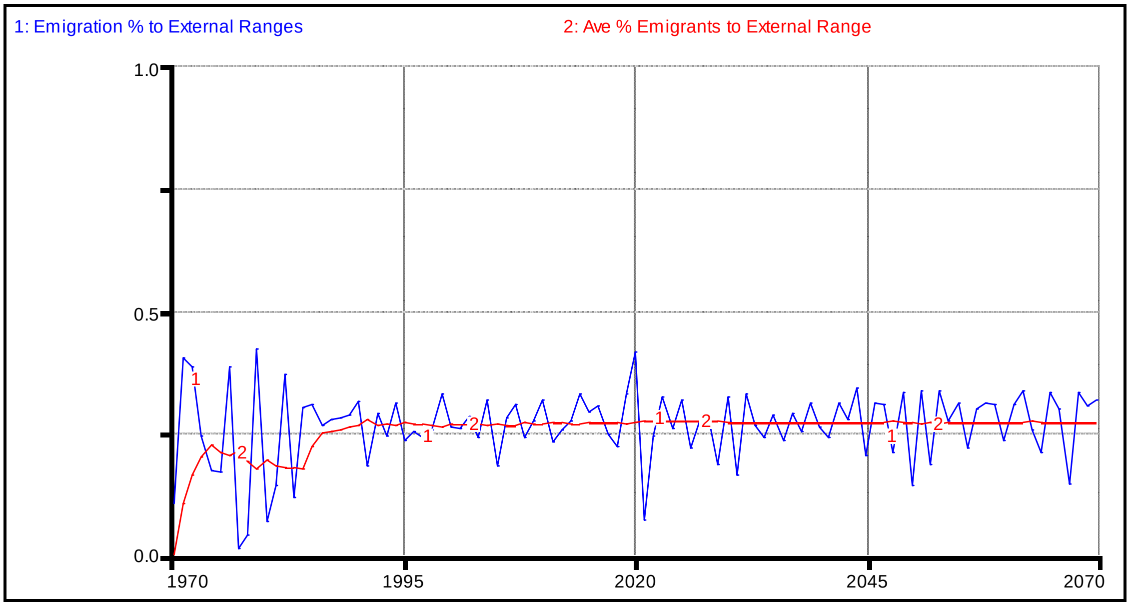


Figure 6.66. Simulated percent of annual bison movement that goes to boundary winter ranges (Gardiner basin and West Yellowstone); based on movement coefficients from Majority Average Model. Graph #1 reflects annual values and Graph #2 reflects a running average. This scenario involves road grooming along corridors PHC, FMC, and FWC.

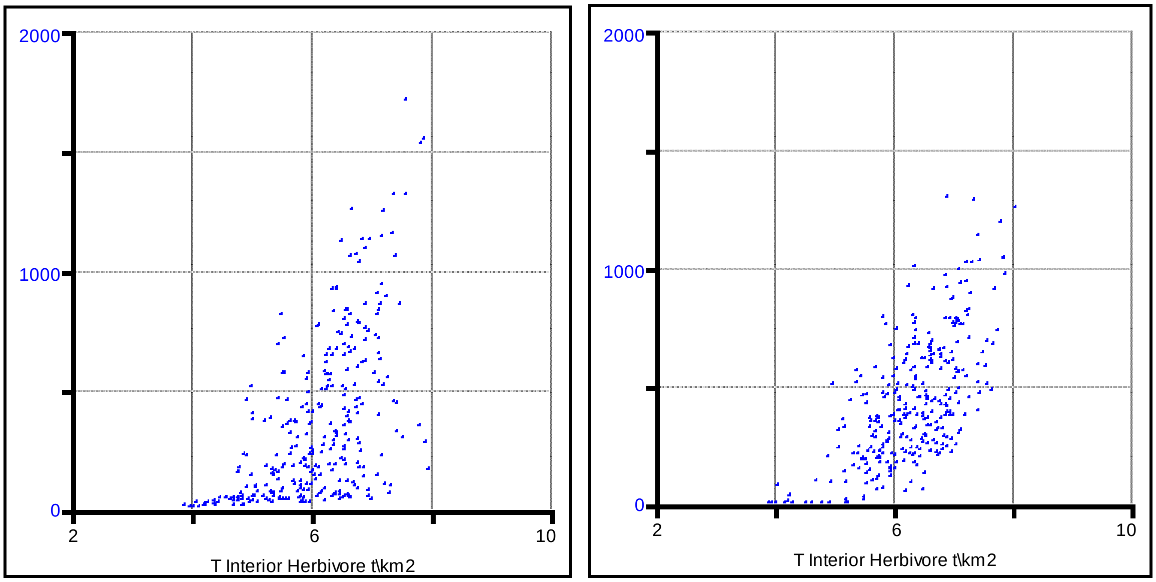


Figure 6.67. Simulated scattergram (300 year simulation) indicating relationship between bison biomass density (tonne/km$^2$) in the interior ranges and the number of bison emigrating to boundary ranges during for the winter season. Graph on the left reflects a no road grooming scenario; graph on right reflects road grooming along corridors PHC, FMC, and FWC. Simulation based on Majority Average Model.

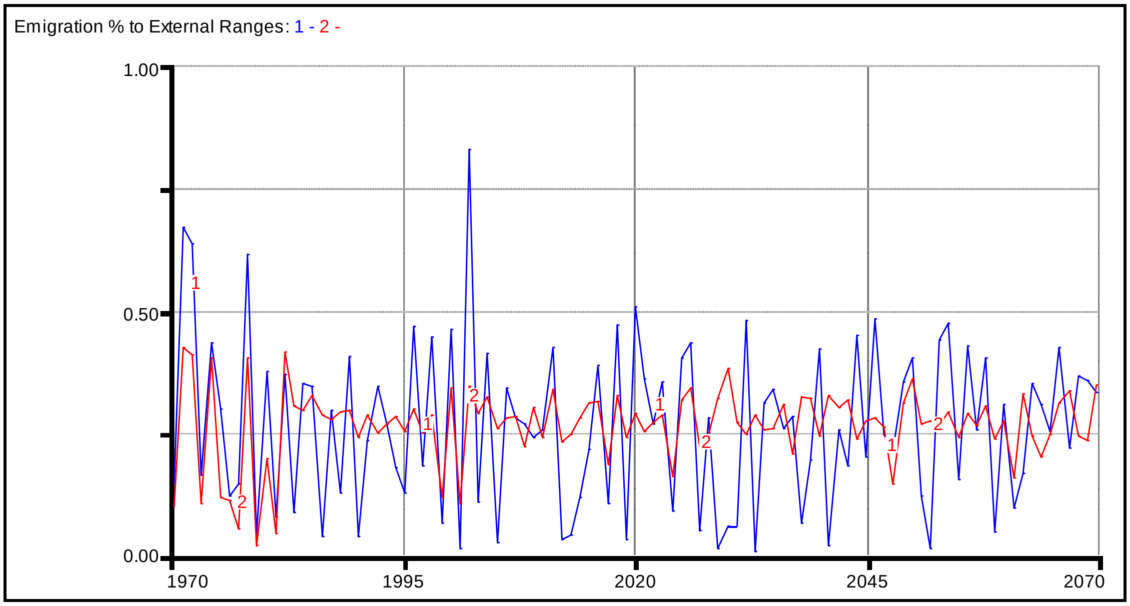


Figure 6.68. Simulated percent of annual movement that goes to boundary winter ranges (Gardiner basin and West Yellowstone); based on movement coefficients from Majority Average Model. Graph #1 reflects a simulation scenario without any road grooming, and Graph #2 indicates scenarios involving road grooming along corridors PHC, FMC, and FWC.

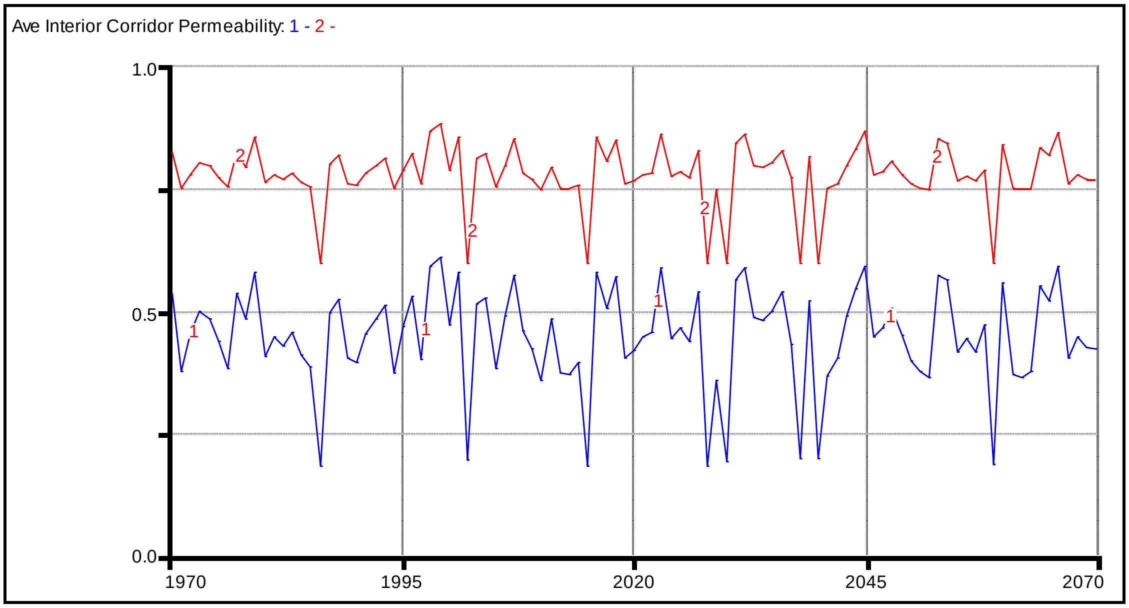


Figure 6.69. Simulated comparison of average YNP interior corridor permeability without (#1) and with (#2) winter road grooming. Simulation based on Majority Average Model.

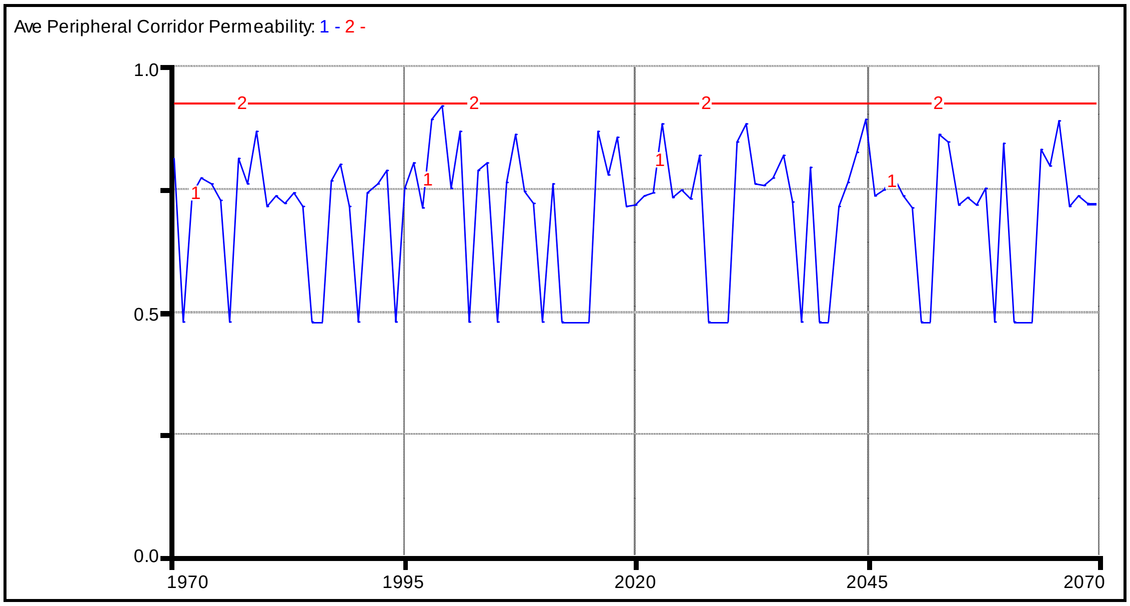


Figure 6.70. Simulated comparison of average YNP boundary corridor permeability without (#1) and with (#2) winter road grooming. Simulation based on Majority Average Model.

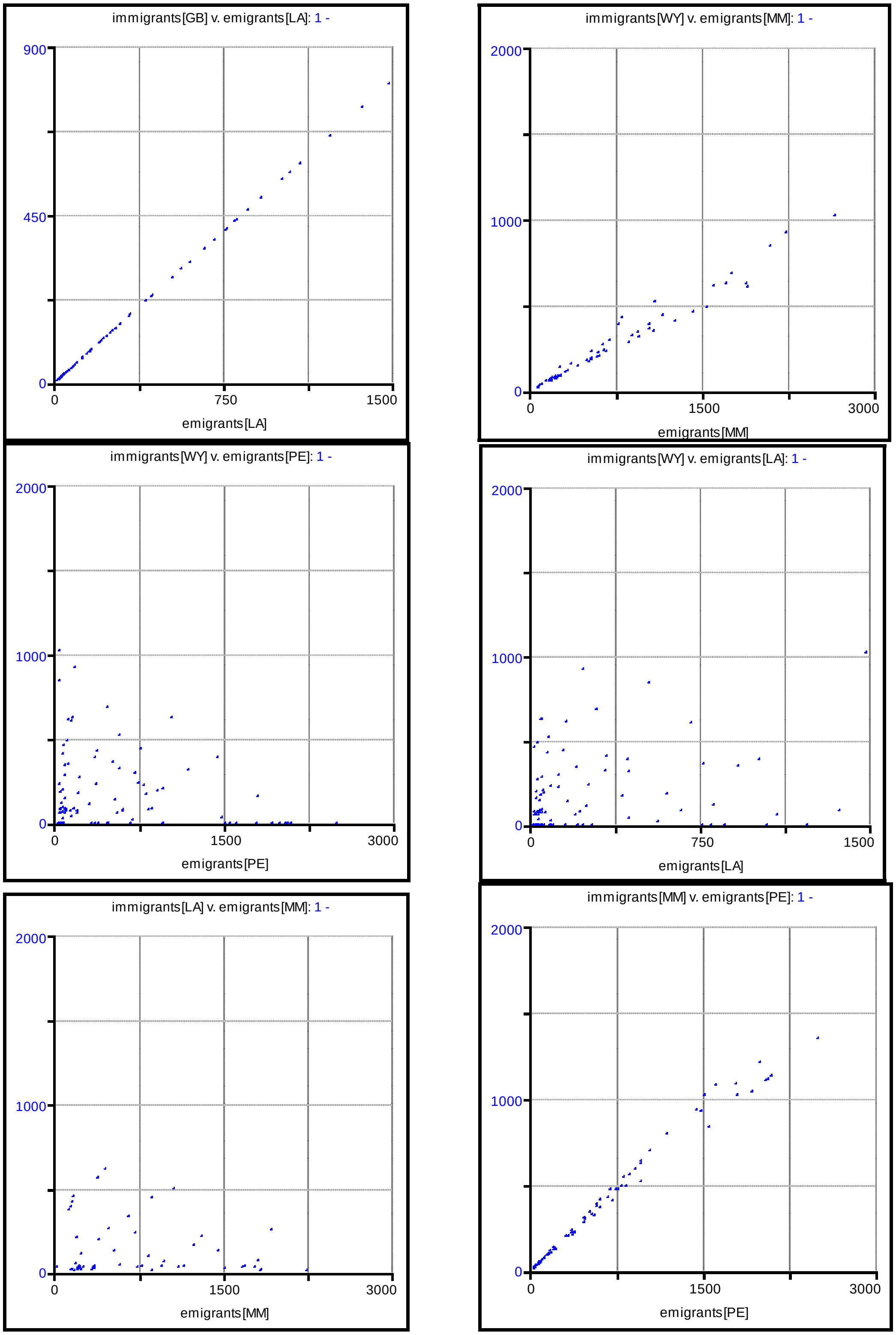


Figure 6.71. Simulated scattergrams between selected range immigration and emigration values. Scenarios do not involve winter road grooming. Simulation based on Majority Average Model.

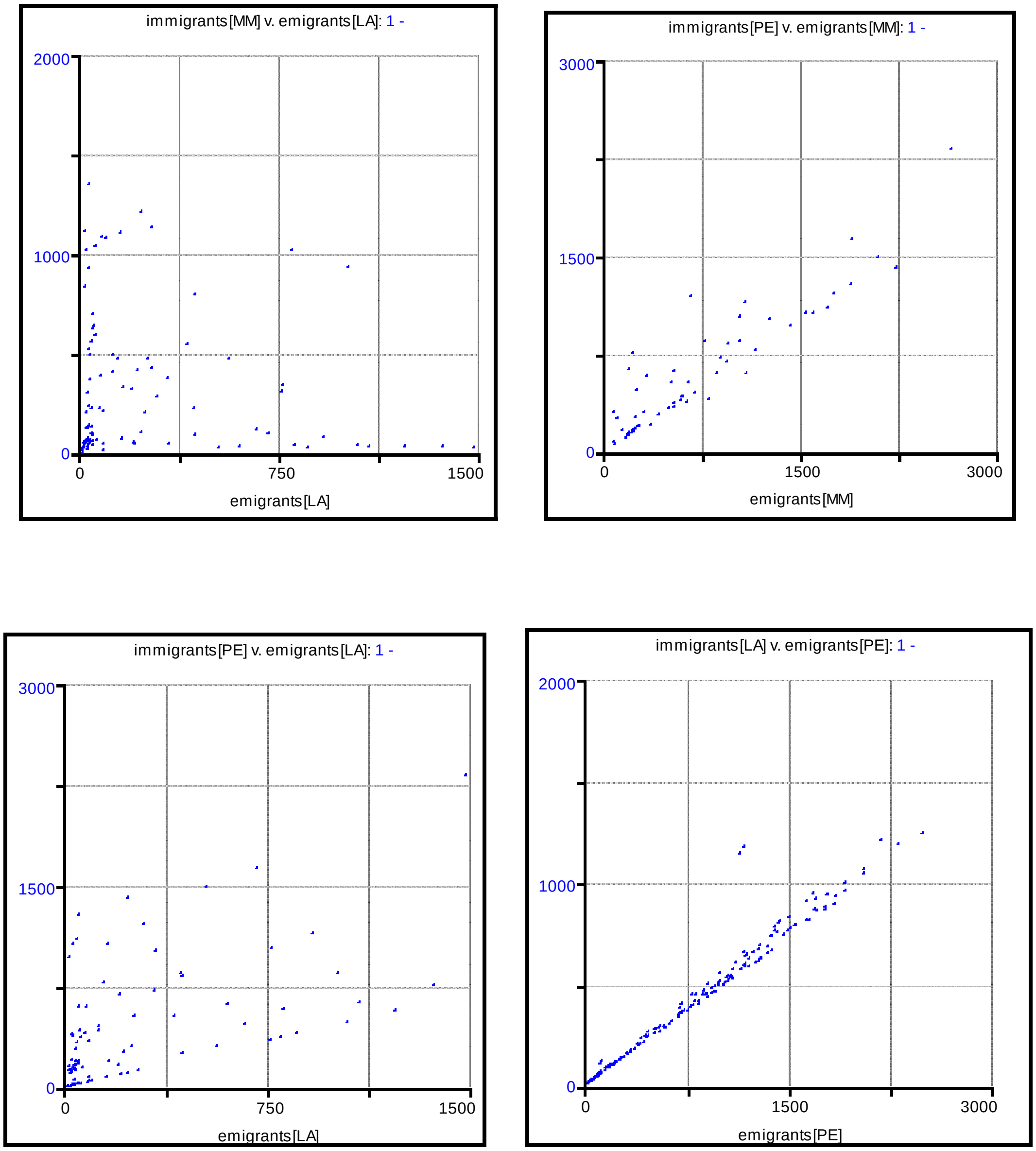


Figure 6.72. Simulated scattergrams between selected range immigration and emigration values. Scenarios do not involve winter road grooming. Simulation based on Majority Average Model.

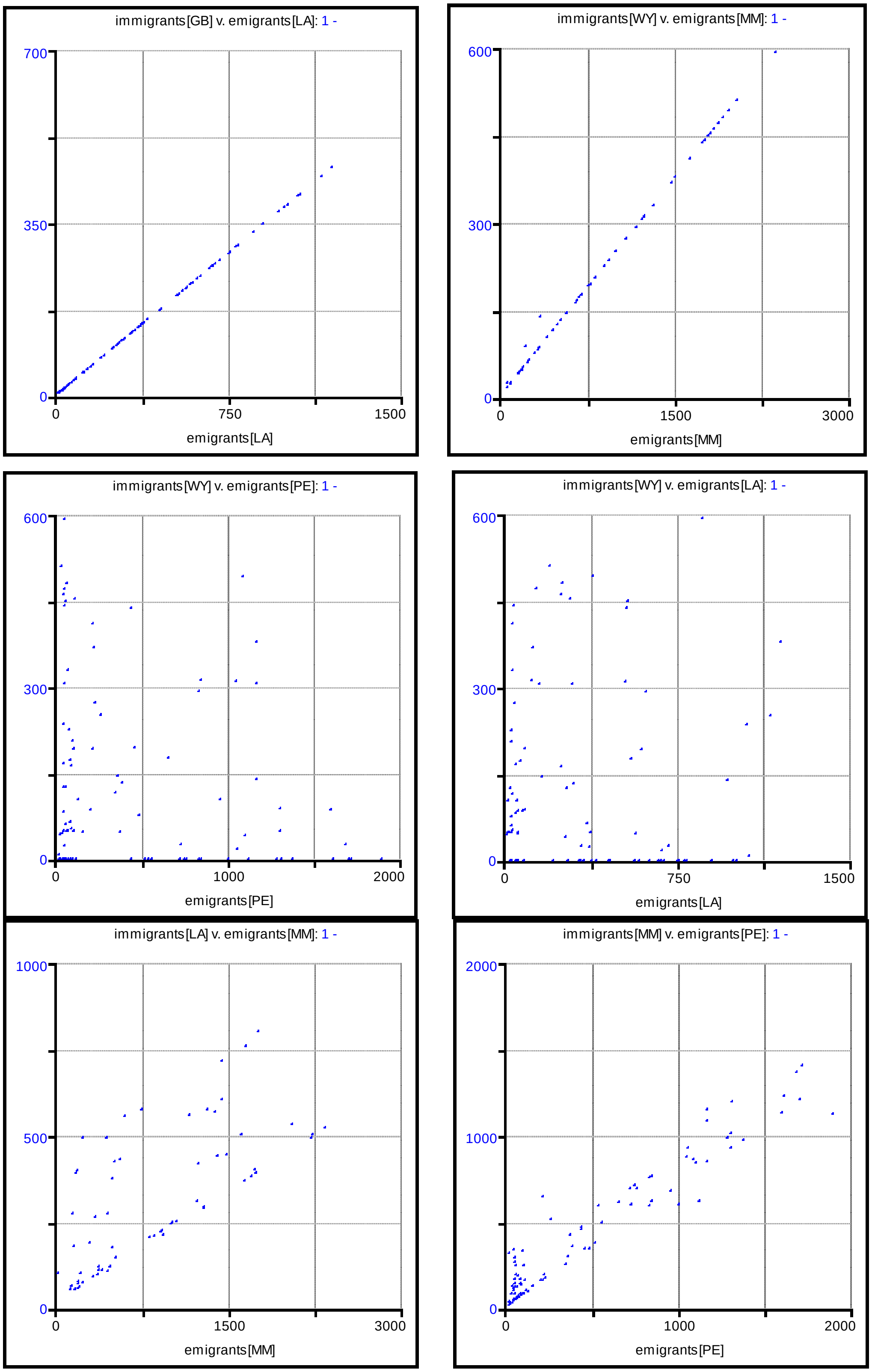


Figure 6.73. Simulated scattergrams between selected range immigration and emigration values. Scenarios include winter road grooming of corridors PHC, FMC, and FWC. Simulation based on Majority Average Model.

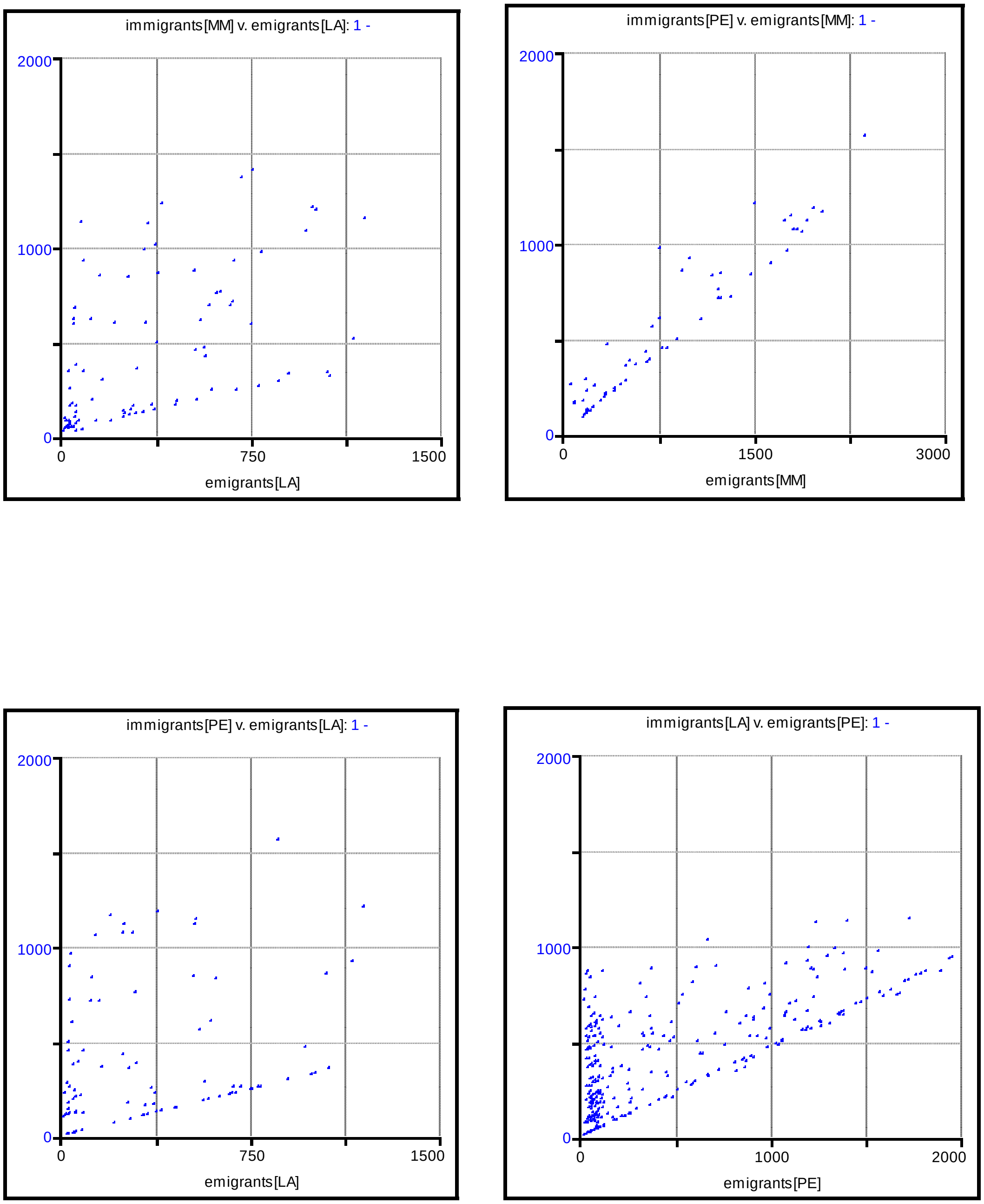
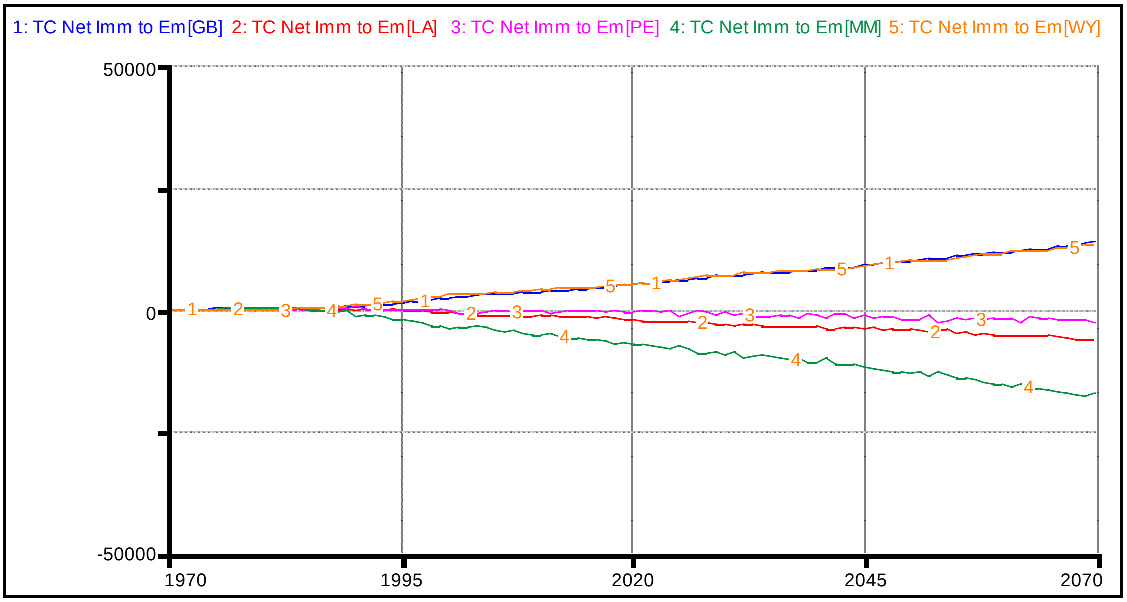


Figure 6.74. Simulated scattergrams between selected range immigration and emigration values. Scenarios include winter road grooming of corridors PHC, FMC, and FWC. Simulation based on Majority Average Model.



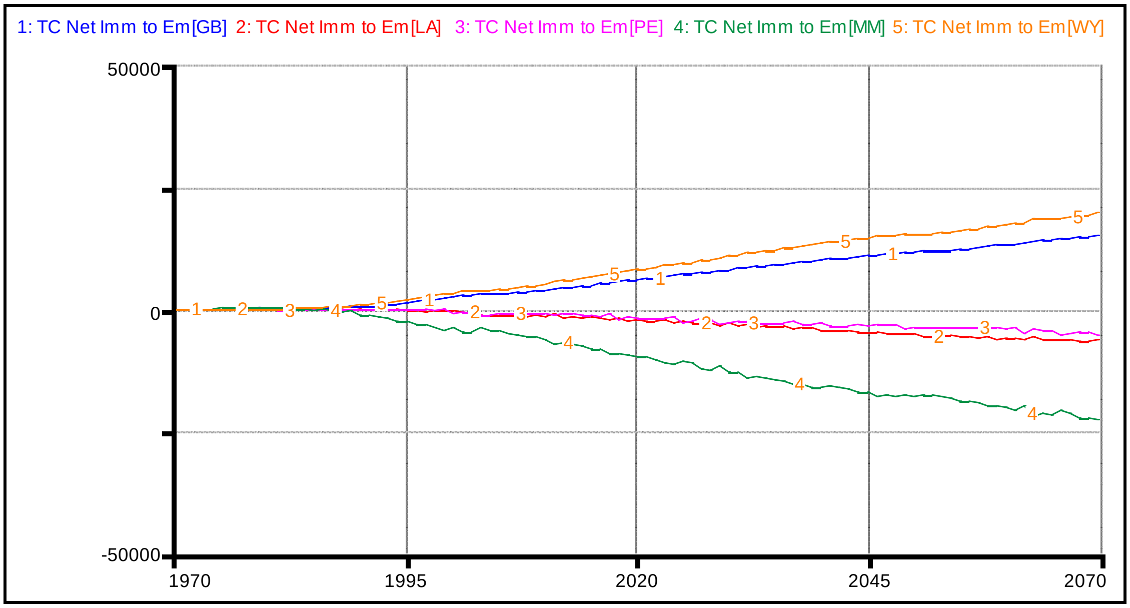


Figure 6.75. Simulated net difference between immigration and emigration from each of the bison winter ranges. Values above 0 represent a net immigration gain, whereas values below 0 indicate that emigration exceeds immigration. Upper graph involves scenario without road grooming and lower graph includes road grooming. Simulation based on Majority Average Model.

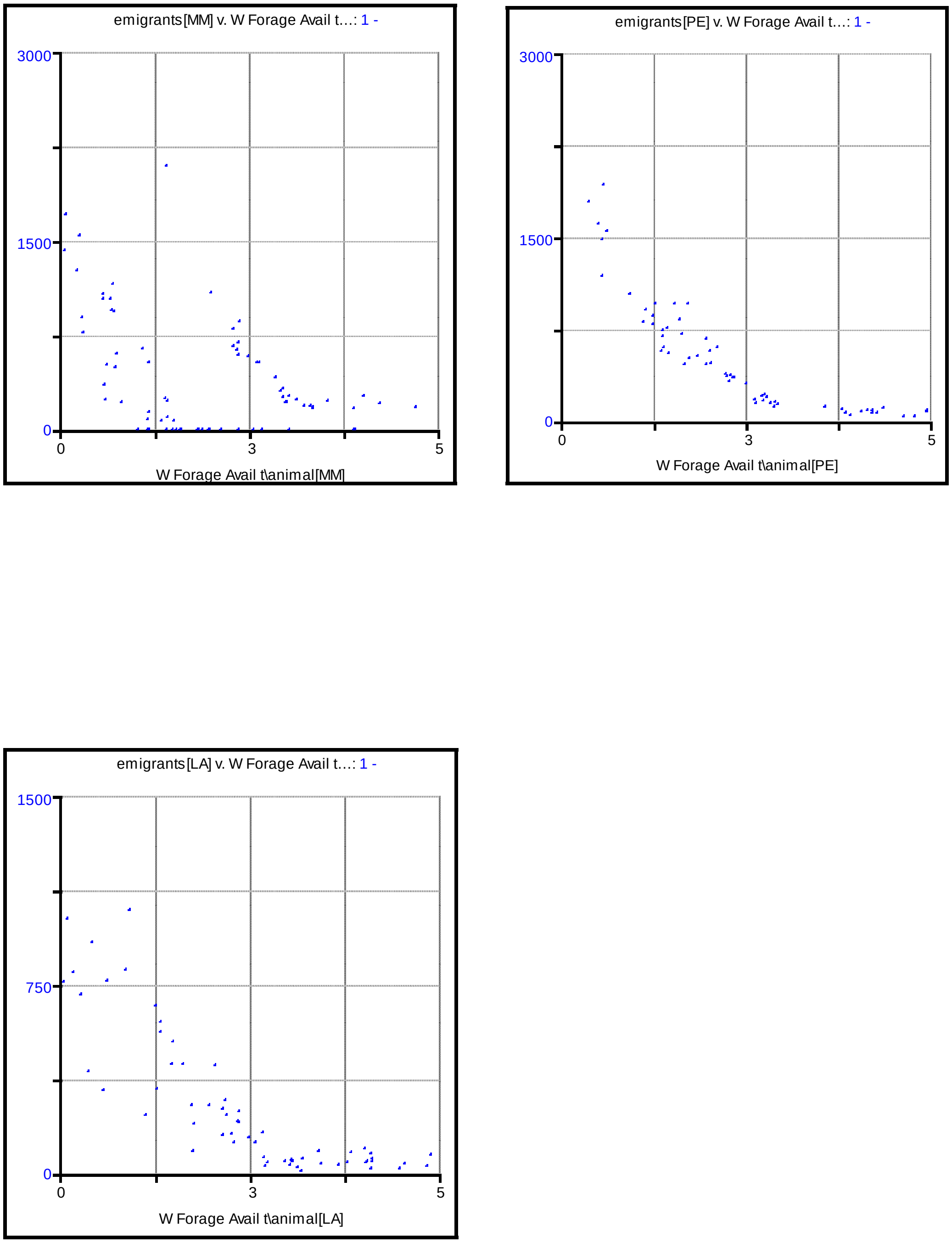
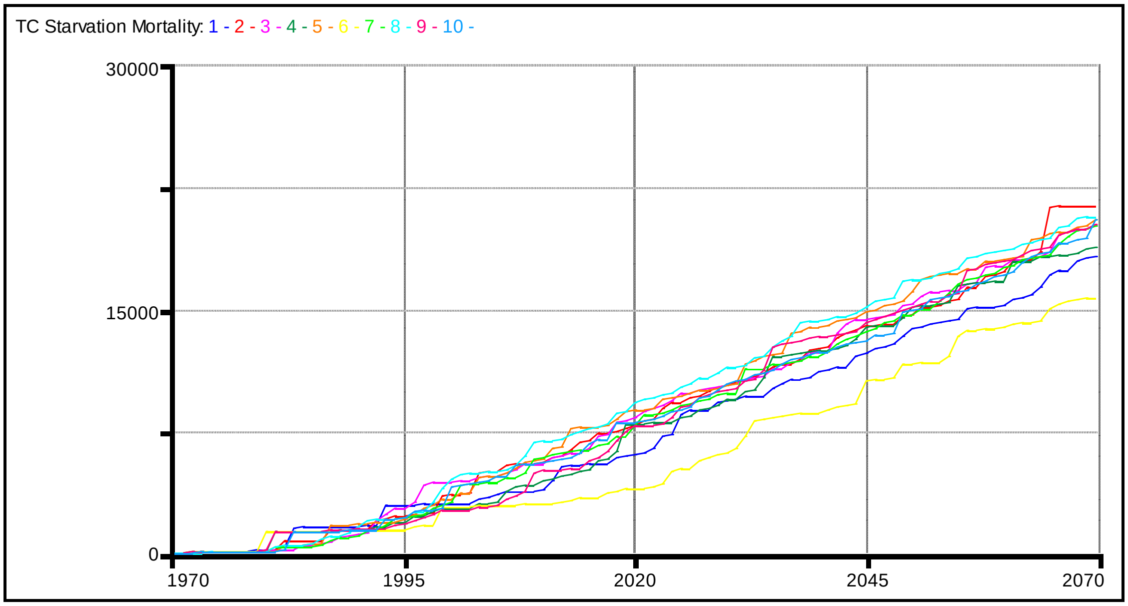


Figure 6.76. Simulated scattergrams between bison emigration values from interior winter ranges and winter forage availability (tonne/bison). Simulation based on Majority Average Model.



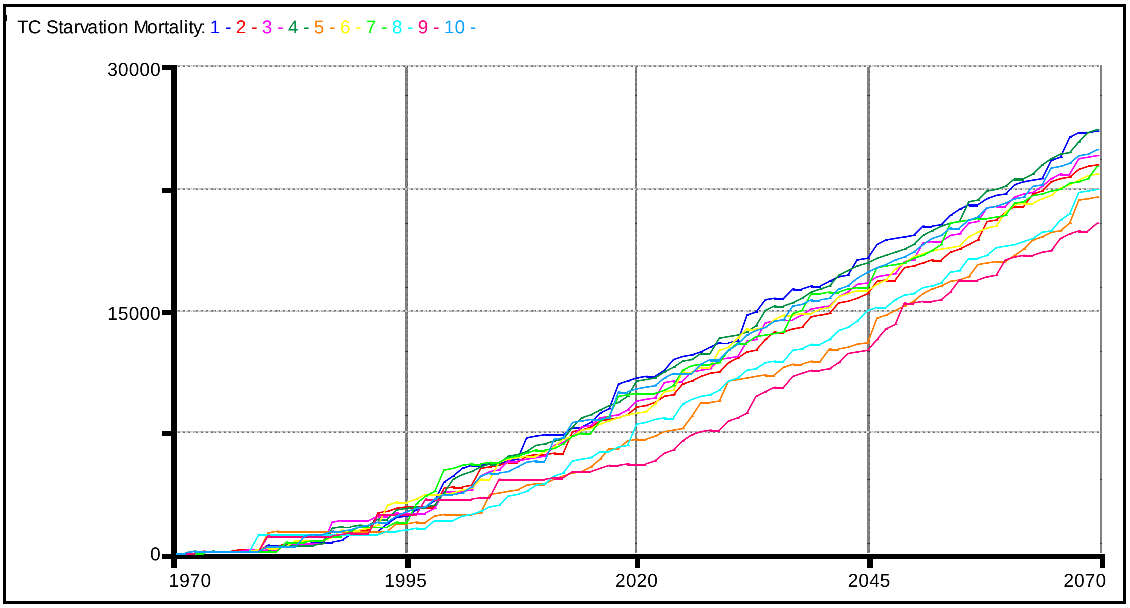


Figure 6.77. Simulated total cumulative level of bison starvation without (above) and with (below) winter road grooming. A series of ten 100 year simulations conducted with random precipitation using majority average model. Simulation based on Majority Average Model.

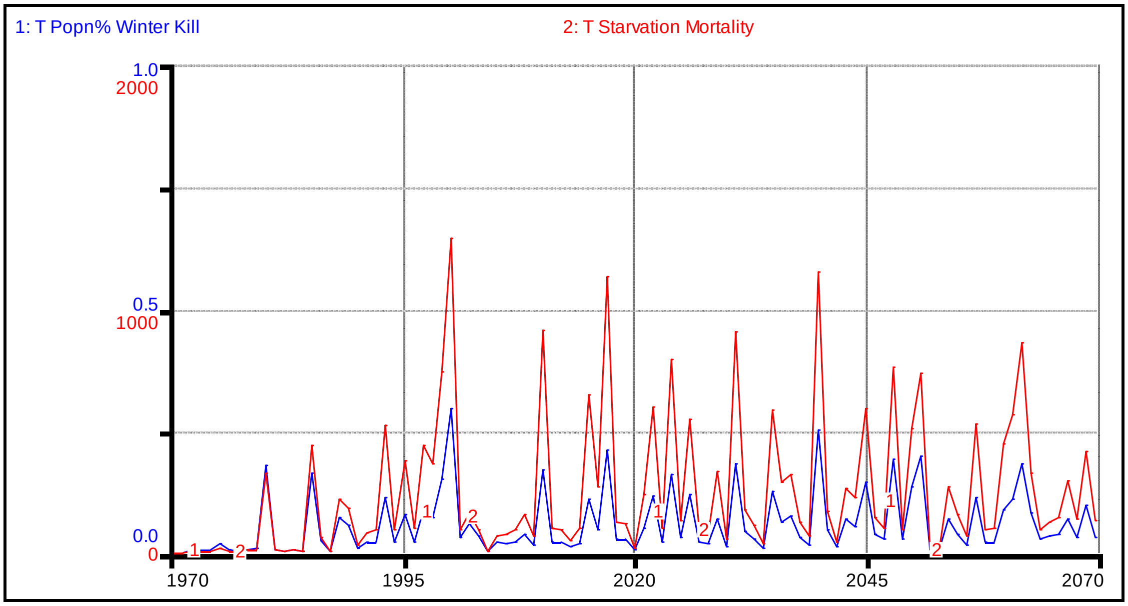


Figure 6.78. Simulated number and percent of bison killed by starvation during the winter season. Graph illustrates the episodic nature of bison die-offs associated with conditions of low forage availability. Simulation based on Majority Average Model.

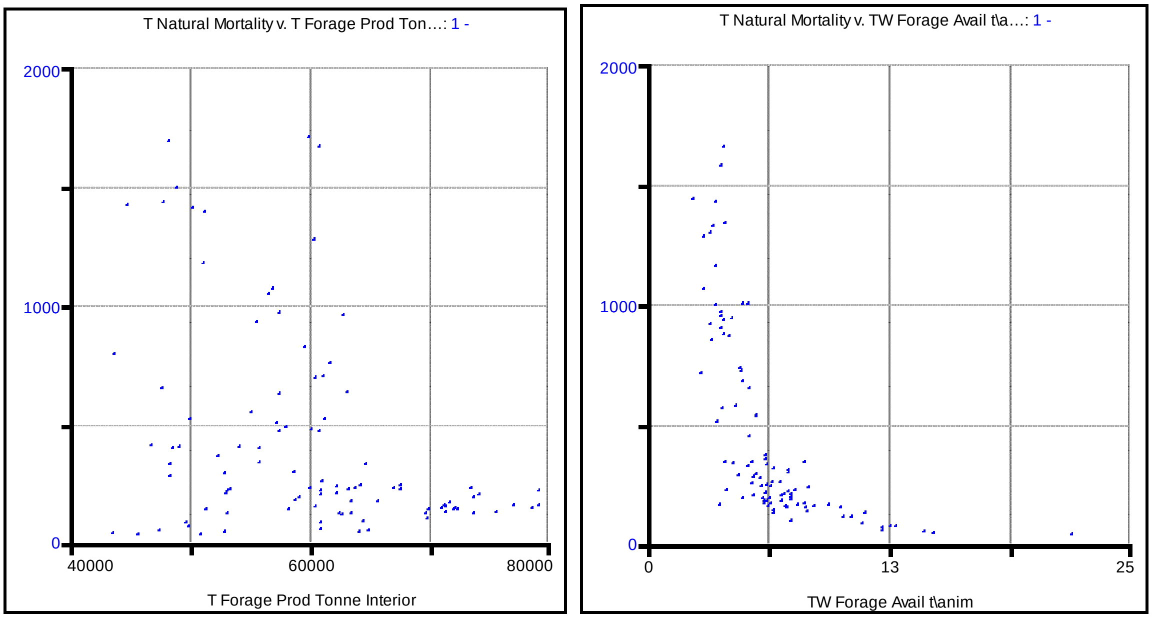
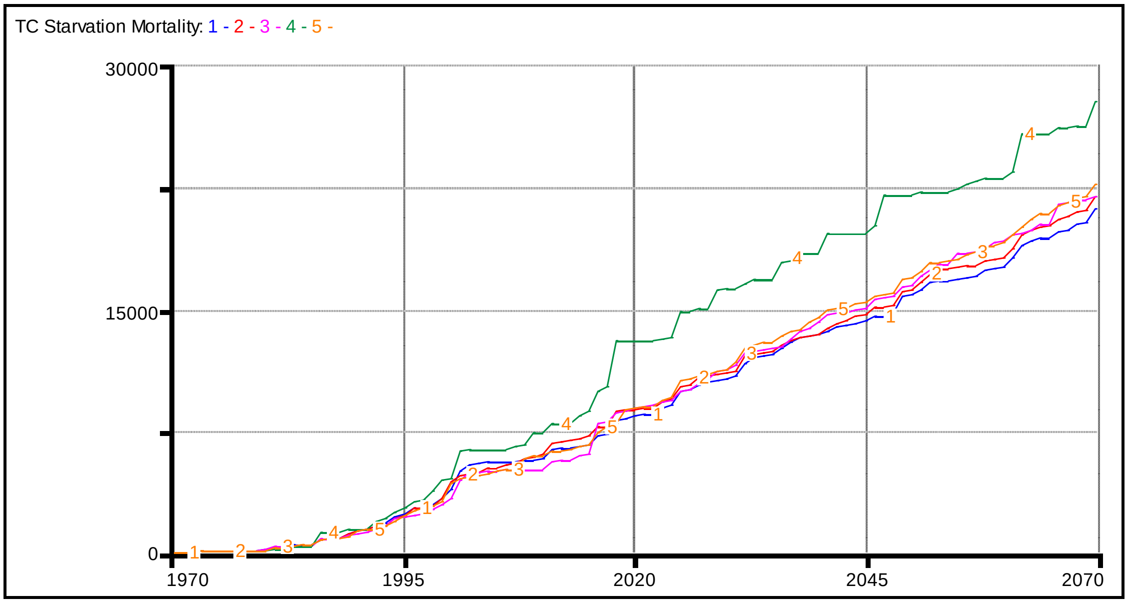


Figure 6.79. Simulated relationships between winter starvation mortality and forage production (left) and forage availability (right) for interior ranges. Simulation based on Majority Average Model.



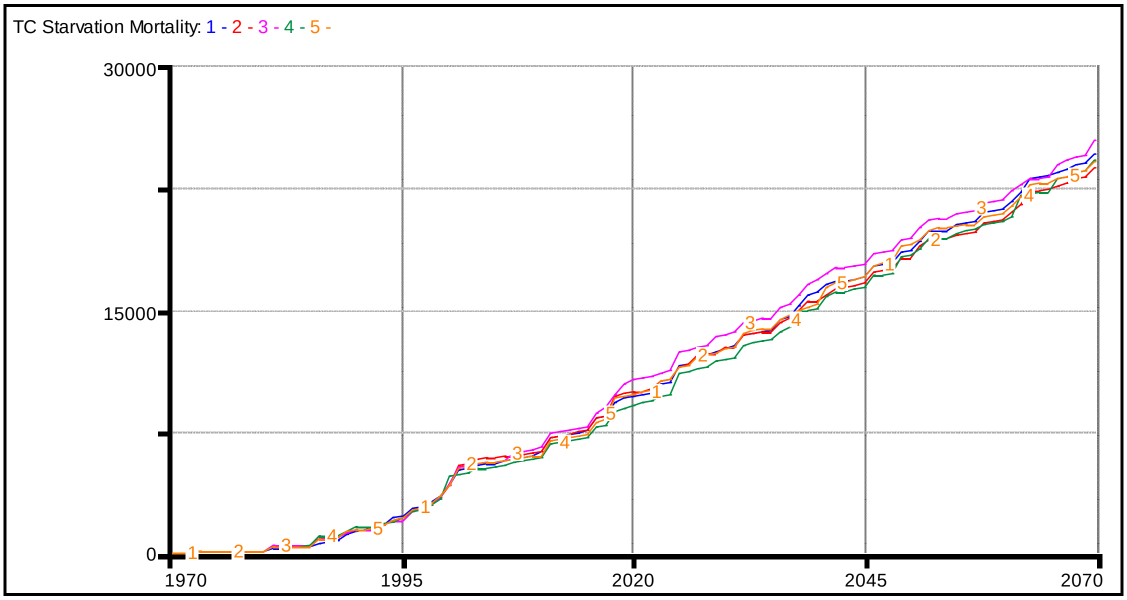
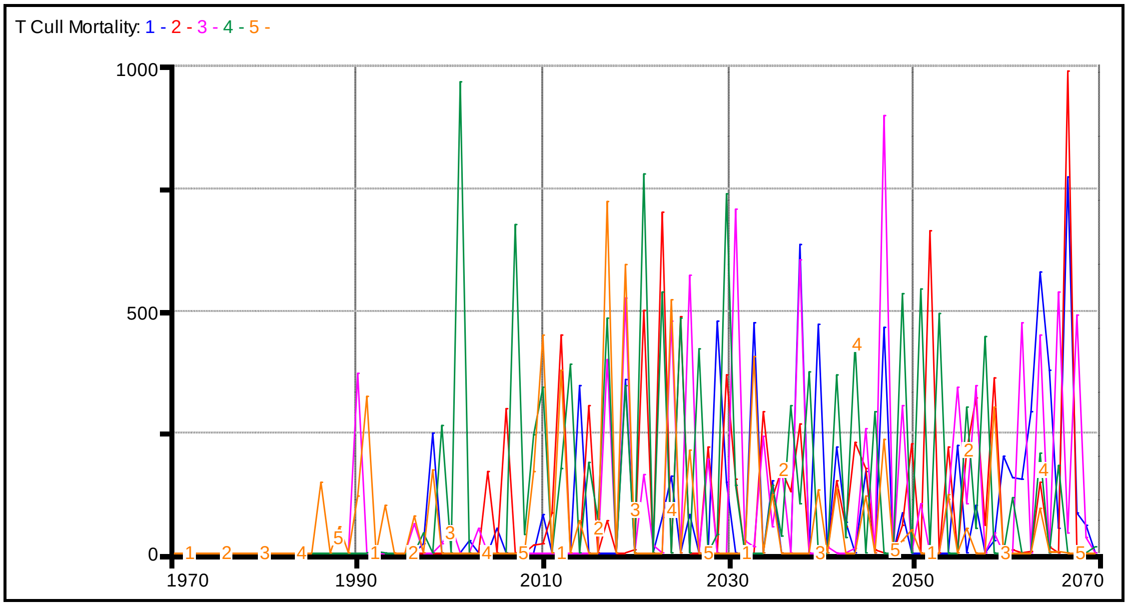


Figure 6.80. Simulated total cumulative bison starvation mortality. Graphs represent different Key Informant Groups (1 through 5). Upper graph represents simulation scenario without winter road grooming, whereas lower graph represents road grooming along corridors PHC, FMC, and FWC.



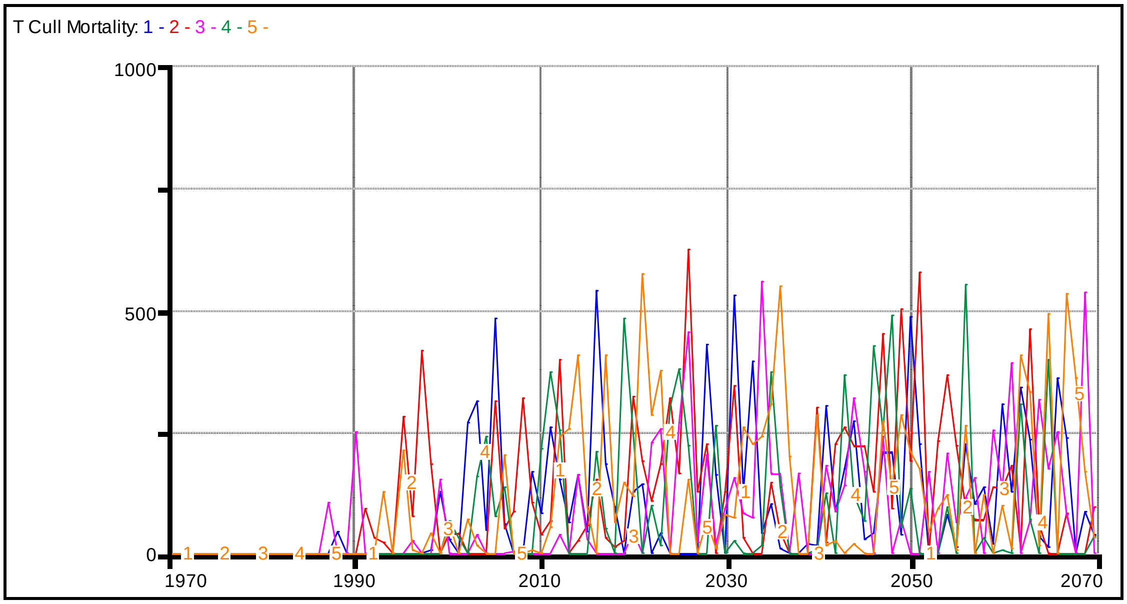
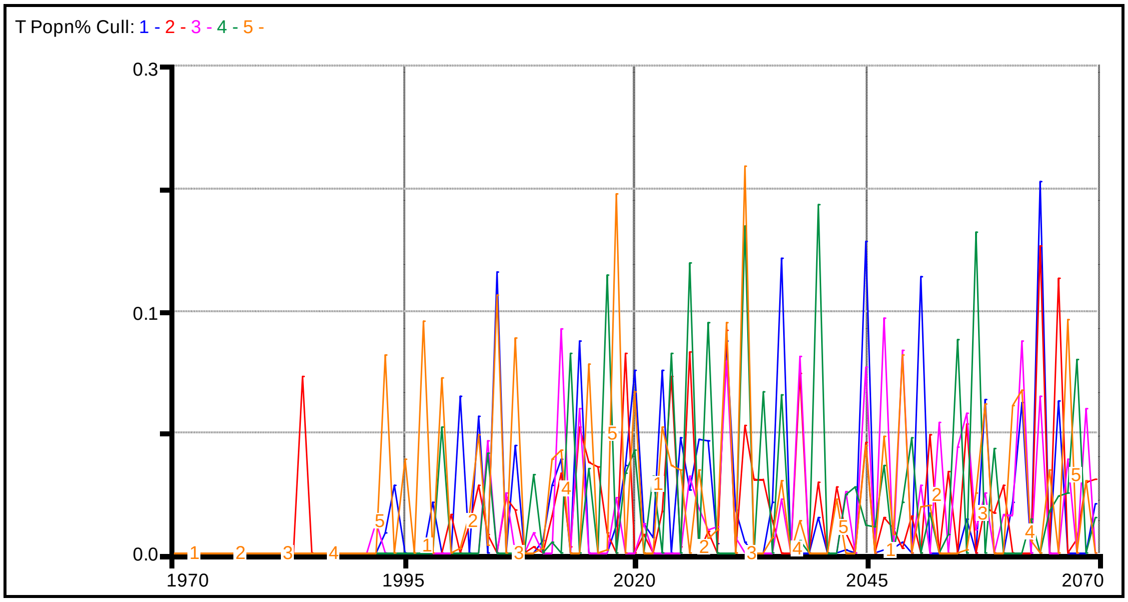


Figure 6.81. Simulated annual number of bison culled from boundary ranges (max tolerance of 200 animals per boundary range). Ten random runs without (upper) and with (lower) winter road grooming. Simulation based on Majority Average Model.



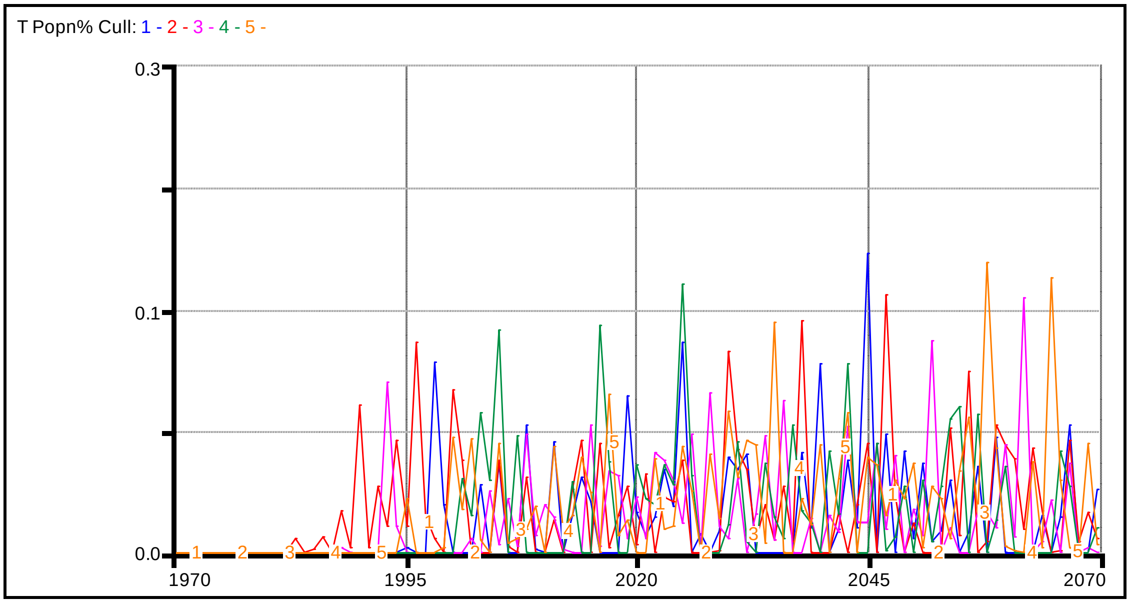
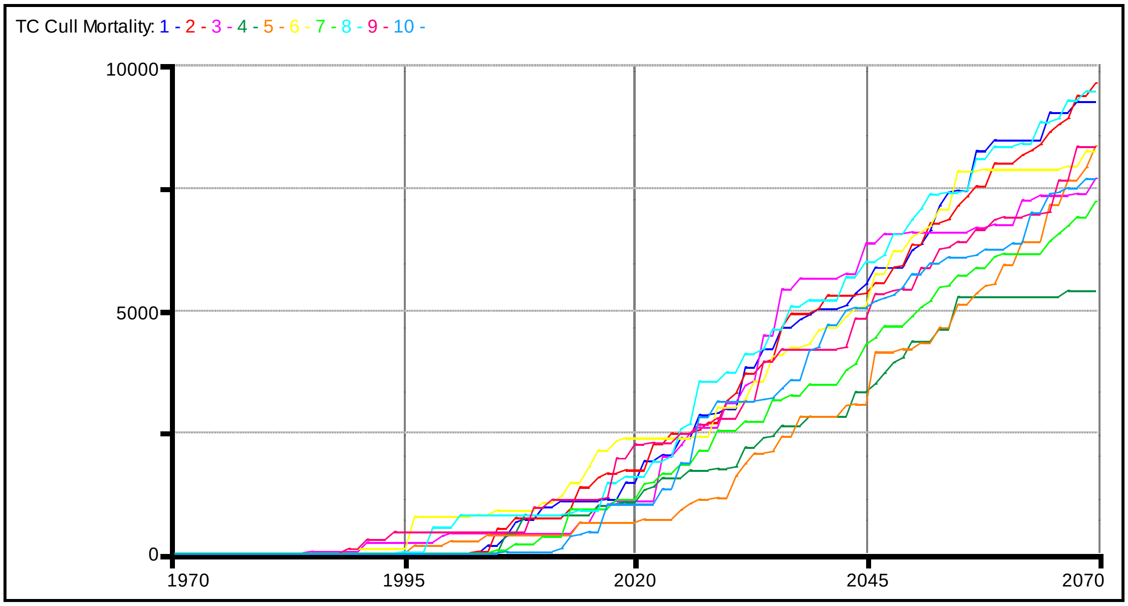


Figure 6.82. Simulated comparison of proportion of YNP bison herd that is killed by cull of boundary herds without (upper) and with winter road grooming (lower). Simulations were 100 years and reflected an identical pattern of random precipitation. Simulation based on Majority Average Model.



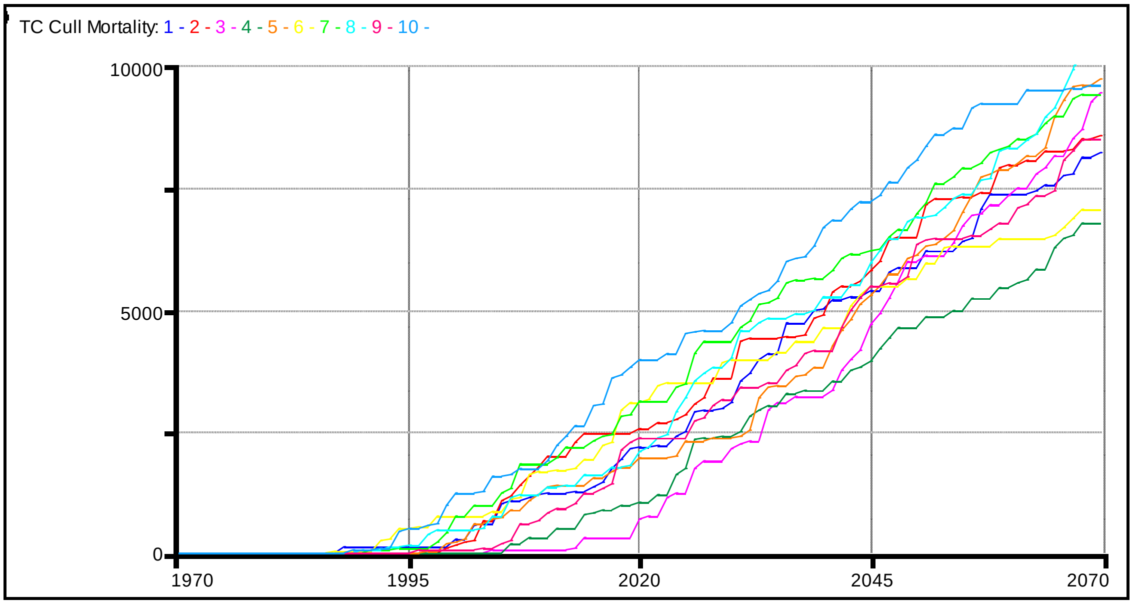
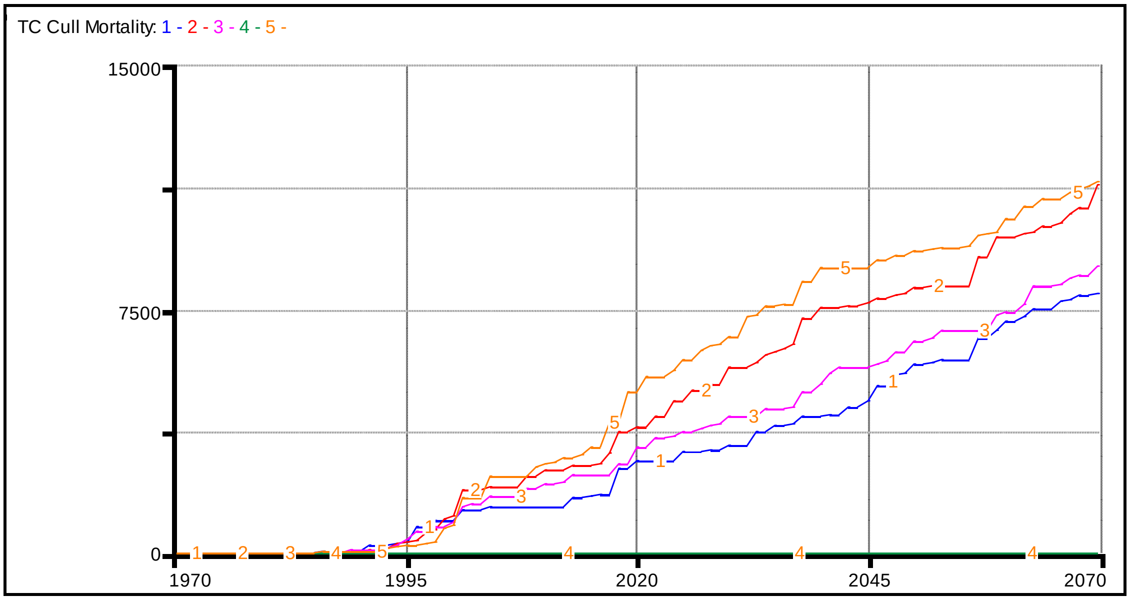


Figure 6.83. Simulated total cumulative number of bison culled from boundary ranges (max tolerance of 200 animals per boundary range) without (above) and with (below) winter road grooming. A series of ten 100 year simulations conducted with random precipitation. Simulation based on Majority Average Model.



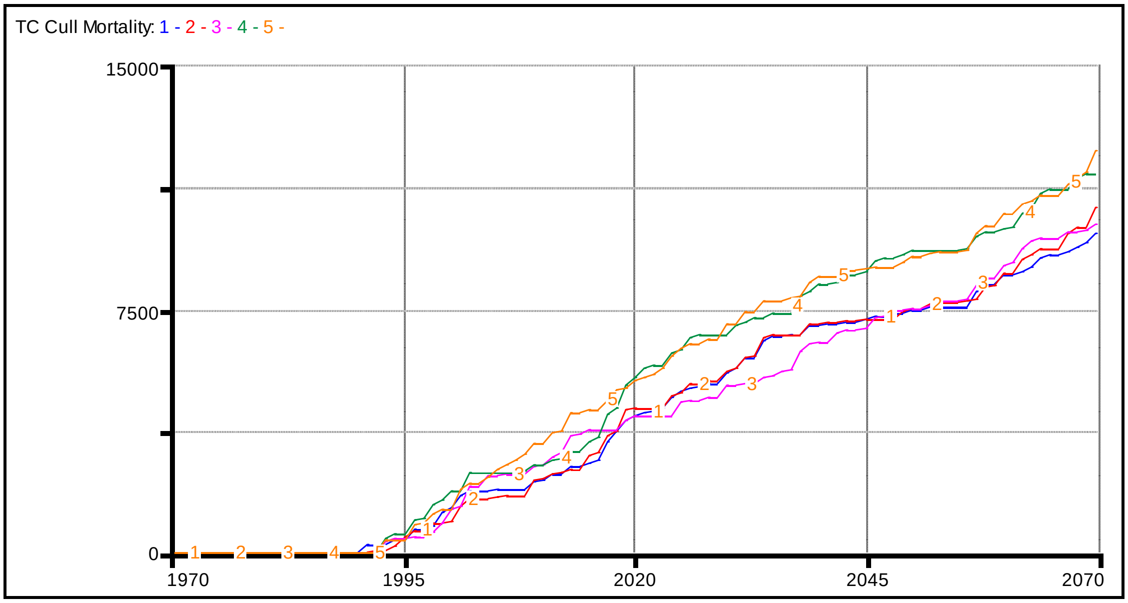


Figure 6.84. Simulated total cumulative cull of excess bison in boundary ranges. Graphs represent different Key Informant Groups (1 through 5). Upper graph represents scenario without winter road grooming, whereas lower graph represents road grooming along corridors PHC, FMC, and FWC.

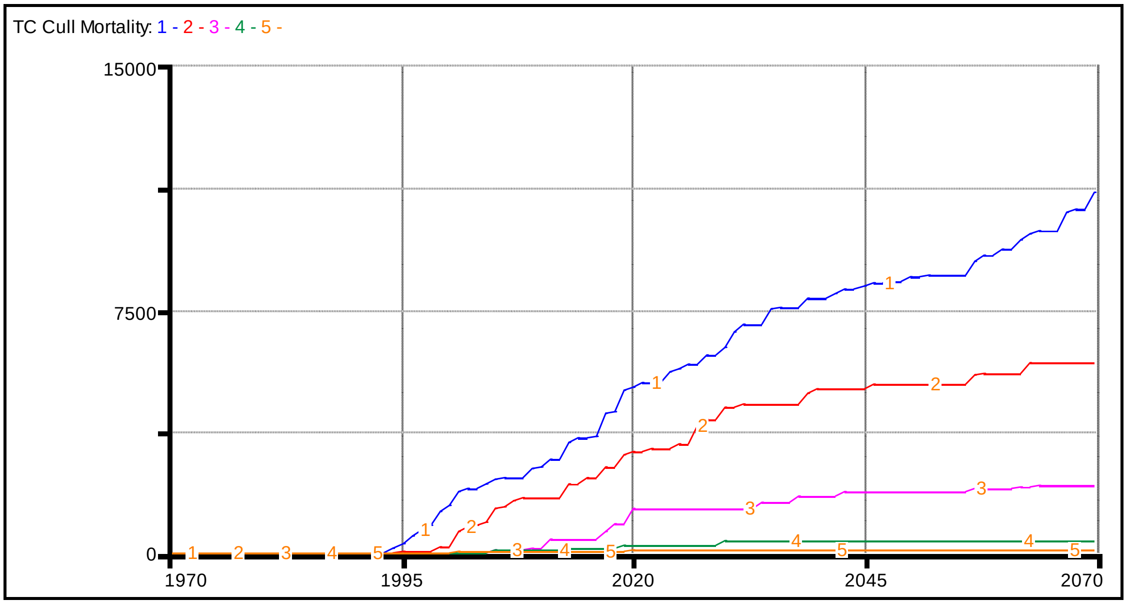


Figure 6.85. Simulated comparison of total cumulative # of bison culled under different maximum bison tolerances of 200, 400, 600, 800, and 1000 for each of the two boundary ranges. Scenarios include winter road grooming of corridors PHC, FMC, and FWC and involve identical series of random precipitation. Simulation based on Majority Average Model.

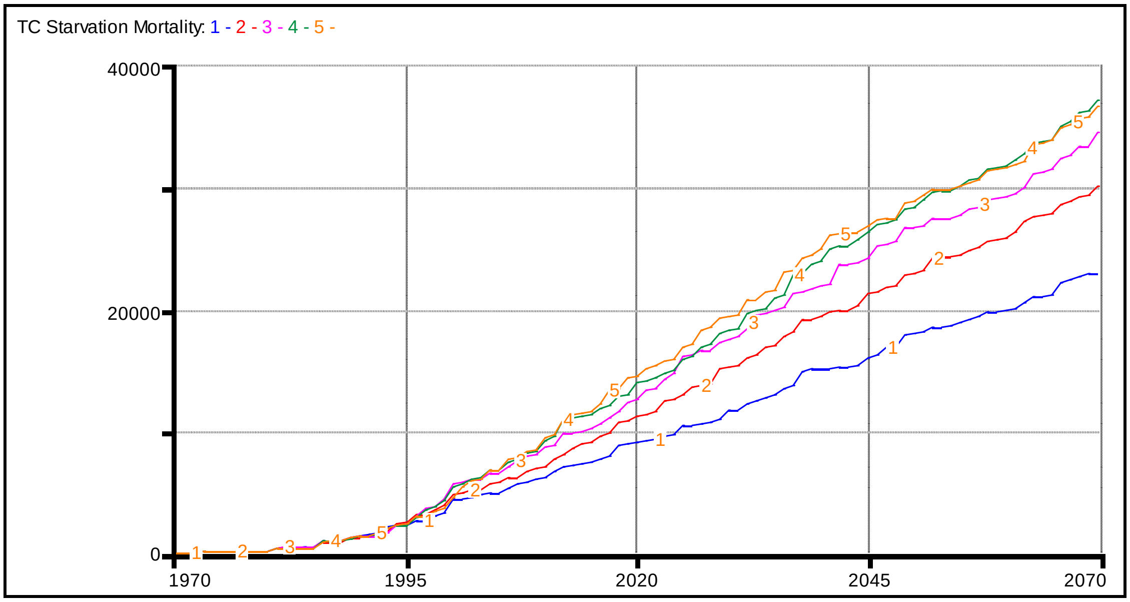


Figure 6.86. Simulated comparison of total cumulative bison starvation under different maximum bison tolerances of 200, 400, 600, 800, and 1000 for each of the two boundary ranges. Scenarios include winter road grooming of corridors PHC, FMC, and FWC and involve identical series of random precipitation. Simulation based on Majority Average Model.

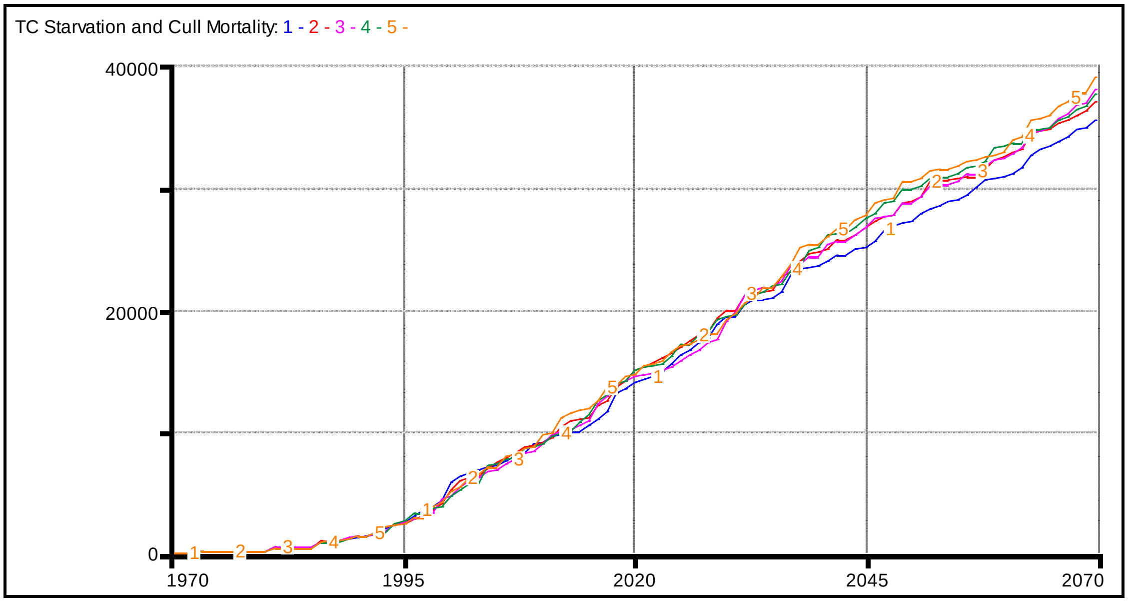


Figure 6.87. Simulated comparison of total cumulative bison cull and starvation under different maximum bison tolerances of 200, 400, 600, 800, and 1000 for each of the two boundary ranges. Scenarios include winter road grooming of corridors PHC, FMC, and FWC and involve identical series of random precipitation. Simulation based on Majority Average Model.

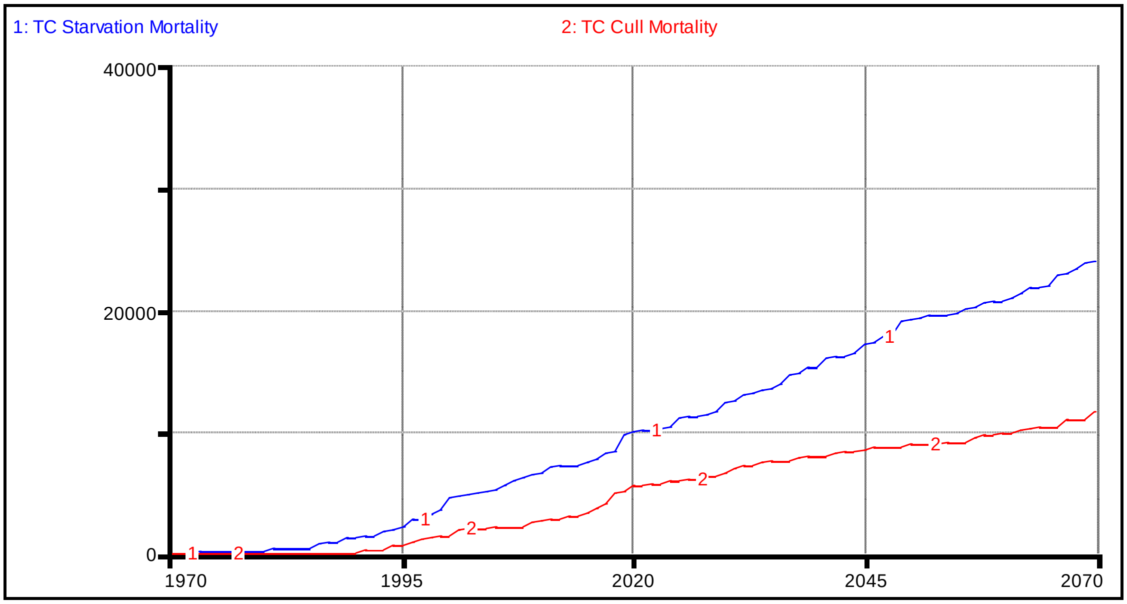
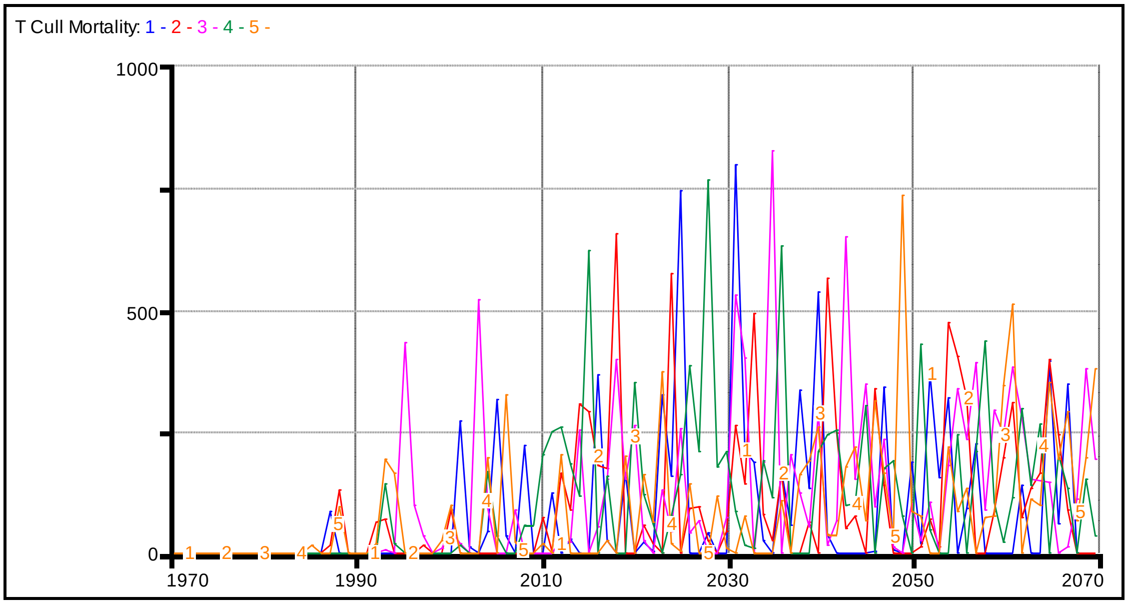


Figure 6.88. Comparison of net mortality attributed to starvation (#1) and cull (#2) during a 100 year simulation involving stochastic precipitation. Scenario includes winter road grooming. Simulation based on Majority Average Model.



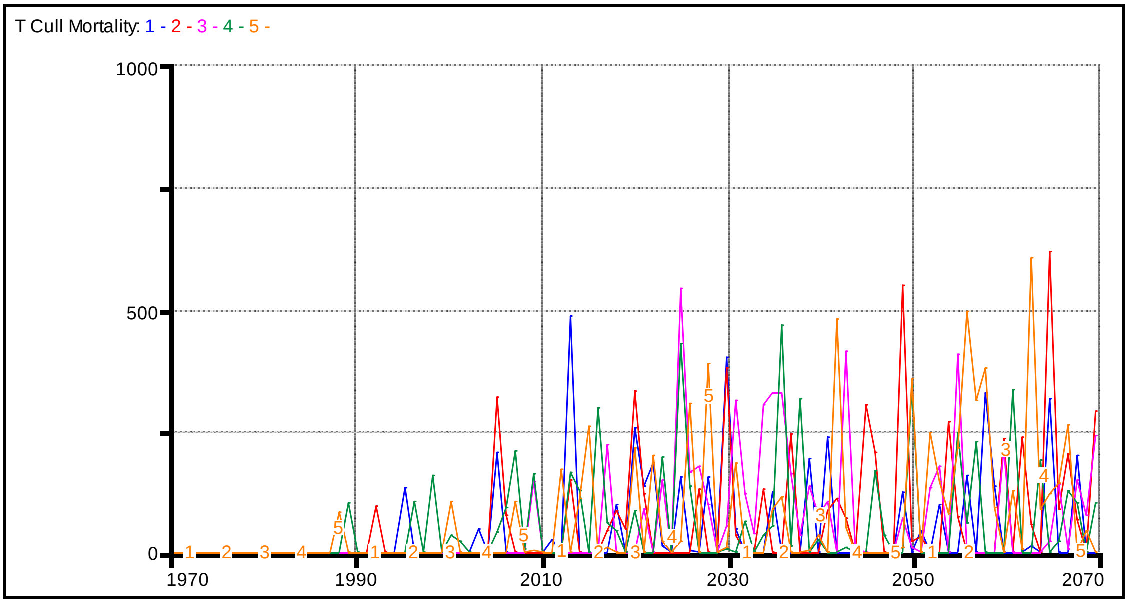
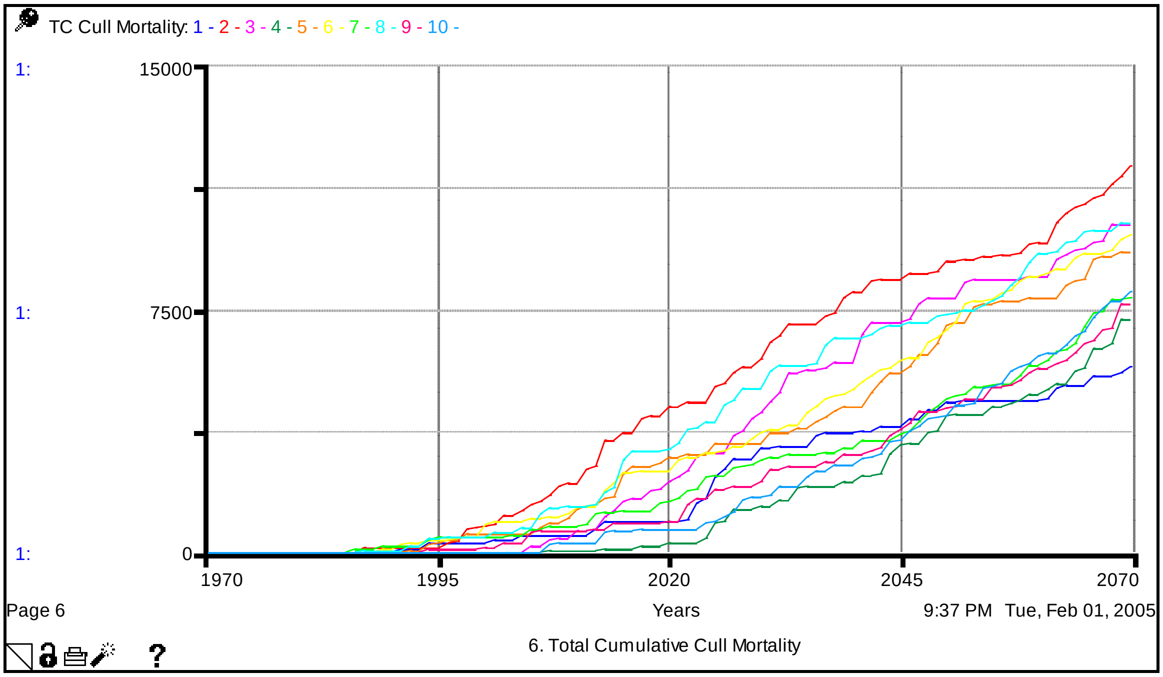


Figure 6.89. Simulated annual bison cull from boundary herds without (above) and with (below) a bison vaccination program. A series of five 100 year simulations conducted with random precipitation. These scenarios involve winter road grooming. Simulation based on Majority Average Model.



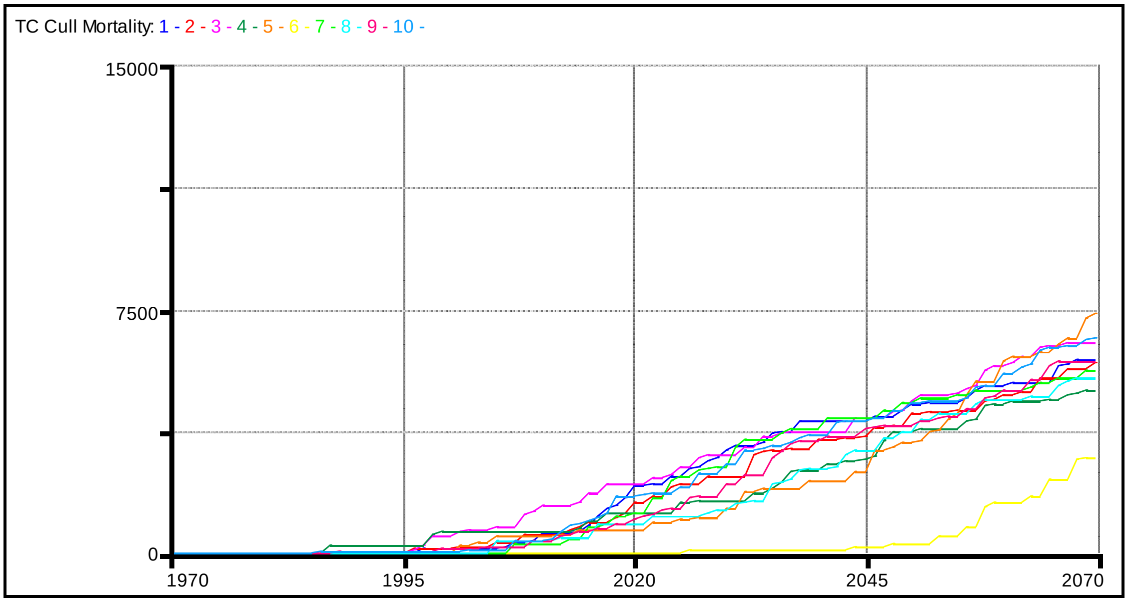


Figure 6.90. Simulated total cumulative level of bison cull without (above) and with (below) a bison vaccination program. A series of ten 100 year simulations conducted with random precipitation. These scenarios involve winter road grooming. Simulation based on Majority Average Model.

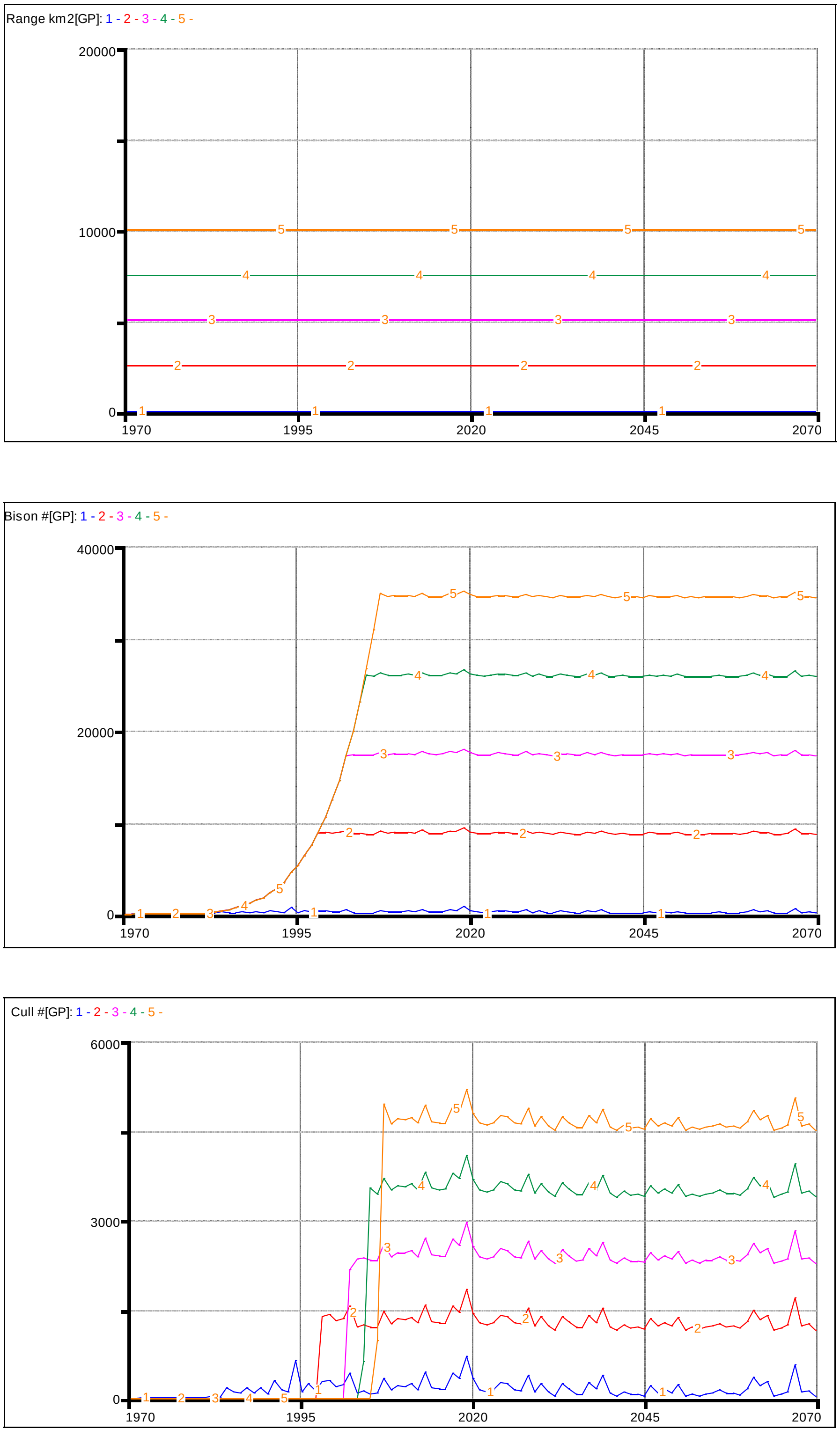


Figure 6.91. Simulation total range area (km$^2$, above), population size (middle) and annual cull (bottom) for a hypothetical "Great Plains" bison population under different scenarios where available area of the Great Plains varies from 0 (#1), 2,000 (#2), 4,000 (#3), 6,000 (#4), 8,000 (#5), and 10,000 (#6) km$^2$. Simulation based on Majority Average Model.

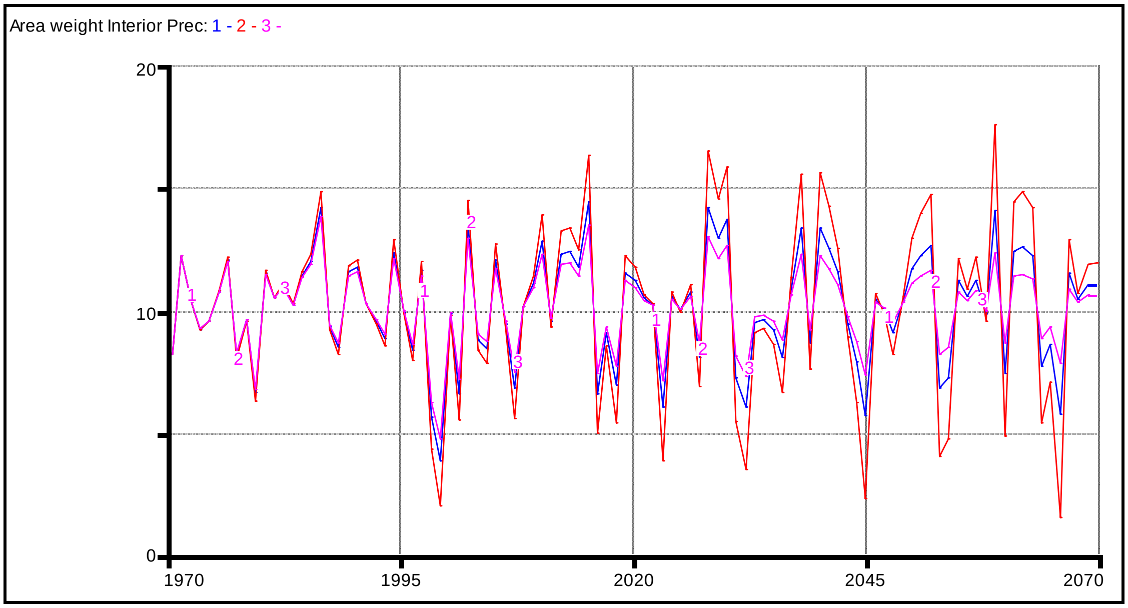


Figure 6.92. Simulated change in area-weighted average precipitation (cm) under three "climate change" scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. Scenario #3 reflects an incremental reduction in precipitation variance such that it is reduced by 50% over a 100 year simulation. All scenarios reflect synchronous variance in precipitation. Simulation based on Majority Average Model.

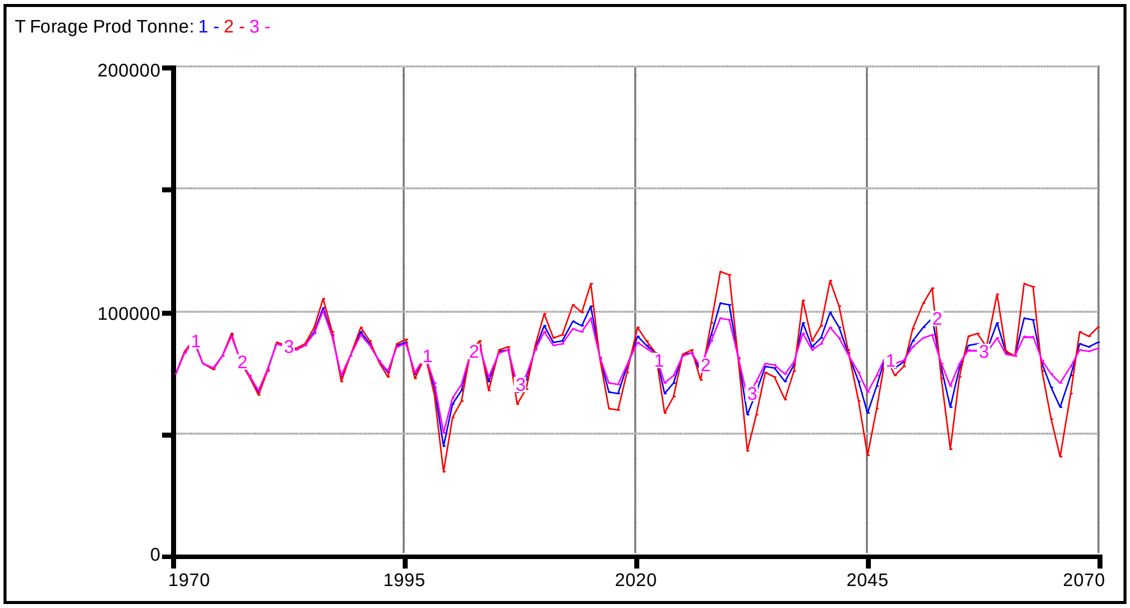


Figure 6.93. Simulated change in forage production (tonne) under three "climate change" scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. Scenario #3 reflects an incremental reduction in precipitation variance such that it is reduced by 50% over a 100 year simulation. All scenarios reflect synchronous variance in precipitation. Simulation based on Majority Average Model.

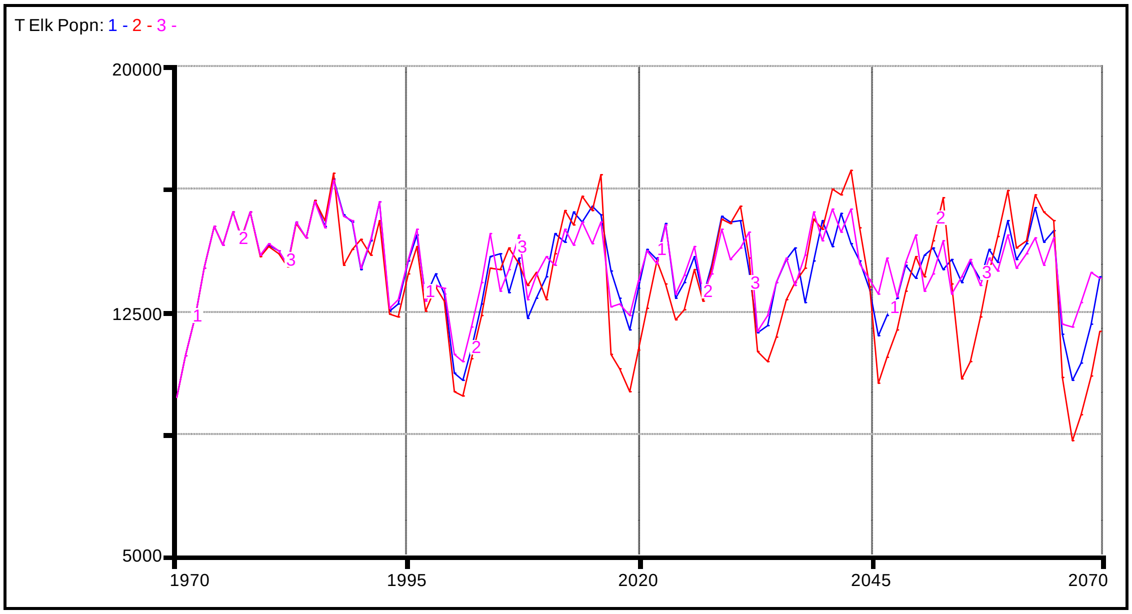


Figure 6.94. Simulated change in total elk populations under three “climate change” scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. Scenario #3 reflects an incremental reduction in precipitation variance such that it is reduced by 50% over a 100 year simulation. All scenarios reflect synchronous variance in precipitation. Simulation based on Majority Average Model.

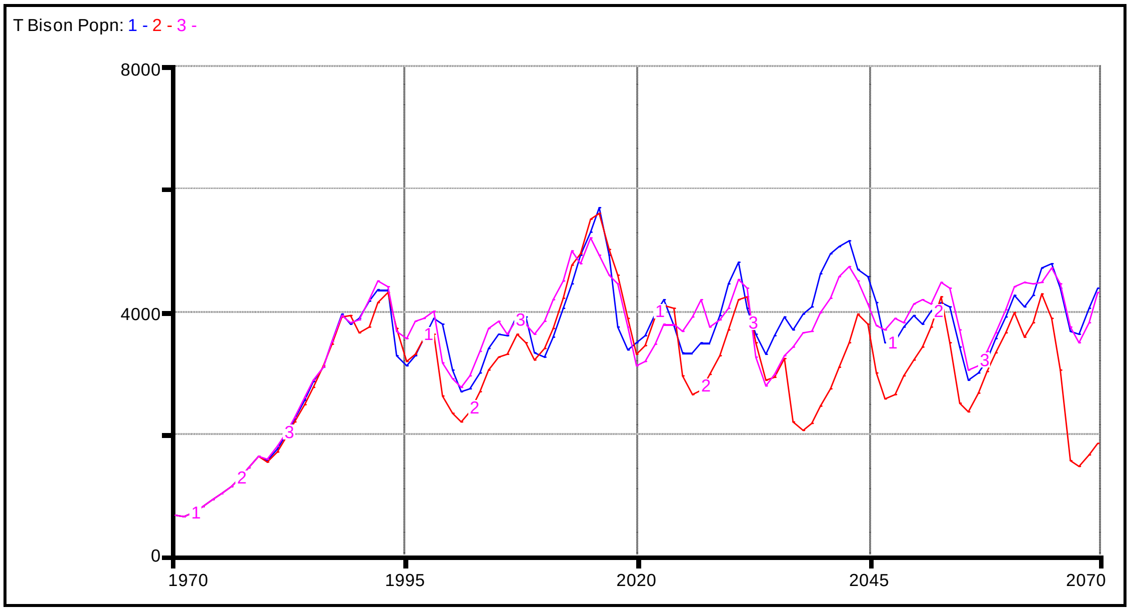


Figure 6.95. Simulated change in bison populations under three “climate change” scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. Scenario #3 reflects an incremental reduction in precipitation variance such that it is reduced by 50% over a 100 year simulation. All scenarios reflect synchronous variance in precipitation. Simulation based on Majority Average Model.

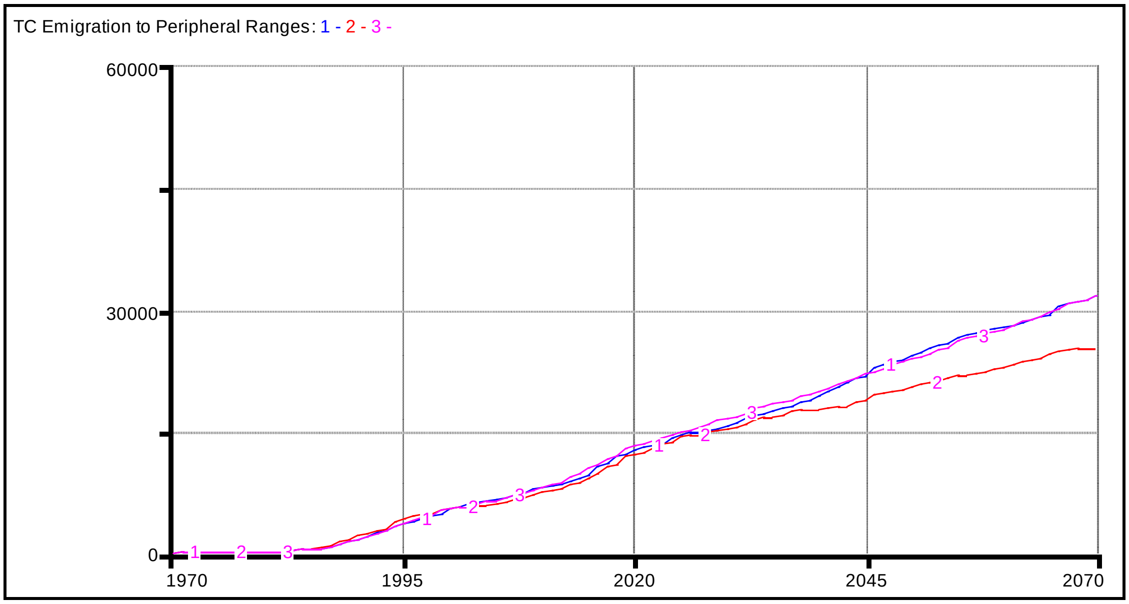


Figure 6.96. Simulated change in total cumulative bison emigration to boundary ranges under three “climate change” scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. Scenario #3 reflects an incremental reduction in precipitation variance such that it is reduced by 50% over a 100 year simulation. All scenarios reflect synchronous variance in precipitation. Simulation based on Majority Average Model.

# 7

# SYNTHESIS AND RECOMMENDATIONS

In 1968, Yellowstone National Park moved from a 33 year (1934-1967) period of culling ungulate populations for achieving predetermined stocking levels to a regime of ecological management under which wildlife populations are allowed to fluctuate in the park without human intervention. Since then, bison management in the YNP area has been dominated by two major linked controversies: 1) the risk to livestock of transmission of brucellosis from bison moving across the boundary; and 2) criticism of the effects of winter use by humans and their machines on bison population dynamics, movements and range expansion, including transboundary movements. This study reviews, integrates and applies knowledge of bison ecology with the specific objective of assessing the nature of bison movements and distribution, and whether grooming roads in YNP induces changes in spatial and population ecology of bison.

The study adopts an Adaptive Environmental Assessment and Management (AEAM) and policy-oriented framework (Blumenthal and Jannink 2000, Clark 2002), including a systems modeling approach (Ford 1999, STELLA u.d.). AEAM is a process of organizing people and their decisions around systems modeling and iterative hypothesis testing (Blumenthal and Jannink 2000). We addressed the issues broadly, defining the ecological and management systems in which road grooming and bison movements create apparent conflict, and to a limited extent evaluated the processes by which management decisions are made and conflicts may be resolved.

Our review of knowledge and the design of a bison movements and population dynamics model enabled us to identify key uncertainties and knowledge gaps and guided recommendations regarding research initiatives and management experiments to improve understanding and offer guidance for future management decisions. Additionally, we recommended approaches to improve the process of creating management policy, drawing on the theories and practices of environmental policy process and collaborative decision making.

## Synthesis

1. The bison of Yellowstone National Park are of ecological and evolutionary significance because they are among less than a dozen free-ranging herds exposed to natural regulation and selection regimes and the only free-ranging plains bison population on the continent that exceeds 2000. Prehistorically, YNP bison ranges were probably the extremes of seasonal migration from large source populations associated with expansive grasslands surrounding the Yellowstone Plateau. Historical accounts indicate that interior ranges also supported resident bison populations.

2. Yellowstone National Park is not a self contained ecosystem, covering only 8,983 km$^2$ or slightly more than 10% of the Greater Yellowstone Ecosystem (80,503

km$^2$). The movements and population dynamics of large mammal populations need to be viewed at spatial scales significantly larger than the park itself.

3. Key informants identified 5 bison winter ranges and 5 winter movement corridors in YNP. Recent GPS location data confirmed the delineation of the ranges and added new information about two additional movement pathways.

4. In northern YNP, two ranges were identified, Lamar Valley (233.8 km$^2$) and Gardiner basin (98.4 km$^2$). The portion of the Gardiner basin bison winter range outside YNP delineated in the 2000 bison management plan included 17.6 km$^2$ of habitat in Zone 2 and 83.3 km$^2$ in Zone 3. Management actions are taken in these areas to reduce the risk of brucellosis transmission from bison to cattle. Three bison winter ranges were defined in central YNP: Pelican Valley (55.2 km$^2$), Mary Mountain (151.8 km$^2$) and West Yellowstone (79.9 km$^2$ spanning the park boundary). Hayden Valley was grouped with the Firehole because of continuous movement back and forth between the two valleys over the Mary Mountain trail throughout the winter. Like Gardiner basin, the portion of West Yellowstone bison winter range outside YNP was delineated based on bison management policy and reflects where 100 bison are tolerated before culling actions are taken as opposed to where bison could forage if allowed to expand freely.

5. Bison in Yellowstone attempt to compensate for declining per capita food resources by range expansion, thus maintaining a relatively stable instantaneous density. However, compensation is not exact; population growth rate declines with density because high quality foraging patches are limited in overall area, are patchily distributed, and depleted first, forcing bison to shift to poorer quality patches as density increases. The likely demographic responses are decreased fecundity and increased juvenile mortality.

6. Apparent isolation of bison in separate winter ranges when populations were small likely reflected high per capita availability of forage and low pressure to move or expand. From the evidence, we infer that as populations grew, the area they used expanded, and distributions eventually coalesced. Anecdotal information on bison movements suggests they can break trail for considerable distances through deep snow, but in addition to forage limitation, knowledge of destination is likely an important motivation.

7. At the present time, there are two relatively separate subpopulations, one on the Northern Range and the other on the Central Range. Some exchange occurs via the Mirror Plateau. In recent years, there have been major migrations from the Central Range to Gardiner basin via the road allowance between Madison Junction and Swan Lake Flats. This migratory pattern would not likely have developed in the absence of the groomed road through the Gibbon Canyon.

8. Snow conditions (e.g. depth, density and snow water equivalence) can have significant impacts on ungulate foraging, survival and movements. In YNP, snow may influence forage availability, energy expenditures, ability to travel, vulnerability to predators and nutritional status of ungulates, including bison. This is a critical consideration in the current management challenge of minimizing contact between bison and cattle as they migrate northward and westward across park boundaries.

9. Snow was deeper and SWE was greater in central YNP than the northern range. Mean February 15th SWE values for central YNP were approximately 20 cm compared to 7.5 cm on the northern range. In addition to snow depth and SWE, other characteristics of snow pack can affect forage availability to ungulates. Key informants identified snow crusts as an important constraint to forage availability for bison, making it difficult or impossible for bison to crater and forcing them to move in search of forage. Growing season precipitation and herbivory also affect forage production and availability.

10. Geothermal activity can also modify snow pack. Thermal features generate heat that can dramatically reduce snow cover and lengthen the growing season in geothermal basins and along the banks of geothermally influenced rivers and streams, thus improving forage availability and reducing travel effort in winter. Geothermal sites may, therefore, be key refugia for bison during severe winters in the Central Range. Reduced snow cover in geothermal areas also reduces movement costs.

11. Removals at the western and northern boundaries to control egress of bison from the park were a direct function of population size, influenced by snow conditions. The relationships were strongest for populations above 1500 for the Central Range and 550 for the Northern Range.

12. Although forage availability influenced by production, use, and snowpack, will continue to be a major factor influencing population increase, distribution and movements, predation may become increasingly important as wolves learn how to kill larger prey. We suggest that wolf predation on bison will continue to increase in the Central ranges, but not on the northern range as long as elk are relatively more abundant there than bison. In systems where wolves show a numerical response to an abundant prey species that is difficult to kill, predation rate on easier prey can be inversely proportional to their density.

13. Strong differences were predicted by the model in immigration and emigration rates between ranges. The Mary Mountain range is clearly the central numerical engine of the YNP bison system. Lamar Valley and Pelican Valley contribute significantly fewer bison to the YNP system. The Gardiner basin and West Yellowstone ranges are clearly net sinks for bison.

14. Information from key informants and results from the YNP Bison Movement and Population Model (based on literature and key informants) suggest that inter-range movements of bison are generally not constrained by winter snowpack in non-road grooming scenarios during most winters. The notable exception to this rule is the Firehole-Mammoth corridor that represents a barrier during all non-road grooming scenarios. Road grooming is likely to have a greater influence on movement of bison between interior ranges (Lamar-Mary Mountain, Mary Mountain-Pelican) than to the peripheral ranges (West Yellowstone, Gardiner basin). Therefore, grooming of winter roads may reduce the variation in and total numbers of bison departing for peripheral ranges during winters of inadequate forage.

15. Bison movement between winter ranges was projected to range from 100 to 4,000 animals, influenced most by per capita forage availability. An average movement of ~1,000 bison occurred in non-road grooming scenarios, and 1200 in road-grooming scenarios.

16. Natural winter mortality is a common, though a highly variable event for bison in the YNP model, representing how the system actually functions. Average simulated annual winter mortality was ~180 bison (5%) for the non-road grooming and 225 for the road-grooming scenario, or about 7% of the YNP herd. However, mortality during occasional extremely harsh winters exceeded 25% of the population.

17. The predicted maximum cull under current boundary management policies periodically exceeded 500 animals, and rarely exceeded 750 animals. Culls exceeded 10% of the total YNP herd in 15% of years in non-road grooming scenarios and 6% of the herd during road grooming scenarios. Cumulative culls during ten 100-year stochastic runs varied considerably, and ranged between annual average culls of 50-90 bison for the non-grooming scenario, and 60-100 for road grooming scenarios. On average, 75 bison would be culled each year from peripheral ranges with or without road grooming.

18. Increasing bison habitat exterior to YNP is an effective strategy to increase the total regional population, but would not be a good strategy to minimize the number of bison that would need to be culled annually in the regional landscape surrounding the park. Although the number of bison to be culled at the boundary of YNP would be significantly reduced in a “repatriation” scenario, a greater number of bison would inevitably be culled in the surrounding region because there would be more bison. For example, the annual cull at the margins of the expanded range would be as follows: (2,500 km$^2$ = 1,250 culls, 5,000 km$^2$ = 2,500 culls, 7,500 km$^2$ = 3,750 culls, 10,000 km$^2$ = 5,000 culls).

19. Gardiner basin has been considered important winter range for bison since at least the 1940s and is an important component of the Northern winter range. In contrast, the Hebgen Lake area north of West Yellowstone offers no unique

ecological value as winter range. It can be considered an expansion area for the Central subpopulation with the capacity to support 100 to 130 bison at the instantaneous density typical for Central Range bison in winter.

20. Since 1997, population monitoring has been somewhat inconsistent and data do not provide the same opportunity for continued analysis as the data collected between 1970 and 1997. A population monitoring program is needed that will provide for: 1) annual estimates of adult population size (> 1 year); 2) fecundity (calf production); 3) winter density distribution, i.e. during the period when distribution is most responsive to forage limitation; 4) inter-annual population rate of increase; and 4) seasonal and annual calf and adult mortality.

21. With the possible exception of the Madison Junction to Mammoth road segment, road grooming likely has not induced range expansion, although roads facilitate bison movements within and between winter ranges where aligned with natural movement corridors. Given the evidence, we concur with the assessments made by Cheville et al. (1998): 1) there is a threshold density effect above which expansion to new ranges occurs and population pressure induces bison to maintain pathways between ranges; and 2) attributing population increase to road grooming rather than the use of groomed roads to population pressure may reverse cause and effect. There is no evidence to suggest that groomed roads have changed population growth rates relative to what may have happened in the absence of road grooming.

22. The two major issues associated with Yellowstone National Park bison management are primarily a consequence of the successful recovery and expansion of bison as a wildlife species and value conflicts resulting from the arbitrary location of the park boundary within a large ecosystem in which people live and derive their livelihoods. Existing organizations and decision processes addressing the two issues have not been effective in defining the common interest or producing stable, broadly supported management plans.

23. The decision processes followed by federal and state agencies to develop the Joint Management Plan appears a divisive, deeply-rooted power-balancing struggle to protect fragmented and overlapping jurisdictions and avoid risk.

24. Both the bison/cattle/brucellosis issue and the winter use issue are highly charged conflicts with public interests having no mechanism for meaningful participation, apart from the low level process prescribed by NEPA. The affected publics are willing to use the courts and sometimes more extreme actions to be heard. The result is ongoing conflict, substantial annual and incremental costs for the agencies in time and resources, and promotion of the notion that more science, more information, will somehow result in wiser outcomes.

## Recommendations

### *Monitoring and Science*

### *1. Yellowstone National Park should implement an internally funded bison population monitoring program that collects and manages data on population size, vital rates and winter distribution in the long term.*

Winter surveys of the YNP bison population provided a nearly continuous, though imprecise, time series of population estimates for a hundred years, between 1902 and 1997. Seasonal surveys of population size, distribution and composition were carried out between 1970 and 1997. This is a prestigious and unparalleled record that provides a rich opportunity for examining the long term dynamics of a large herbivore population subject to management and environmental perturbations. The survey system was altered in 1998 when a study was initiated to evaluate and redesign the aerial census program (Hess 2002). Building on that study, we offer recommendations for a population monitoring program that will serve the management needs of the agencies (Figure 7.1).

Well designed winter surveys can provide the basis for estimating annual rate of increase and density distribution patterns in relation to forage availability and other environmental stressors. Summer census during the breeding season when bison are aggregated in large groups within a few small areas provides an opportunity for efficient census (accuracy and precision) and for classifying a large number of bison into recognizable sex and age classes. The population monitoring protocol (Figure 7.1) is adapted from Hess (2002). It incorporates aerial census, winter distribution surveys, and a ground-based composition survey. The protocol is designed to compliment research on the effects of climate, forage production, herbivory, snow pack, and density on demography and spatial ecology of bison in YNP and on boundary ranges in Montana.

Census in early winter will account for bison subject to subsequent winter mortality; density dependent and independent processes will operate on these animals during the winter. Hess (2002) found that group size declined over winter in a log-linear manner and dispersion increased as winter progressed. The most favorable winter census conditions occur in early winter, December or January when bison are still in relatively large groups, yet have moved from high elevation ranges, providing for more efficient census than later in the winter. Winter surveys should be conducted during cold weather when few animals are in forested areas. Distinguishing calves from older bison from an aircraft is difficult in winter. However, experienced observers are able to do so. If this measure can be recorded, the change in calf: adult ratio from summer (August census) to December or January would provide an estimate of pre-winter calf survival. Further, the change in estimated adult (> 1 year) population from time $t$ to $t + 1$ would provide a measure of population increase not inflated by calves. An independent estimate of the rate of increase $LN(N_{t+1}/ N_t)$ can be provided from the number of adult (> 1 year) bison estimated during the breeding season in years $t$ and $t + 1$ . During the breeding season (late July to early August) bison are concentrated in large aggregations in few areas (typically three) in open valleys. Aggregation at this time of year provides the opportunity for aerial photo survey of most of the population, reducing variance due to sampling error. Hess (2002) recommended at least one replicate of both the winter and summer censuses to be certain that anomalous conditions during one seasonal survey did not produce a biased estimate that could lead to a spurious conclusion about population change. Population trends are of limited value in the absence of data on vital rates. Age and sex ratio data are critical to understanding population dynamics. Population composition surveys should be carried out during or shortly before the breeding season when all age and sex classes are aggregated. At least 50% of each sub-population should be classified. Sampling should occur throughout the area occupied by bison. Detailed recommendations on census methods and bias compensation (habitat and group size effects) are offered by Hess (2002).

The capacity to describe the dynamics of bison population and spatial ecology depends on sustaining consistent long term monitoring such as the program carried out between 1967 and 1997.

### *2. Yellowstone National Park should define a minimum viable bison population for the Northern Range.*

The bison population on the Northern range has existed as a semi-independent subunit and exhibits biological traits (genotypes, fetal growth, tooth wear patterns) distinctive from Central range bison. Historical data indicates that most of the northern range bison may migrate into the Gardiner basin during harsh winters, returning to the Lamar Valley unless removals occur. The potential exists for most of the population to be culled if it exits the park. Seasonal migration between low elevation, low snow cover range in the Gardiner basin and high elevation summer range is an ecological phenomenon not supported by the current management system. If the northern range is depopulated, grazing by bison would also become a lost ecological process in the northern range until it becomes recolonized by Central range bison. Current research by Dr. J. Gross (NPS, Fort Collins) will contribute to defining population viability for national park herds (Gross and Wang 2005). A specific PVA analysis is recommended for the Northern herd to provide a threshold size and structure below which culling may adversely affect population viability. We perceived no threat to the viability of the Central population from boundary control at West Yellowstone.

### *3. Yellowstone National Park should encourage and coordinate research focused on reducing key uncertainties over a full range of densities as the population fluctuates in response to environmental stochasticity or management actions.*

Research on bison population ecology, and distribution and movement behaviour in YNP has been conducted in the short to intermediate term (>30 years). Researchers have been able to study the system for discrete periods during their professional careers. Basic research is needed on bison population ecology and behaviour focusing on the full range of density dependent and independent influences on the population and its spatial behavior over meaningful periods of time (>50 years). Considerable research has been carried out on plant herbivore dynamics in the Northern Range generating a wealth of knowledge about density dependence in elk populations. Similar research is needed for bison.

Key uncertainties identified in this review deserving of particular research attention are:

- Threshold depth/density of snow at which low and high density forage-limited bison cannot move through corridors in search of better foraging conditions.
- Terrain characteristics (slope, ruggedness) that affect the above snow depth/density threshold preventing movements.
- Snowpack characteristics in the Pelican Valley in relation to other ranges.
- The relationship (shape and scale of the curve) between winter forage availability, bison density and bison over-winter mortality.
- The relationship (shape and scale of the curve) between winter forage availability and probability of bison movement.
- Density related effects of bison on vegetation communities and terrain, especially geothermal habitat.
- There was contradictory opinion whether the unroaded Mirror Plateau Corridor is a functional barrier to movements in winter between the Pelican Valley and the Lamar Valley when bison numbers are high and per capita forage is limited.
- Inter-range variability in forage productivity in response to precipitation and growing season length. In particular, one key informant suggested the growing season is shortest in the Pelican Valley range because of a long period of snow cover typically followed by spring flooding.
- Relationship between incidence of sero-positive bison and proportion of the herd that has been vaccinated.
- Systematic research has not been carried out on the ability of bison to move through snow under the variety of circumstances present in Yellowstone National Park.
- Snow conditions in the Pelican Valley are limited to subjective observations rather than consistent records from strategically-placed snow stations. Two modeling efforts thus far have not been able to precisely model the dynamic of snow conditions in this isolated valley of the park. Calibration of models in one location of the park does not allow large scale inference.
- The future role wolf predation plays in bison population dynamics is uncertain in Central Yellowstone ranges and is likely increasing at present. Mechanisms underlying how YNP wolves limit bison abundance and distribution have received limited attention.
- There is uncertainty of the extent of the interchange between the Northern and Central bison herds. This information is important for understanding how to conserve the spatial and genetic structuring of this population and maintenance of bison on the Northern Range under current boundary management.
- Data now being obtained from GPS collars will allow key questions about movement ecology to be addressed, including the timing and extent of movements in relation to plant phenology, snow conditions, forage production and utilization. In addition, with this technology research is now possible to address questions

about the effects of roads and other anthropogenic or natural features on movements about which some uncertainty remains.

The YNP bison population will continue to experience perturbations and high amplitude fluctuations in the long term providing ongoing opportunities to study ecological dynamics at varying densities. A systems-based approach to understanding the dynamics of the YNP bison subpopulations can exploit these anticipated meteorological and management perturbations and use them to learn about key uncertainties.

### *4. An adaptive management experiment should be designed to test permeability of the Firehole to Mammoth corridor under varible snow conditions with a specific focus on the road section between the Madison Administrative Area and Norris Junction.*

The road segment through the Gibbon Canyon is the single area in the park where snow cover in combination with steep terrain may deter bison movements in the absence of grooming and snow compaction by over snow vehicles. Beginning in the mid 1990s, bison learned to migrate along the road allowance and adjacent habitat between the Madison Junction and the Northern Range near Gardiner Montana. In some recent winters, large numbers of bison have used this migration pathway. Bison from the Central Range may reach and be subject to management actions at both the western and northern boundaries. To date there is no evidence that Northern Range bison have moved to the western boundary. Under the current management plan for bison, it is possible that the defined tolerance for bison emigration to the northern boundary of the park could be satisfied early in the winter by bison moving from the Central subpopulation. If large numbers of Northern Range bison move to the boundary later in the winter in response to severe conditions, there is risk that most of the northern subpopulation could be subject to removal, leaving the Northern Range of the park ecologically impaired. Furthermore, there is evidence that rare alleles are unevenly distributed among subpopulations (Gross and Wang 2005); depopulation of the Northern Range could place genetic diversity at risk.

An experiment is warranted to test the hypothesis that the Central population's movement to the Northern Range is possible only with grooming of the snow pack on the road, in particularly in the Gibbon Canyon. This action was previously proposed. Readers are referred to a settlement agreement approved on October 27, 1997, in federal court, Washington D.C. that called for the NPS to prepare an environmental assessment evaluating the closure of groomed road segments in YNP to study the effects of groomed roads on bison movements. An environmental assessment was completed in November 1997 evaluating options for temporary closures of sections of the road system in winter including the section identified here (NPS 1997). The experiment recommended here should be designed to test the effectiveness of unaltered snow pack as a barrier to winter movements between the Central and Northern Ranges in relation to varying environmental conditions including forage production, winter severity, and population size.

### *5. Yellowstone National Park should install a SNOTEL or Snow course station in the Pelican Valley, monitor snow conditions in*

*the Pelican-Hayden Corridor, and re-evaluate the two existing snow models.*

Winter conditions in the Pelican Valley have been described as the most severe among bison winter ranges in Yellowstone National Park (Meagher 1971, 1974:12, Meagher et al. 2002:135). It has the highest elevation (7800 ft) and the longest duration of snow cover (late October to early May) among winter ranges. Meagher (1971), citing reports from ranger ski patrols, described snow depth in the Pelican Valley as "usually a few inches deeper than those of the Lake snow course", with average depths of 40 to 45 inches. In addition, the east-west orientation of the Pelican Valley exposes it to packing from the prevailing wind. The harshness of this environment and trapping effect of snow in the undisturbed corridor between Pelican Valley and Hayden Valley were the basis for the argument that in the absence grooming of winter roads the Pelican winter range is self-regulating, and with road grooming the "domino effect" of bison emigrating from Pelican drives expansion of bison to the western boundary of the park. However, snow conditions in the Pelican Valley and the Pelican-Hayden corridor have not been systematically measured nor have the effects of snow on foraging and movements studied. Snow conditions in the Pelican Valley and Northern range predicted with the two models yielded discordant results. The Yellowstone Snow Model (Wockner et al. 2002) generates SWE values closer to observed Lake SNOTEL station values than the LANGUR Model (Chapter 4). The latter model generated mid February SWE values for the Pelican Valley similar to the Northern Range and were clearly discordant with the common view that conditions are the most severe in the Pelican Valley and least severe on the Northern Range among bison winter ranges in YNP. Clearly, this discrepancy needs to be addressed. Furthermore, there needs to be well designed research on the effects of snow (SWE, depth and density) on foraging, movements, and population dynamics of bison.

## *Adaptive and Collaborative Management Structures and Processes*

Managing bison or any other natural resource within the context of a large ecosystem that includes complex, partially understood interactions between biotic and physical elements of the environment, people, their endeavors, and competing value systems, is enormously challenging. While good science is necessary to inform wise decisions, scientific knowledge is typically developed and championed by people in a discipline without reference to knowledge from the many disciplines and multitude of values that bear on management of an ecosystem. Similarly, single agencies are not mandated to manage human activities and ecological processes across jurisdictions and agencies must necessarily work together to achieve outcomes in keeping with the common interest of society. Collaboration is necessary to define what is acceptable; science is necessary to define what is possible; organizing people to use knowledge to design and implement management in the face of uncertainty is fundamental.

The issues of managing transboundary movements of bison to contain the risk of brucellosis transmission to livestock and winter use management in YNP as it affects bison movements have been dealt with separately despite broad overlaps in the interests of stakeholders engaged in these issues. Existing organizations and decision processes addressing these issues have not been effective in defining the common interest or producing stable, broadly supported plans. For successful resolution of YNP bison management conflicts, new organizational structures and decision processes are needed to provide legitimacy, integrative problem solving, shared learning, and decision-making among resource agencies and citizens at scales meaningful to stakeholders. The recommendations offered in this section reflect the need for a new approach to management planning, and the key roles of science and systems modeling for aiding multi-party decision-making, where change is inevitable and uncertainty and unpredictability are inherent properties of the ecosystem.

### *6. Engage the U.S. Institute for Environmental Conflict Resolution in an independent situation assessment that includes advice on designing an integrated agency and public involvement planning strategy to represent the common interest.*

The 1998 Environmental Policy and Conflict Resolution Act (P.L. 105-156) created the U.S. Institute for Environmental Conflict Resolution[61] to assist parties in resolving environmental conflicts involving federal agencies or interests. The Institute provides assistance in consensus-based processes, such as negotiated rule-making, community-based collaborations, and policy dialogues.

The Institute should be engaged to do the following:

- Using document analysis and stakeholder surveys, thoroughly assess the range of issues and interests of those affected by or engaged actively in bison management in the YNP/Montana transboundary area and in winter use management in YNP, including agencies and publics;
- Survey representative stakeholders (agencies and publics) about their perspectives on public involvement and interagency coordinated planning;
- Assess the effectiveness of current management planning structures and processes, including public involvement;
- Propose options for organizational structures and processes for policy-oriented integrative planning, including higher levels of public involvement than currently practiced;
- Draft charters (Terms of Reference) for each organizational body (see below for suggested organization).

We suggest consideration of an organizational structure (framework) that provides for integrated agency and public involvement, shared learning and valued-based integrative decision-making, informed by expert knowledge and decision support models and other tools. The framework consists of three interacting bodies (Figure 7.2):

1) An interagency planning team representing the agencies holding authority;

2) A multi-party working group representing affected interests, including agency managers and public interest representatives; and

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[61] U.S. Institute for Environmental Conflict Resolution, 130 S. Scott Ave. • Tucson, AZ 85701 • Tel. (520) 670-5299, Fax (520) 670-5530

3) An interdisciplinary science council serving the information and analytical needs of both the planning team and the working group.

The interagency planning team would negotiate a goal-driven, results-based management plan for bison in YNP and adjacent Montana, informed by input from the working group and the interdisciplinary science council. The working group would work with the planning team to reach agreements on the issues to be addressed in the management plan, and on goals and objectives, and to develop criteria for assessing and selecting the most appropriate management alternatives. The interdisciplinary science council would be responsible for integrating a broad range of knowledge and skills in both natural and social sciences, developing models to support and inform value-based decision-making, designing management experiments, and recommending basic research for YNP and GYE to fill information gaps. Both the planning process and organizational structures would be authorized by the authorities under a common agreement (e.g. Memorandum of Understanding). The MOU would define agency roles and responsibilities, ground rules for cooperation, the decision process, available resources, designated representation on the interagency planning team, and direct interactions between the planning team and the other two bodies.

We recommend using a problem solving model (Webne-Behrman 1998:52) for decision-making by the planning team and the working group, based on facilitated interest-based negotiation practice. Each body would require a specific charter that defines its task, decision process, ground rules, membership, communications strategy, and reporting relationships. Shoulder to shoulder working relationships between the interagency planning team and the working group would be desirable (Figure 7.2).

> *7. The Yellowstone Center for Resources (YCR) should play a lead role among agencies and researchers in coordinating data sharing and data-base management, research and monitoring of bison and other research relevant to bison ecology and management, by developing a stable collaborative science and management framework.*

A variety of research interests are engaged or have been engaged in more or less independent studies on bison ecology, epidemiology and management of brucellosis, ecology of other species, and ecological processes or human activities that affect bison in Yellowstone National Park. Independent scientists can engage in research in the park under a permit system that does not require them to contribute to the park data base or management programs of the park, or indeed to provide data. Coordination of research has been left largely to outside organizations such as the Greater Yellowstone Interagency Coordination Committee under which the Greater Yellowstone Interagency Brucellosis Committee functions. Between 1997 and 2003, the U.S. Geological Survey attempted to coordinate research on bison ecology and the effects of removals on population viability. Numerous researchers typically associated with universities have carried out independent research.

Fragmentation of effort and inefficient coordination and use of knowledge have been the rule rather than the exception. Mandate conflicts between agencies, competition between research groups and individual researchers for funding, and failure to share data to protect publication rights are all recognized as contributing to the fragmented science effort. In the absence of coordination, there is a risk that researchers who work independently in specific geographic areas or for relatively short periods of time may come to narrow or ill considered conclusions.

The authors are aware of a substantial volume of data on bison ecology in the park that has neither been published nor shared with YCR. The data are proprietary, held by research camps or independent scientists who do not communicate with or trust each other. Internally, concerns were expressed to the authors about the limited opportunity for input by YCR scientists and managers into management plans, EAs, EIS and rule making in which bison are an aspect.

YCR should define personnel and financial resources necessary to coordinate the science effort and sustain a core applied research program.

### *8. Develop or refine appropriate systems models and other decision support tools to help agencies and other stakeholders to understand key uncertainties and system properties, and to evaluate outcomes of management scenarios defined through value-based decision processes.*

Systems models allow participants to evaluate alternatives today that reveal potential futures and consider uncertainties rather than waiting to evaluate outcomes of actual management interventions. System models, such as the one developed in this assessment, should be encouraged to evolve through time as new information is revealed by scientific study, or as new possible management actions are proposed by stakeholder interests. The primary role of these models is not to reveal “truth”, but to assist stakeholders in understanding the emergent properties of how the system functions, to assist YNP managers in identifying key uncertainties that prevent improved management strategies, and to help stakeholders distinguish perceived from real problems.

### *9. The National Park Service should increase its support for the appropriate agencies to secure key winter range for bison and other wildlife adjacent to the park in the Northern range.*

The Gardiner basin is part of a prehistoric seasonal range use system for bison occupying the Northern range. Under current circumstances, it can be considered refuge habitat for bison during severe winters, serving a role similar to geothermally influenced refuge habitat in the Central Range. The bison management plan presumed that the lands north of Yellowstone National Park in the Gardiner basin would be free of cattle after the winter of 2001-2002. However, the Church Universal and Triumphant is still running cattle on the Royal Teton Ranch (RTR) adjacent to the park. Consequently, Step 1 of the management plan is still in place on the north side. Removing cattle from this area was a critical underpinning of the bison management plan and a goal of a $13 million federal-private land exchange initiative of 1999. The Record of Decision requires in Step 1 that the agencies “cooperate with RTR to develop a Bison Management Plan for the Royal Teton Ranch that is consistent with the provisions of the Joint Management Plan.”

The NPS is engaged in low key discussions with the Church Universal and Triumphant in defining the terms of an agreement consistent with the bison management plan, including removal of cattle from RTR holdings. NPS is encouraged to step up its efforts to obtain an agreement to secure winter range for bison adjacent to the park as refuge habitat during extreme winters.

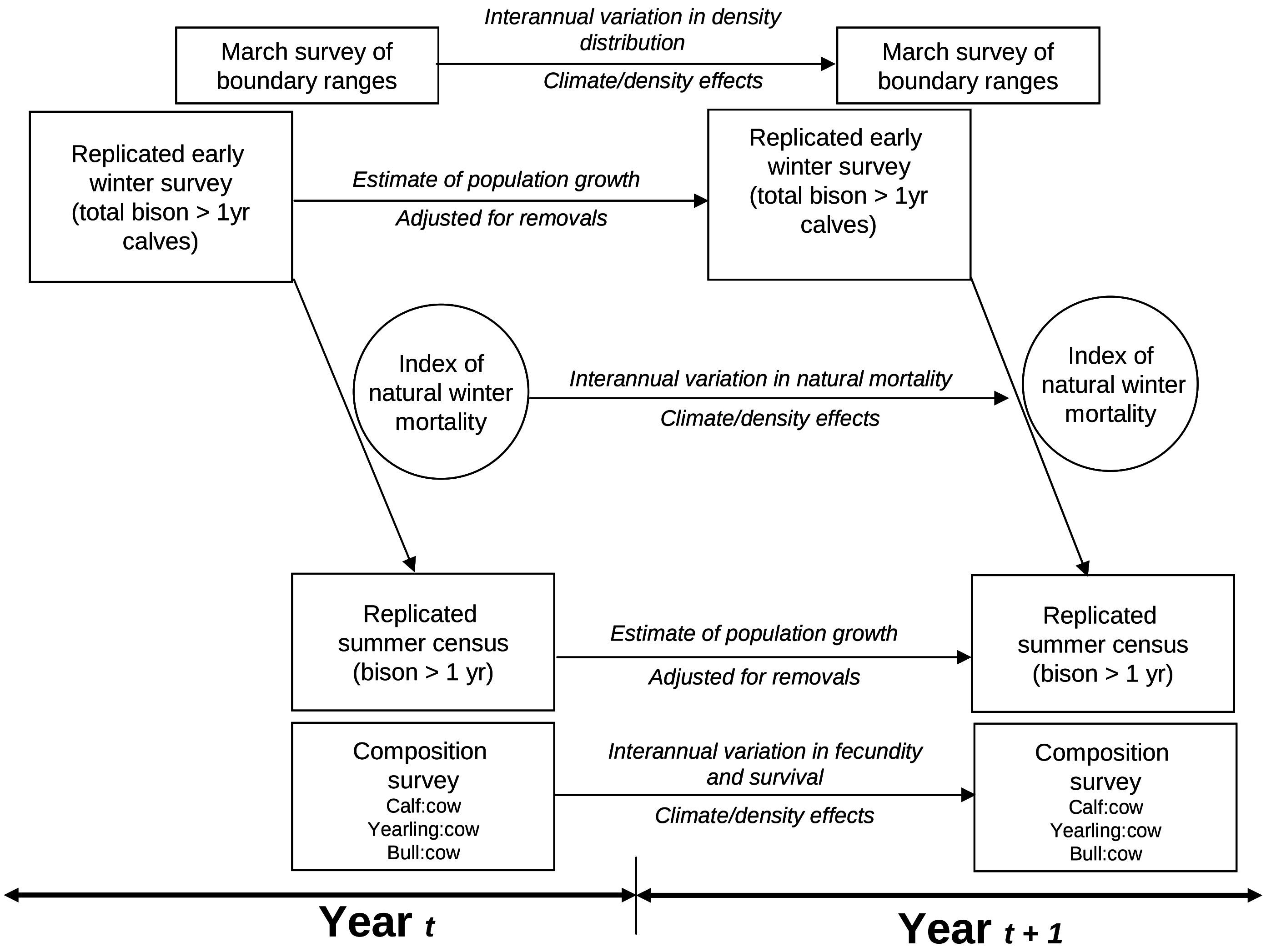

Figure 7.1. Conceptual diagram of a population monitoring program for bison in Yellowstone National Park. Adapted from Hess (2002).

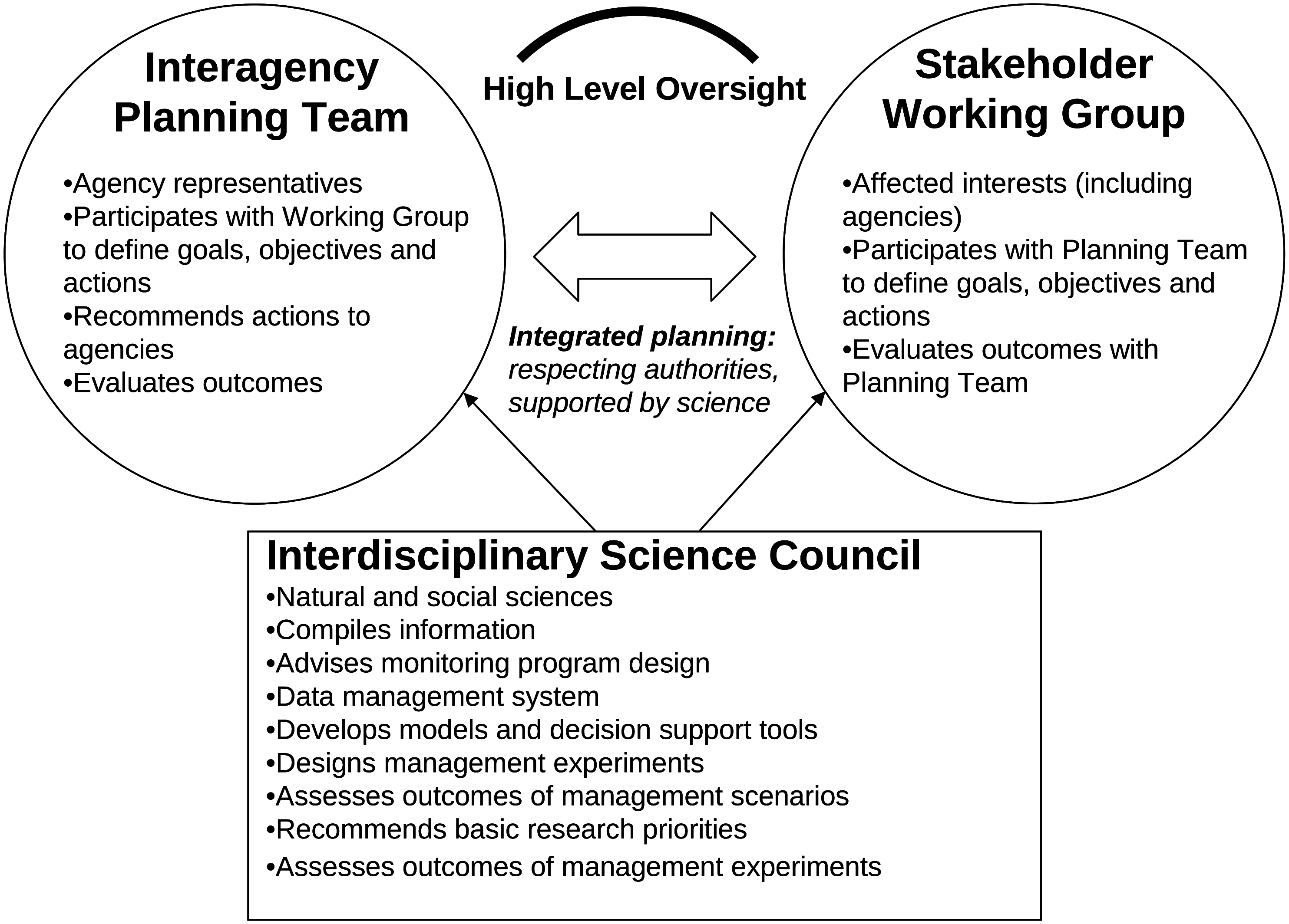

Figure 7.2 Organizational framework for collaborative and adaptive management of YNP/Montana bison.

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# APPENDIX I

# KEY INFORMANT INTERVIEWS
# JULY 15 – AUGUST 13, 2004

| | | | |
|---|---|---|---|
| Aune, Keith | Montana Fish, Wildlife & Parks | Chief of research and technical services | July 22, 2004<br>August 10, 2004 |
| Backus, Alison | Montana State University - Natural History Media | Masters Candidate | August 2, 2004 |
| Bjornlie, Dan | Wyoming Fish and Game | Trophy game division, Lander | August 12, 2004 |
| Brewster, Wayne | Yellowstone Center for Resources, Yellowstone National Park | Deputy Director | July 26, 2004 |
| Cain, Steven | Grand Teton National Park | Supervisory Wildlife Biologist | August 11, 2004 |
| Caron, Rick | Yellowstone National Park | Chief Maintenance | July 29, 2004 |
| OTHER ROAD CREW | Yellowstone National Park | 12 maintenance equipment operators | July 29, 2004 |
| Clark, Tim | Yale University | Professor | August 11, 2004 |
| Garrott, Robert | Montana State University | Professor | August 2, 2004 |
| Gogan, Pete | Montana State University; USGS Northern Rocky Mountain Science Center | Adjunct Associate Professor; Wildlife Research Biologist | July 21, 2004 |
| Gross, John | National Park Service | Ecologist | July 21, 2004 |
| Irby, Lynn | Montana State University | Professor, retired | August 13,2004 |
| Jerde, Chris | University of Alberta | PhD candidate | June 24 and July 27, 2004 |
| Johnson, Ann | Yellowstone Center for Resources, Yellowstone National Park | Chief Archaeologist | July 28, 2004 |
| McClure, Craig | Yellowstone National Park | Resource Manager | August 9, 2004 |
| McNulty, Dan | University of Minnesota | Wolf and bison ecologist | August 5, 2004 |
| Meagher, Mary | Yellowstone National Park | Bison biologist, retired | July 15, 16, and 27, 2004 |
| Miles, Wes | Yellowstone National Park | Norris District Ranger | August 9, 2004 |
| Olenicki, Tom | Montana State University | PhD candidate | August, 13, 2004 |
| Olexa, Ed | USGS Northern Rocky Mountain Science Center | Wildlife Biologist | July 21, 2004 |
| Olliff, Tom | Yellowstone Center for Resources, Yellowstone National Park | Natural Resources Branch Chief | August 3, 2004 |
| Plumb, Glenn | Yellowstone Center for Resources, Yellowstone National Park | Supervisory Wildlife Biologist | August 4, 2004; July 23, 2004 |
| Reinhart, Dan | Yellowstone National Park | Resource Manager | August 3, 2004 |
| Renkin, Roy | Yellowstone Center for Resources, Yellowstone National Park | Vegetation and Fire Ecologist | August 4, 2004 |
| Roffe, Tom | United States Fish and Wildlife Service | Veterinarian | July 22, 2004 |
| Ross, Dave | Yellowstone National Park | West Yellowstone District Ranger | August 6, 2004 |
| Sacklin, John | Planning and Compliance, Yellowstone National Park | Chief of Planning | July 23, 2004 |
| Schneider, Kevin | Planning and Compliance, Yellowstone National Park | Planner | July 23, 2004 |
| Smith, Doug | Yellowstone Center for Resources, Yellowstone National Park | Yellowstone Wolf Project leader | July 26, 2004 |

|  |  |  |  |
|---|---|---|---|
| Taper, Mark | Montana State University | Associate Professor | July 27, 2004 |
| Wallen, Rick | Yellowstone Center for Resources, Yellowstone National Park | Yellowstone Bison Project leader | July 23, 2004 |
| Watson, Fred | California State University, Monterey |  |  |
| White, PJ | Yellowstone Center for Resources, Yellowstone National Park | Yellowstone Ungulate Project leader | July 28, 2004 |
| Young, Dennis | Yellowstone National Park | Madsion District Ranger | August 9, 2004 |

# APPENDIX II

# GROUP MODELING WORKSHOPS

## Yellowstone Center For Resources

### *Workshop 1: October 20, 2004, Mammoth, Wyoming*

**Participants:**Wayne Brewster, Lynn Irby, Dan McNulty, Tom Olenicki, Tom Oliff , Glenn Plumb, Dan Reinhart, Roy Renkin, Bob Seibert, Doug Smith, Rick Wallen, PJ White

### *Workshop 2: October 30, 2004, Emigrant, Montana*

**Participants:** Kevin Schneider, Rick Wallen
**Regrets:** Glenn Plumb

### *Workshop 3: February 25-26 , 2005, Lake Louise, Alberta*

**Participants:** Glenn Plumb, Rick Wallen

## Montana Workshop, October 21, 2004, MFWP Office, Bozeman, Montana

**Participants:**
Montana Fish Wildlife and Parks: Kurt Ault, Kieth Aune
USDA/APHIS: Ryan Clark
USFWS: Tom Roffe
**Regrets**: Jack Rhyan

## Wyoming Workshop, October 25, 2004, WGF Office, Jackson Wyoming

**Participants:**
National Parks Service, GTNP: Steven Cain, Sarah Dewey
Wyoming Game and Fish Department: Dan Bjornlie
Wildlife Conservation Society: Joel Berger
**Regrets**: Sue Consolo-Murphy, Tim Clark

## Meagher Research Group Workshop, October 27, 2004, Emigrant, Montana

**Participants:** Mary Meagher, Mark Taper, Anne Johnson
**Regrets:** D. J. Schubert, Chris Jerde

## USGS Workshop, October 28, 2004, Montana State University, Bozeman, Montana

**Participants:**
USGS: Peter Gogan
University of Colorado: Mike Coughenhauer
**Regrets**: John Gross, Ed Olexa

# APPENDIX III

# ENVIRONMENTAL NON-GOVERNMENT ORGANIZATIONS WORKSHOP

## October 29, 2004

Yellowstone Inn and Conference Center
1515 West Park
Livingston, MT. 59047
10:00 a.m. – 5:00 p.m.

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**American Buffalo Foundation**
Joe Gutkoski, Secretary
Bozeman, MT

**American Wildlands (did not attend)**
Rob Ament, Executive Director
Bozeman, MT

**Barb Abramo**
West Yellowstone, MT

**Bear Creek Council (did not attend)**
David Keltner, Chair
Gardiner, MT

**Buffalo Field Campaign**
Mike Mease
West Yellowstone, MT

**Defenders of Wildlife (did not attend)**
Minnette Johnson
Missoula, MT

**Fund for Animals (did not attend)**
Andrea Lococo, Rocky Mountain Coordinator
Jackson, WY

**The Fund for Animals (did not attend)**
D.J. Schubert, Ranch Manager/Wildlife Biologist
Murchison, TX

**Gallatin Wildlife Association**
Glenn Hockett, President
Bozeman, MT

**Greater Yellowstone Coalition**
Amy McNamara, National Parks Director
Bozeman, MT

**Greater Yellowstone Wildlife Alliance**
William C. Patric
Bozeman, Montana

**George Nell**
Gardiner, MT

**HBNA (Horse Butte Neighborhood Association)**
Karrie Taggart
Horse Butte Neighbors of Buffalo
West Yellowstone, MT

**Horse Butte Neighbors of Buffalo**
Liz Kearney, Newsletter Editor
West Yellowstone, MT

**Humane Society of the United States**
Northern Rockies Regional Office
Dave Pauli, Director
Billings, MT

**Intertribal Bison Cooperative (did not attend)**
Fred DuBray
Rapid City, SD

**Jackson Hole Conservation Alliance**
Dr. Franz Camenzind
Jackson Hole, WY

**Dr. Mary Meagher**
Cinnebar Basin, MT

**Montana Conservation Voters**
Jeanne-Marie Souvigney, Program Director
Livingston, MT

**Montana Wildlife Federation (National Wildlife Federation) (did not attend)**
Craig Sharpe, Executive Director
Helena, MT

**National Parks Conservation Association**
Tony Jewett, Senior Director
Helena, MT

**National Parks Conservation Association**
Patricia “Patti” Borneman, Program Coordinator
Northern Rockies Region
Helena, MT
**Natural Resources Defense Council (did not attend)**
Charles M. Clusen
Director, National Parks Project
Natural Resources Defense Council
Washington, DC

**The Nature Conservancy**
Laura Hubbard, Project Manager
Montana Field Office
Helena, MT

**Rocky Mountain Elk Foundation (did not attend)**
Peter J. Dart, President and CEO
The Rocky Mountain Elk Foundation
Missoula, MT

**Sierra Club (did not attend)**
Kathryn Hohmann
Bozeman, Montana

**Society for Range Management**
Jeff Mosley, SRM 2004 Board of Directors
Dept. of Animal and Range Science
Montana State University
Bozeman, MT

**Society for Range Management**
International Mountain Section
Jim Knight, PhD
Dept. of Animal and Range Science
Montana State University
Bozeman, MT

**Wildlife Conservation Society (did not attend)**
Craig Groves
Bozeman, MT

**Wilderness Society, Northern Rockies Chapter (did not attend)**
Bob Ekey
Bozeman, MT

**Wyoming Wildlife Federation (did not attend)**
Cathy Purves
Western Wyoming Field Director
Lander, WY

**Facilitator:** Dennis Phillippi, Bozeman Montana
**Coordinator**: Traci Weller, Bozeman MT
**Investigators**: C. Gates, B. Stelfox, T. Muhly, Calgary AB

# APPENDIX IV

# BISON WINTER ROAD USE MONITORING STUDIES

Three major studies regarding bison use of groomed roads and interactions with Over Snow Vehicles (OSV) have been conducted in Yellowstone National Park (YNP). The first (Kurz et al. 2000, Reinertson et al. 2002) was initiated in winter 1997-1998 and was conducted during four subsequent winters. The purpose was to assess the level and frequency of groomed road use by bison and generate a data set on bison use of groomed roads to serve as a basis for comparison with future monitoring efforts. Four types of data were collected: ground survey observations, automated point photos, groomer surveys and aerial surveys (Reinertson et al. 2002). Random crepuscular and daytime ground surveys of bison were conducted along three road sections in YNP, the road from Pelican Valley to Canyon, the road from Gibbon Canyon to Golden Gate and roads in the Madison-Firehole area. The Pelican Valley to Canyon section was monitored all five years of the study, the Gibbon Canyon to Golden Gate section was monitored the final four years of the study and the Madison area was monitored the final 2 years. Two-person teams recorded all bison observations along the road section, including data on group size, sex/age composition, location (UTM), group behaviour (foraging, resting, traveling), snow depth, habitat, time of day, winter weather conditions, distance from road, type of road use (i.e. crossing or linear use), direction of travel if on road, and location of entry and exit from road. Point photo data was collected at eight locations, Swan Lake, Roaring Mountain, Norris Junction, Gibbon Meadows, Otter Creek, Mary Mountain Trailhead, the North Geologic overlook and Buffalo Ford. Photographs were taken every 90 minutes with a view of the road. Snow and weather conditions were also recorded at each photo station. During grooming, groomer operators recorded all bison observations, including date, time and section of groomed road where sighting occurred, and reaction of the bison to the groomer. Aerial surveys and radio-telemetry of bison were conducted to monitor large-scale movements and distribution of the population within the study area.

A concurrent study was conducted by Bjornlie and Garrott (2001) in the Madison-Firehole area of YNP, during the winters of 1997-1998 and 1998-1999. Road sections between Old Faithful, Madison Junction, West Yellowstone and Norris were surveyed and data from trail monitors was gathered to study bison movements and use of winter roads. Three-person crews traveled one of 6 survey routes each day, attempting to locate all bison along the route. The location, age and sex composition, and behaviour (traveling, foraging or resting) of bison were recorded in addition to the number of bison traveling along the road for > 50 m. Trail monitors were located at the Mary Mountain trail and Gneiss Creek trail. SWE data were collected from the Canyon SNOTEL station to correlate snowpack conditions with bison distribution.

A third study (Davis et al. 2004, White et al. 2004) was initiated in winter 2002-2003 to collect data on interactions between wildlife, including bison, and OSV's on groomed roads and also examined whether responses of wildlife to snowmobiles and snow coaches differed, and whether levels of human activity and behavioural responses of wildlife differed between commercially guided and unguided groups of snowmobiles. The study was repeated in 2003-2004 for comparison (White et al. 2004) and is expected to continue into the future. Data were collected on number and type of OSV's entering each park gate, and SWE data was collected from SNOTEL stations in YNP. Three, two-person crews used snowmobiles or wheeled vehicles to conduct repeated surveys of wildlife distribution and responses to motorized vehicles along eight road sections (Madison to Old Faithful, Canyon Village to Lake Butte, Madison to West Yellowstone, Mammoth to Lamar Valley, Norris to Madison, Mammoth to Norris, Fishing Bridge to West Thumb, Canyon Village to Norris, Fishing Bridge to Sylvan Pass). Surveys were conducted during daylight hours only, at all times of the week and sections were surveyed without replacement. Observers traveled along a road segment until they located a wildlife group, at which time they stopped and observed the wildlife until a motorized vehicle (OSV on groomed roads and wheeled vehicle along plowed roads) entered the area (within 500 m). Observers then began recording the interaction between the motorized vehicle user and wildlife. For each observation of a bison group along a survey route the time of observation, habitat type (aquatic, burned forest, unburned forest, wet meadow, dry meadow, geothermal), group size and composition, and activity of the group (standing, traveling, resting) was recorded. Categories for measuring motorized vehicle user responses to wildlife were: no visible interaction, stop their vehicles, dismount vehicle, approach wildlife or impede and/or hasten wildlife. Categories for measuring wildlife responses to OSV users were: no visible reaction, look at vehicles or activity then resume behaviour, travel away from activity, attention/alarm behaviour, flight from activity or defense behaviour.

## Road Use Patterns by Bison

Most bison observed were not on roads; 7.9% (519) of bison groups were observed on the road along the Pelican Valley to Canyon road section, 7.2% (251) of bison groups were on the road along the Gibbon Canyon to Golden Gate road section and 12.8% (118) of bison groups were on the road along the Madison road section (Reinertson et al. 2002). When bison were observed on roads, 95% were traveling linearly along the road (Kurz et al. 2000). Photographs recorded bison on the road 14.4% of the time and 9.75% of groomer observations were of bison on the road.

Kurz et al. (2000) reported the percent of bison observed on roads for each road section and total number of bison groups observed on each road section (Table 1). The highest percent of bison observed on roads occurred along the Gibbon Canyon and Elk Park to Gibbon Meadows sub-sections of the Gibbon Canyon to Golden Gate road, and along the Mud Volcano to Buffalo Ford and Hayden Valley (north of Mud Volcano to Mary Mountain trailhead) sub-sections of the Pelican Valley to Canyon road. Bison were most likely to travel on groomed roads from Gibbon Canyon to Gibbon meadows and from Buffalo Ford to the Mary Mountain trailhead. In the case of the former road section, the high percentage of bison found on roads may be due to restriction of bison to narrow valleys, which also contain roads, because of steep topography along the movement corridor between foraging areas (Kurz et al. 2000). The latter road section may have been relatively heavily used because of frequent traveling back and forth along the road between feeding areas (Kurz et al. 2000).

Davis et al. (2004) and White et al. (2004) monitored wildlife/OSV interactions between December and April. In 2002-2003 they conducted 332 surveys totaling 11,182 km while observing 4,269 groups of wildlife (2,294 groups of bison) and 3,020 interactions. In 2003-2004, 402 surveys were conducted totaling 11,389 km with 4,940 wildlife observations (2,597 bison) and 3,174 interactions. Road segments were categorized into low and high use based on frequency of interactions per kilometer surveyed (Davis et al. 2004). The number of bison groups and bison/OSV interactions observed along each road section is indicated in Table 2 for 2002-2003 and Table x for 2003-2004. Overall, bison were observed on groomed roads during 159 of 1,668 observations (9.5%) in 2002-2003 and 311 of 2,597 observations (12.0%) in 2003-2004. Bjornlie and Garrott (2001) recorded 19% of bison travel was on roads. Unfortunately, these studies do not indicate the percentage of sightings of bison on roads by road section therefore it is difficult to compare patterns of road use with Kurz et al. (2000); however, it is clear that bison more frequently used corridors between Madison and Old Faithful and Canyon to Lake Butte (i.e. the road through Hayden Valley) with relatively high frequency. The sections most used by bison are also the sections where interactions between bison and OSV's are most frequent.

The pattern of road use by bison was not consistent among winters. In 1997-1998, bison were observed on roads 8% of the time in December and January, 25% of the time in February and 38% of the time in March (Kurz et al. 2000). In 1998-1999, bison were observed on roads 8% of the time in December, 15% of the time in January, 23% of the time in February and 35% of the time in March (Kurz et al. 2000). In 1999-2000, bison were observed on the road 12% of the time in December, 33% of the time in January, 10% of the time in February and 36% of the time in March (Kurz et al. 2000); similar patterns were observed the following two winters (Reinetrson et al. 2002). Snow depths also varied, increasing monthly as winter progressed (Kurz et al. 2000). Bjornlie and Garrott (2001) found that bison use of roads peaked in late fall and early spring, and was lowest during the OSV season. It appears bison travel along roads more frequently in late winter/early spring, perhaps in relation to snow depth and spring greenup. However, all movement (on roads and trails) increased during late winter (Bjornlie and Garrott 2001). In March, roads are plowed, which may affect bison use of roads (Kurz et al. 2000); additionally peak movement in the spring coincided with meltoff and greenup at lower elevations, which may also affect bison movements. Increased travel by bison along linear corridors during early spring could also be due to an increase in effort to find forage once snowpack begins to melt (Bjornlie and Garrott 2001).

A greater number of bison traveled along roads during an above-average SWE winter (1998-1999) more than a below average SWE winter (1997-1998). SWE was a significant predictor of road use by bison (Bjornlie and Garrott 2001). Greater use of roads by bison, both annually and seasonally, as snow depth and/or SWE increases suggests a correlation between snow conditions and bison use of roads. However, all of these studies were short term and the majority were conducted during below average to average SWE winters. It is impossible to determine from these studies whether snow conditions are a causative mechanism for road use.

## Interactions Between Bison and OSV's

Of all the recorded interactions between OSV's and wildlife, 48% (2,984) involved groups of snowmobiles, 12% (722) involved snowcoaches and 40% (2453) involved wheeled vehicles (Davis et al. 2004, White et al. 2004). In 2002-2003, 13% of snowmobile groups impeded or hastened wildlife movement and 25% of snow coach groups impeded or hastened wildlife movement (Davis et al. 2004) Although snowcoaches appear to have a greater impact on wildlife, they make up a smaller percentage of OSV interactions with wildlife. Additionally, there was a notable discrepancy in the type of OSV causing impede/hasten interactions in wildlife. In 2003, snow coaches and snowmobiles accounted for 68% and 32%, respectively, of impede/hasten interactions compared to 2004, when snow coaches and snowmobiles accounted for 22% and 78%, respectively, of impede/hasten interactions.

In 2002-2003 the majority of OSV users had no reaction to wildlife (59%), 18% stopped and observed wildlife, 13% dismounted, 8% approached and only 1% impeded and/or hastened wildlife (Davis et al. 2004). The majority of bison groups (78%) had no response to OSV's, only 9% of groups showed alarm behaviour, moved away from the OSV users or showed defense behaviour. The likelihood of observing an active response in bison increased as snowmobile group size increased and odds of observing an active response in bison were significantly higher for commercially guided groups than unguided groups, although sample size of guided groups was very small (< 10% of interactions). Guided groups appeared more likely to approach wildlife than unguided groups (Davis et al. 2004). In the subsequent winter, a similar percentage of people had no visible reaction to wildlife (White et al. 2004). More OSV users stopped to observe animals in 2004, but the numbers of users that dismounted the OSV and approached wildlife decreased. Wildlife was impeded and/or hastened by OSV users more often in 2004 (6%) compared to 2003 (1%). The responses of most wildlife species to OSV users was minor; 58% of wildlife responses were categorized as no apparent response, 18% as look/resume, 11% as attention/alarm, 9% as travel, 4% as flight, and <1% as defense. In bison, 84% of interactions were 'no apparent response' or 'look-and-resume'.

Active responses in bison caused by bison/OSV interactions varied depending on vehicle type, location of bison, composition of bison group and composition of OSV group. The odds of observing an active response in bison were 20 times greater when bison were on the road than when they were off road (Davis et al. 2004). Active responses were also more likely as the number of juveniles in a bison group increased, but decreased as the number of adult males in the group increased (White et al. 2004). The odds of observing an active response by bison were greater as snowmobile group size increased and were greater if a snow coach was in the group (White et al. 2004). Odds of observing an active response was greater when the bison group was traveling rather than resting and as interaction time increased (up to 20 minutes; White et al. 2004). Bjornlie and Garrott (2001) found that when traveling on roads, 53% of bison groups encountering OSV's had negative interactions, of which 68% of those interactions involved running from 50 m to 4 km.

Administrative OSV users (e.g. park staff) were more likely to stop and view wildlife but guided groups were more likely to approach wildlife when stopped. In 2003-2004, 70% of guided groups passed wildlife without stopping, compared to 45% of administrative groups. Of those that stopped, 7% of guided groups approached wildlife whereas 1% of administrative groups approached wildlife.

Groomers are more likely to cause active responses than other OSV types (snowcoaches and snowmobiles). Over half (51%) of bison encounters with road groomers resulted in bison running (Kurz et al 2000). Grooming typically occurred between 3 pm to 2 am yet no bison sightings were recorded after 10 pm (Kurz et al. 2000) suggesting bison rarely travel at night. Bjornlie and Garrott (2001) also found little evidence of bison traveling along roads at night in the Madison-Firehole area. Because bison appear to rarely travel at night (Kurz et al. 2000, Bjornlie and Garrott 2001), grooming could be conducted later at night (after 10 pm) to mitigate impacts of groomers on bison. Bison response to OSV use is likely minor as there was no evidence of population level effects of OSV use on bison (Davis et al. 2004, White et al. 2004).

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Appendix IV, Table 1**.** Percentage of bison observations and number of bison groups observed on roads for each road section surveyed. Data from Kurz et al. (2000) conducted in winters of 1997-1998, 1998-1999 and 1999-2000.

| **Road Segment** | **Road Sub-section** | **Percent of Bison Observations on Roads** | **Total Number of Bison Groups Observed** |
|---|---|---|---|
| Pelican Valley to Canyon | Mary Bay to Fishing Bridge Junction | 12 | 31 |
| | Fishing Bridge Junction to Cascade Picnic area | 18 | 50 |
| | Mud Volcano to Buffalo Ford | 28 | 76 |
| | Hayden Valley (north of Mud Volcano to Mary Mountain trailhead) | 26 | 68 |
| | Otter Creek to Canyon Junction | 13 | 37 |
| Gibbon Canyon to Golden Gate | Golden Gate to Indian Creek | 8 | 7 |
| | Roaring Mountain | 8 | 7 |
| | Frying Pan Spring to Bijah Spring | 11 | 9 |
| | Ranger Museum | 12 | 10 |
| | Elk Park to Gibbon Meadows | 27 | 23 |
| | Gibbon Canyon | 34 | 29 |

Appendix IV, Table 2. Bison observations and interactions with OSV's in winter of 2002-2003. Data table from Davis et al. (2004).

| Road Segment | Total km surveyed | Bison Groups Observed | Groups Observed per km surveyed | Interactions Observed | Interactions Observed per km surveyed |
|---|---|---|---|---|---|
| Madison to Old Faithful | 1451 | 675 | 0.47 | 599 | 0.41 |
| Madison to West Yellowstone | 1305 | 232 | 0.18 | 228 | 0.17 |
| Canyon to Norris | 590 | 20 | 0.03 | 16 | 0.03 |
| Madison to Norris | 998 | 113 | 0.11 | 85 | 0.09 |
| Mammoth to Norris | 655 | 74 | 0.11 | 50 | 0.08 |
| Mammoth to Lamar Valley | 3570 | 621 | 0.17 | 389 | 0.11 |
| Canyon to Lake Butte | 1506 | 498 | 0.33 | 300 | 0.20 |
| West Thumb to Fishing Bridge | 1134 | 55 | 0.05 | 41 | 0.04 |

Appendix IV, Table 3. Bison observations and interactions with OSV's in winter of 2003-2004. Data table from White et al. (2004).

| **Road Segment** | **Total km surveyed** | **Bison Groups Observed** | **Groups Observed per km surveyed** | **Interactions Observed** | **Interactions Observed per km surveyed** |
|---|---|---|---|---|---|
| Madison to Old Faithful | 1569 | 1350 | 0.86 | 981 | 0.63 |
| Madison to West Yellowstone | 1415 | 1118 | 0.79 | 887 | 0.63 |
| Canyon to Norris | ND | ND | ND | ND | ND |
| Madison to Norris | 578 | 199 | 0.34 | 127 | 0.22 |
| Mammoth to Norris | 710 | 145 | 0.20 | 97 | 0.14 |
| Mammoth to Lamar Valley | 2354 | 942 | 0.40 | 742 | 0.32 |
| Canyon to Lake Butte | 2073 | 1055 | 0.51 | 294 | 0.14 |
| West Thumb to Fishing Bridge | 1798 | 106 | 0.06 | 31 | 0.02 |
| West Thumb to South Entrance | 256 | 9 | 0.04 | 3 | 0.01 |
| West Thumb to Old Faithful | 636 | 16 | 0.03 | 12 | 0.02 |