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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The history and enormity of issues leading to this study have touched the professional or personal lives of a broad spectrum of Americans, including federal and state civil servants and citizens who care passionately about the integrity of Yellowstone National Park, bison conservation, or protection of livestock against reinfection with a zoonotic organism nearing eradication in the industry. Given the strong polarization among interests involved in these environmental conflicts, the authors feel privileged to have been welcomed by key informants to engage in exploration of their knowledge and insights, and in many cases to have been provided with unpublished data contributing to our assessment and recommendations. Foremost among those we wish to acknowledge as contributing to the assessment is Dr. Mary Meagher, whose passionate concerns for the conservation of Yellowstone bison and the integrity of the Yellowstone Park ecosystem have been uncompromising. We encourage her to continue analyzing the as yet unrealized potential of a data set spanning more than 30 years, complimented by experience in the Yellowstone ecosystem exceeding the duration of most professional careers in wildlife management. In contrast, Rick Wallen, the current bison biologist with the National Park Service, is just beginning to develop a research and management program. We thank Rick for contributing information and his insights to the assessment and hope in return that the report contributes to the development of his program. We are grateful to both Rick Wallen and Dr. Doug Smith for the experience and insights we gained while riding the Mary Mountain Trail with them in October 2004. Finally, we wish to acknowledge the enormous contribution to the project by Traci Weller of Bozeman, Montana. Traci organized and scheduled the interviews and workshops, recorded the dialogue and prepared transcripts. Her competency and humor sustained us through the arduous interview schedule.

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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.

5. Initial Bison Popn Metrics	
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.

6. Natural Mortality Rate	
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

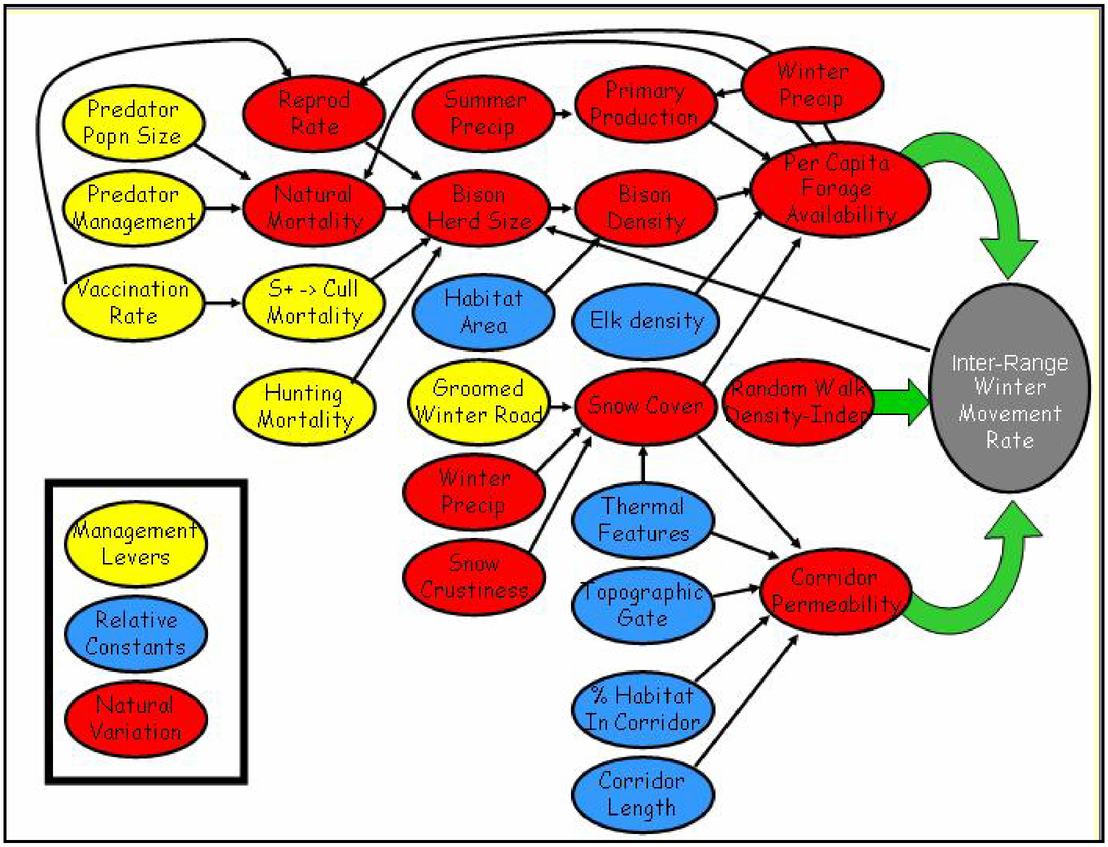


Figure 6.1. Impact Hypothesis Diagram (IHD) used as basis for YNP Bison Distribution Model. The structure of this diagram was based on information gathered at key informant workshops.

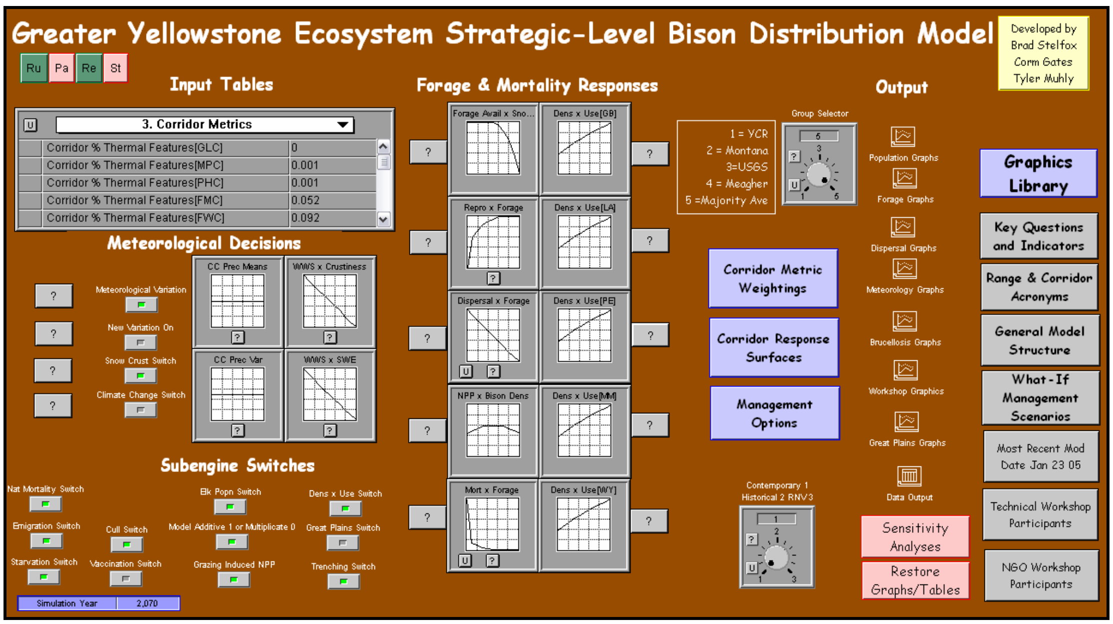


Figure 6.2. Master Panel of the YNP Bison Distribution Model.

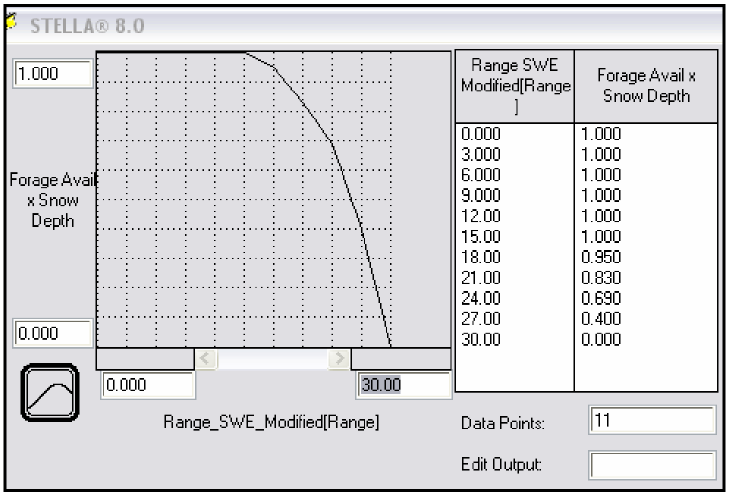


Figure 6.3. Relationship between bison winter forage availability and Snow Water Equivalence (cm).

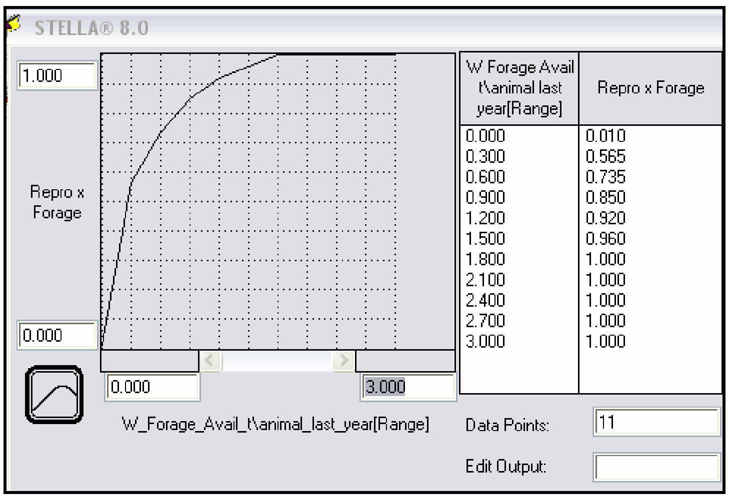


Figure 6.4. Relationship between bison winter forage availability and index of reproductive performance. A value of 1 returns a maximum population growth rate of 0.2.

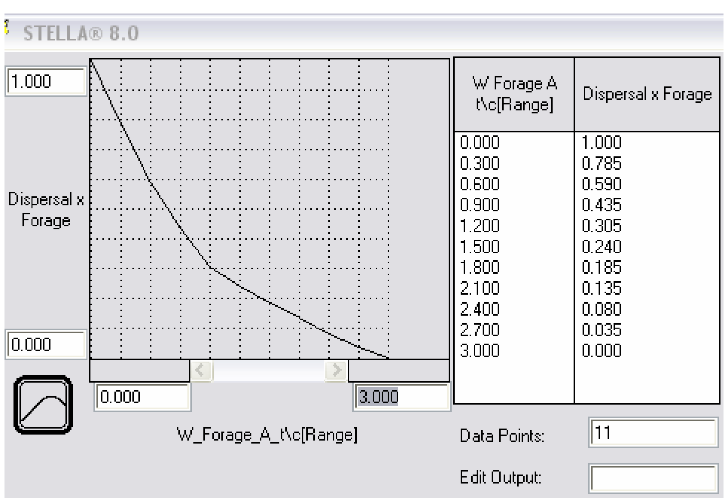


Figure 6.5. Relationship between winter forage availability (tonne/bison) and probability that bison move from current winter range to another winter range.

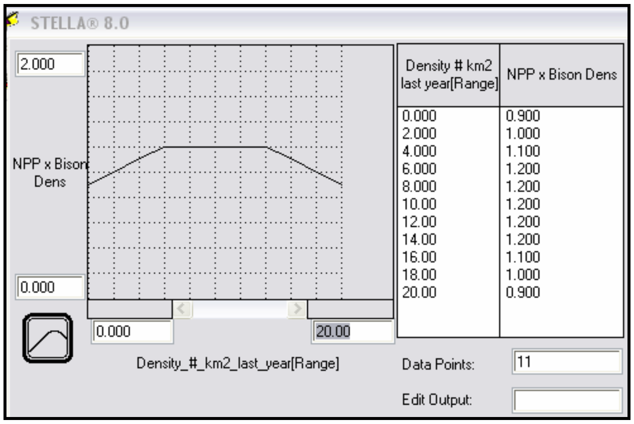


Figure 6.6. Relationship between bison density and net primary productivity modifier. This relationship reflects the understanding that very low and very high levels of herbivory can reduce primary production below long term average values. Intermediate herbivory levels, in contrast, can lead to modest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

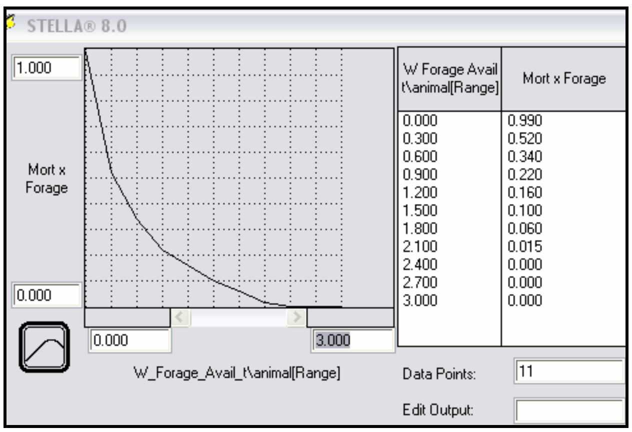


Figure 6.7. Relationship between winter forage availability (tonne/bison) and overwinter bison mortality rate. In this model, no mortality effect occurred until forage availability declined below 2.2 tonne/bison. Rapidly increased levels of starvation mortality occur once forage availability declines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

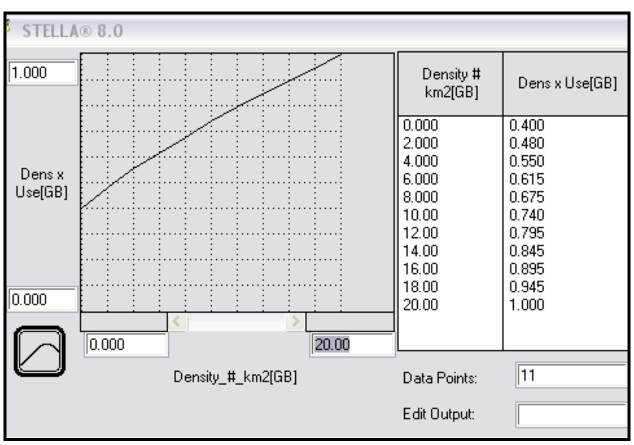


Figure 6.8. Relationship between bison density and proportion of winter range used. This relationship reflects the observation by several of the key informants that use of winter bison range is influenced by bison density. An identical relationship was used for all winter ranges.

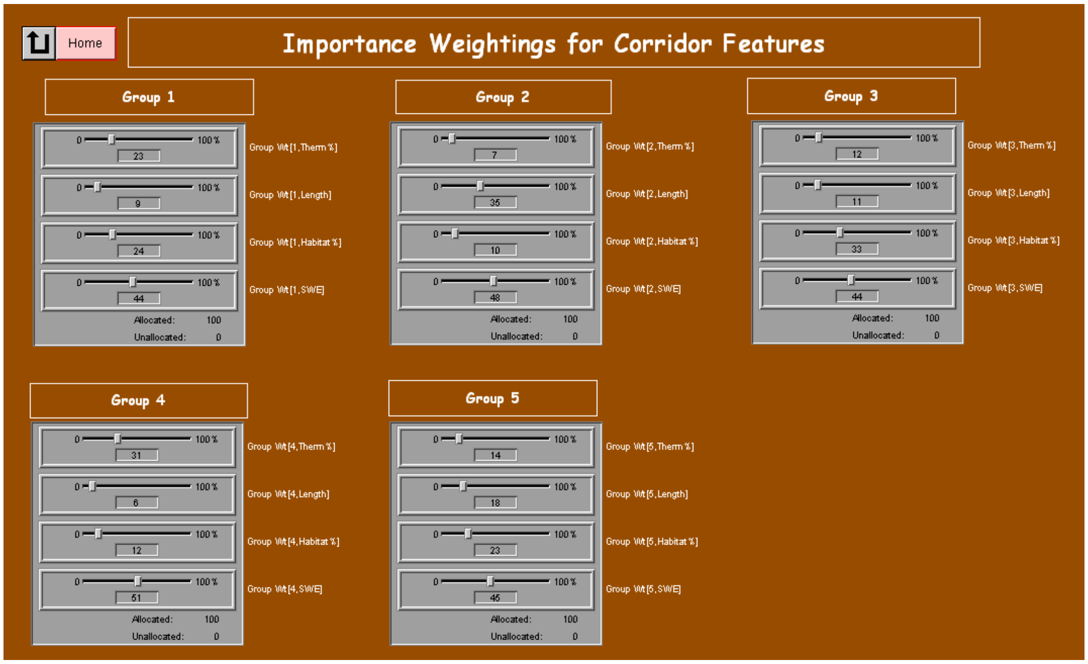


Figure 6.9. Importance weightings attributed to corridor metrics from each of the Key Informant Groups.

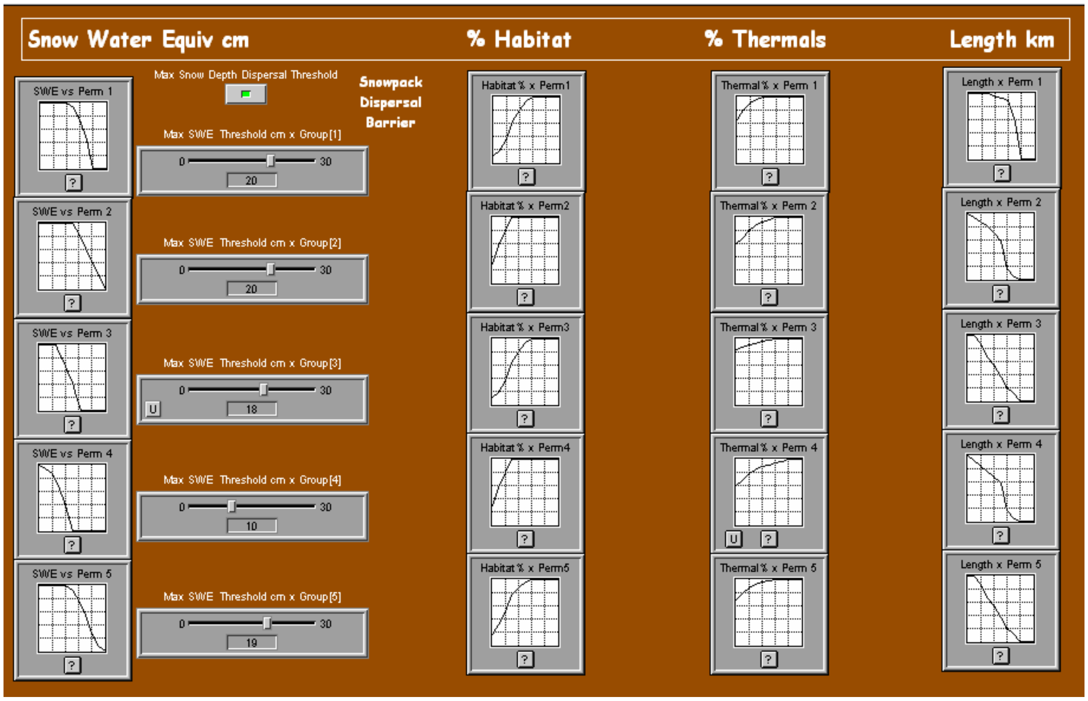


Figure 6.10. Corridor permeability response surfaces provided by each of the Key Informant Groups.

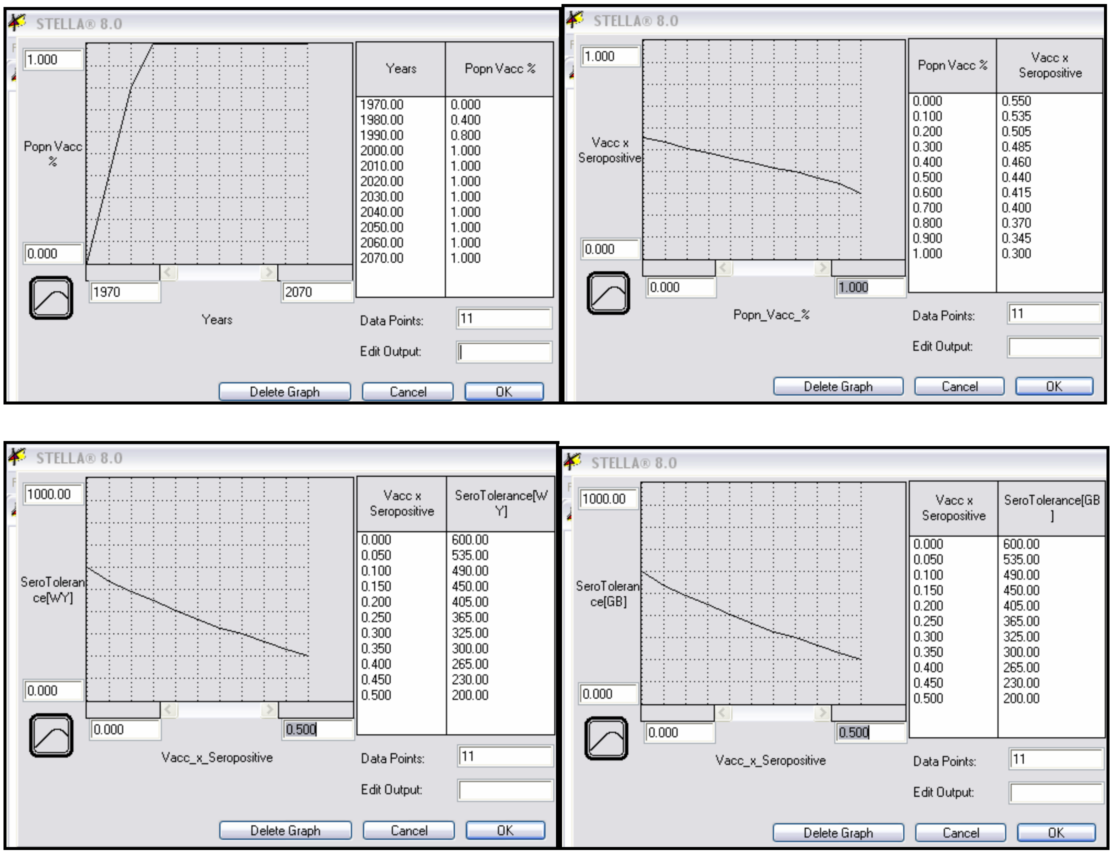


Figure 6.11. Initial user-defined input relationships for a “hypothetical” bison brucellosis vaccination program. The graph in the upper left describes the number of years required to complete a full vaccination of the YNP herd. The graph in the upper right describes the relationship between the percent 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.

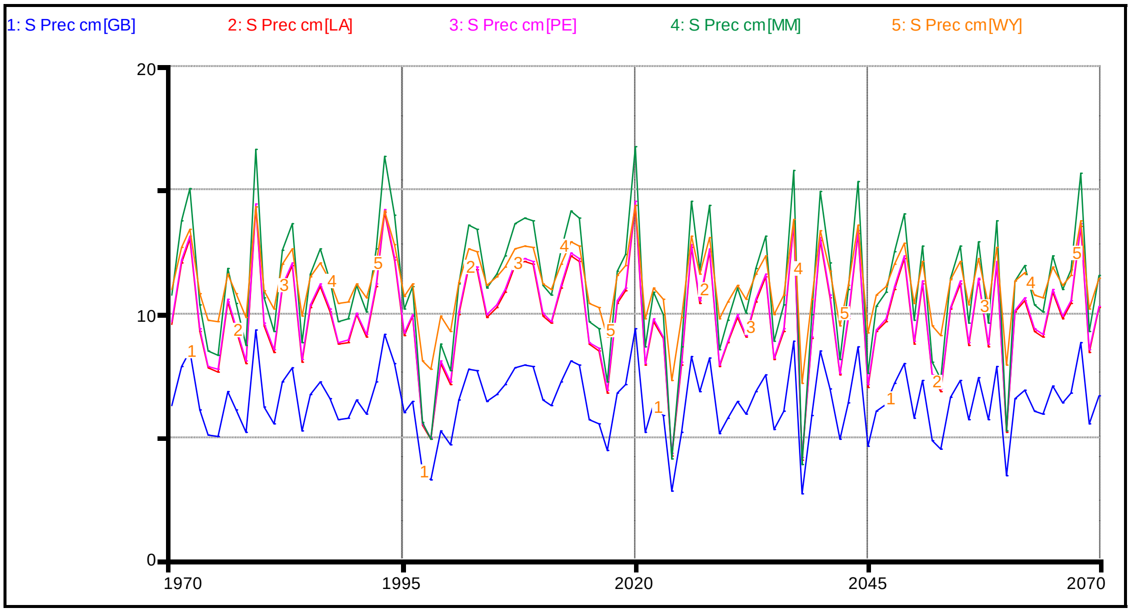


Figure 6.12. Simulated summer precipitation (cm) in each bison winter range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

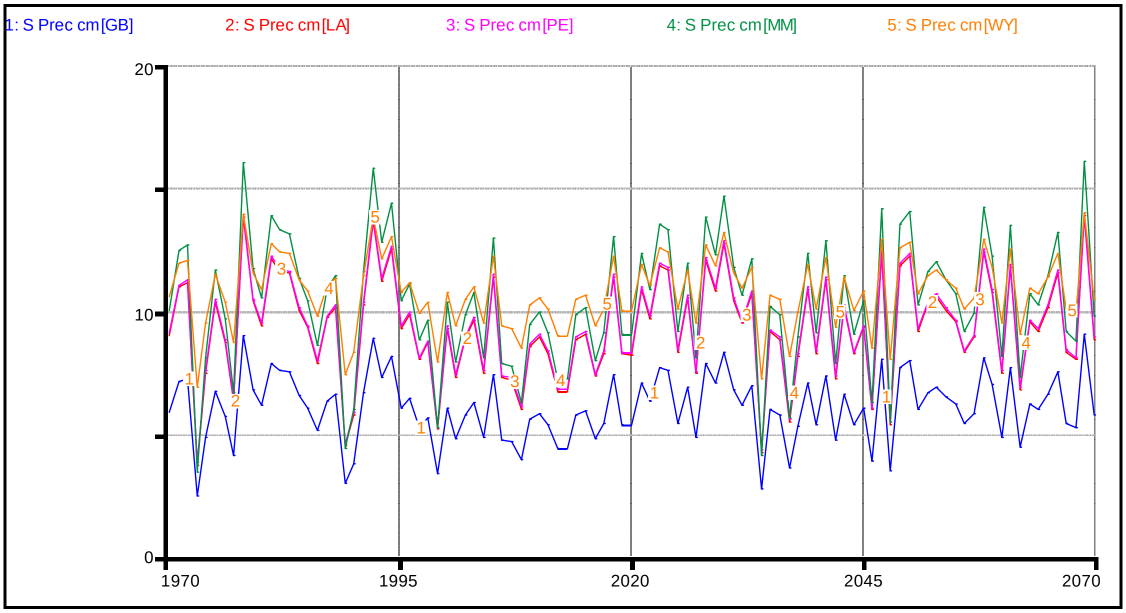


Figure 6.13. Simulated summer precipitation (cm) in each bison winter range. Simulation Run #2. Random precipitation sequence was synchronous among winter bison ranges.

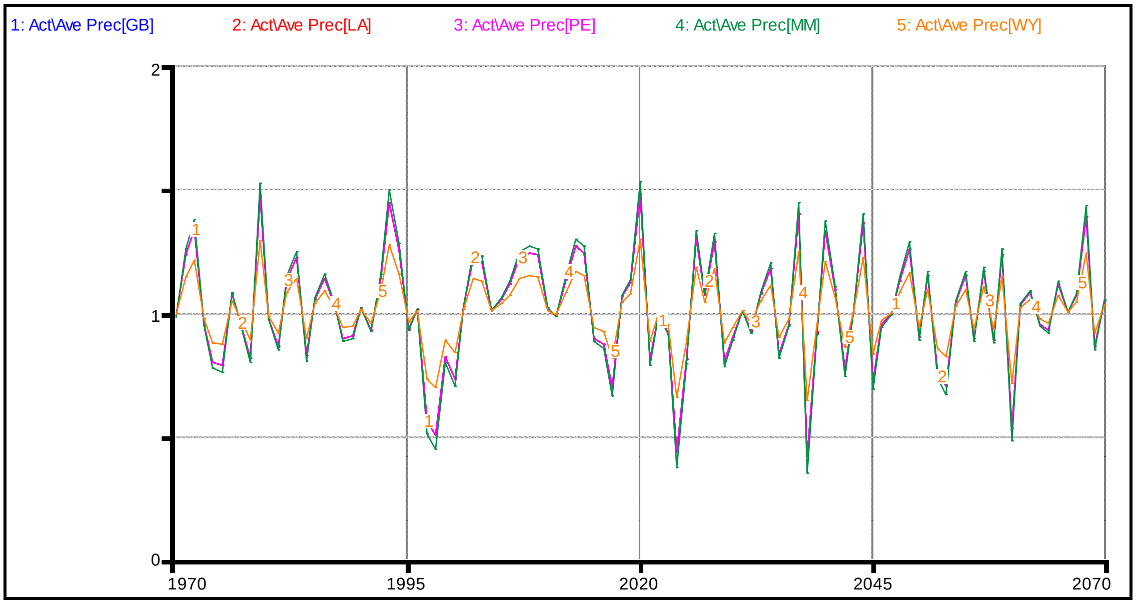


Figure 6.14. Simulated ratio of actual to average summer precipitation in each bison winter range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

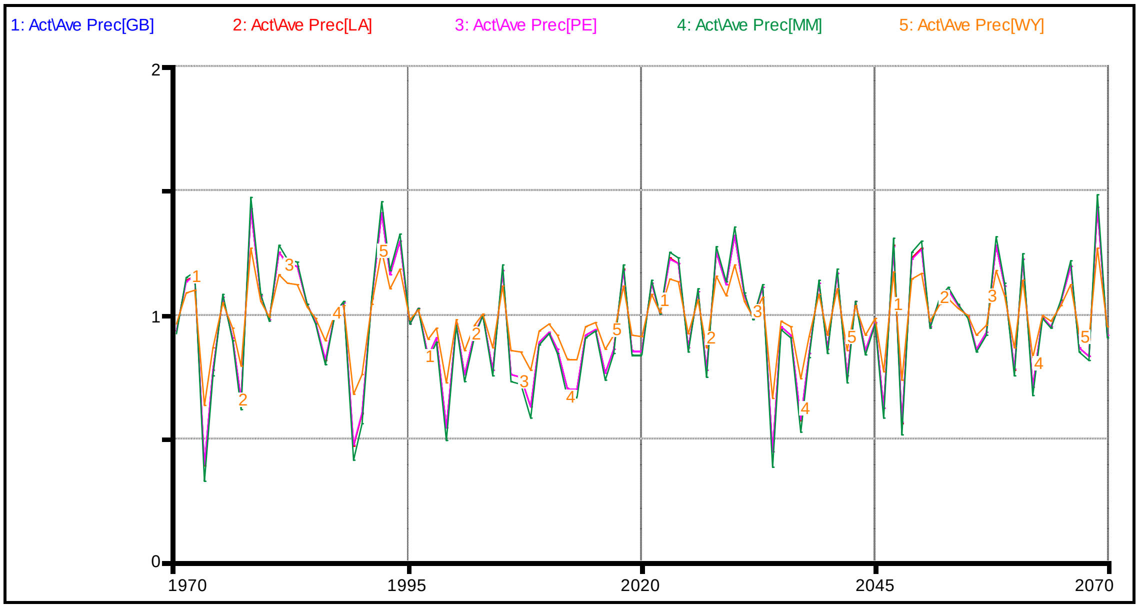


Figure 6.15. Simulated ratio of actual to average summer precipitation in each bison winter range. Simulation Run #2. Random precipitation sequence was synchronous among winter bison ranges.

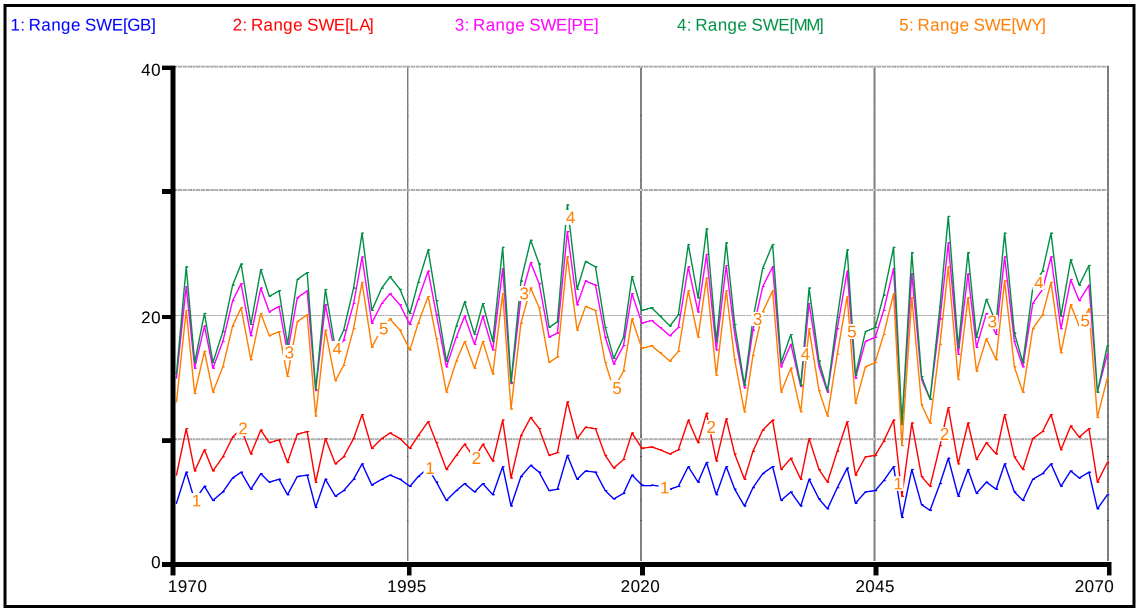


Figure 6.16. Simulated snow water equivalence (SWE) in each range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

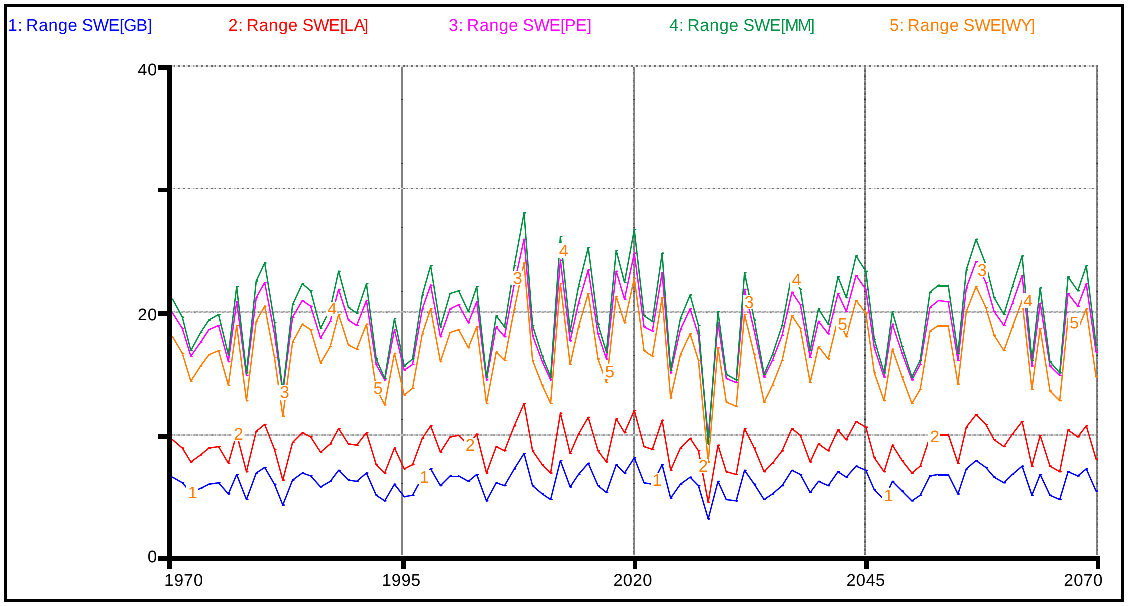


Figure 6.17. Simulated snow water equivalence (SWE) in each range. Simulation Run #2. Random precipitation sequence was synchronous among winter bison ranges.

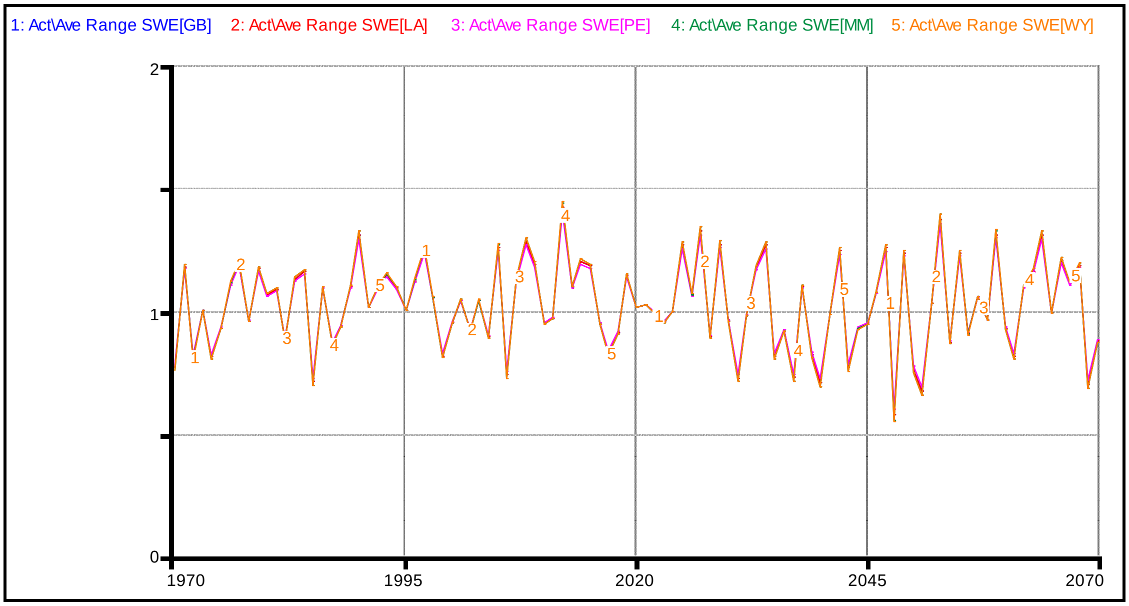


Figure 6.18. Simulated ratio of actual to average snow water equivalence in each range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

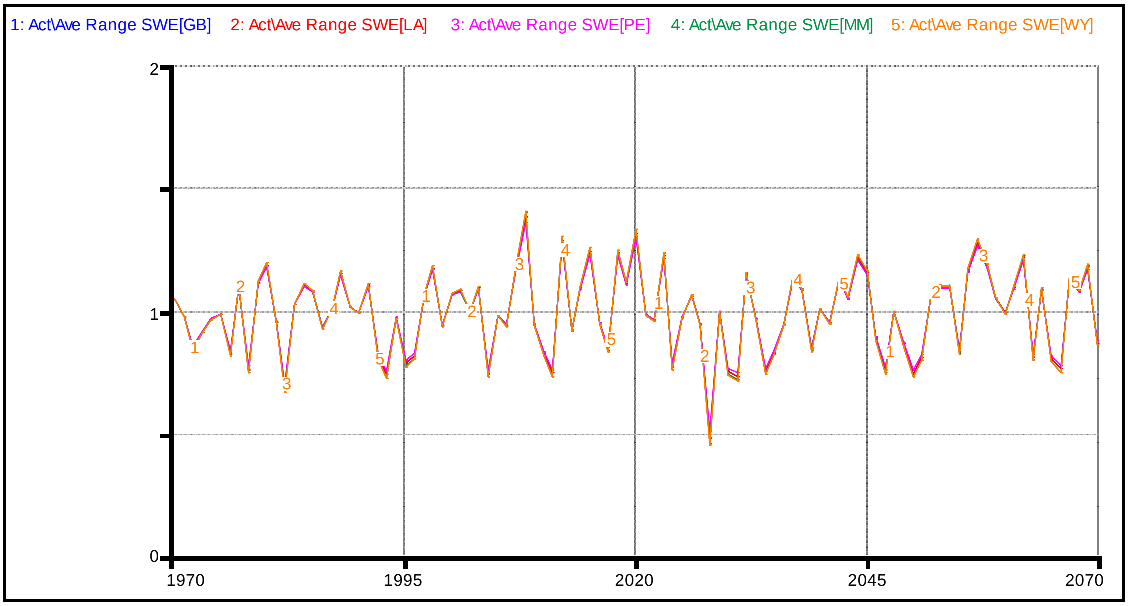


Figure 6.19. Simulated ratio of actual to average snow water equivalence in each winter range. Simulation Run #1. Random precipitation sequence was synchronous among winter bison ranges.

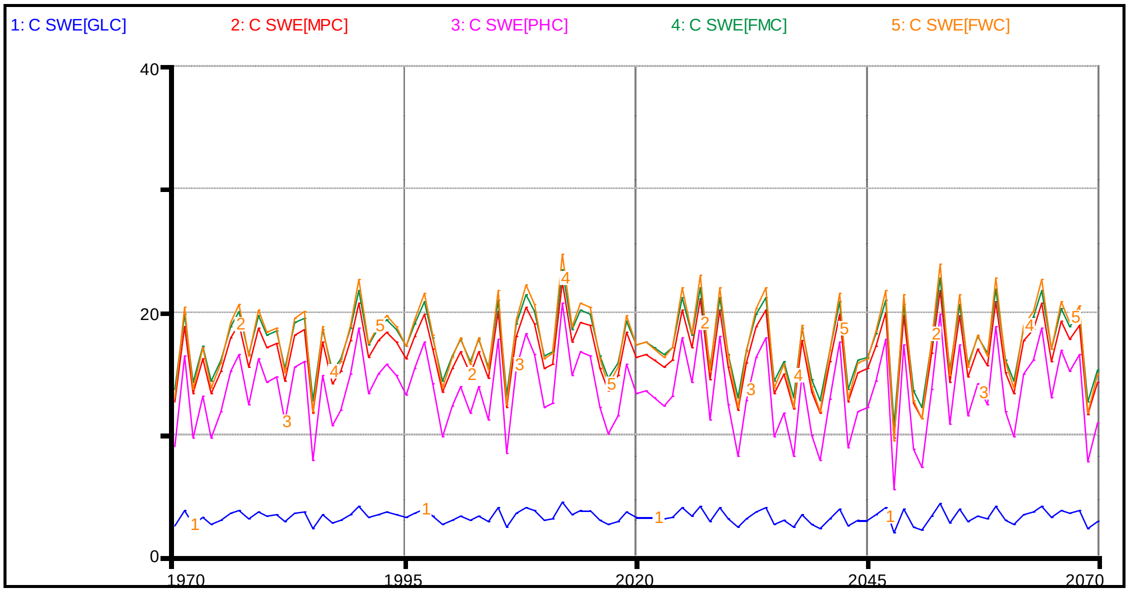


Figure 6.20. Simulated snow water equivalence (SWE) in each corridor. Simulation Run #1. Random precipitation sequence was synchronous among corridor routes.

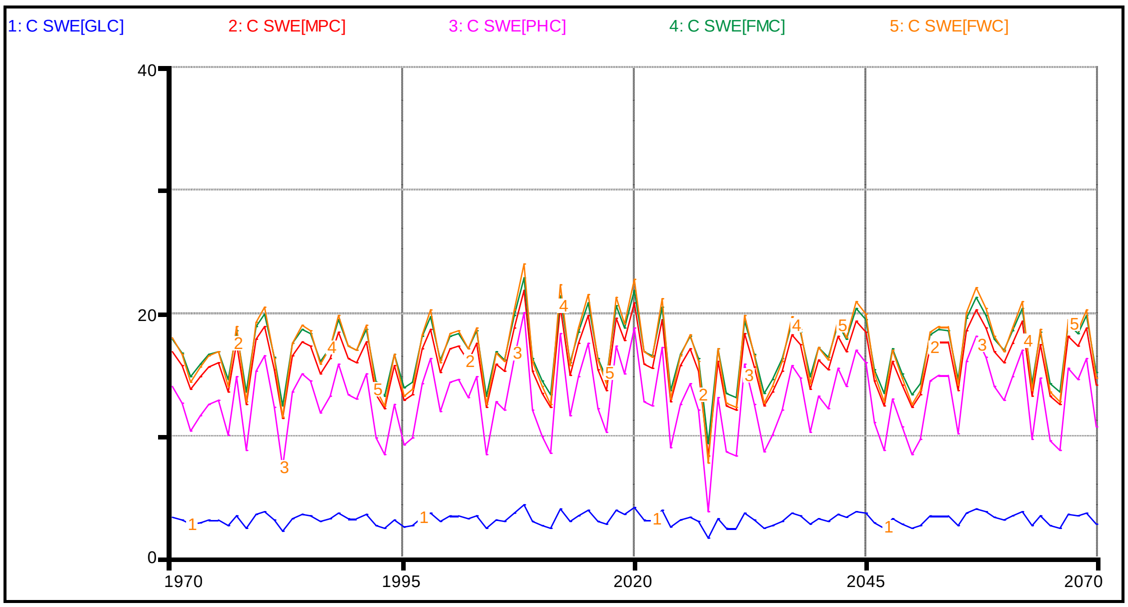


Figure 6.21. Simulated snow water equivalence (SWE) in each corridor. Simulation Run #2. Random precipitation sequence was synchronous among corridor routes.

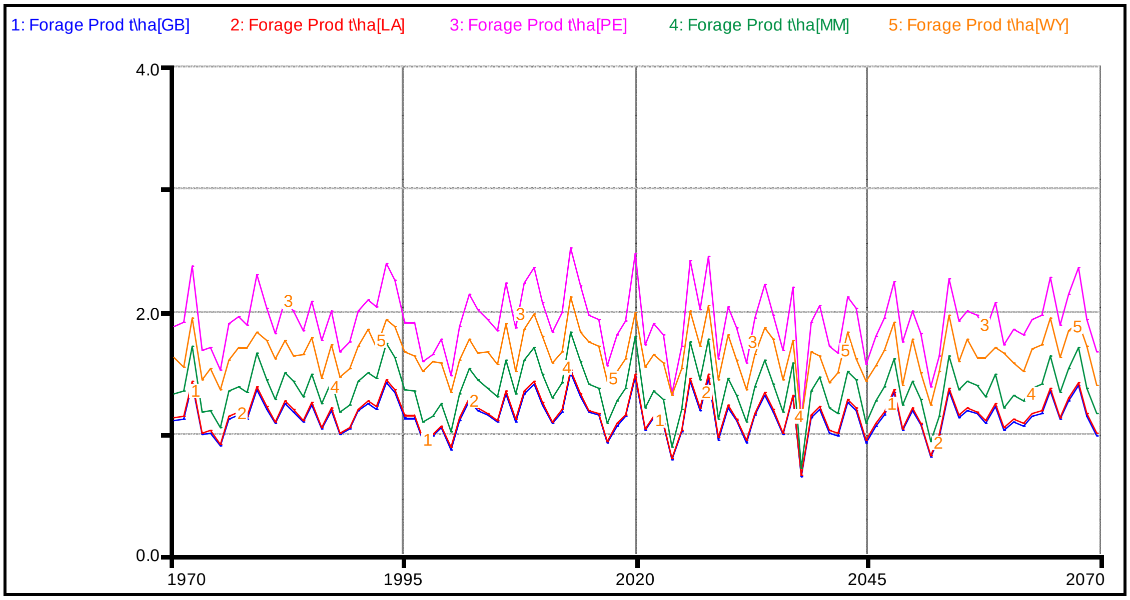


Figure 6.22. Simulated annual winter range forage production rate (tonne/hectare/year). Simulation Run #1. Random precipitation sequence was synchronous among corridor routes.

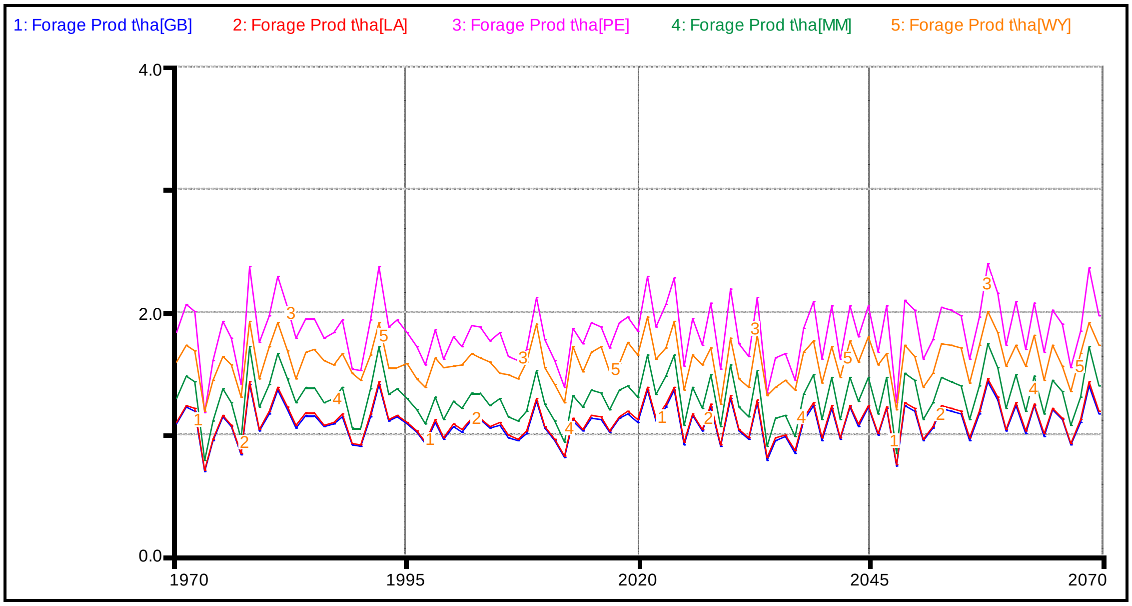


Figure 6.23. Simulated annual winter range forage production rate (tonne/hectare/year). Simulation Run #2. Random precipitation sequence was synchronous among corridor routes.

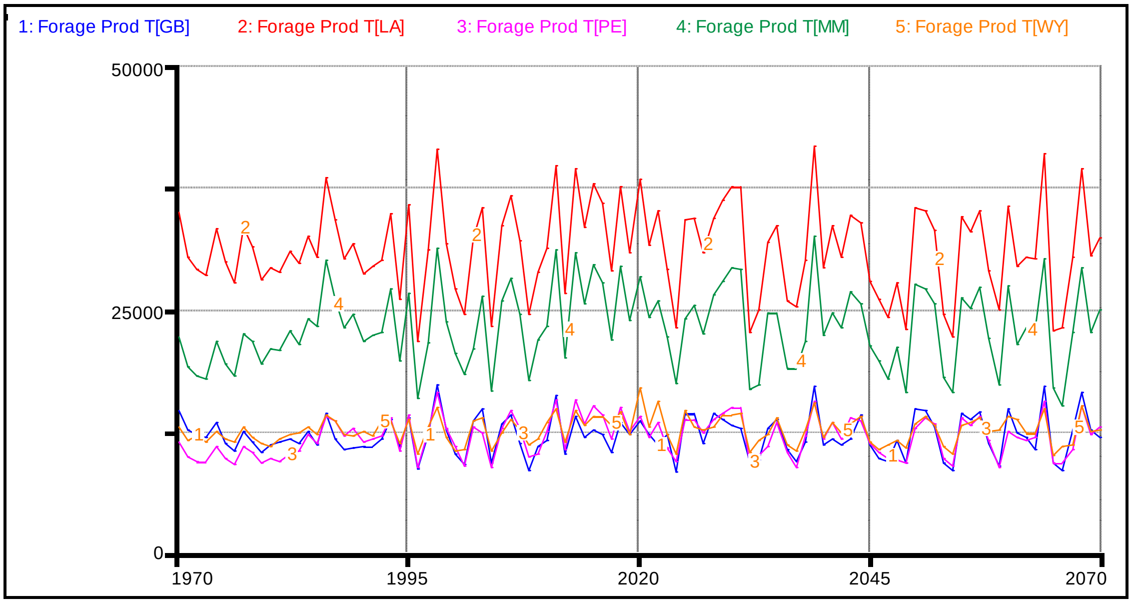


Figure 6.24. Simulated annual forage production (tonne) on winter ranges. Simulation Run #1 was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

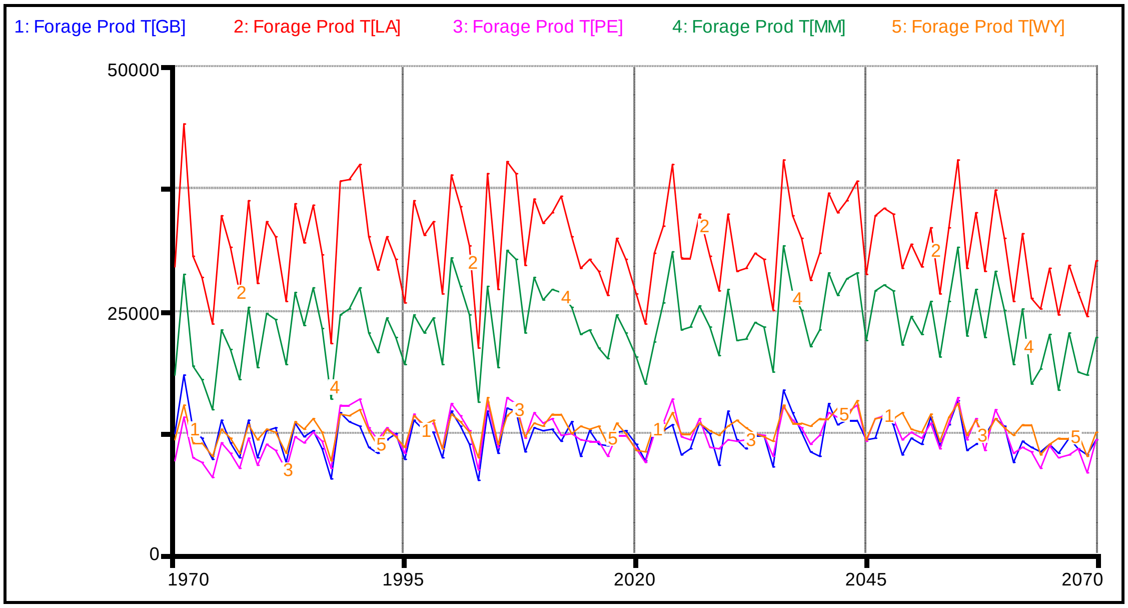


Figure 6.25. Simulated annual forage production (tonne) on winter ranges. Simulation Run #2 was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

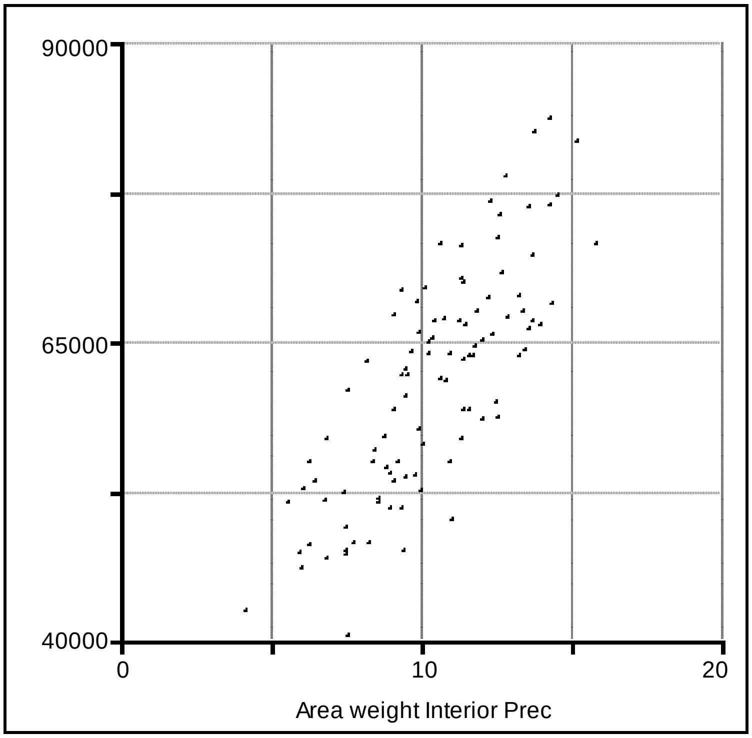


Figure 6.26. Simulated relationship between forage production (tonne; Y-axis) and area-weighted summer precipitation (cm) of interior winter ranges. Simulation was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

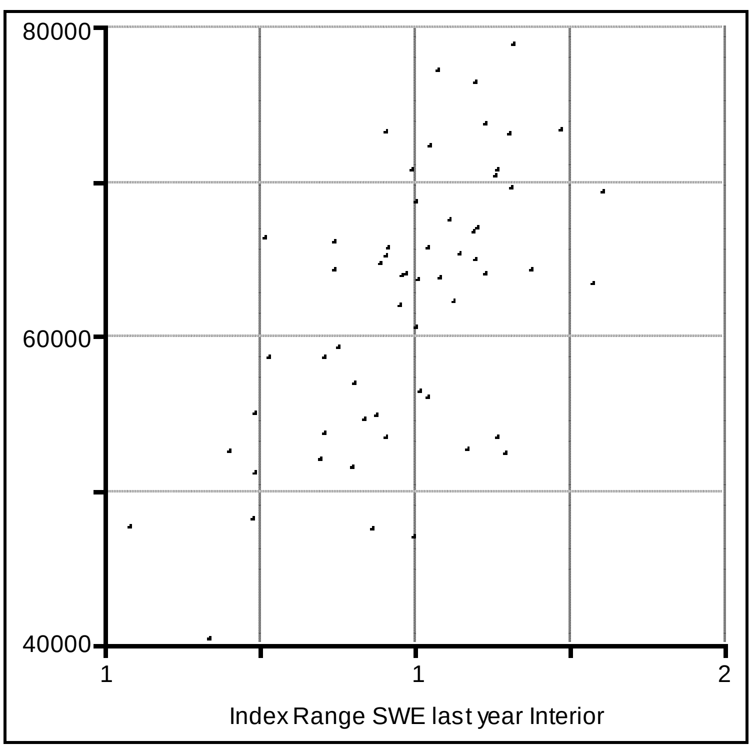


Figure 6.27. Simulated relationship between forage production (tonne; Y-axis) and previous winter snowpack (measured in SWE) of interior ranges. Simulation was 100 years and reflected a synchronous pattern of random precipitation for each winter range.

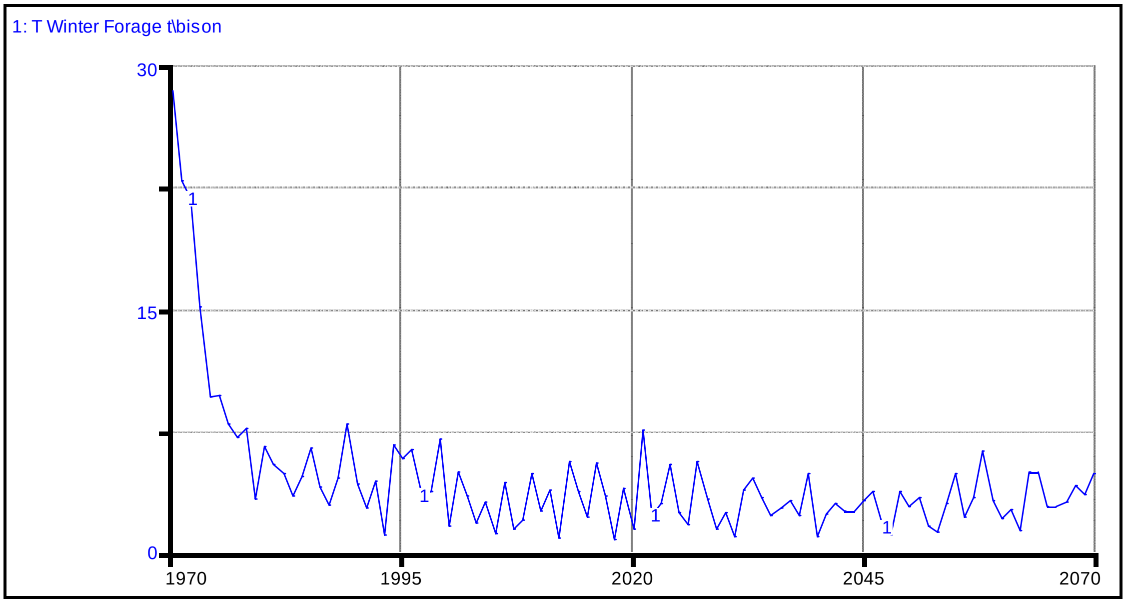


Figure 6.28. Simulated temporal pattern in winter forage availability (tonne forage (dry weight) per bison) using majority average model. The initial reduction in forage availability reflects the initialization of the model with the 1970 populations and their subsequent population growth.

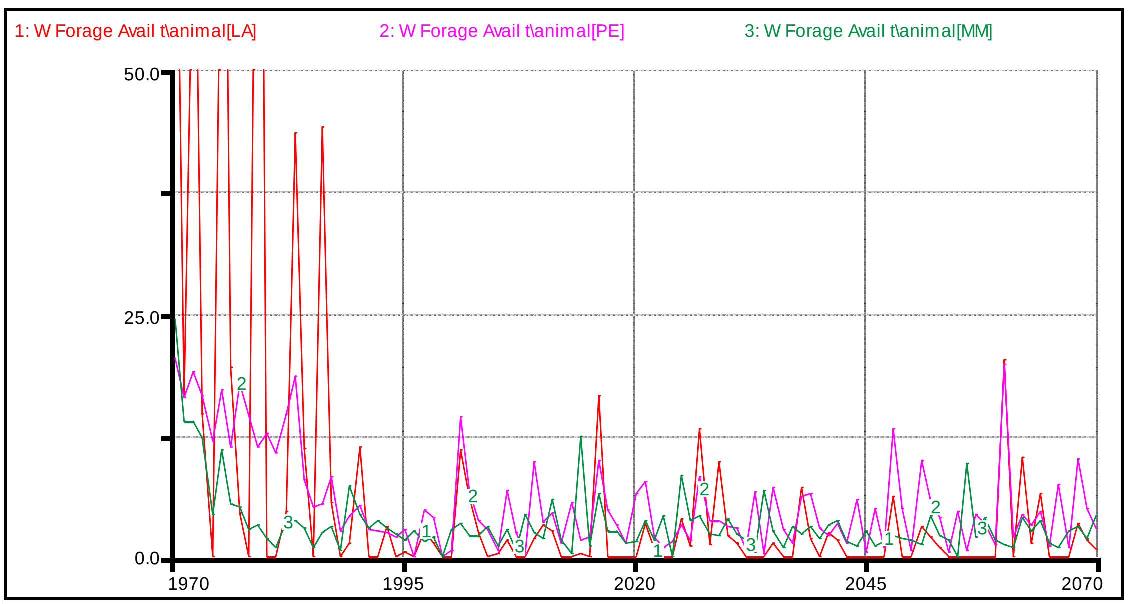


Figure 6.29. Simulated temporal pattern in winter forage availability (tonne forage (dry weight) per bison) using majority average model. The initial reduction in forage availability reflects the initialization of the model with the 1970 populations and their subsequent population growth. High inter-annual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

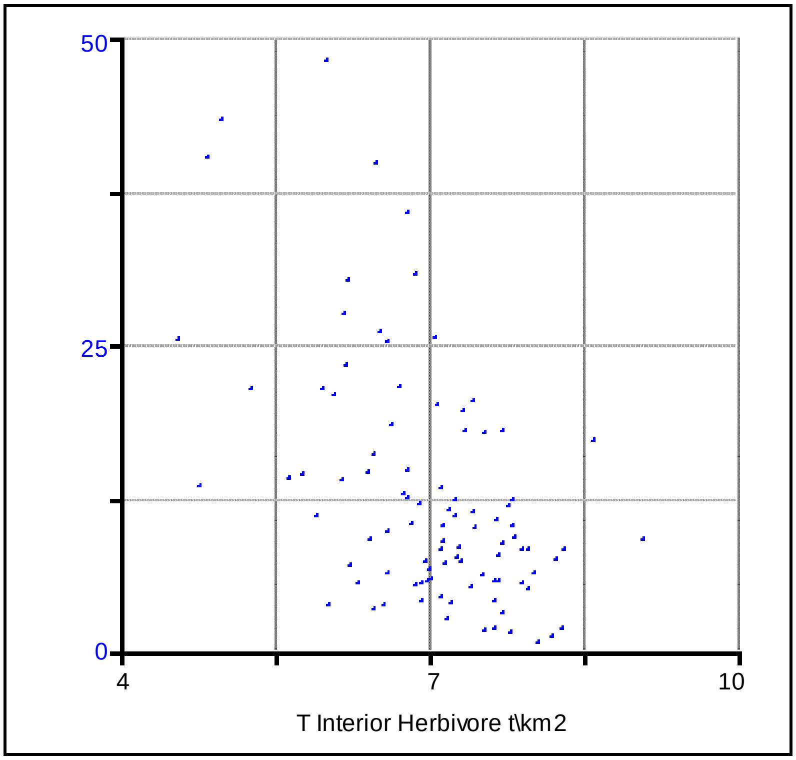


Figure 6.30. Simulated relationship between herbivore (bison and elk) biomass density (x axis; tonne/km^2) and availability of bison winter forage availability (tonne/bison; y-axis) for all of the interior ranges. Simulation based on majority average model.

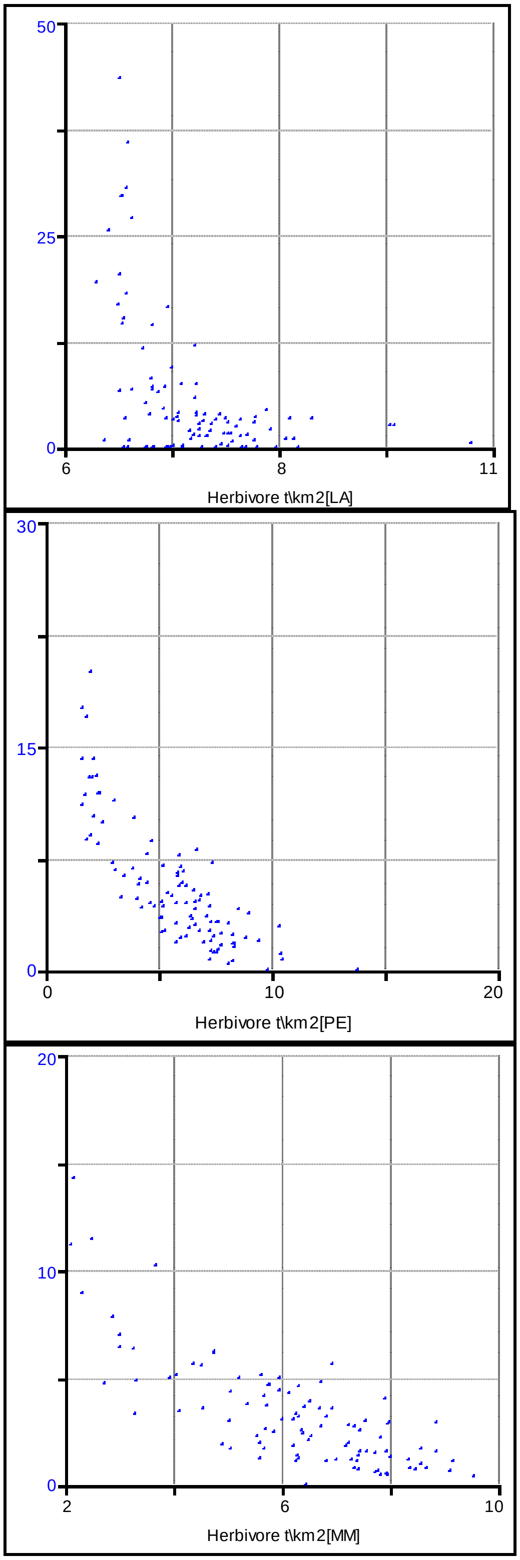


Figure 6.31. Simulated relationship between herbivore (bison and elk) biomass density (x axis; tonne/km^2) and availability of bison winter forage (tonne/bison; y-axis) for each of the interior ranges. Lamar (upper), Pelican (center), and Mary Mountain (lower). Simulation based on majority average model.

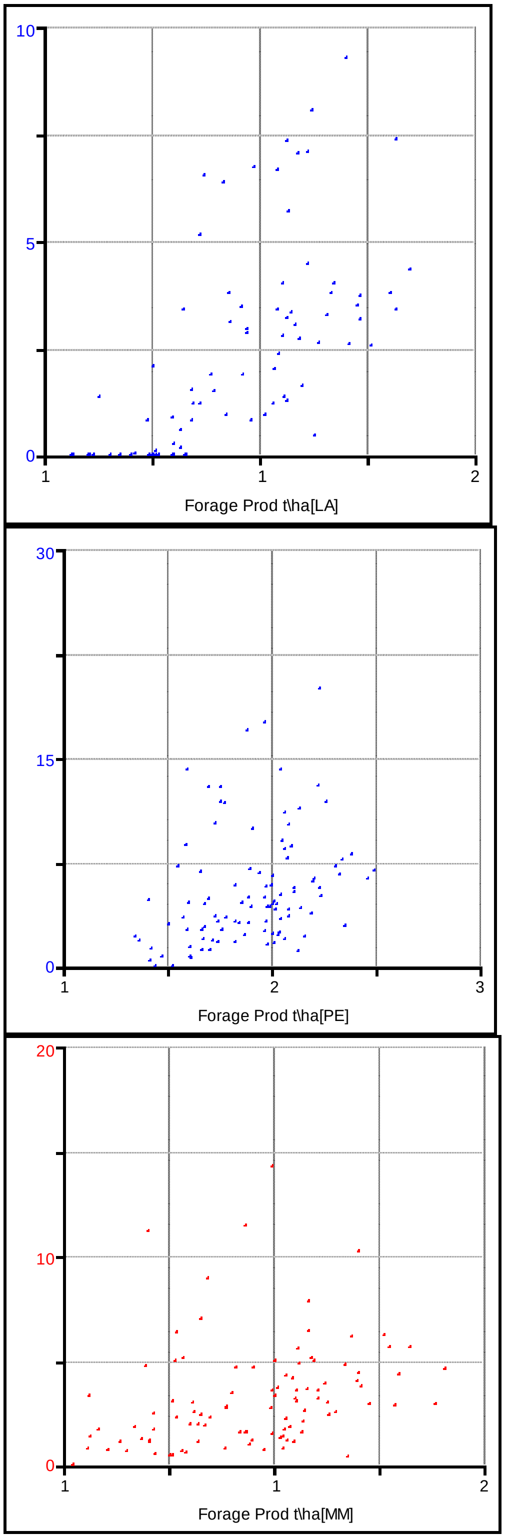


Figure 6.32. Simulated relationship between forage production (x axis; tonne/ha) and availability of bison winter forage availability (tonne/bison; y-axis) for each of the interior ranges. Lamar (upper), Pelican (center), and Mary Mountain (lower). Simulation based on majority average model.

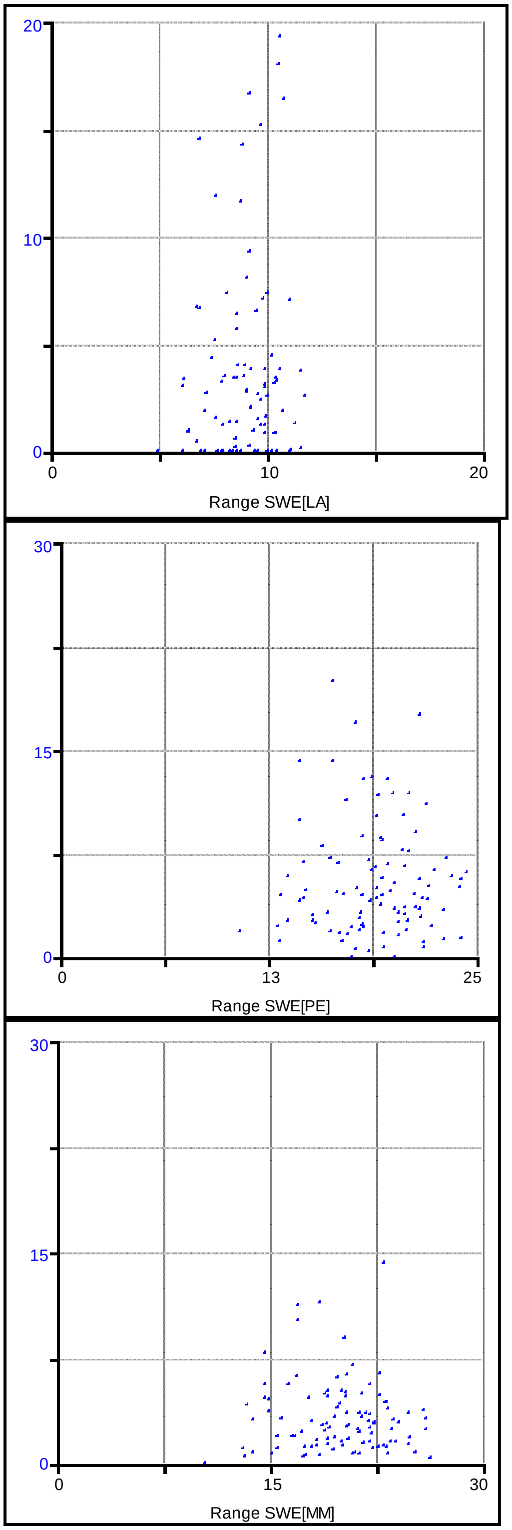
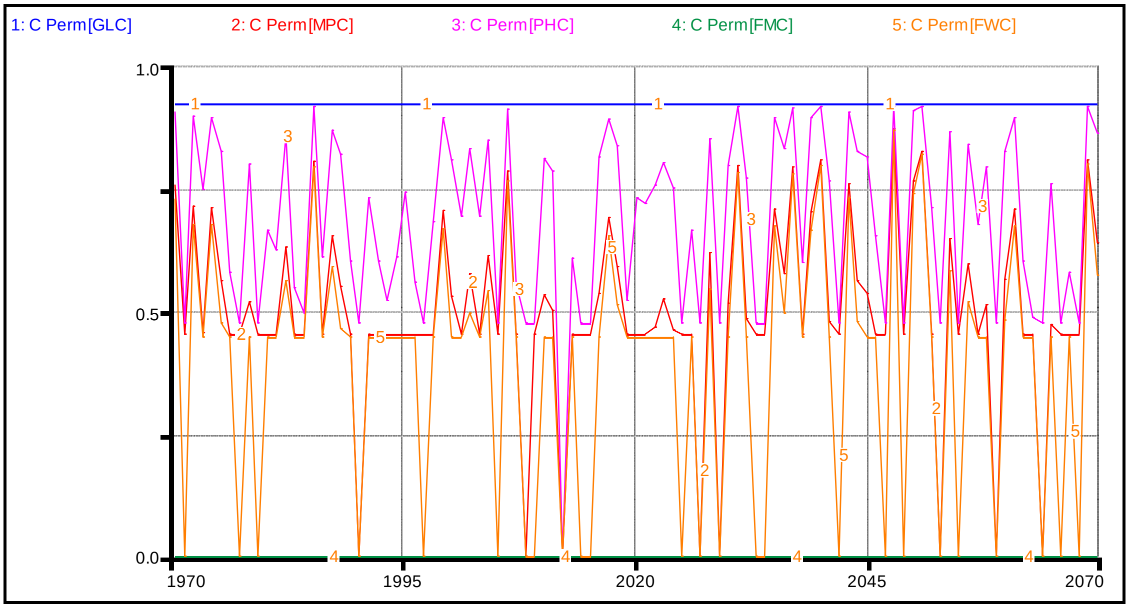


Figure 6.33. Simulated relationship snowpack water equivalent (x axis; cm) and availability of bison winter forage availability (tonne/bison; y-axis) for each of the interior ranges. Lamar (upper), Pelican (center), and Mary Mountain (lower). Simulation based on majority average model.



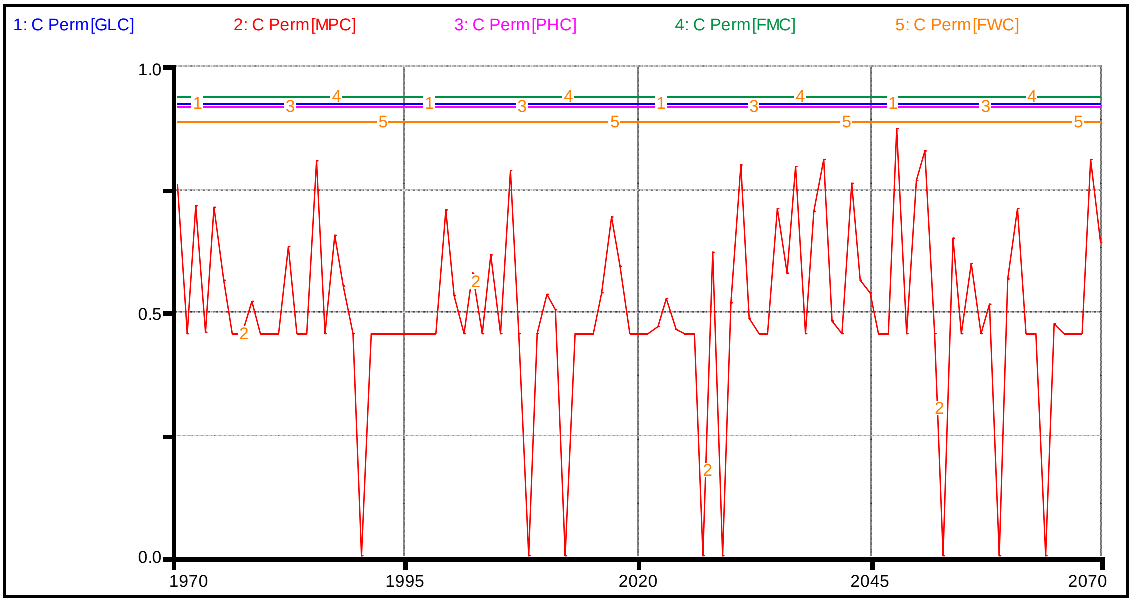
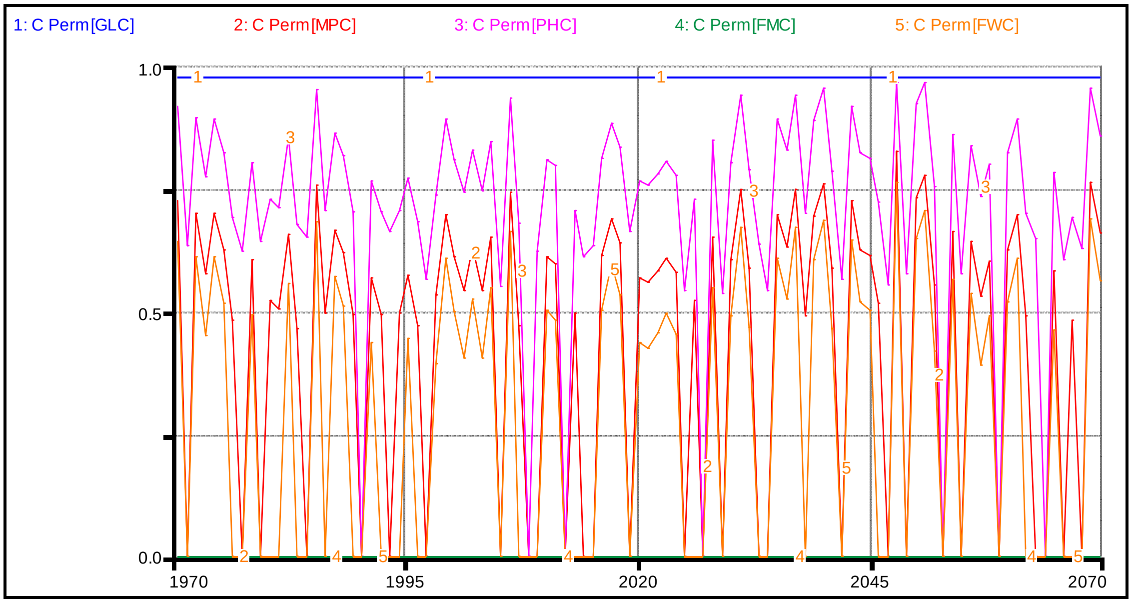


Figure 6.34. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided by Key Informant Group 1. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road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



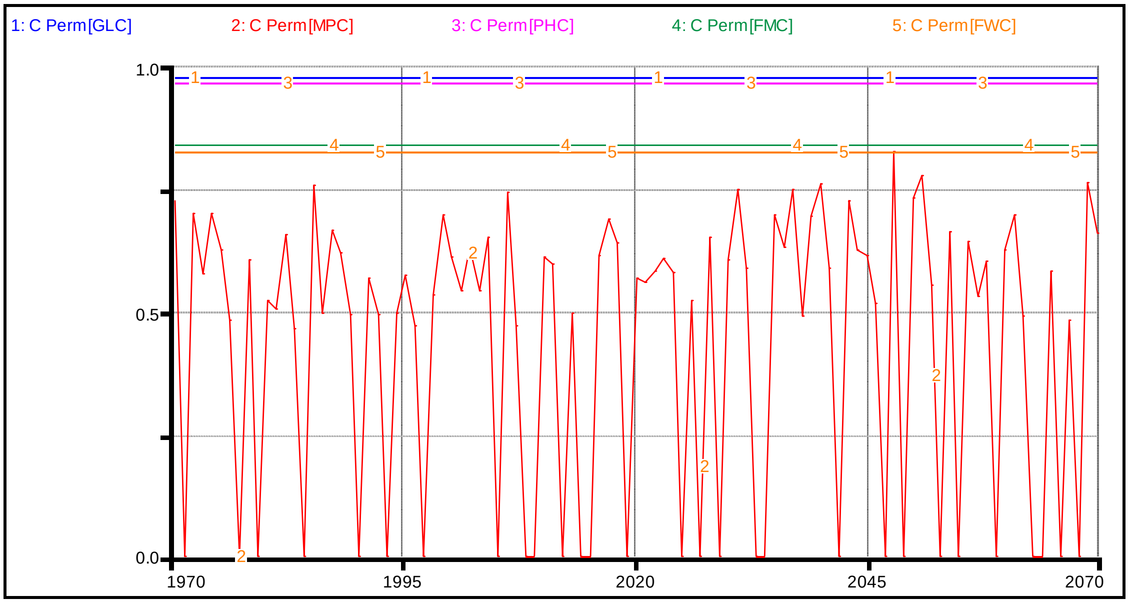
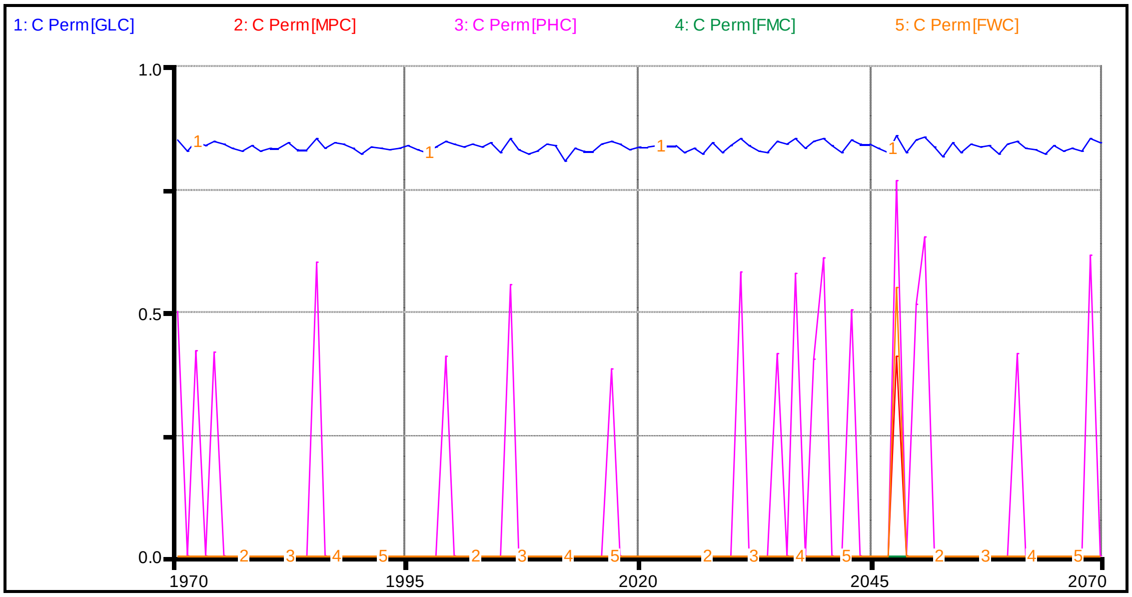


Figure 6.36. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided by Key Informant Group 3. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road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



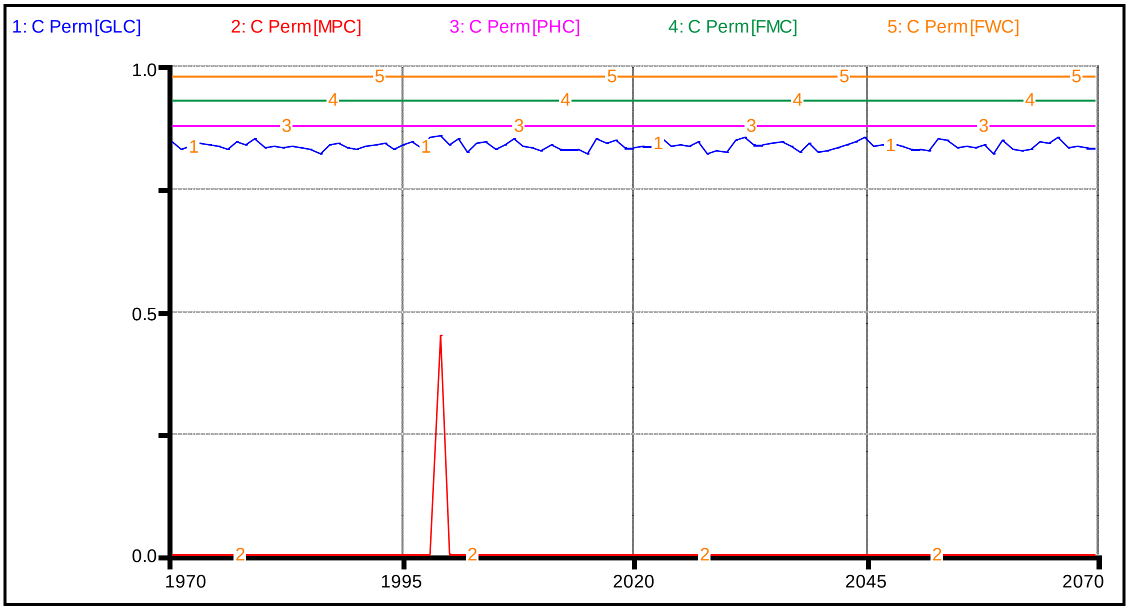
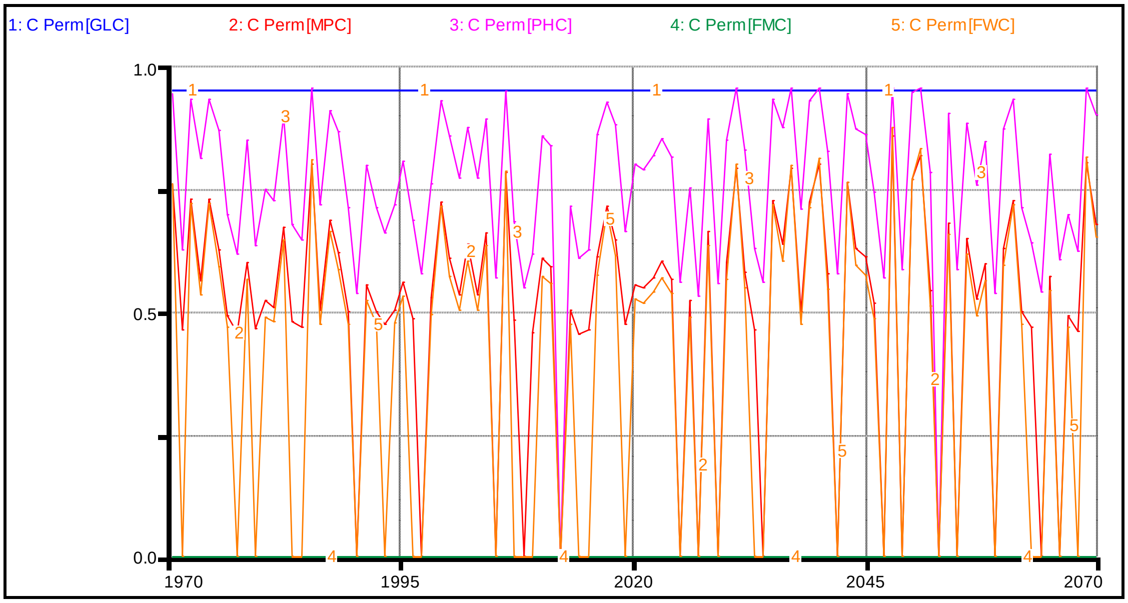


Figure 6.37. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided by Key Informant Group 4. The upper graph represents a scenario without road grooming, whereas the lower graph reflects road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



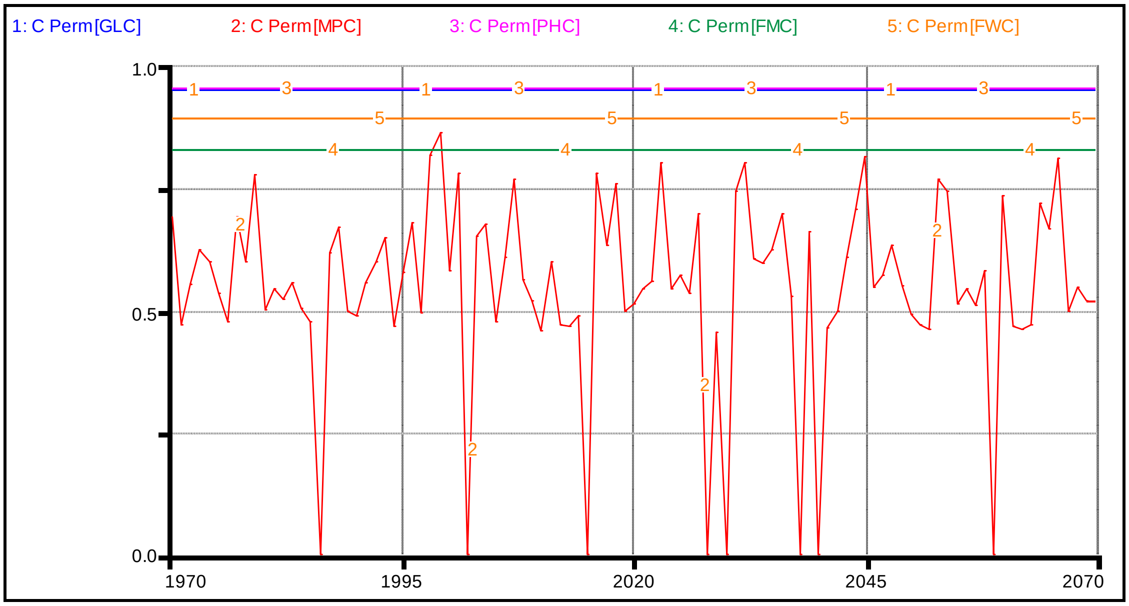


Figure 6.38. Simulated change in corridor permeability (0 represent no permeability and 1 represents complete permeability) based on corridor descriptor weighting values provided from Majority Average Group (average of Group 1, 2, and 3. The upper graph represents a scenario without road grooming, whereas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

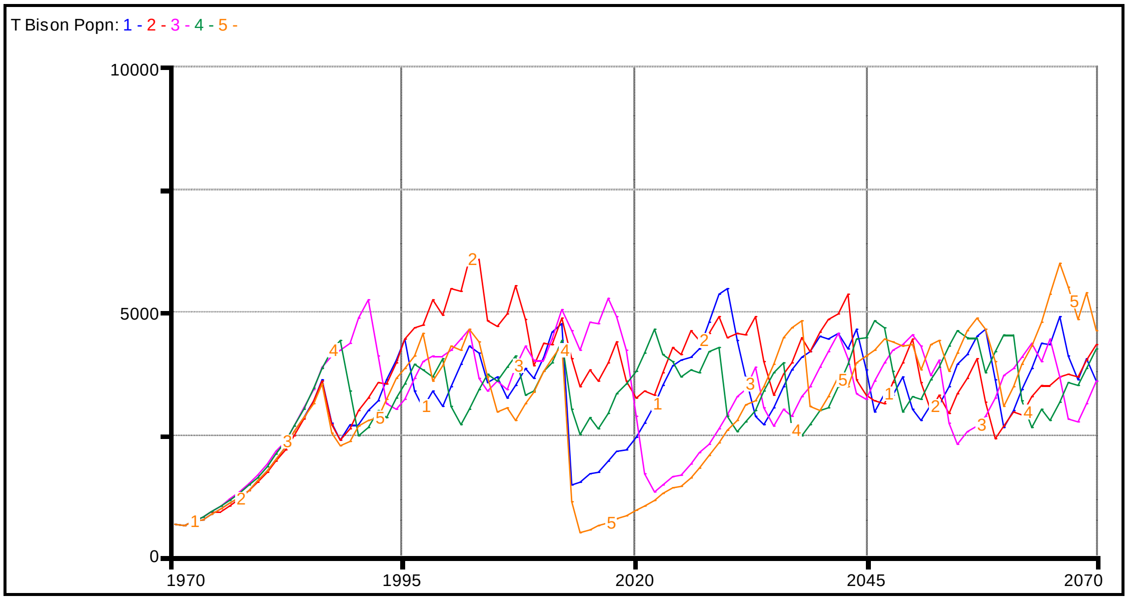


Figure 6.39. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #1. This scenario involves no winter road grooming.

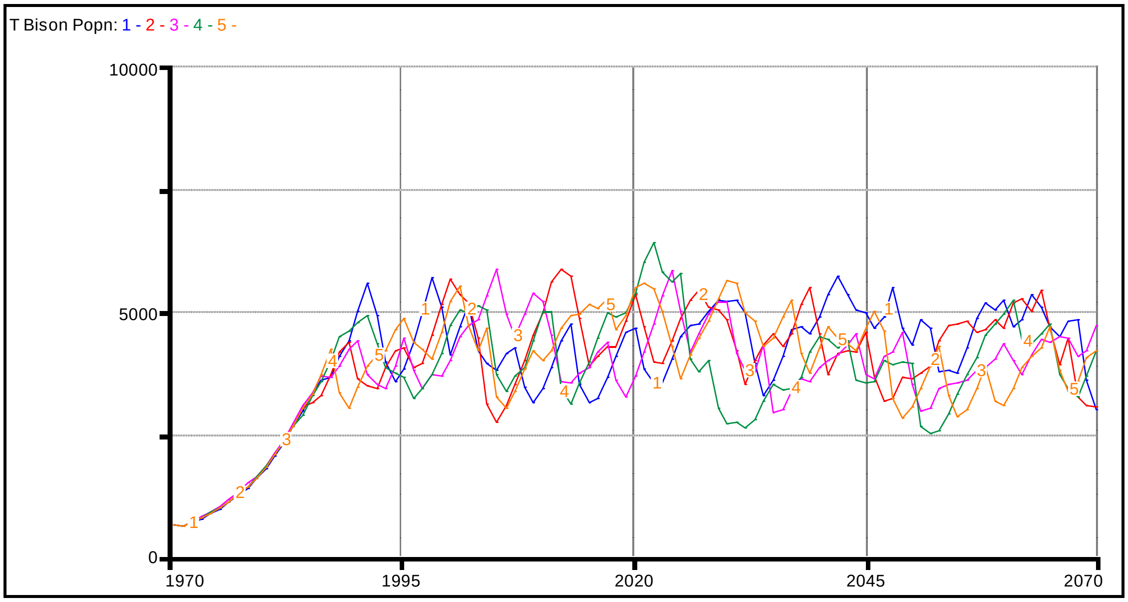


Figure 6.40. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #1. This scenario includes winter road grooming along corridors PHC, FMC, and FWC.

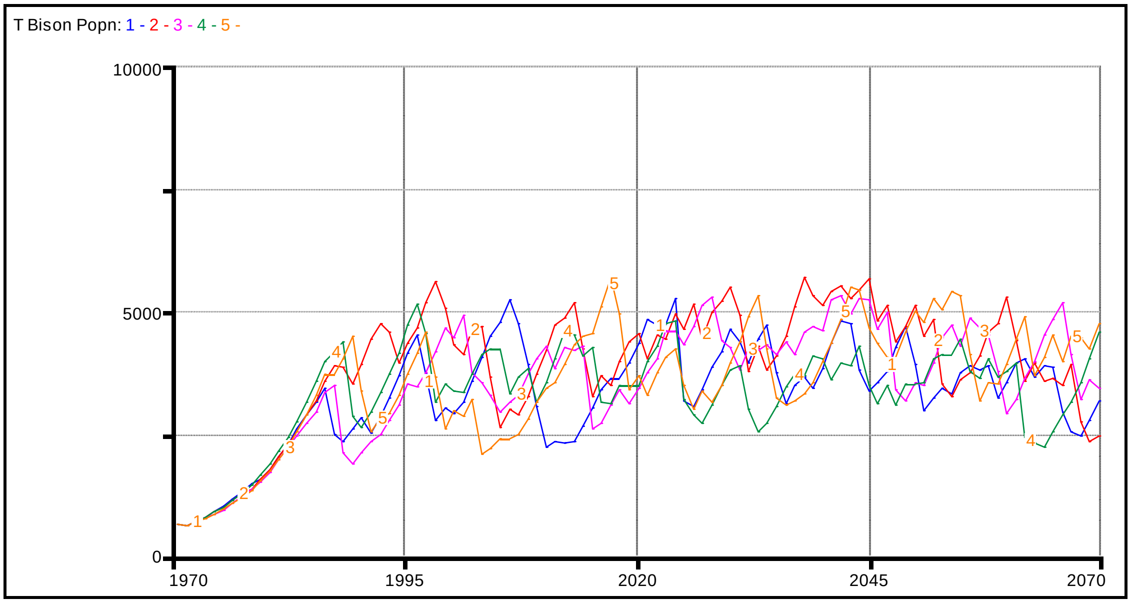


Figure 6.41. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #2. This scenario does not involve winter road grooming.

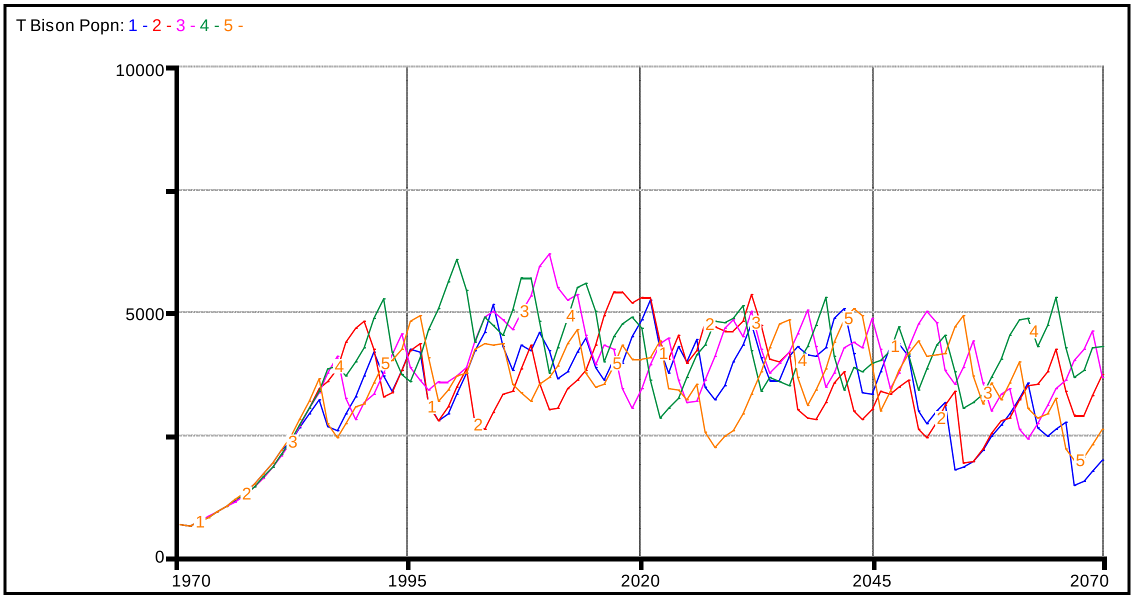


Figure 6.42. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #2. This scenario includes winter road grooming along corridors PHC, FMC, and FWC**.**

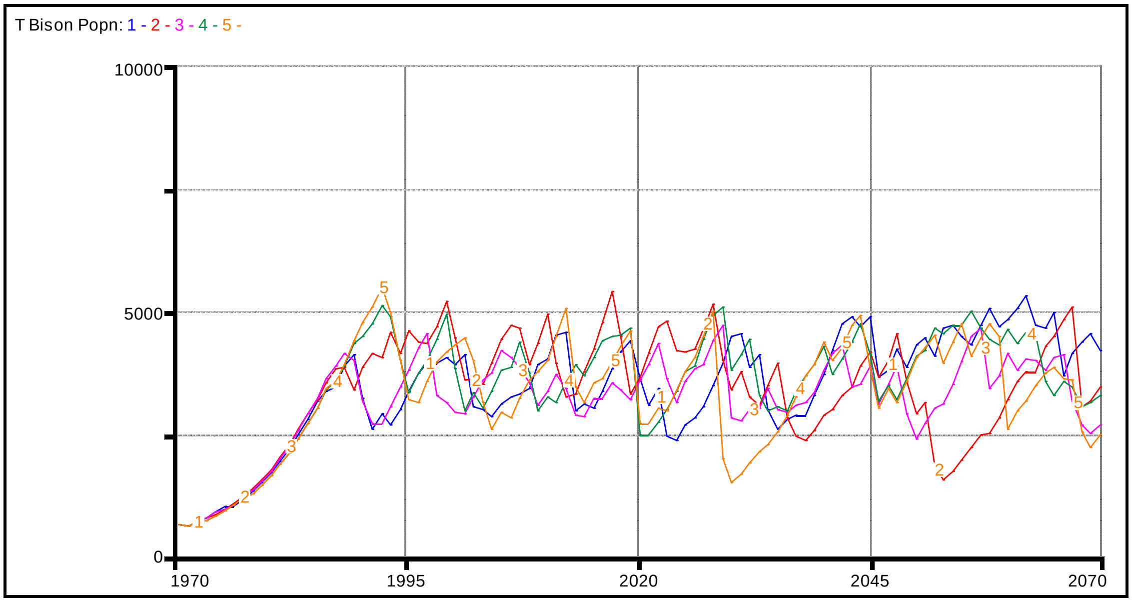


Figure 6.43. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #3. This scenario does not involve winter road grooming.

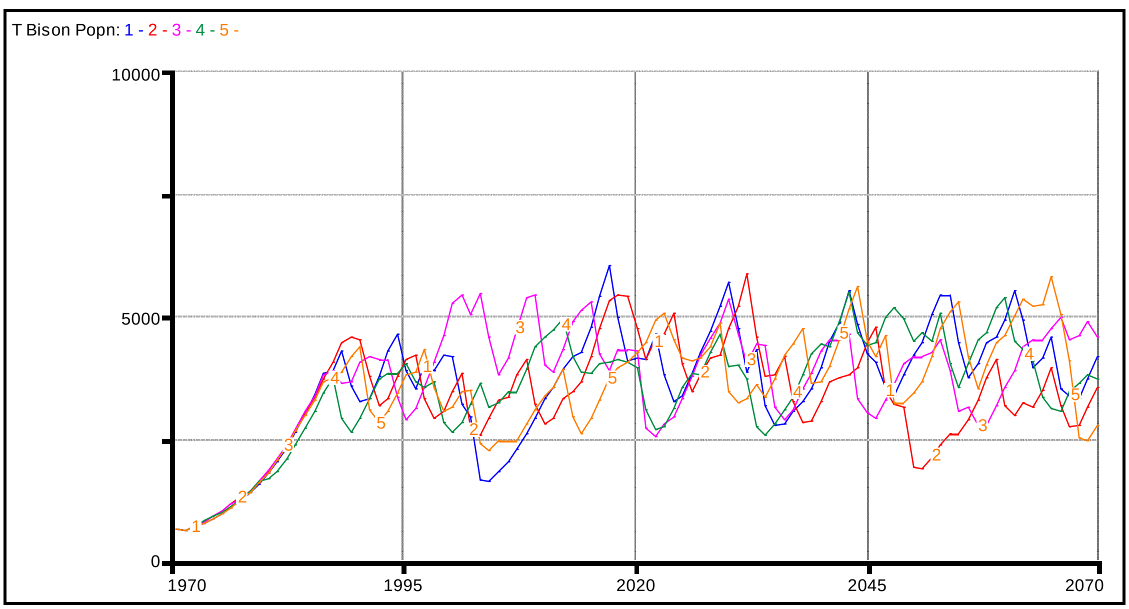


Figure 6.44. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #3. This scenario includes winter road grooming along corridors PHC, FMC, and FWC.

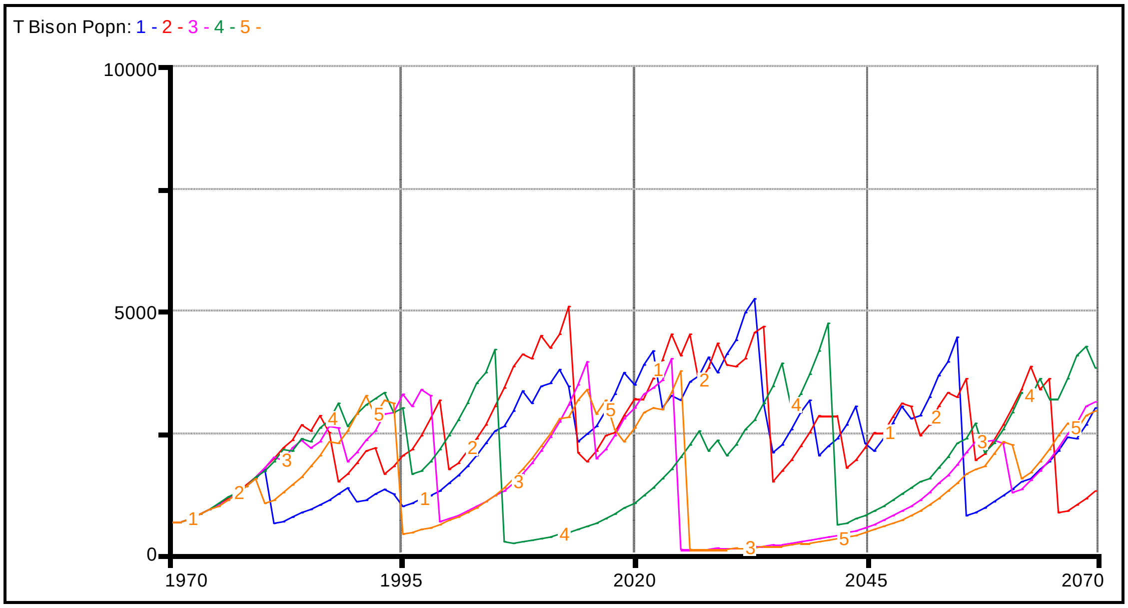


Figure 6.45. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #4. This scenario does not involve winter road grooming.

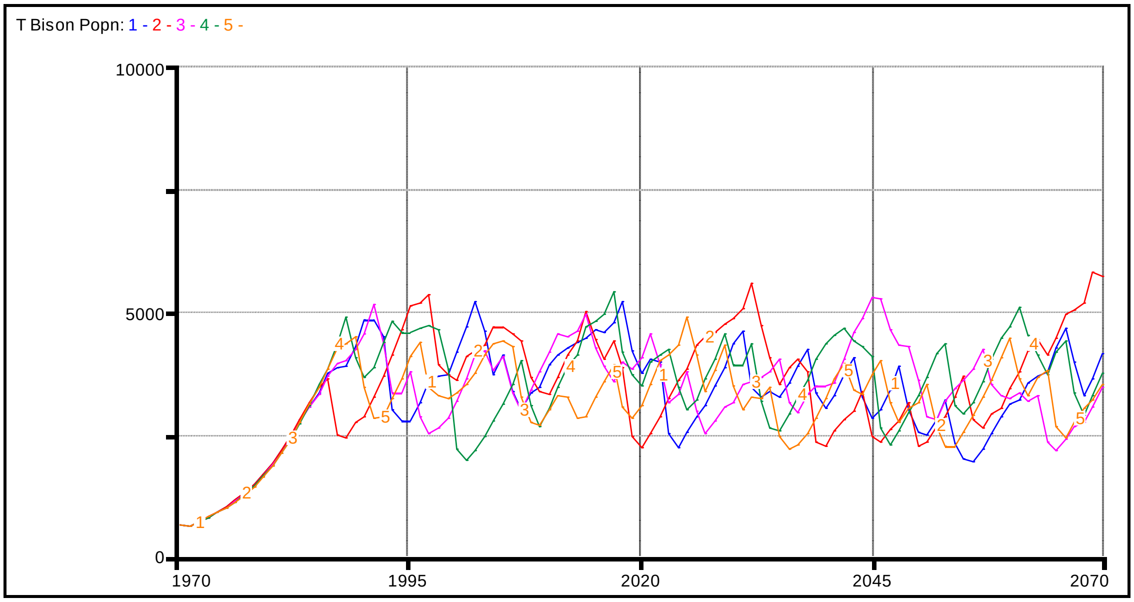


Figure 6.46. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Key Informant Group #4. This scenario includes winter road grooming along corridors PHC, FMC, and FWC.

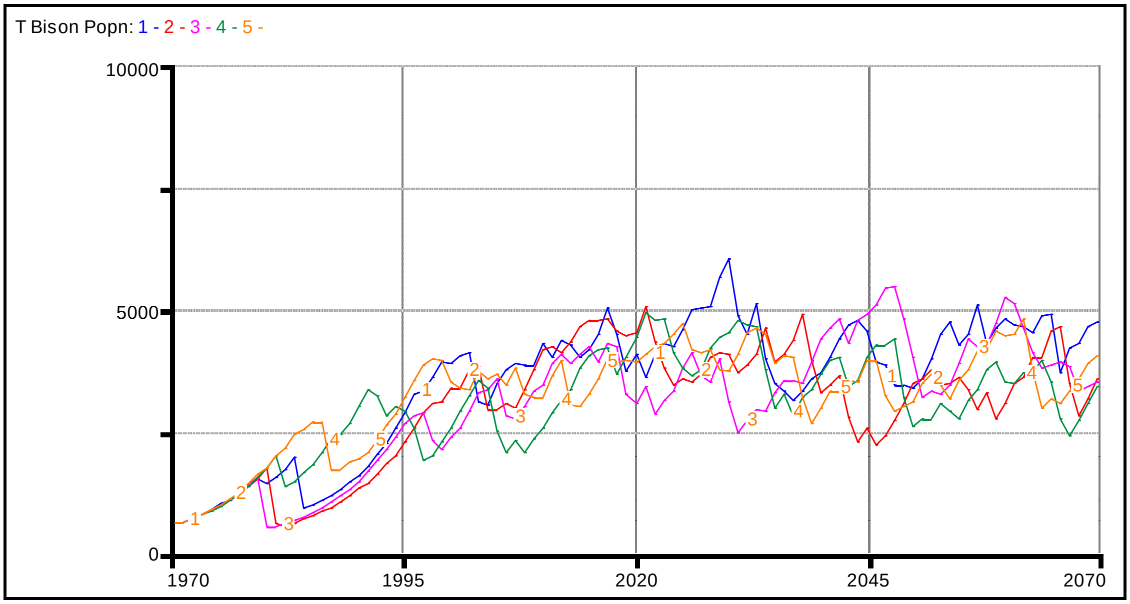


Figure 6.47. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Majority Average Model (average of Group 1, 2, and 3). This scenario does not involve winter road grooming.

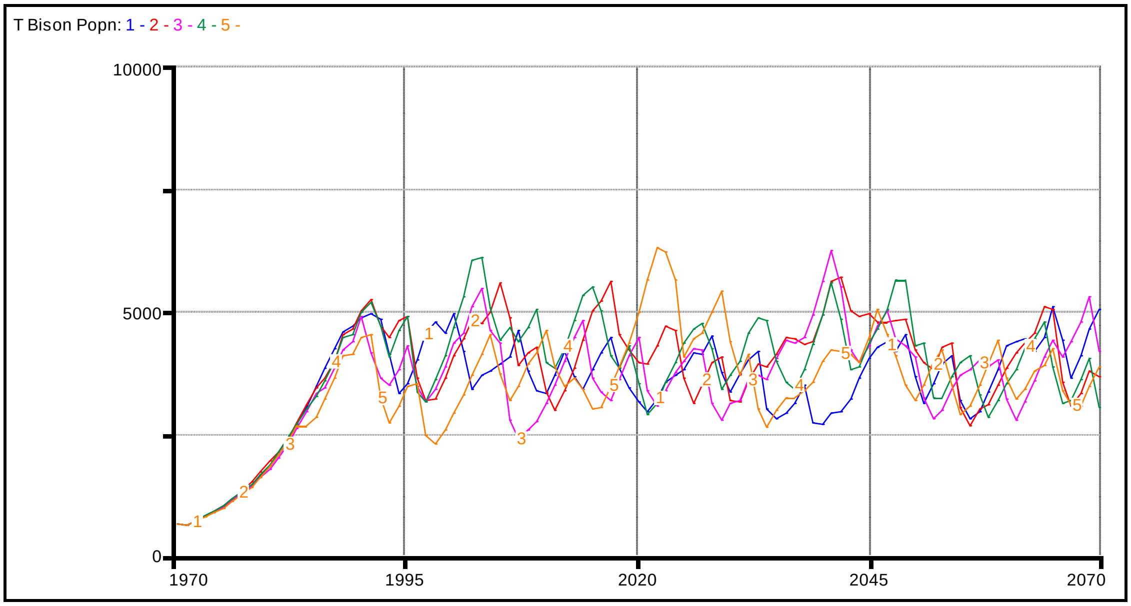
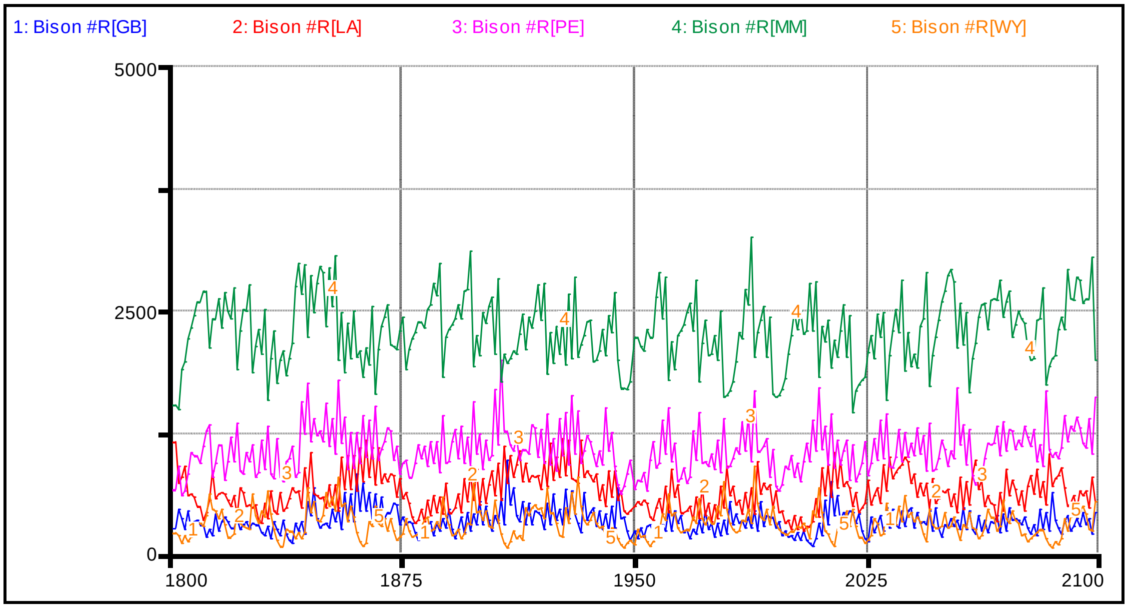


Figure 6.48. Simulated temporal variation (five 100 year simulations with random precipitation) in total YNP bison population based on input values of Majority Average Model (average of Group 1, 2, and 3). This scenario includes winter road grooming along corridors PHC, FMC, and FWC.



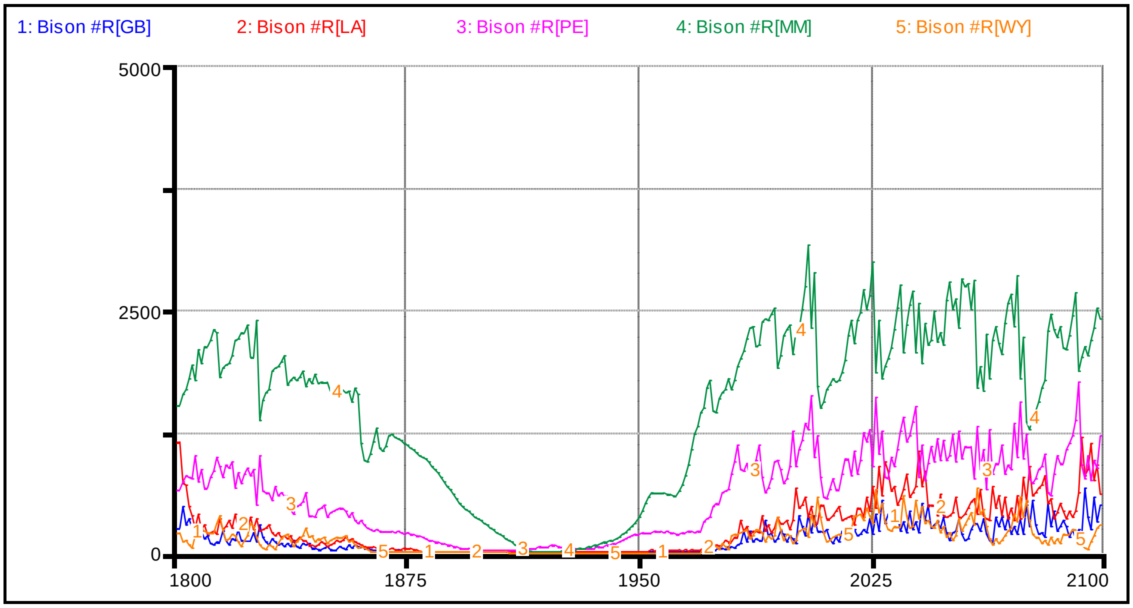
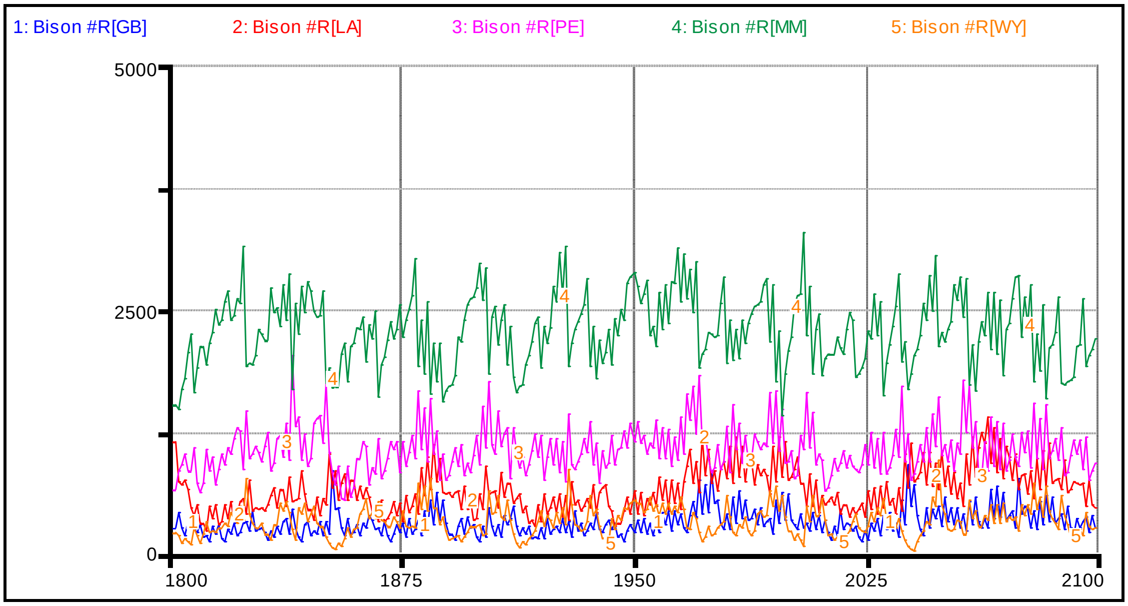


Figure 6.49. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #1. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



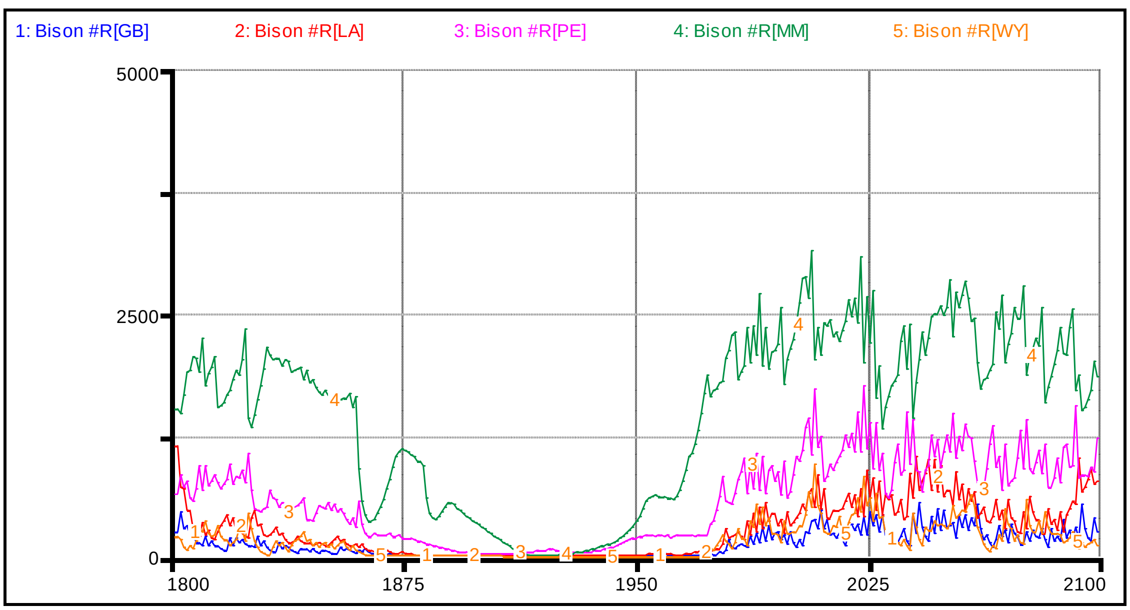
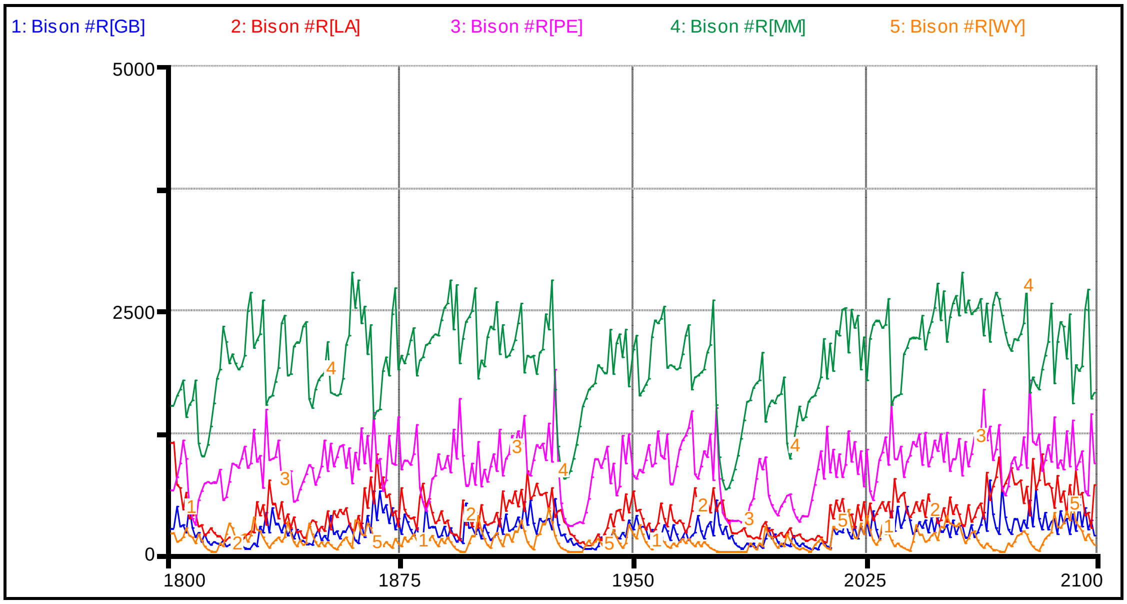


Figure 6.50. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #2. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



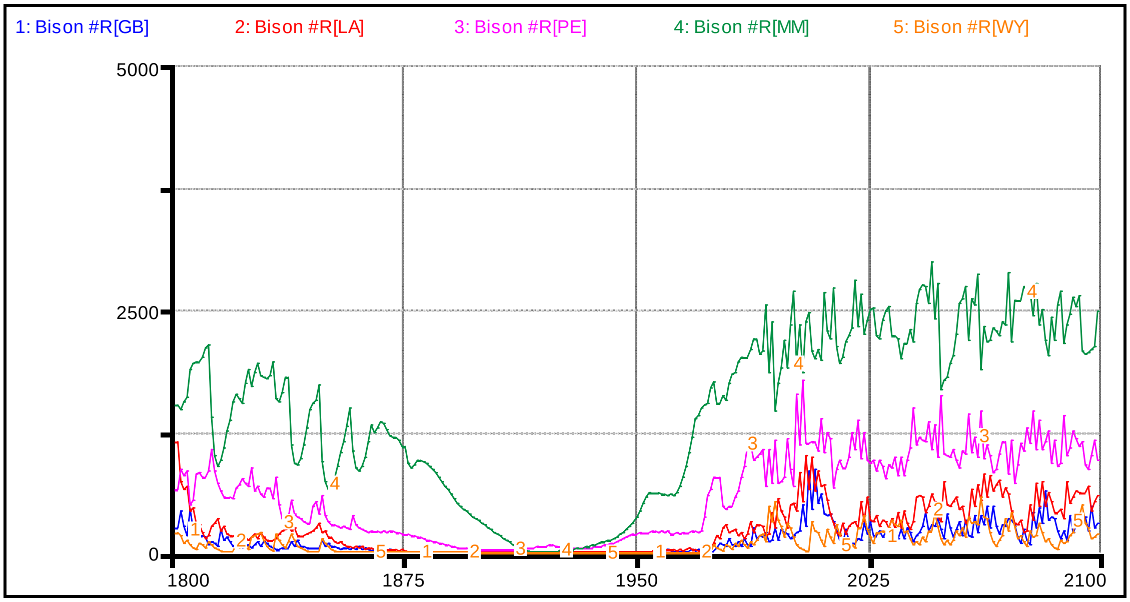
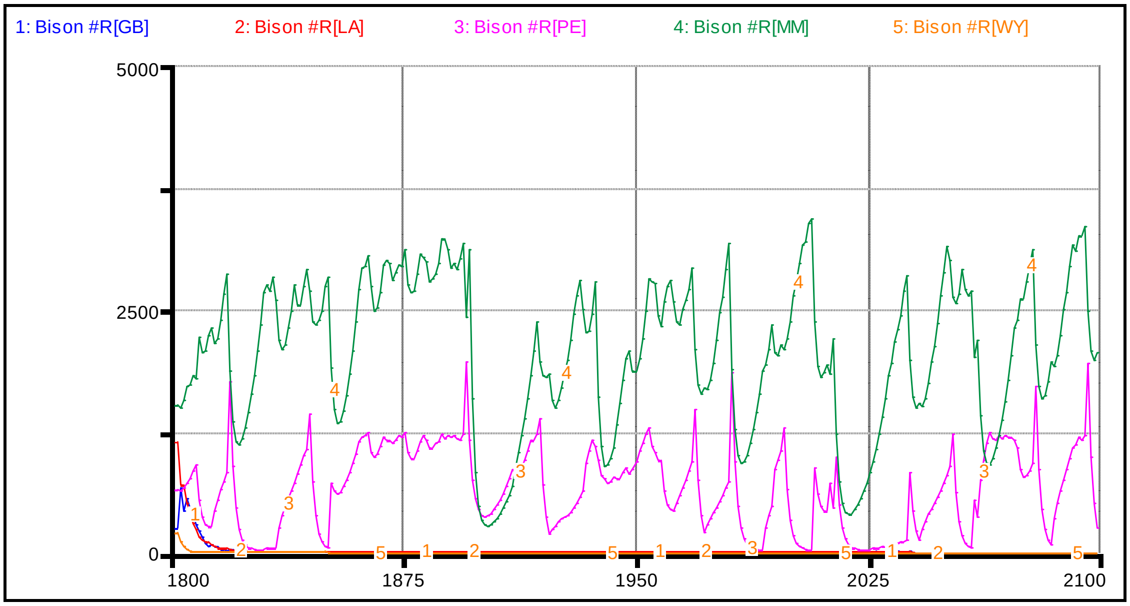


Figure 6.51. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #3. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



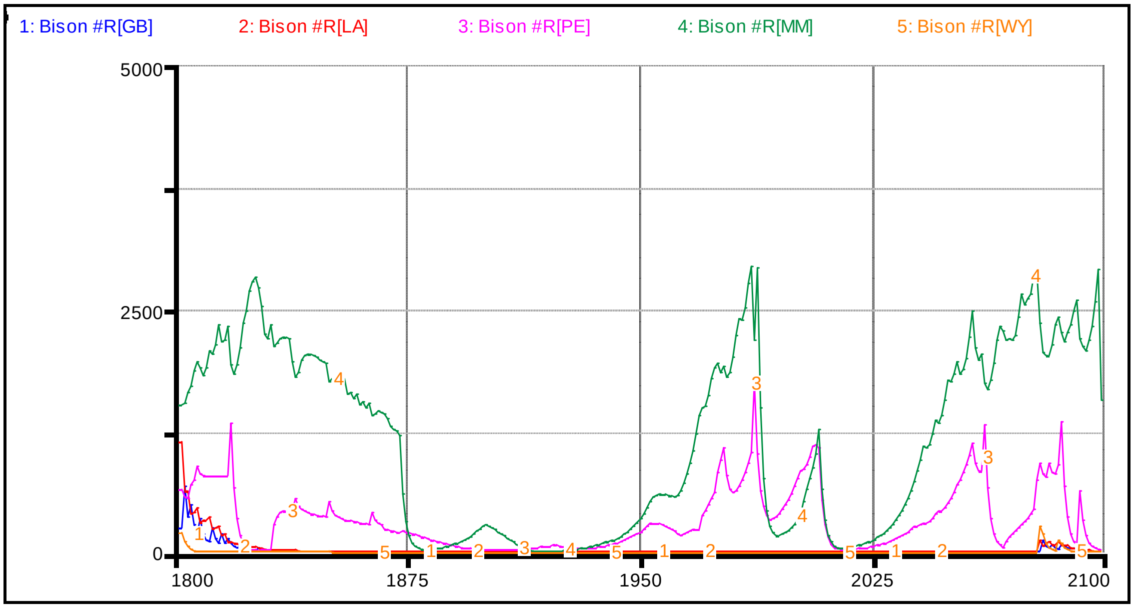
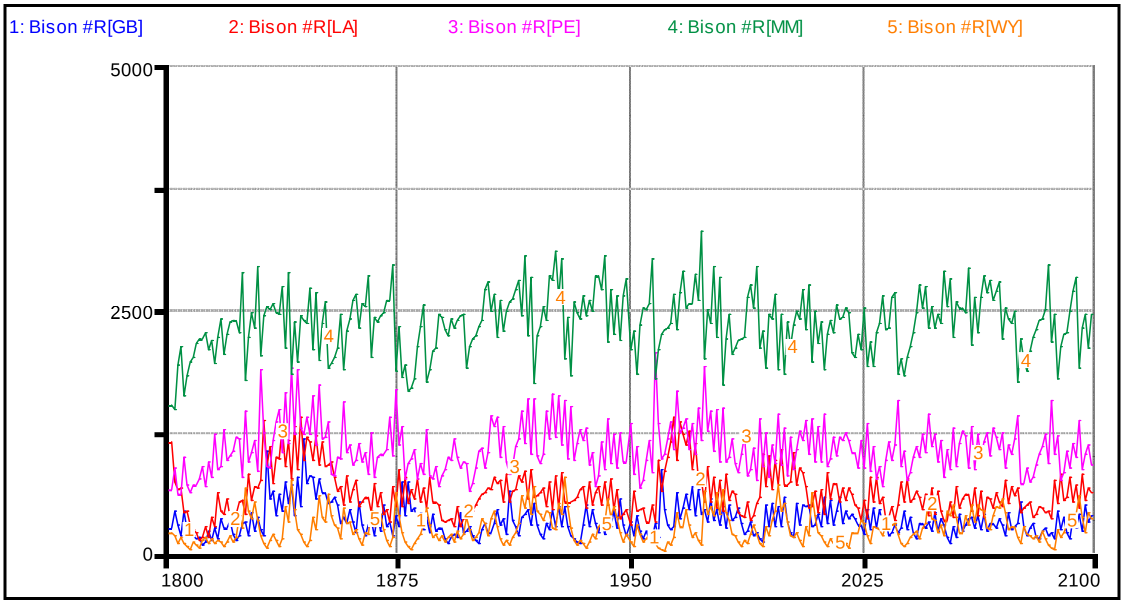


Figure 6.52. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Key Informant Group #4. The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these simulations.



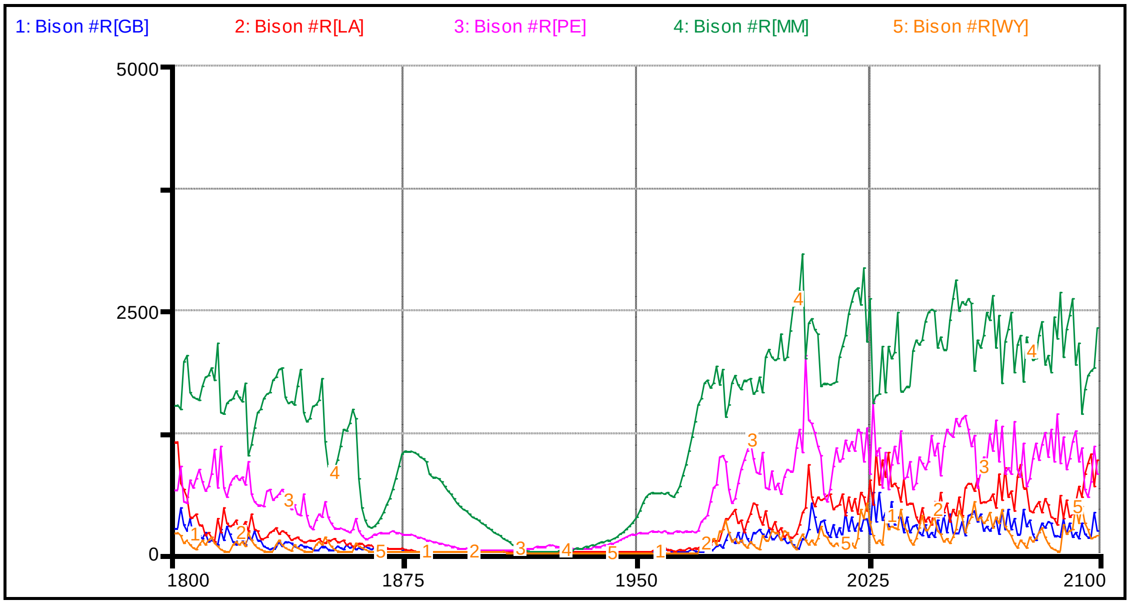
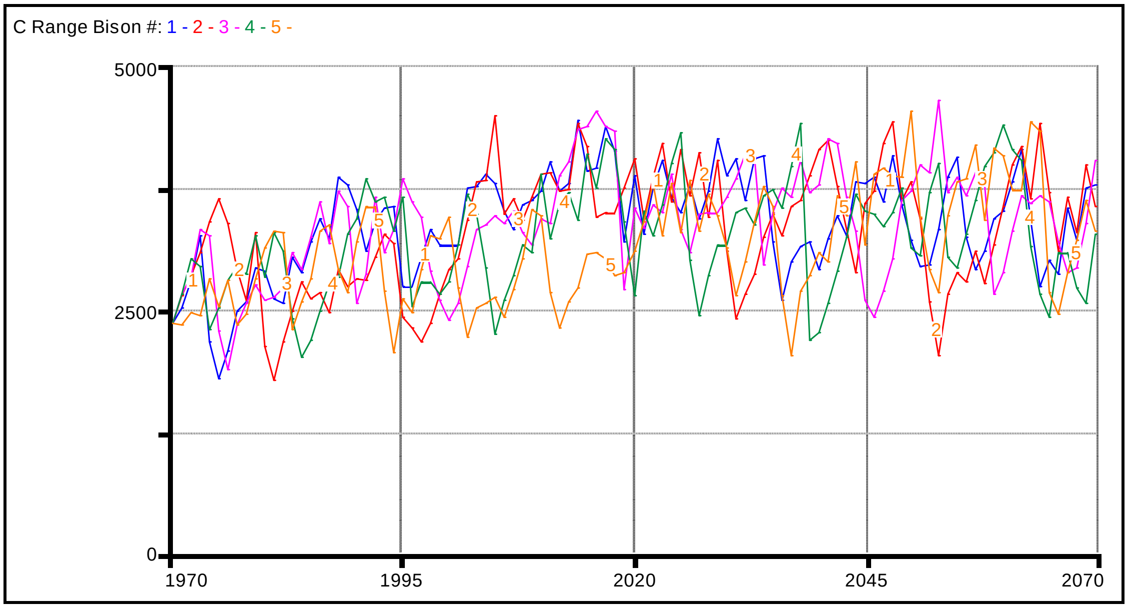


Figure 6.53. Simulated temporal variation (1800 to 2100) in population size of each winter range based on input values from Majority Average Model (average of Group 1, 2, and 3). The lower graph incorporates YNP bison depopulation events of the 1800's and early 1900's. No road grooming occurred in these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



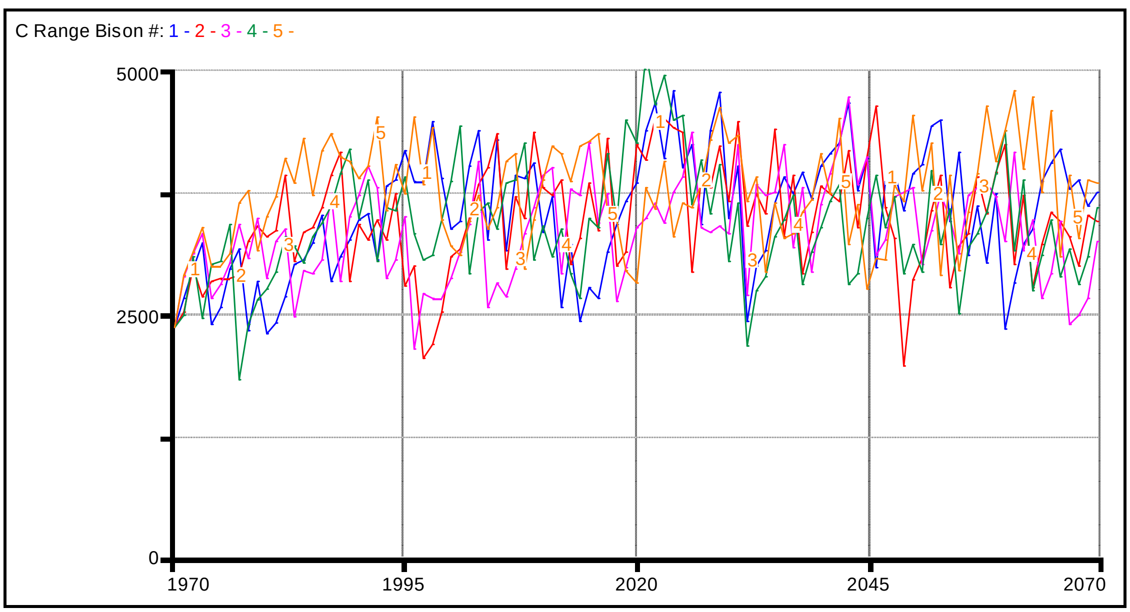


Figure 6.54. Simulated comparison of bison population in the Central Range without (upper) with (lower) road grooming. Simulations were 100 years and reflected stochastic precipitation patterns. Simulation based on Majority Average Model.

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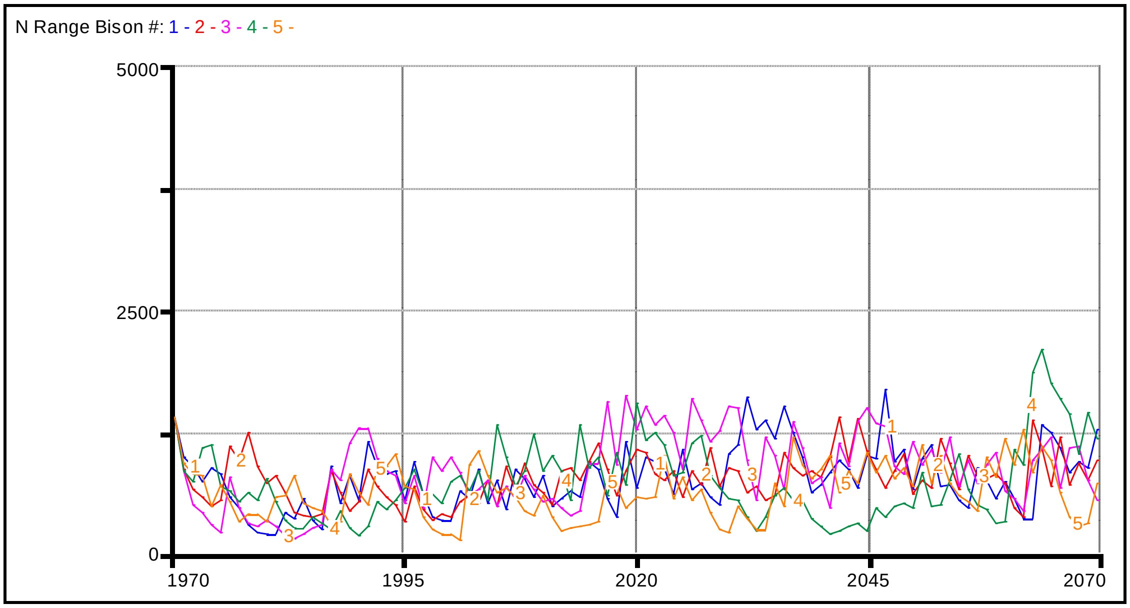

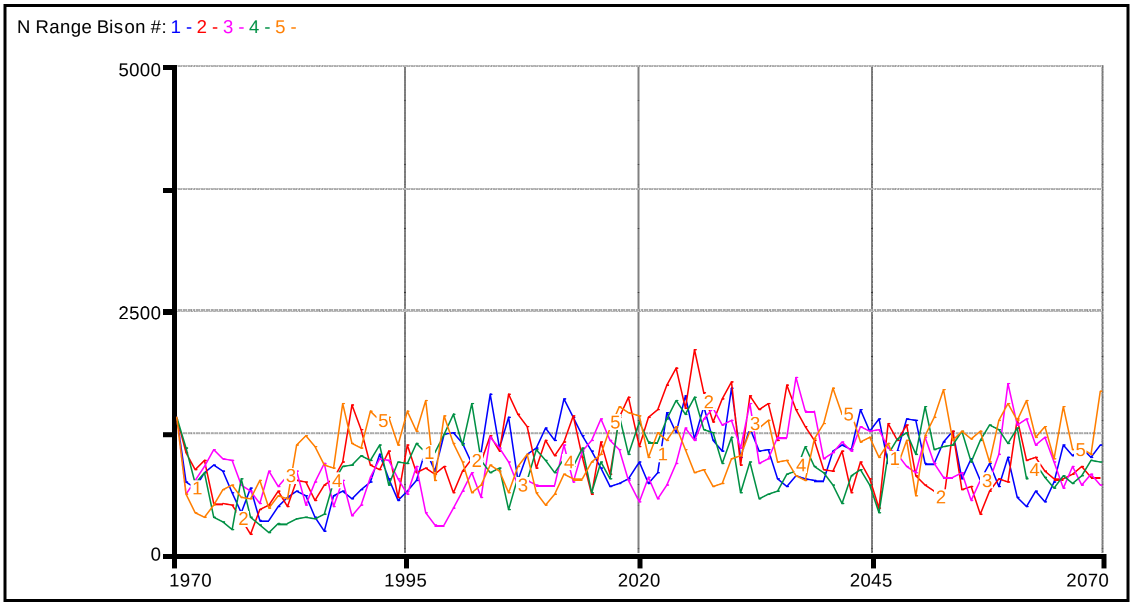

Figure 6.55**.** Simulated comparison of bison population in the Northern Range without (upper) with (lower) road grooming. Simulations were 100 years and reflected stochastic precipitation patterns. Simulation based on Majority Average Model.

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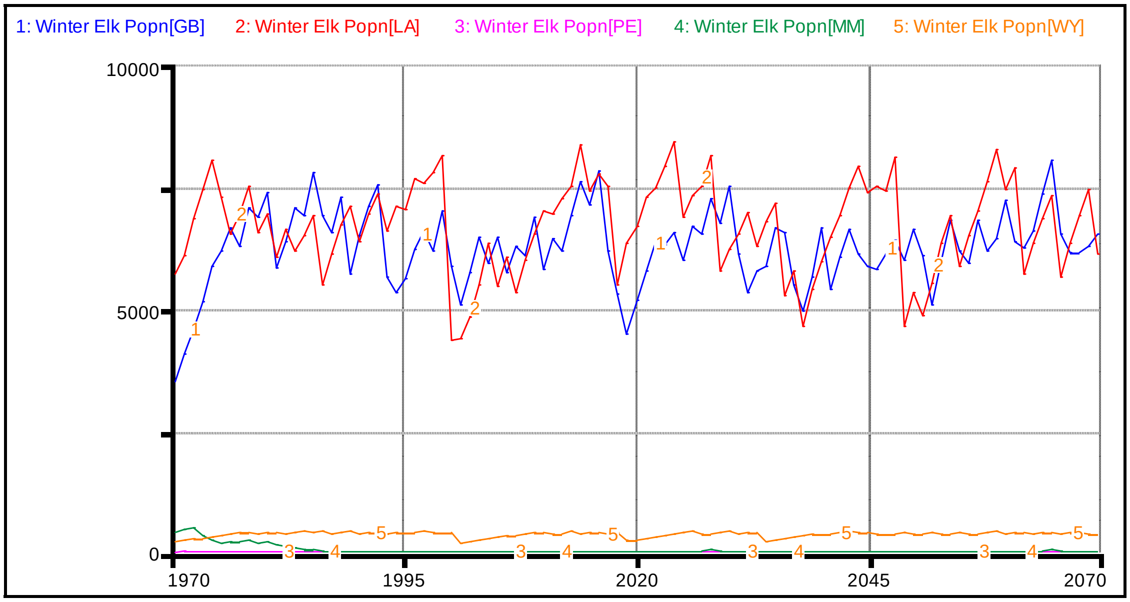


Figure 6.56. Simulated variance in elk populations on winter bison range based on simple population model where fecundity and mortality are influenced by forage availability relative to requirements. Simulation based on Majority Average Model.

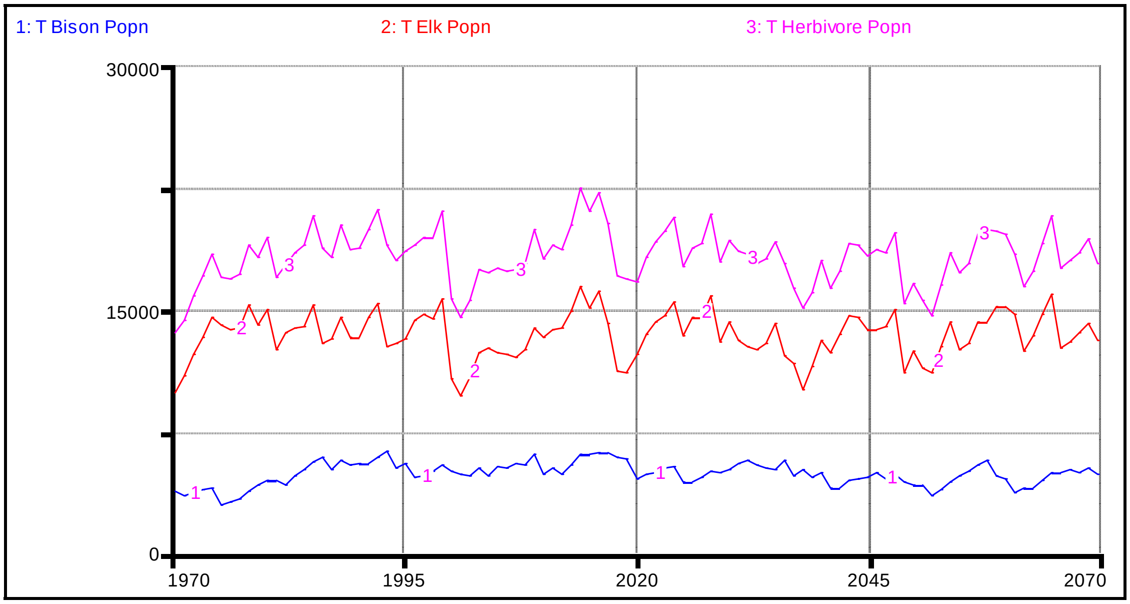
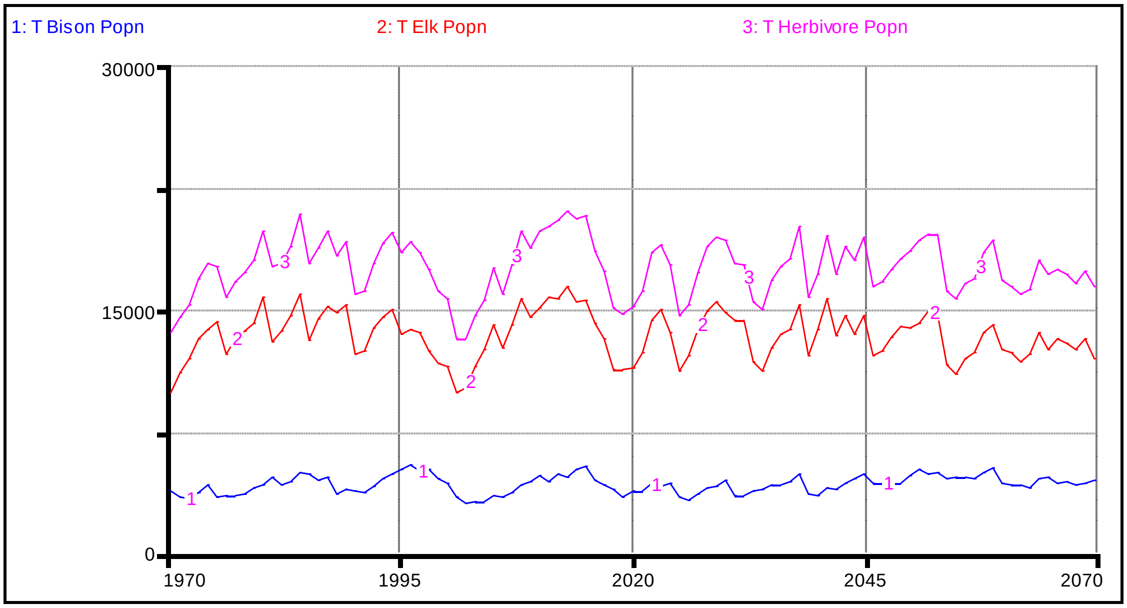


Figure 6.57. Simulated variance in bison, elk, and total herbivore populations on winter bison range to illustrate the relative temporal abundance of these two major herbivore species. Simulation based on Majority Average Model.



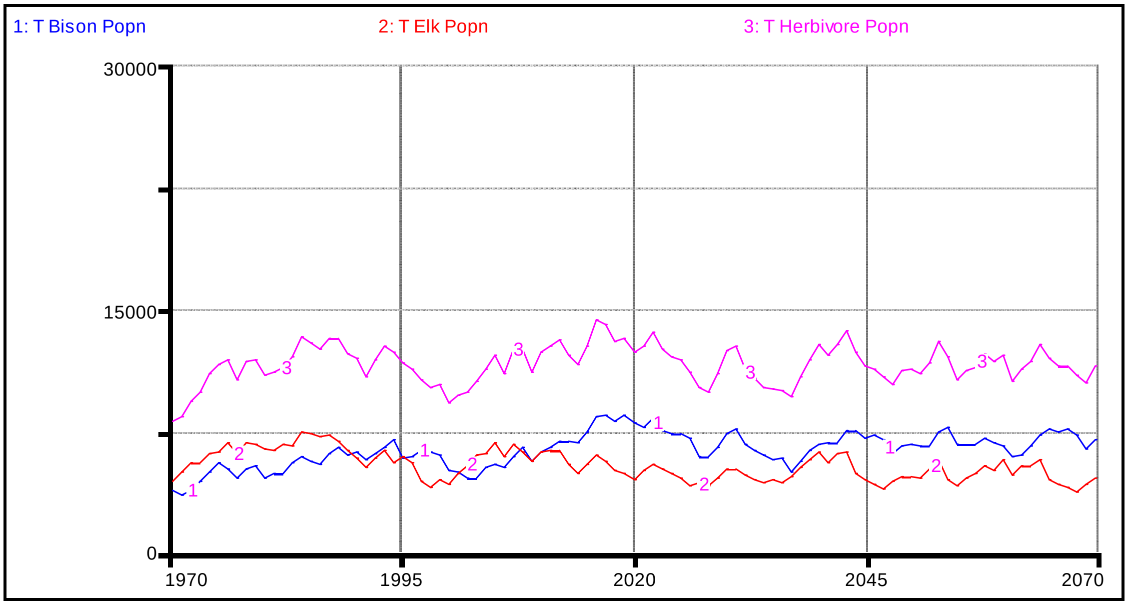
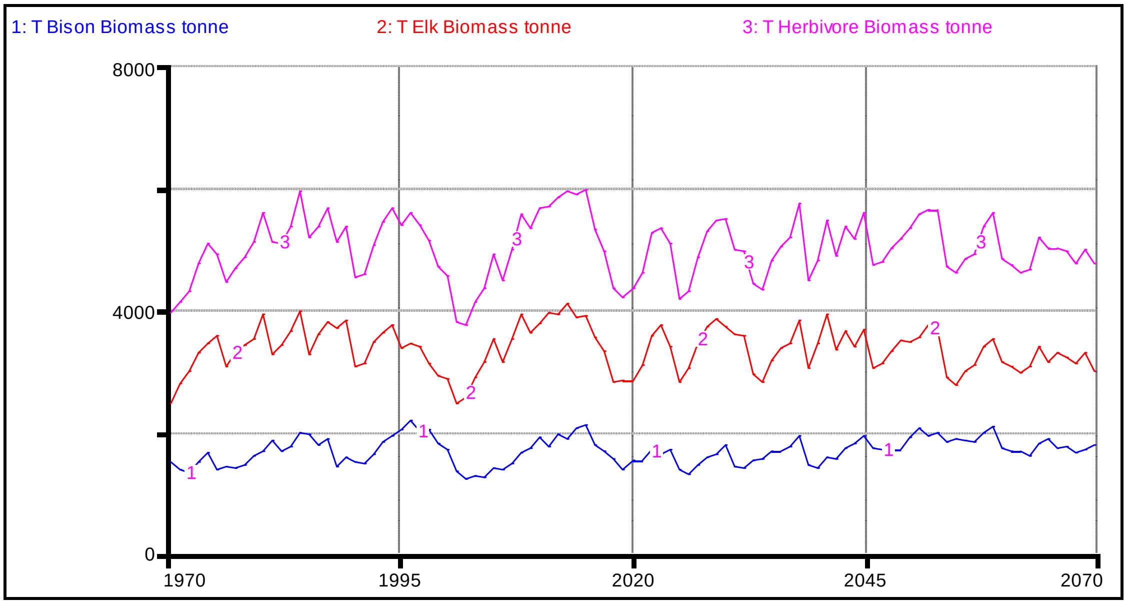


Figure 6.58. Simulated variance in bison and elk population on winter bison range to illustrate the relative temporal abundance of these two major herbivore species. Upper graph illustrates range of natural variability under current system, and lower graph illustrates a “what-if” scenario where elk populations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



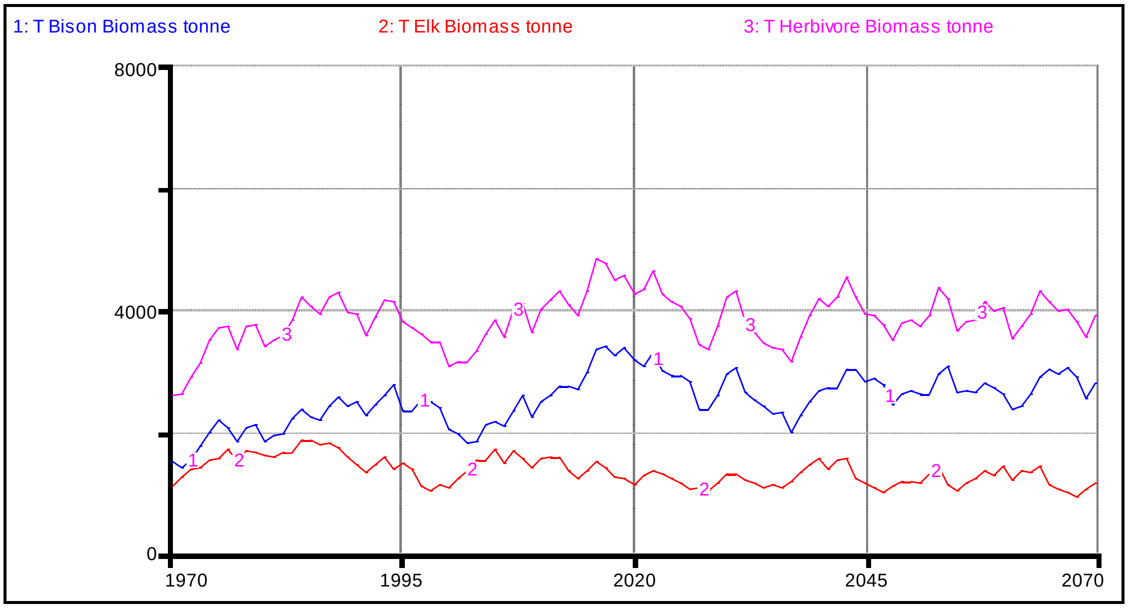
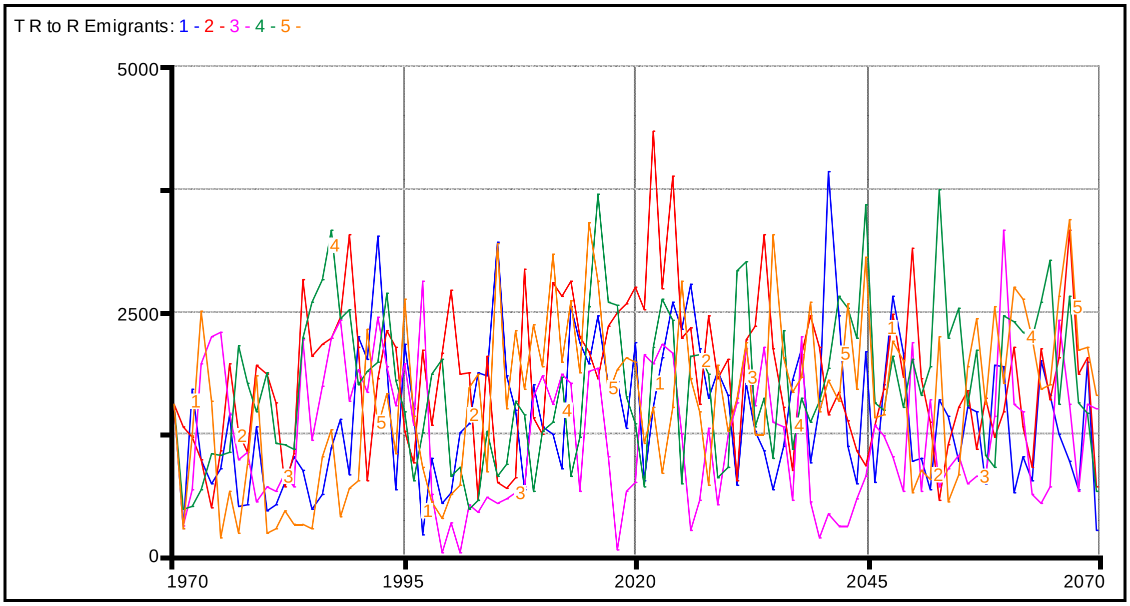


Figure 6.59. Simulated variance in bison and elk biomass (tonne) on winter bison range to illustrate the relative temporal abundance of these two major herbivore species. Upper graph illustrates range of natural variability under current system, and lower graph illustrates a "what-if" scenario where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



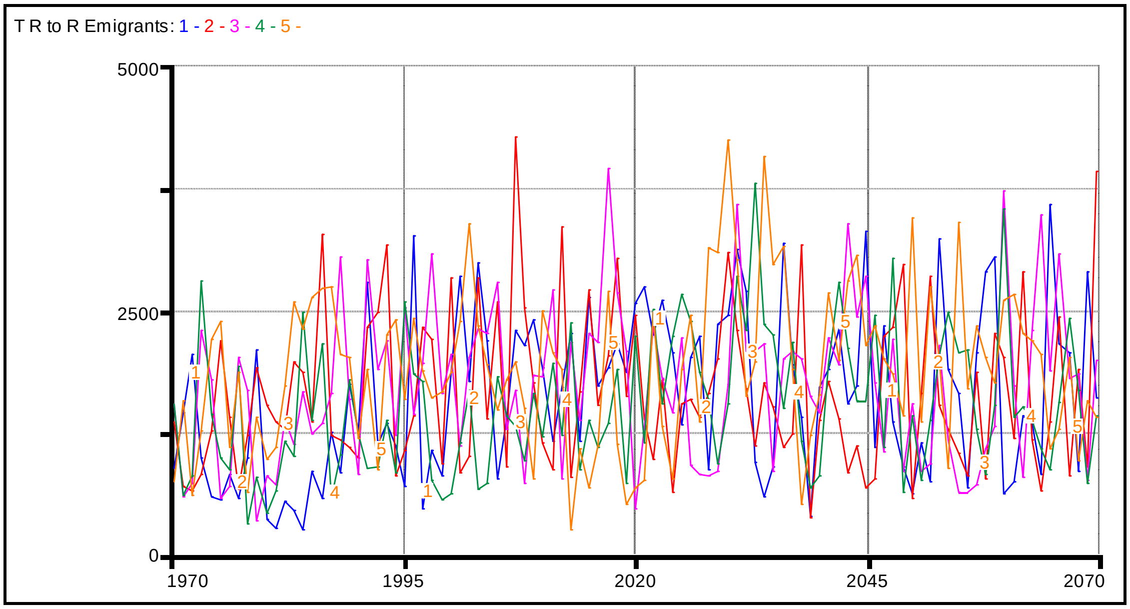
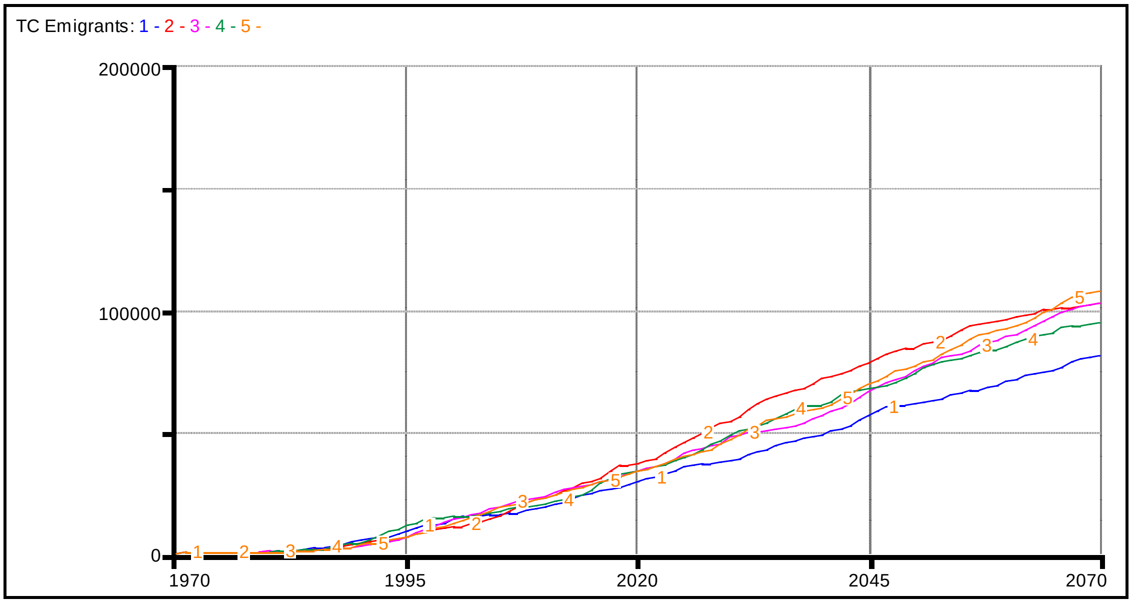


Figure 6.60. Simulated total annual movement of bison between winter ranges; graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario without any road grooming, and the lower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



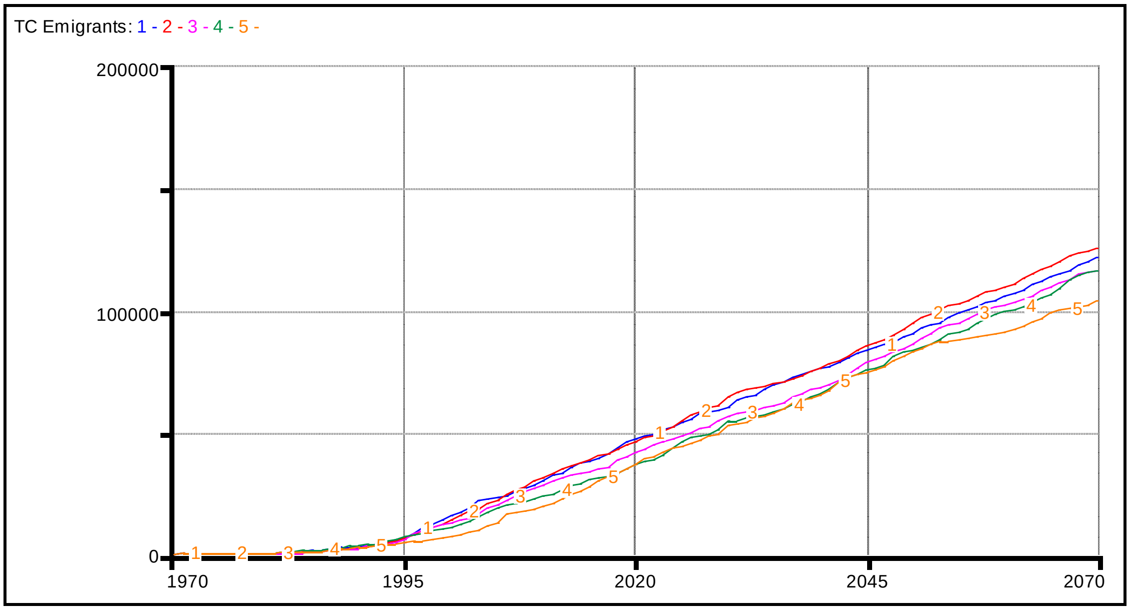
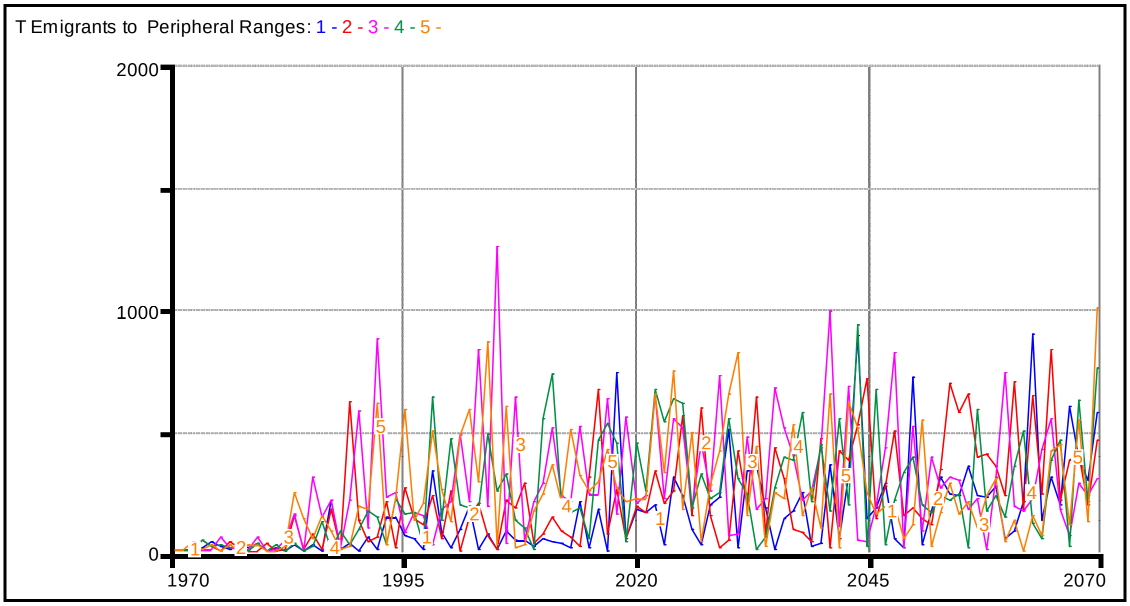


Figure 6.61. Simulated total cumulative movement of bison between ranges; graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario without any road grooming, and the lower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



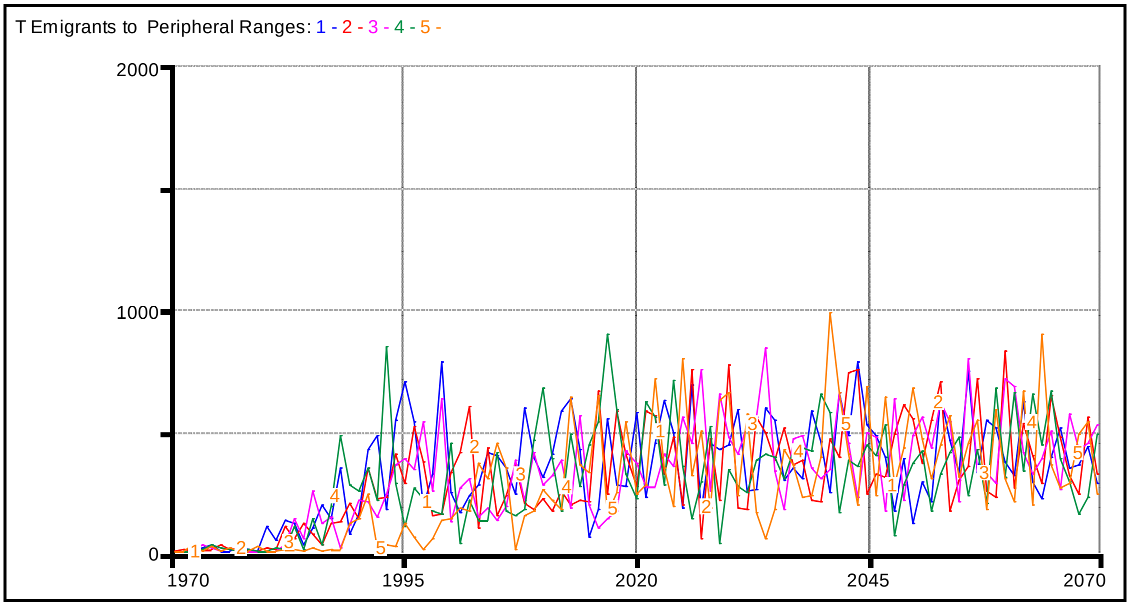


Figure 6.62. Simulated total annual movement of bison to boundary winter ranges (Gardiner basin and West Yellowstone); graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario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

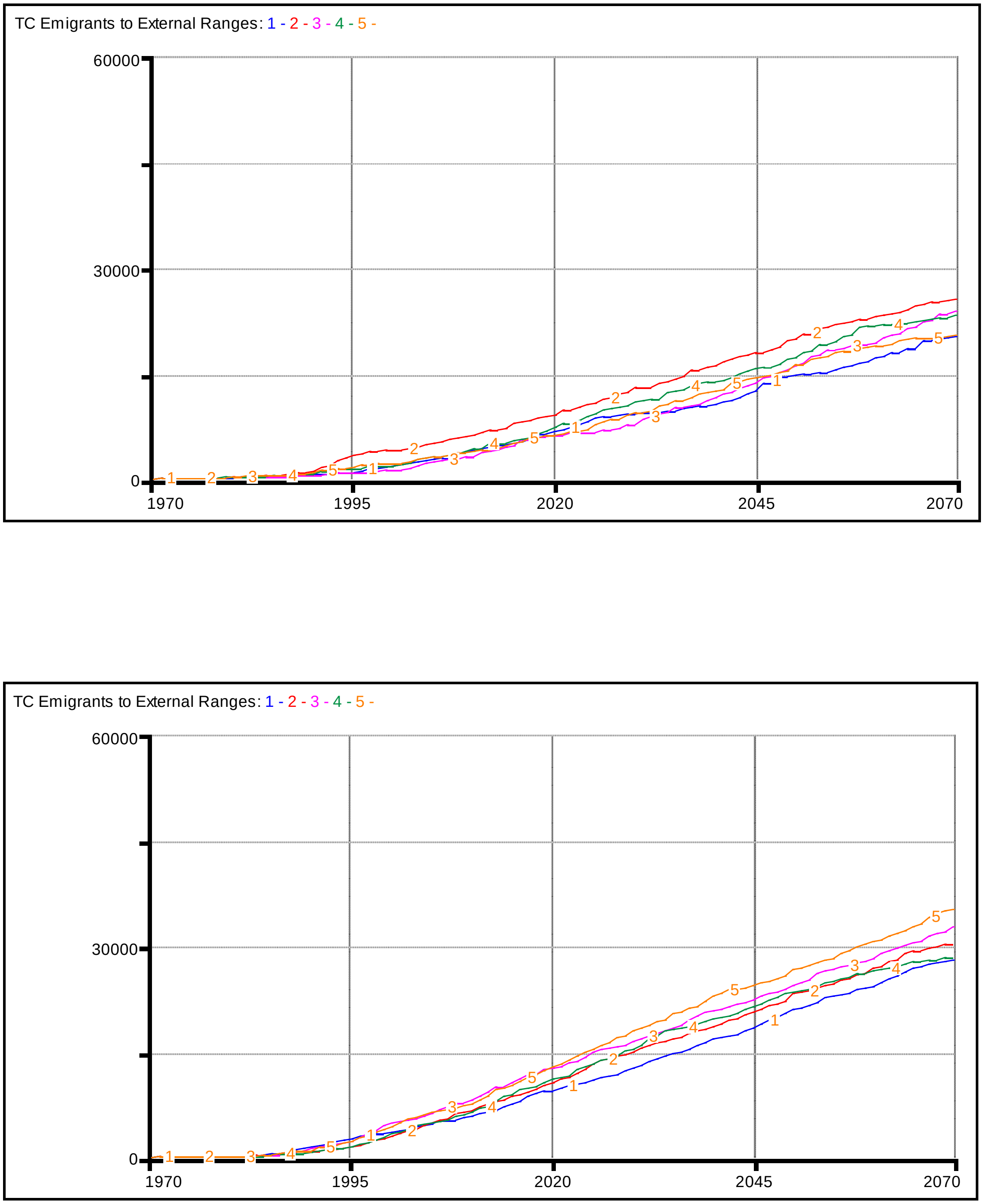


Figure 6.63. Simulated total cumulative movement to boundary winter ranges (Gardiner basin and West Yellowstone); graphs illustrate five 100 year simulations involving stochastic precipitation and using movement coefficients from Majority Average Model. The upper graph reflects a simulation scenario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

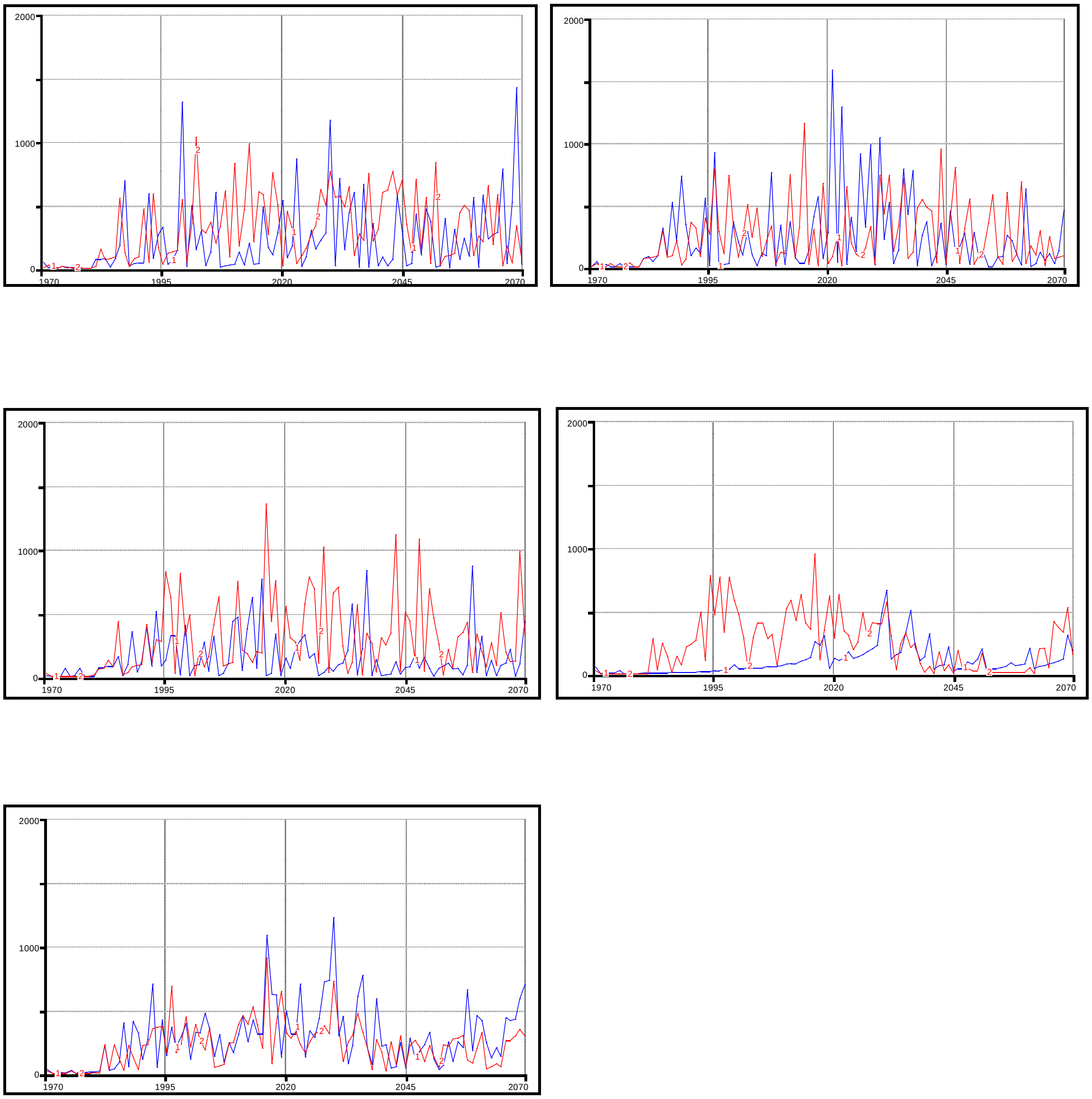


Figure 6.64. Simulated annual movement from interior to boundary winter ranges (Gardiner basin and West Yellowstone); graphs are based on input values from each Key Informant Group. Simulation #1 reflects a scenario without road grooming, and scenario #2 indicates a scenario involving road grooming along 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).

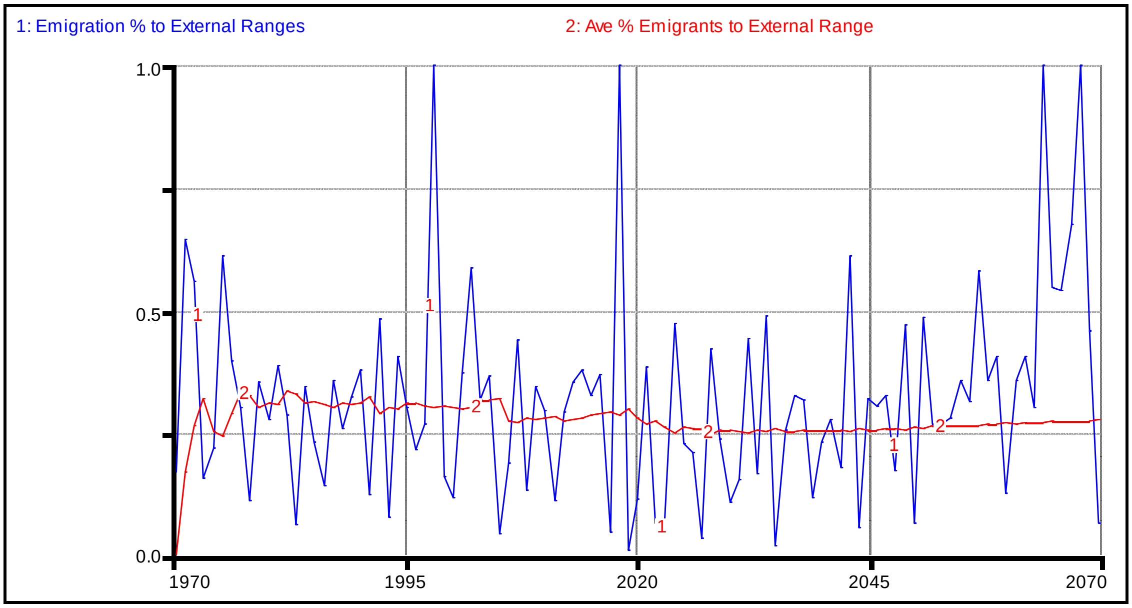


Figure 6.65. Simulated percent of annual bison movement that goes to boundary winter ranges (Gardiner basin and West Yellowstone); based on movement coefficients from Majority Average Model. Graph #1 reflects annual values and Graph #2 reflects a running average. No road grooming occurred during this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

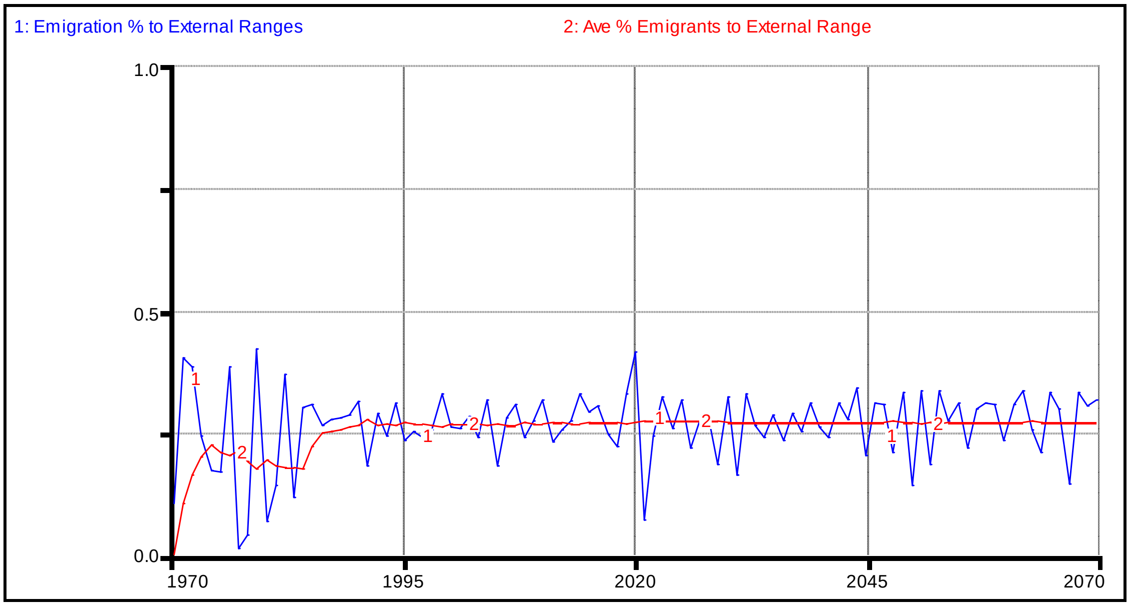


Figure 6.66. Simulated percent of annual bison movement that goes to boundary winter ranges (Gardiner basin and West Yellowstone); based on movement coefficients from Majority Average Model. Graph #1 reflects annual values and Graph #2 reflects a running average. This scenario involves road grooming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

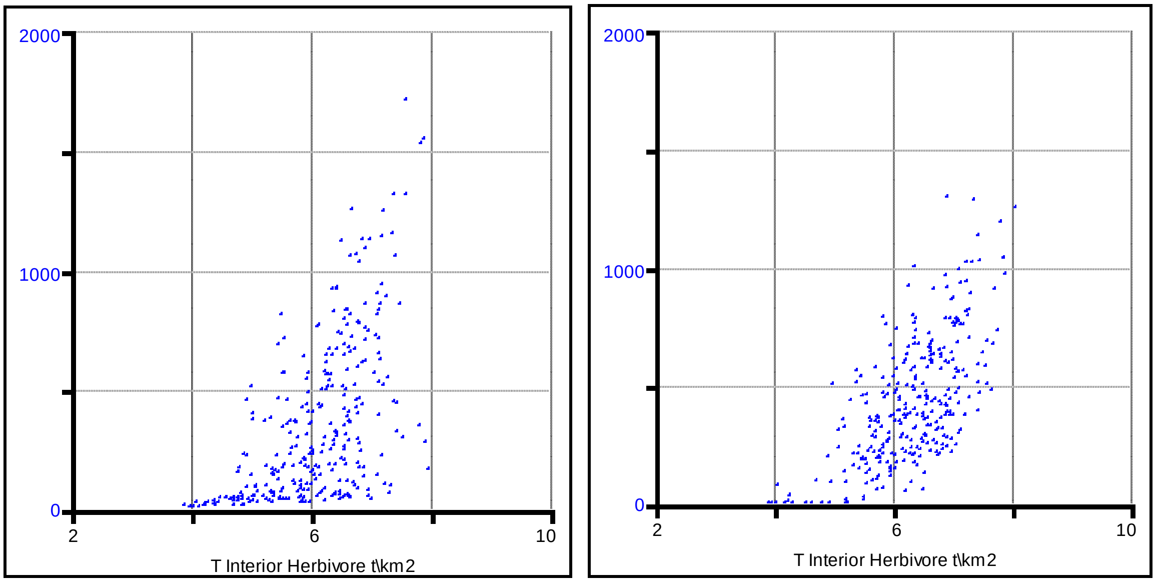


Figure 6.67. Simulated scattergram (300 year simulation) indicating relationship between bison biomass density (tonne/km^2) in the interior ranges and the number of bison emigrating to boundary ranges during for the winter season. Graph on the left reflects a no road grooming scenario; graph on right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

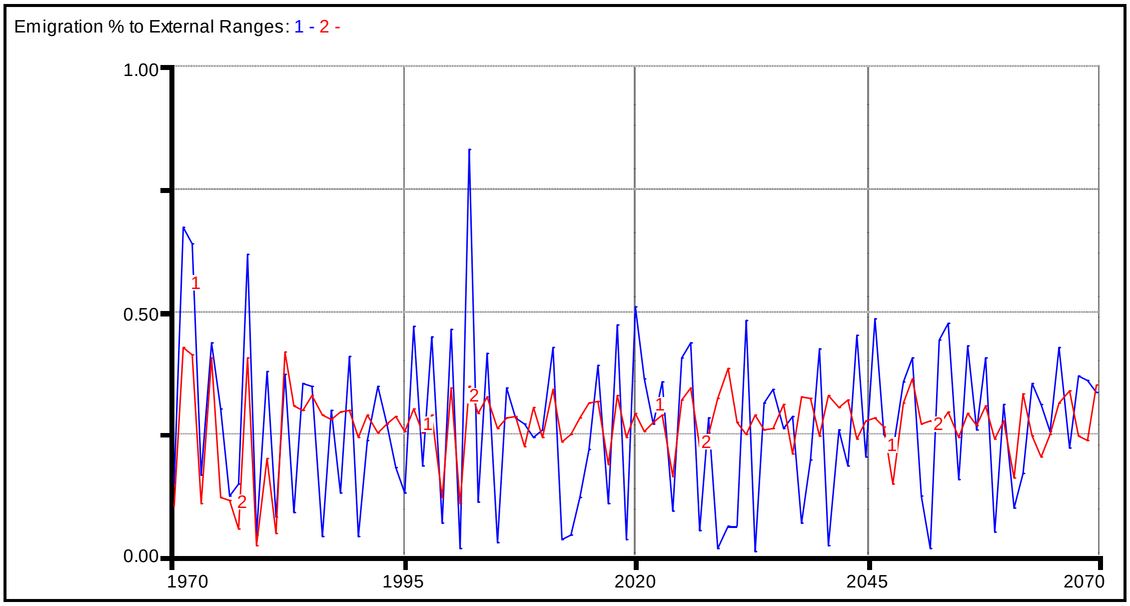


Figure 6.68. Simulated percent of annual movement that goes to boundary winter ranges (Gardiner basin and West Yellowstone); based on movement coefficients from Majority Average Model. Graph #1 reflects a simulation scenario without any road grooming, and Graph #2 indicates scenarios involving road grooming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

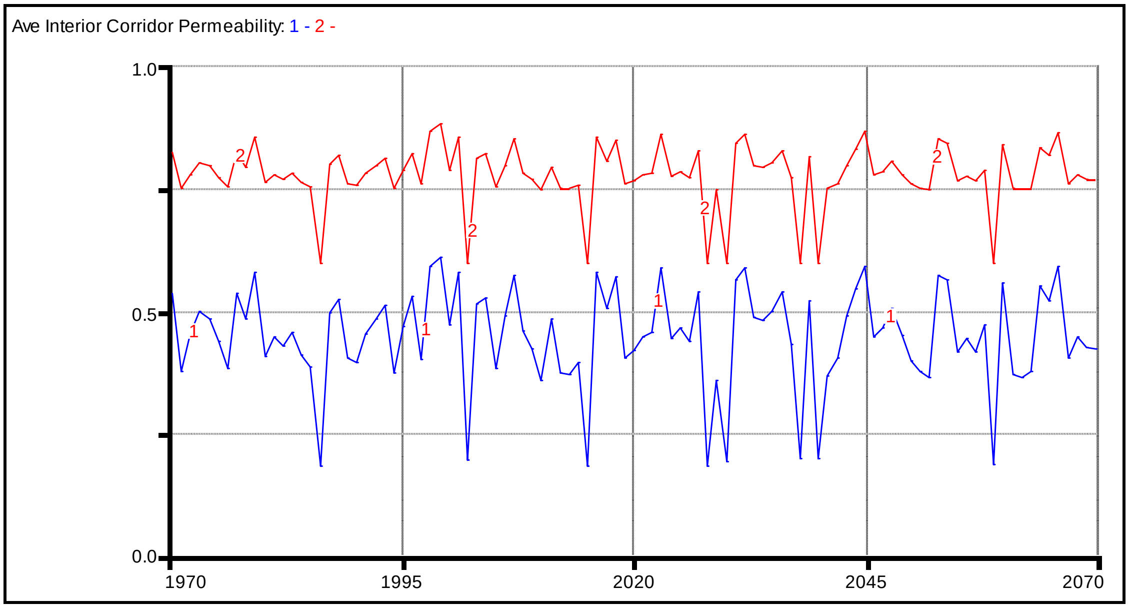


Figure 6.69. Simulated comparison of average YNP interior corridor permeability without (#1) and with (#2) winter road grooming. Simulation based on Majority Average Model.

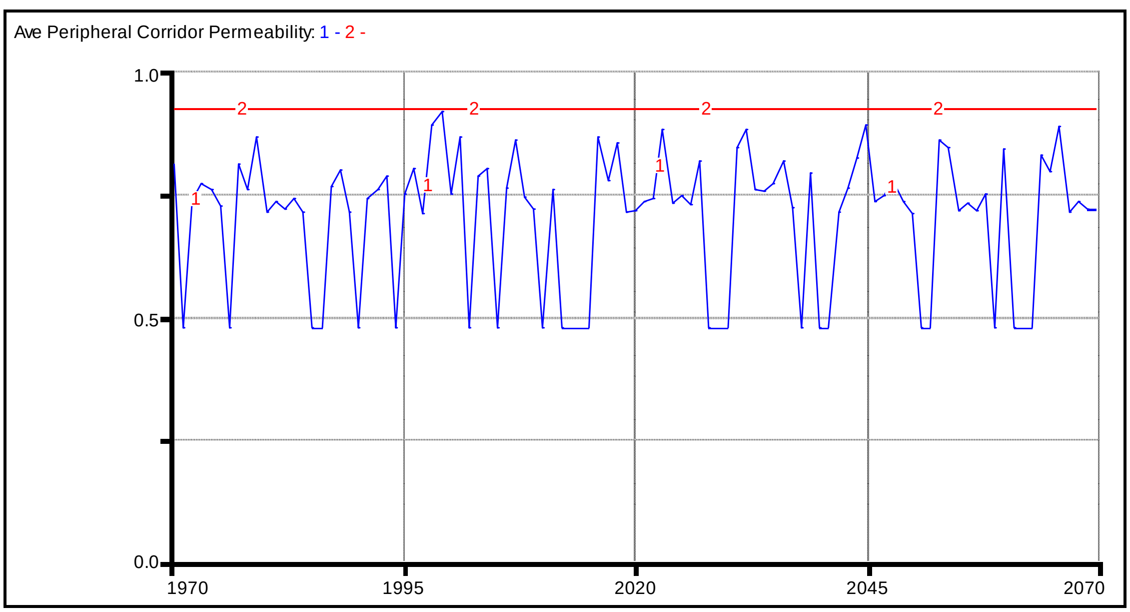


Figure 6.70. Simulated comparison of average YNP boundary corridor permeability without (#1) and with (#2) winter road grooming. Simulation based on Majority Average Model.

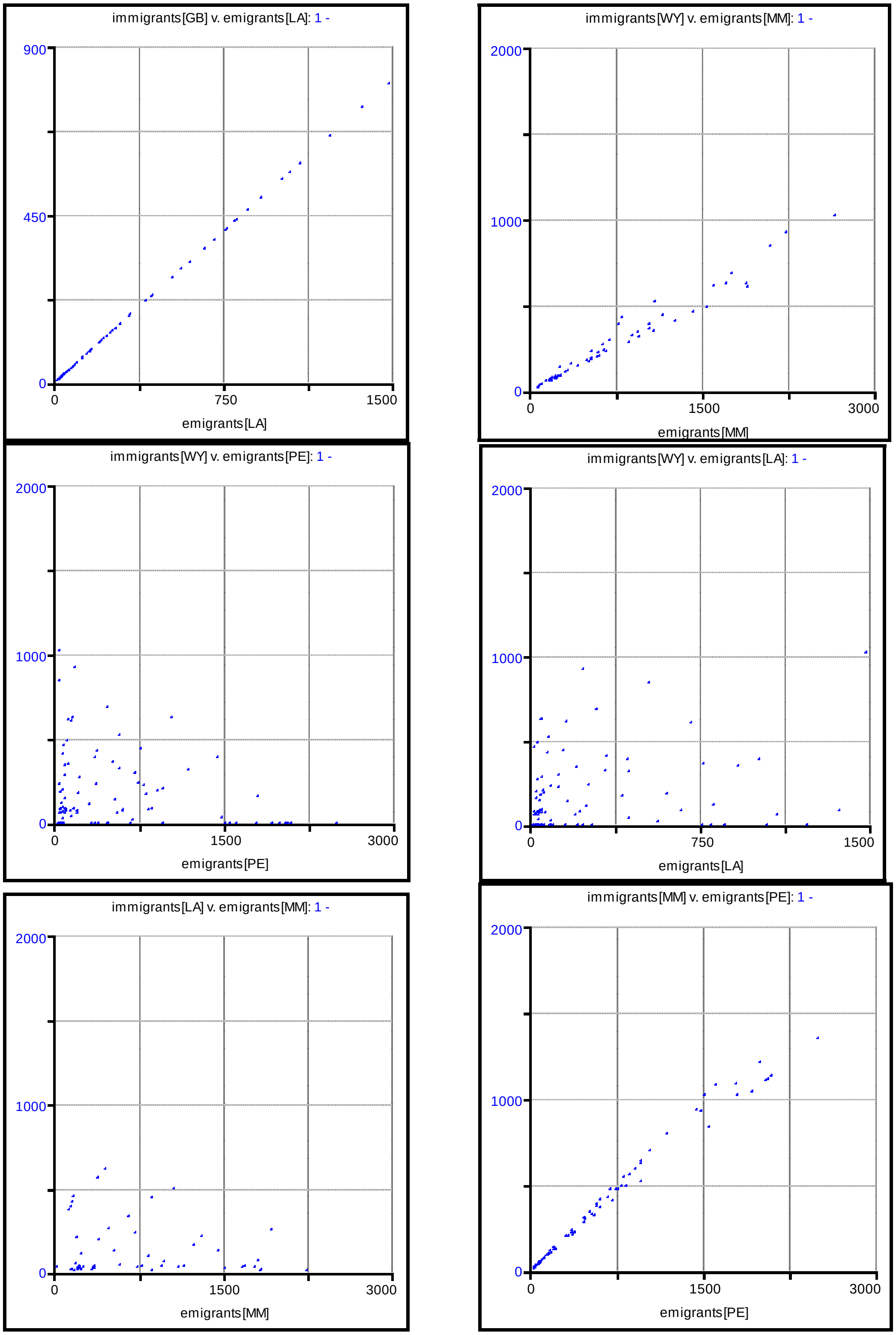


Figure 6.71. Simulated scattergrams between selected range immigration and emigration values. Scenarios do not involve winter road grooming. Simulation based on Majority Average Model.

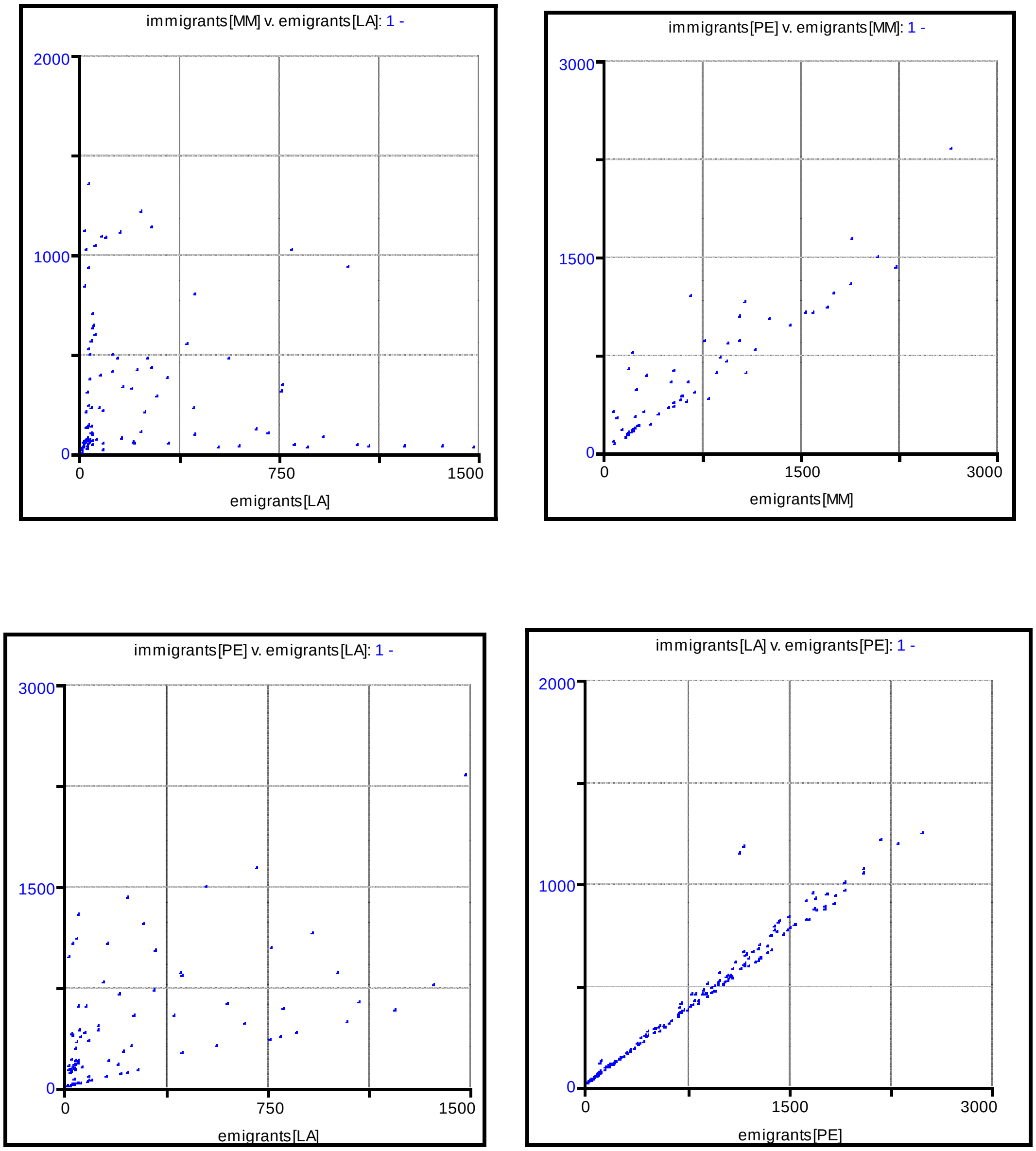


Figure 6.72. Simulated scattergrams between selected range immigration and emigration values. Scenarios do not involve winter road grooming. Simulation based on Majority Average Model.

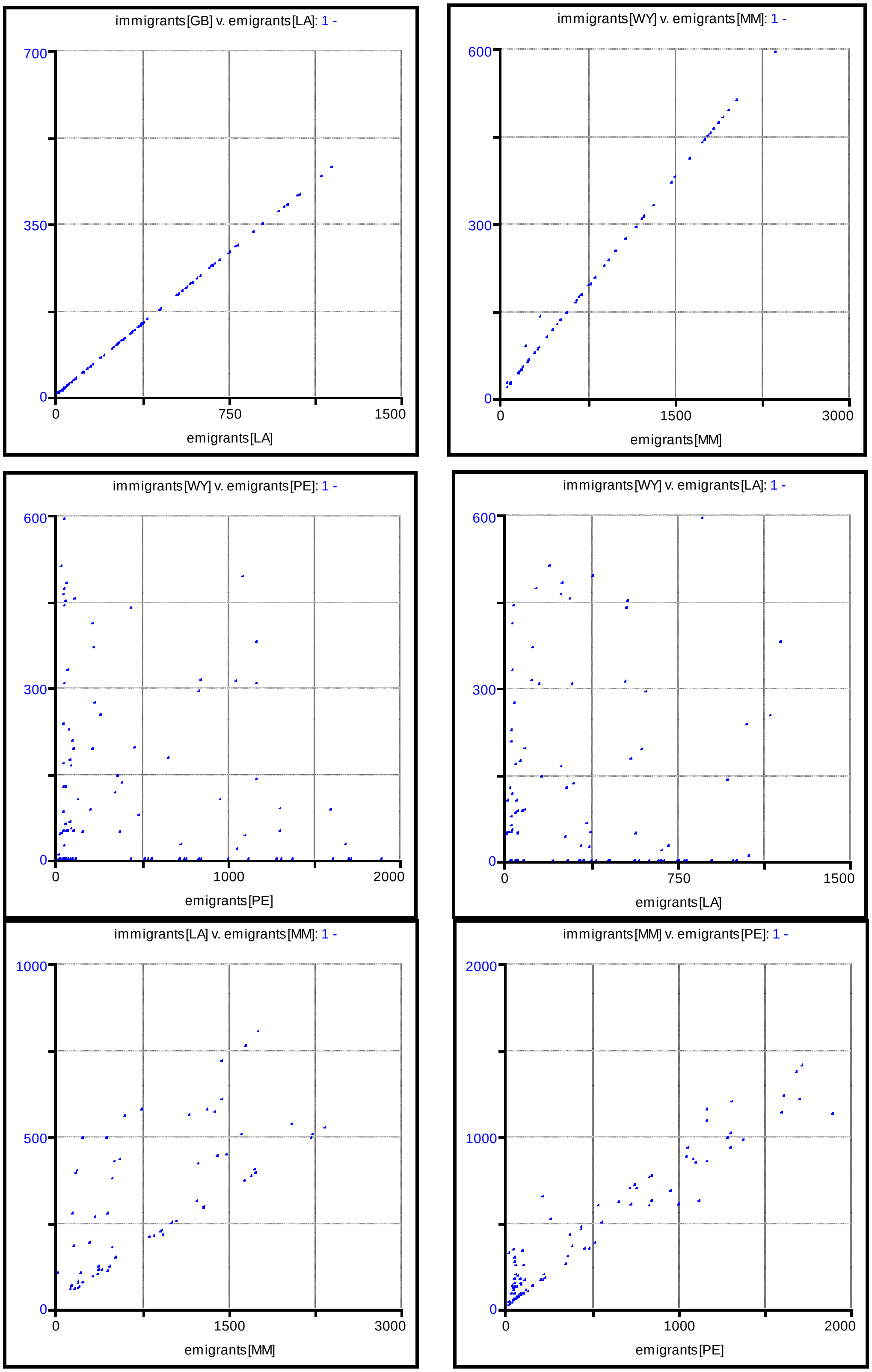


Figure 6.73. Simulated scattergrams between selected range immigration and emigration values. Scenarios include winter road grooming of corridors PHC, FMC, and FWC. Simulation based on Majority Average Model.

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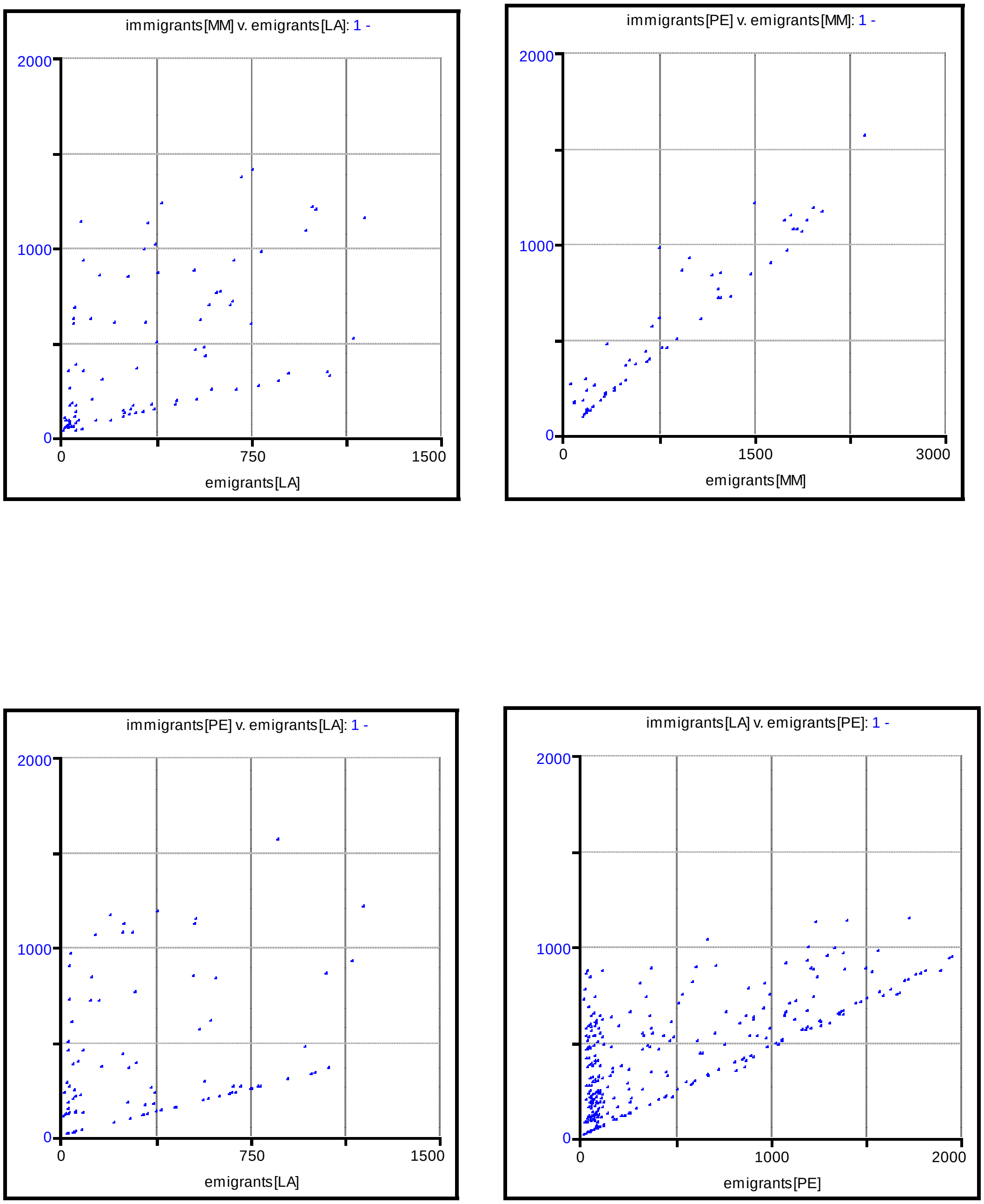
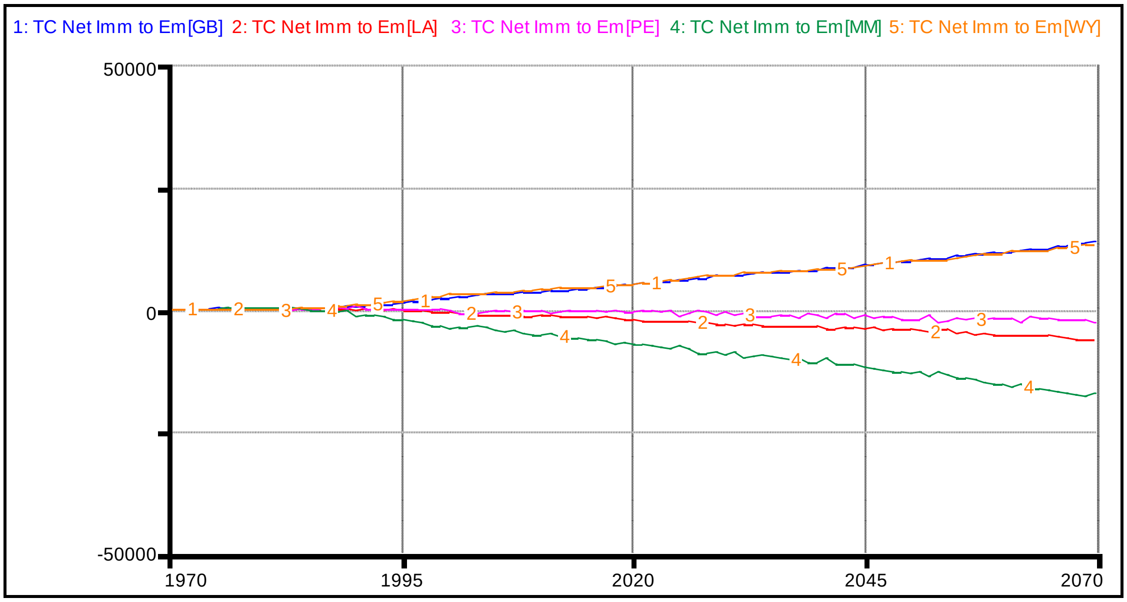


Figure 6.74. Simulated scattergrams between selected range immigration and emigration values. Scenarios include winter road grooming of corridors PHC, FMC, and FWC. Simulation based on Majority Average Model.



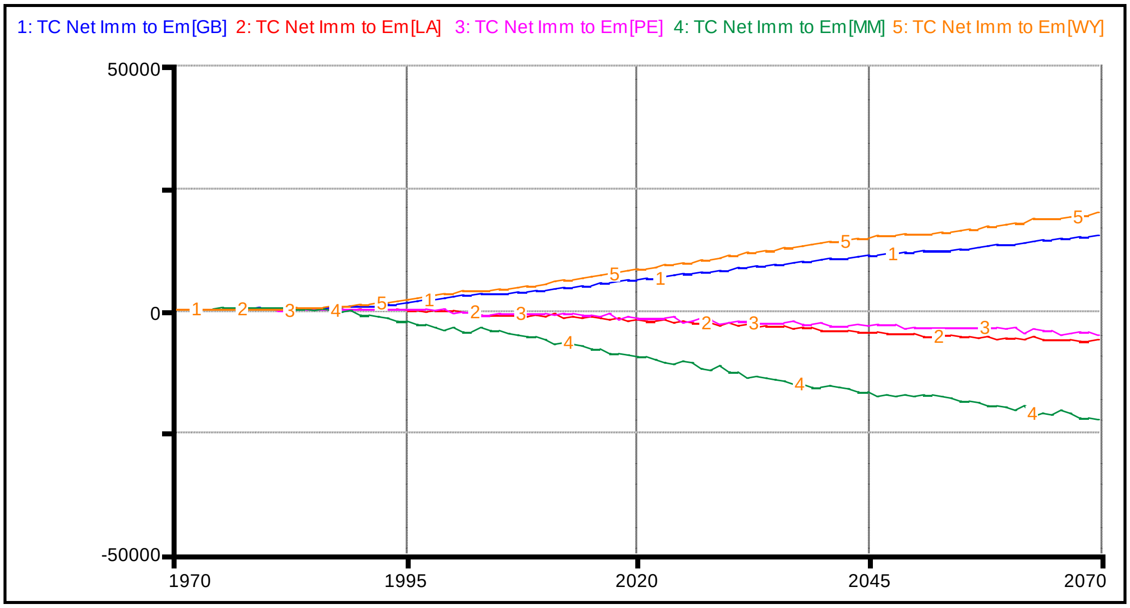


Figure 6.75. Simulated net difference between immigration and emigration from each of the bison winter ranges. Values above 0 represent a net immigration gain, whereas values below 0 indicate that emigration exceeds immigration. Upper graph involves scenario without road grooming and lower graph includes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

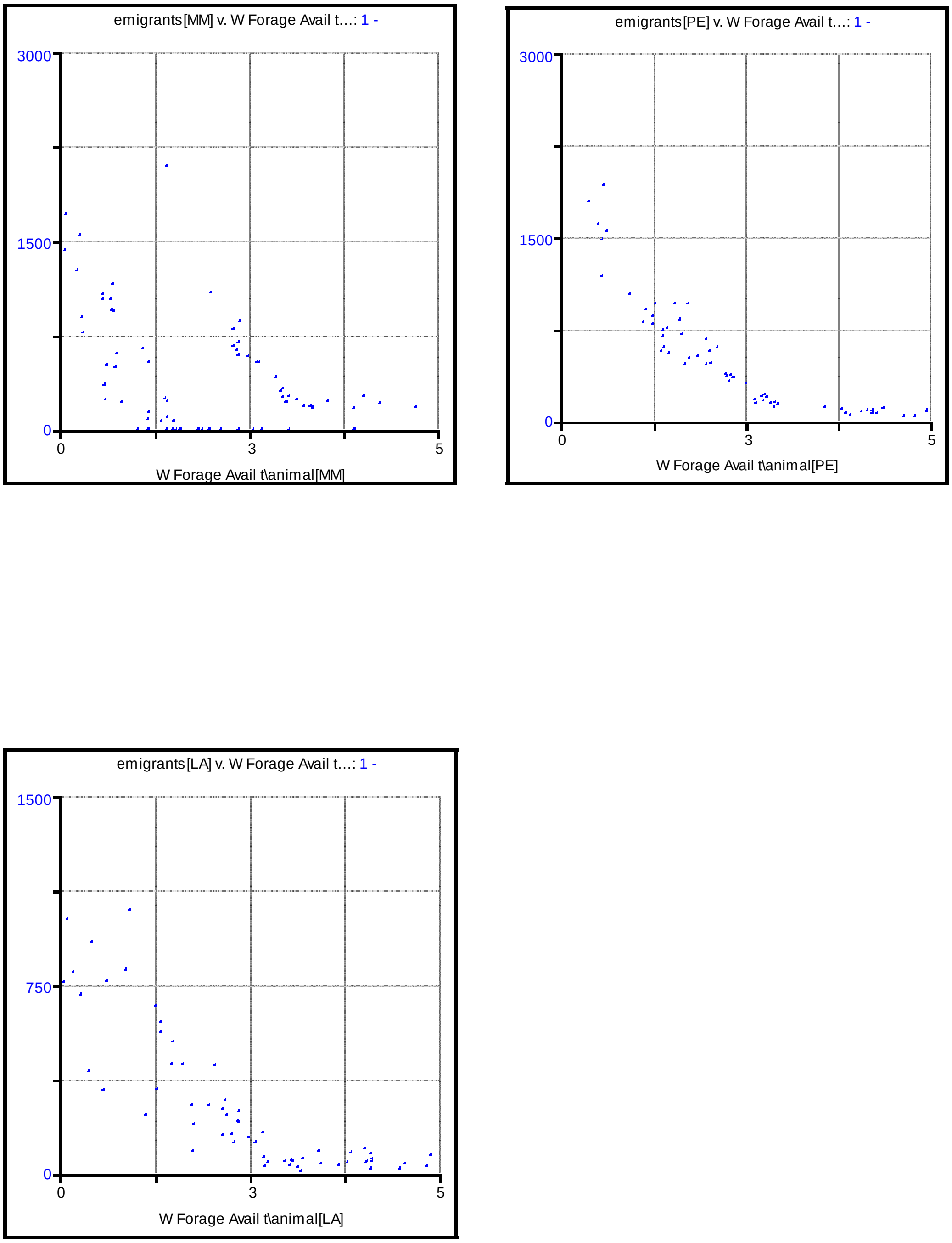
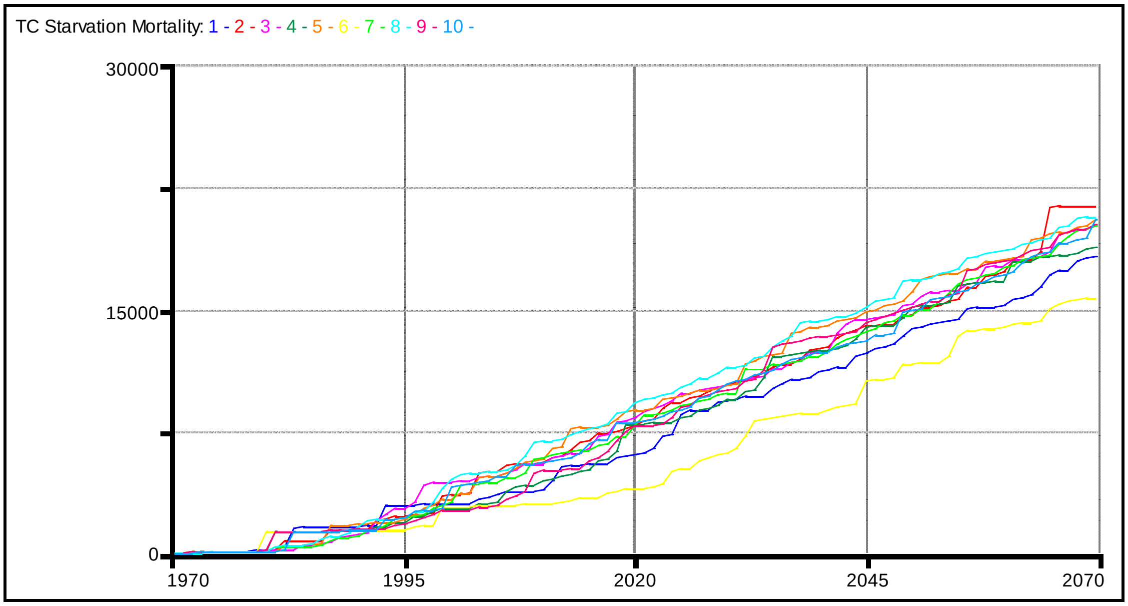


Figure 6.76. Simulated scattergrams between bison emigration values from interior winter ranges and winter forage availability (tonne/bison). Simulation based on Majority Average Model.



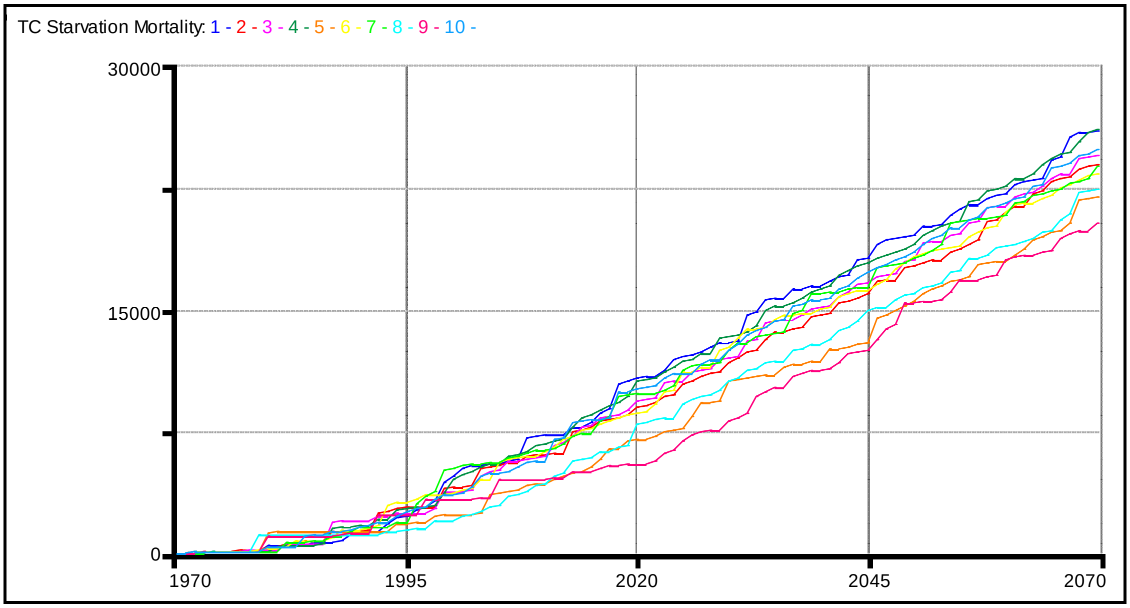


Figure 6.77. Simulated total cumulative level of bison starvation without (above) and with (below) winter road grooming. A series of ten 100 year simulations conducted with random precipitation using majority average model. Simulation based on Majority Average Model.

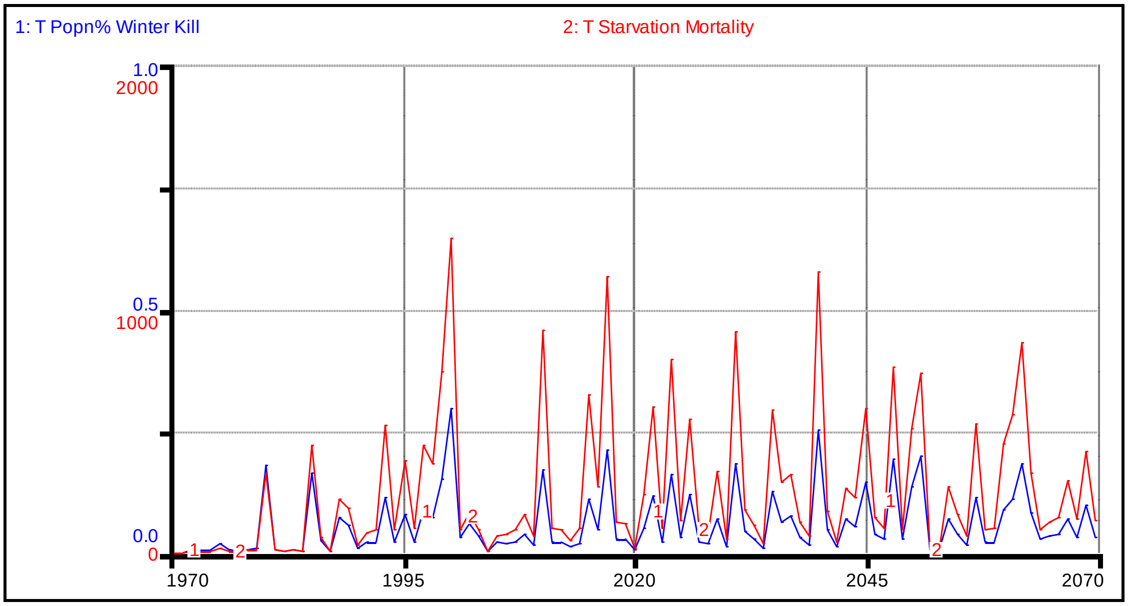


Figure 6.78. Simulated number and percent of bison killed by starvation during the winter season. Graph illustrates the episodic nature of bison die-offs associated with conditions of low forage availability. Simulation based on Majority Average Model.

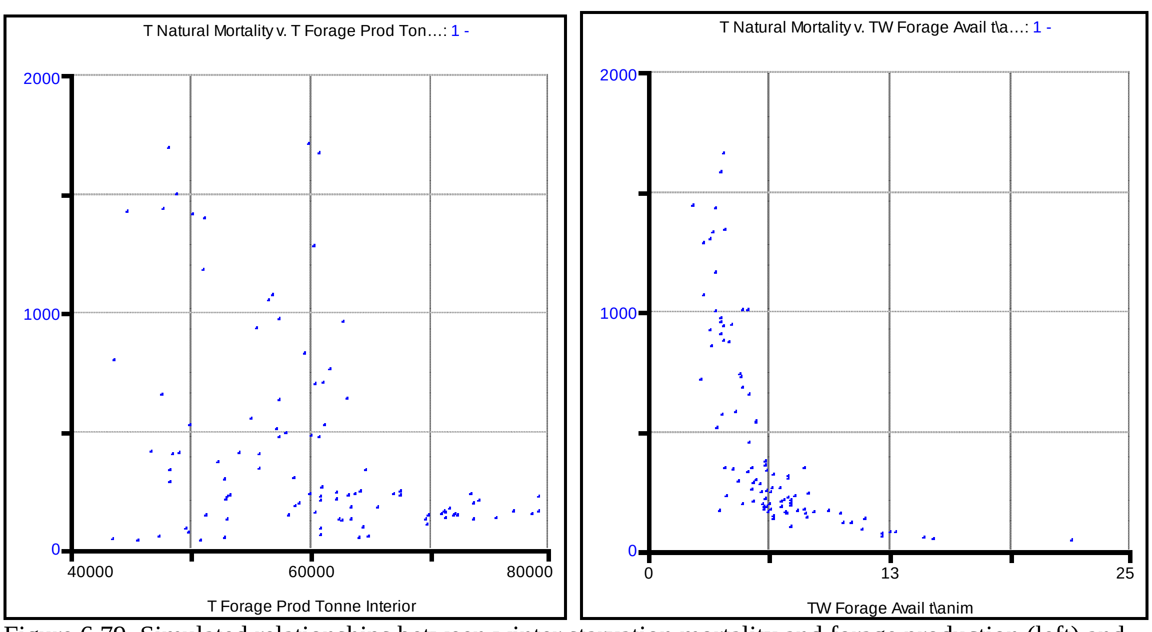
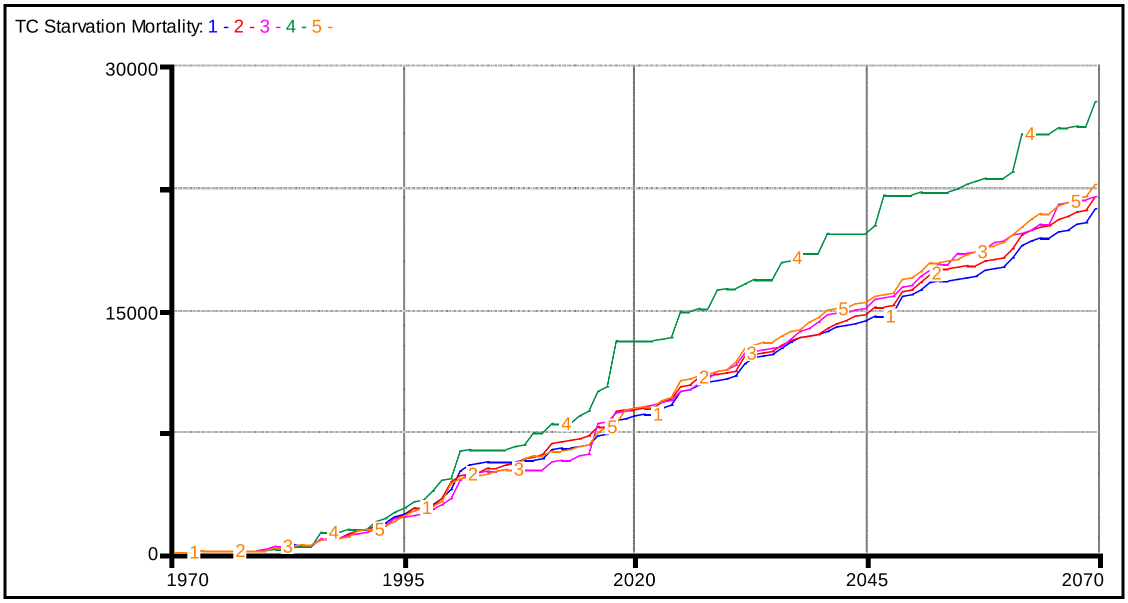


Figure 6.79. Simulated relationships between winter starvation mortality and forage production (left) and forage availability (right) for interior ranges. Simulation based on Majority Average Model.



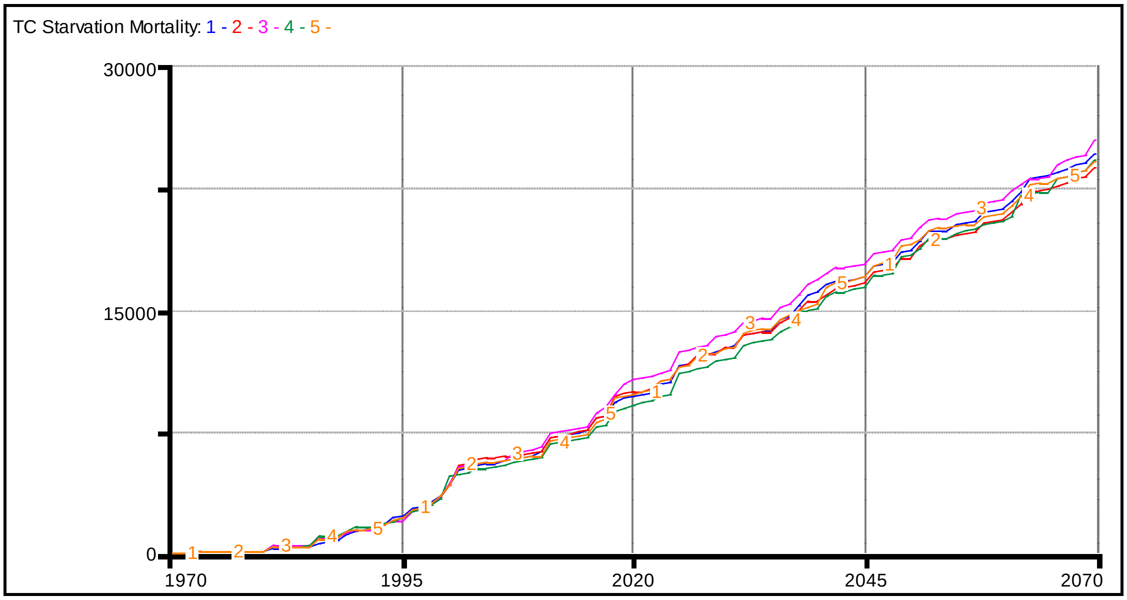
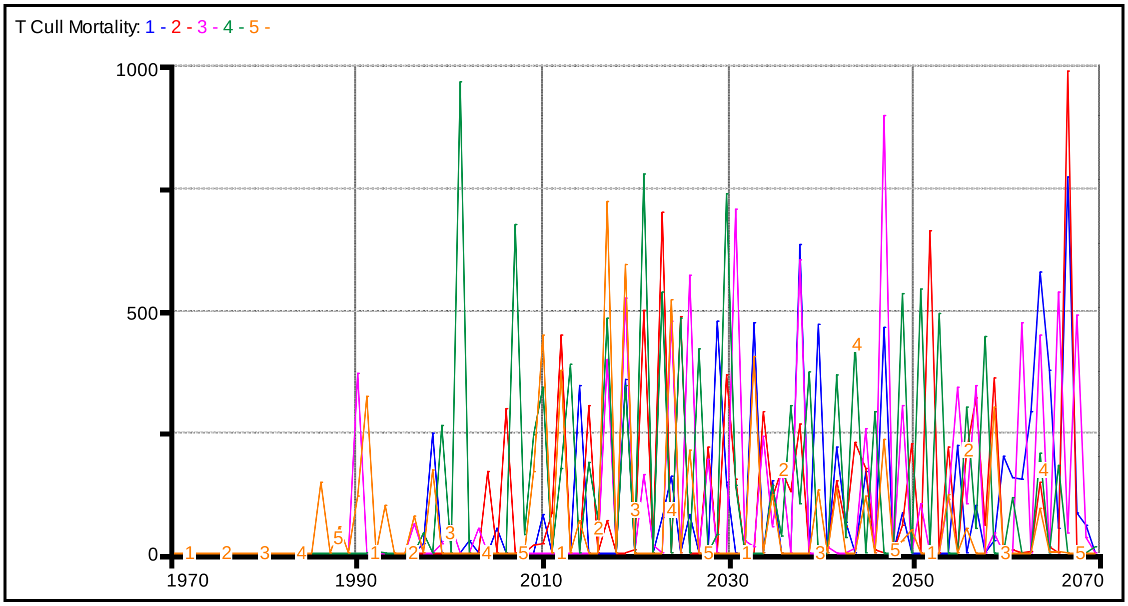


Figure 6.80. Simulated total cumulative bison starvation mortality. Graphs represent different Key Informant Groups (1 through 5). Upper graph represents simulation scenario without winter road grooming, whereas lower graph represents road grooming along corridors PHC, FMC, and FWC.



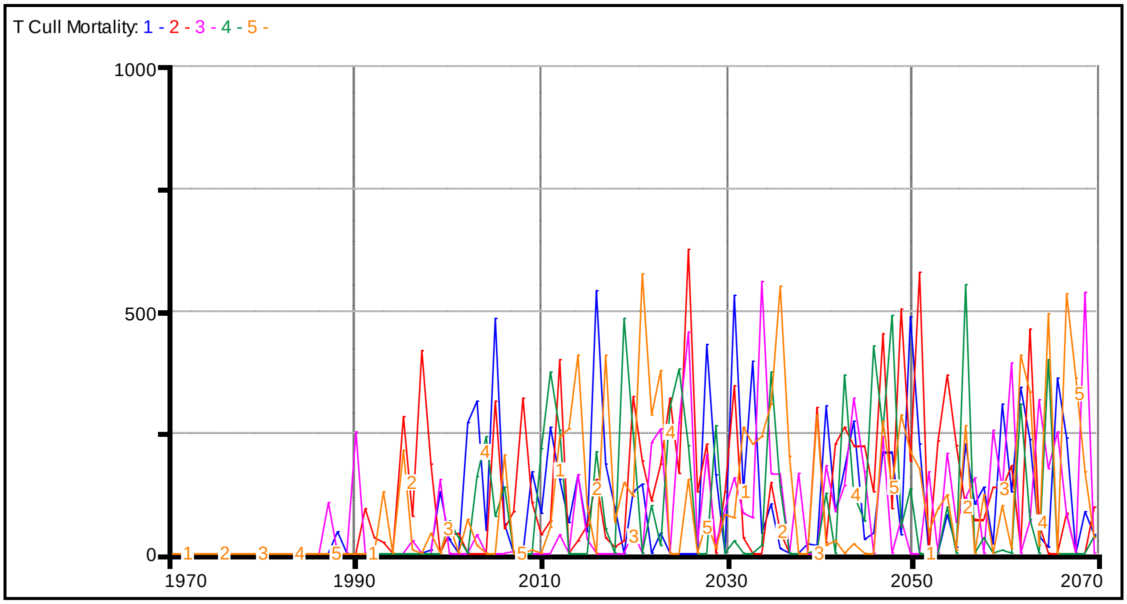
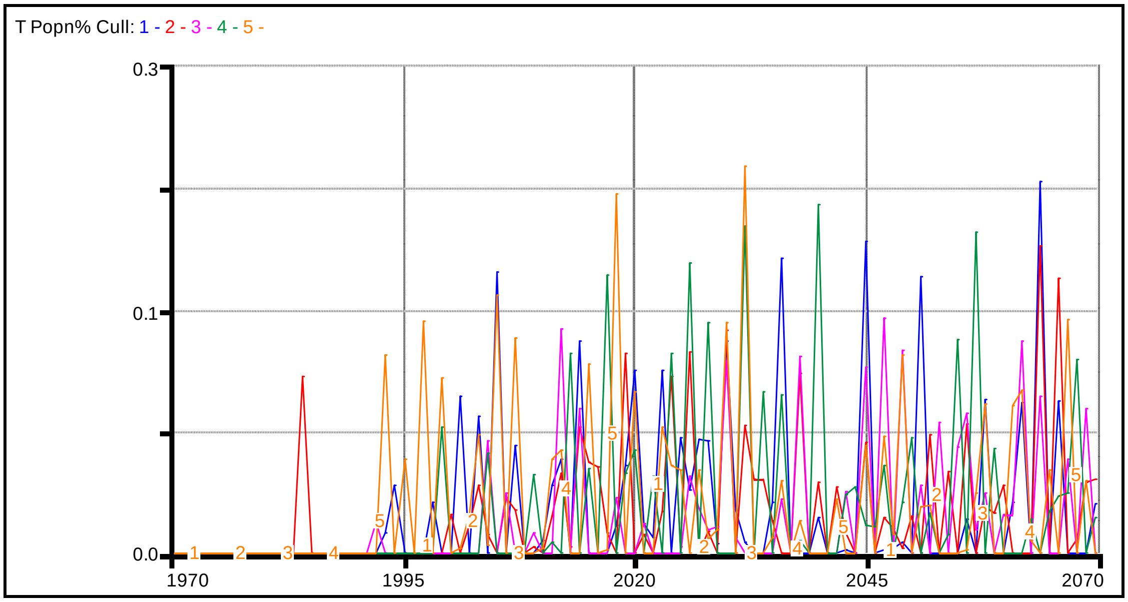


Figure 6.81. Simulated annual number of bison culled from boundary ranges (max tolerance of 200 animals per boundary range). Ten random runs without (upper) and with (lower) winter road grooming. Simulation based on Majority Average Model.



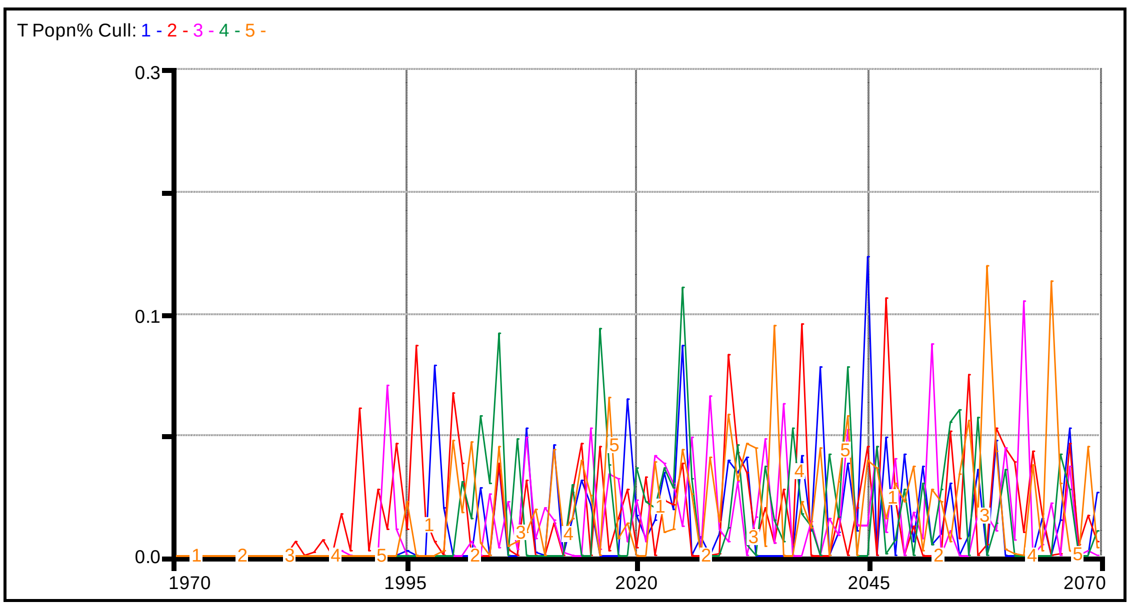
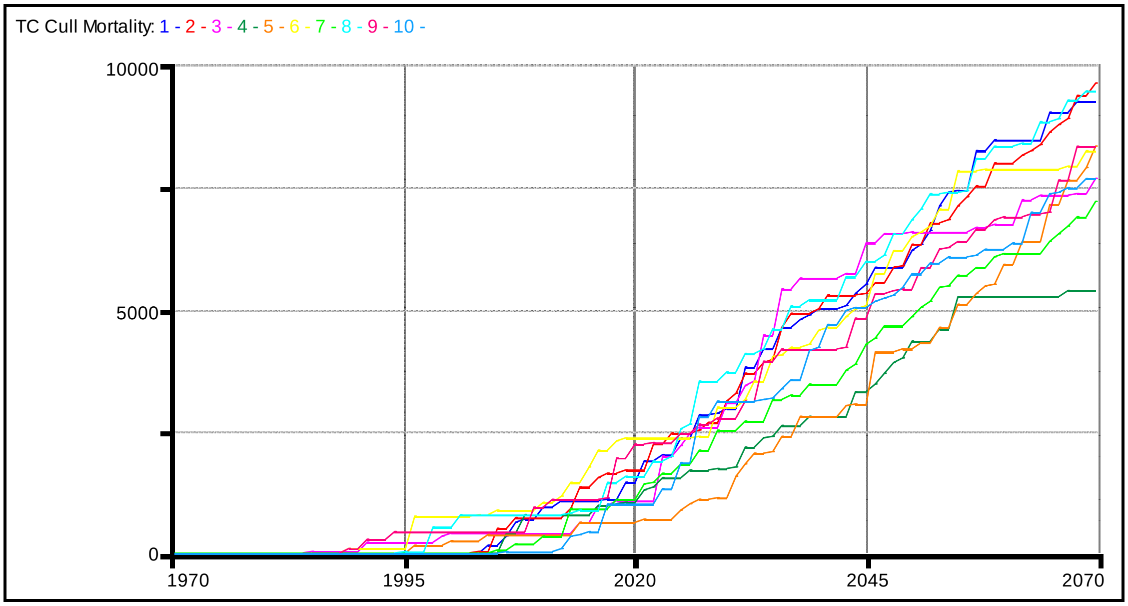


Figure 6.82. Simulated comparison of proportion of YNP bison herd that is killed by cull of boundary herds without (upper) and with winter road grooming (lower). Simulations were 100 years and reflected an identical pattern of random precipitation. Simulation based on Majority Average Model.



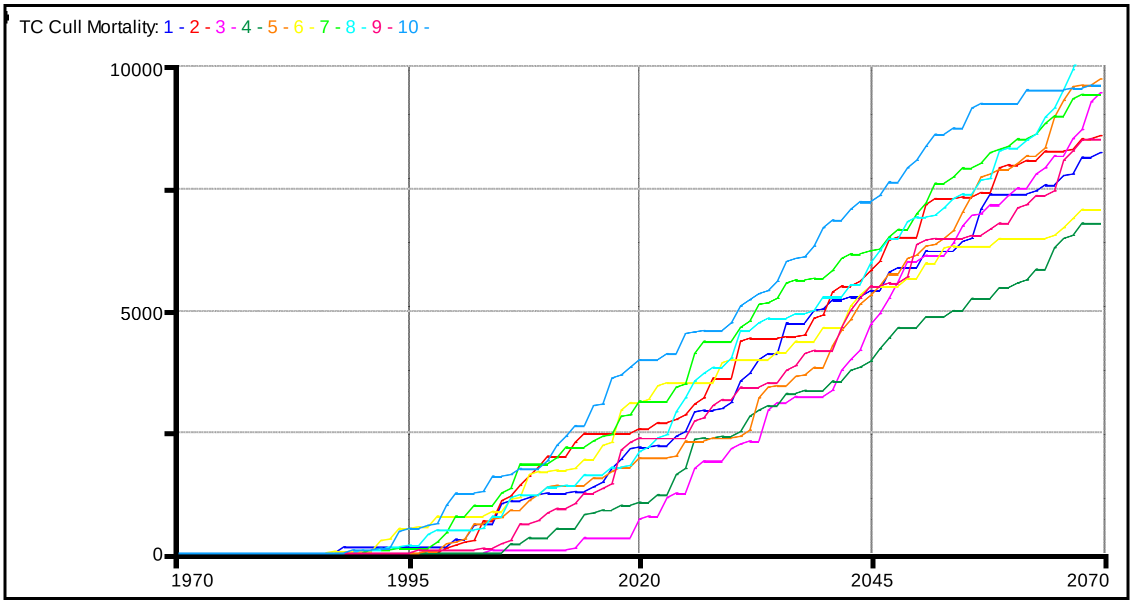
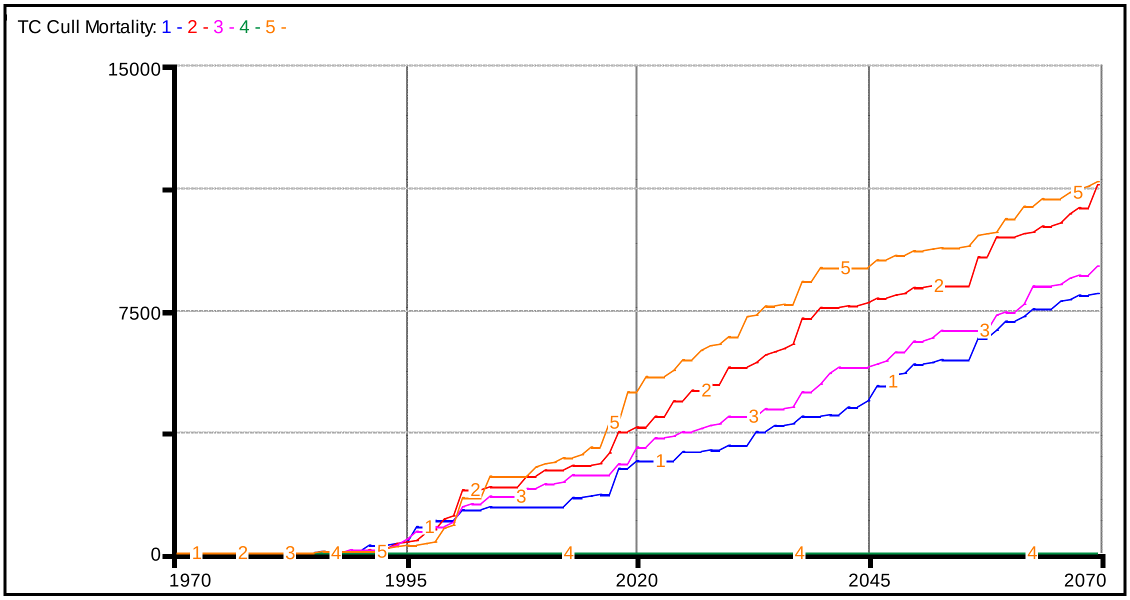


Figure 6.83. Simulated total cumulative number of bison culled from boundary ranges (max tolerance of 200 animals per boundary range) without (above) and with (below) winter road grooming. A series of ten 100 year simulations conducted with random precipitation. Simulation based on Majority Average Model.



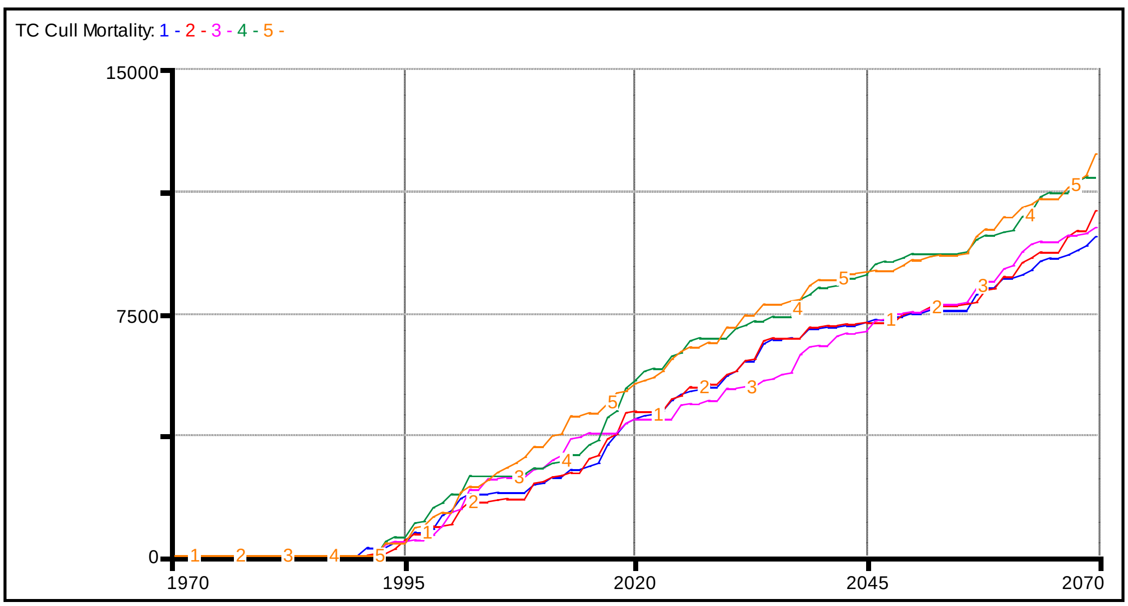


Figure 6.84. Simulated total cumulative cull of excess bison in boundary ranges. Graphs represent different Key Informant Groups (1 through 5). Upper graph represents scenario without winter road grooming, whereas lower graph represents road grooming along corridors PHC, FMC, and FWC.

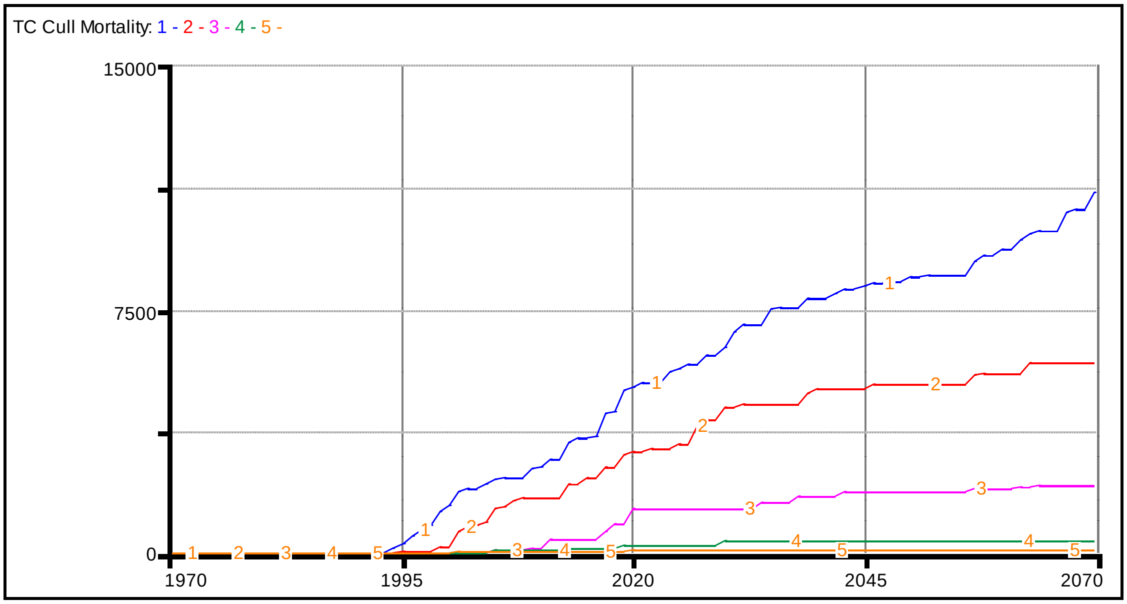


Figure 6.85. Simulated comparison of total cumulative # of bison culled under different maximum bison tolerances of 200, 400, 600, 800, and 1000 for each of the two boundary ranges. Scenarios include winter road grooming of corridors PHC, FMC, and FWC and involve identical series of random precipitation.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

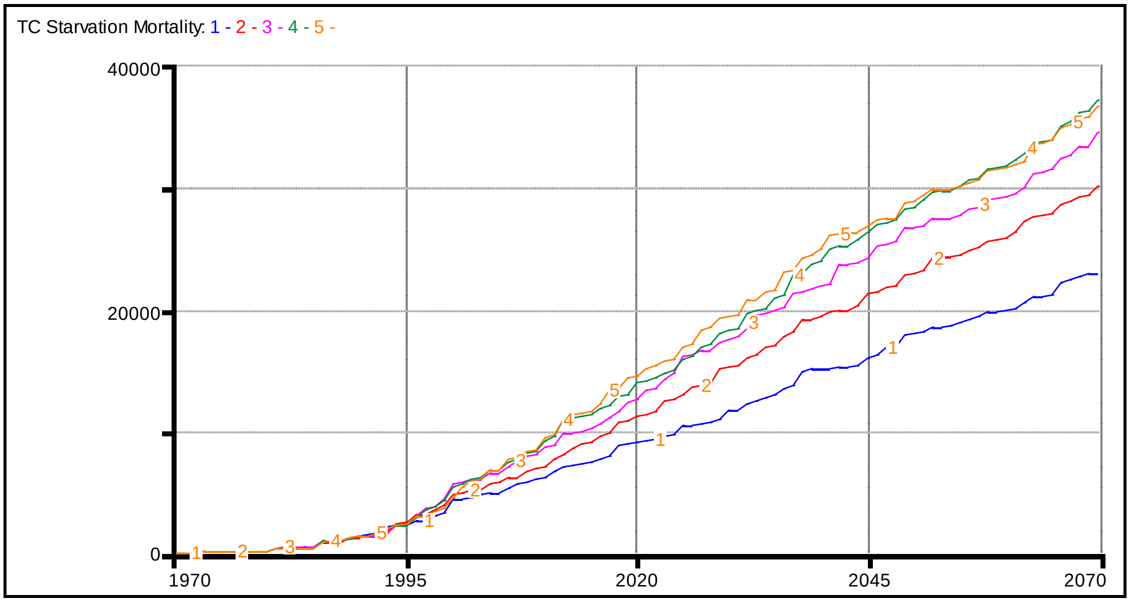


Figure 6.86. Simulated comparison of total cumulative bison starvation under different maximum bison tolerances of 200, 400, 600, 800, and 1000 for each of the two boundary ranges. Scenarios include winter road grooming of corridors PHC, FMC, and FWC and involve identical series of random precipitation.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

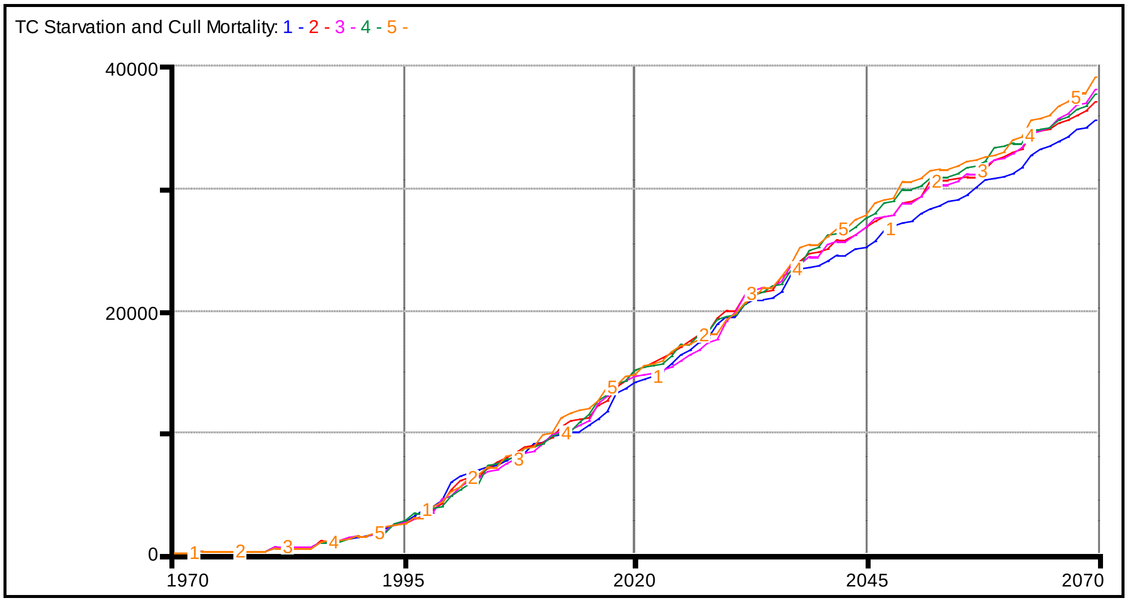


Figure 6.87. Simulated comparison of total cumulative bison cull and starvation under different maximum bison tolerances of 200, 400, 600, 800, and 1000 for each of the two boundary ranges. Scenarios include winter road grooming of corridors PHC, FMC, and FWC and involve identical series of random precipitation.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

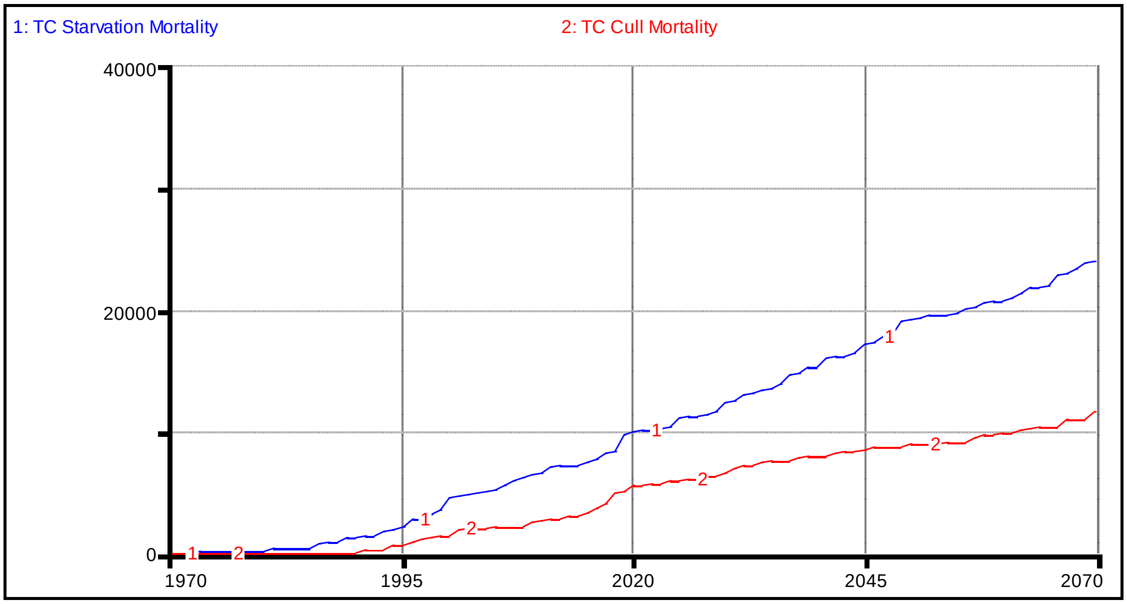
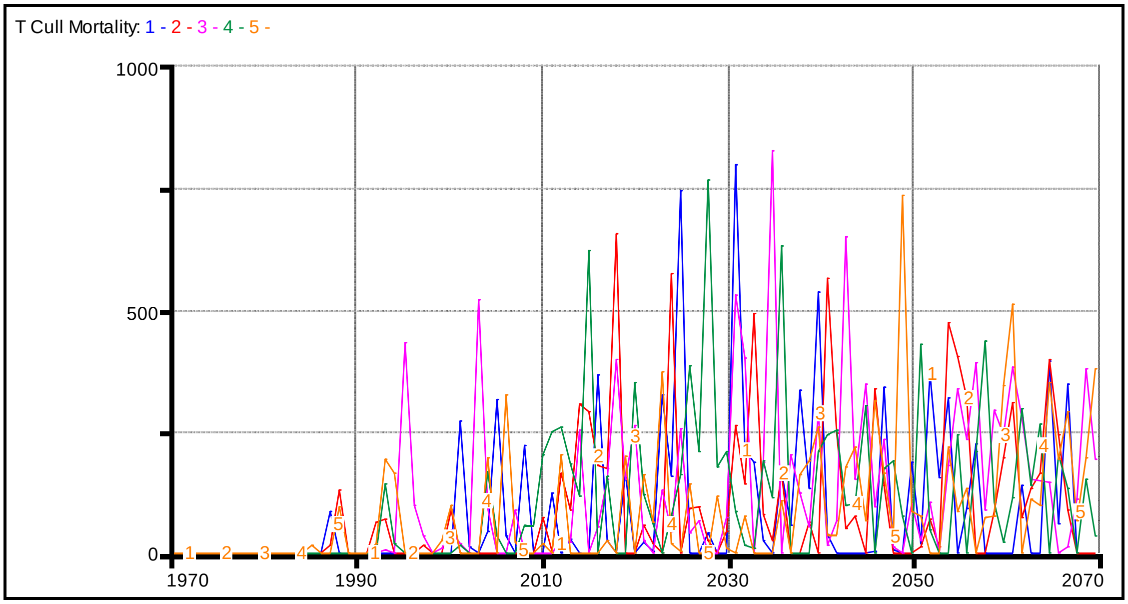


Figure 6.88. Comparison of net mortality attributed to starvation (#1) and cull (#2) during a 100 year simulation involving stochastic precipitation. Scenario includes winter road grooming. Simulation based on Majority Average Model.



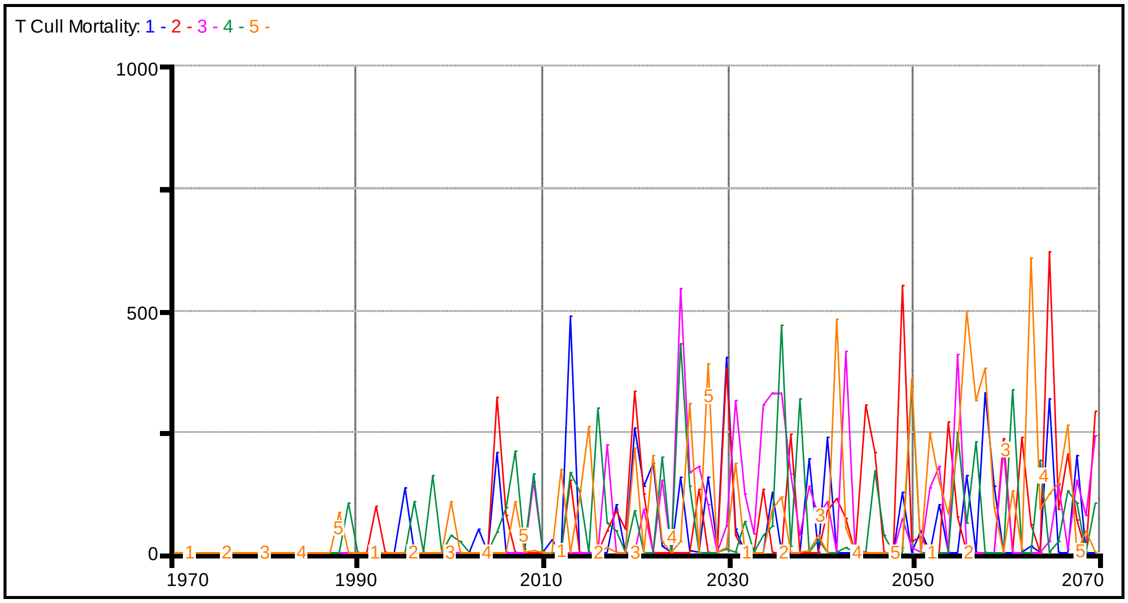
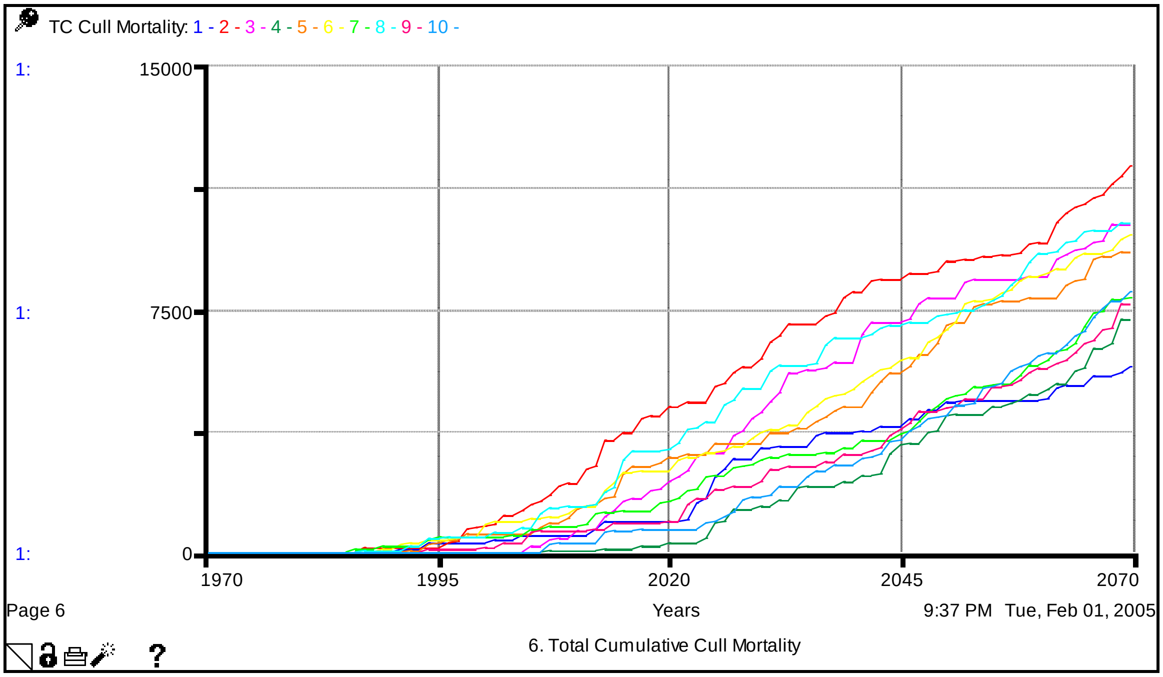


Figure 6.89. Simulated annual bison cull from boundary herds without (above) and with (below) a bison vaccination program. A series of five 100 year simulations conducted with random precipitation. These scenarios involve winter road grooming. Simulation based on Majority Average Model.



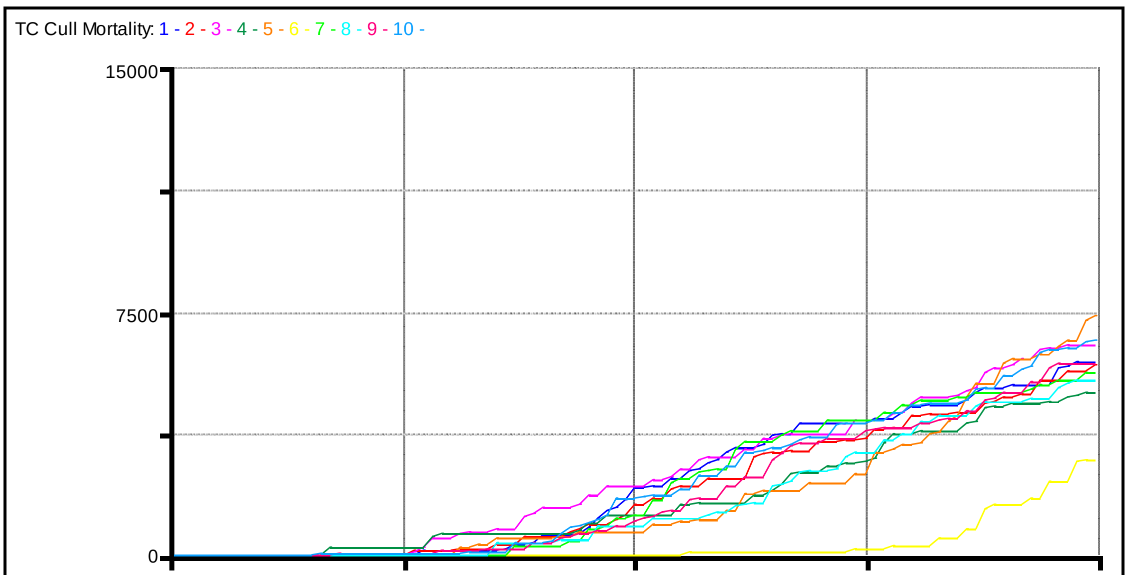


Figure 6.90. Simulated total cumulative level of bison cull without (above) and with (below) a bison vaccination program. A series of ten 100 year simulations conducted with random precipitation. These scenarios involve winter road grooming. Simulation based on Majority Average Model.

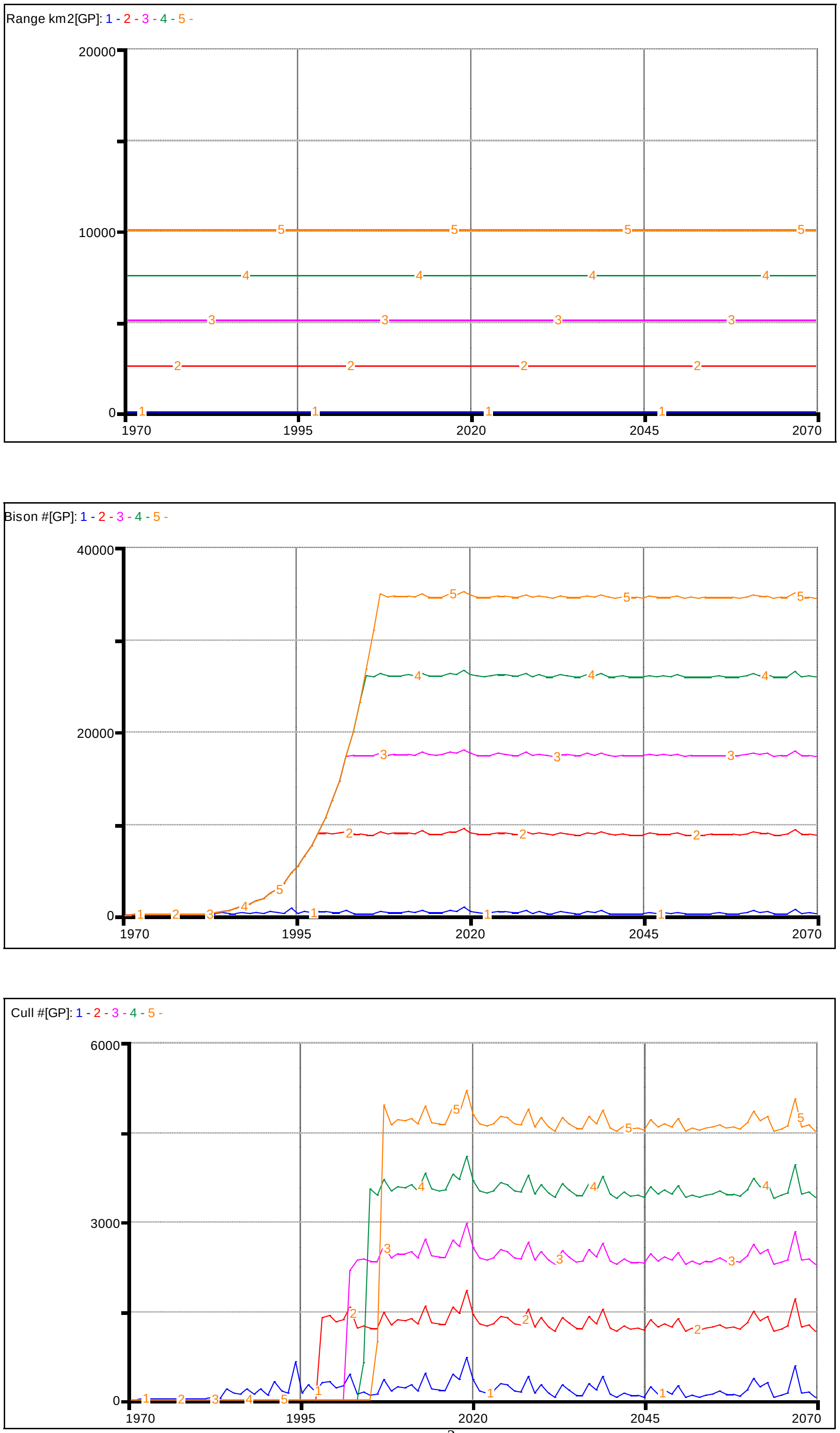


Figure 6.91. Simulation total range area (km^2, above), population size (middle) and annual cull (bottom) for a hypothetical "Great Plains" bison population under different scenarios where available area of the Great Plains varies from 0 (#1), 2,000 (#2), 4,000 (#3), 6,000 (#4), 8,000 (#5), and 10,000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

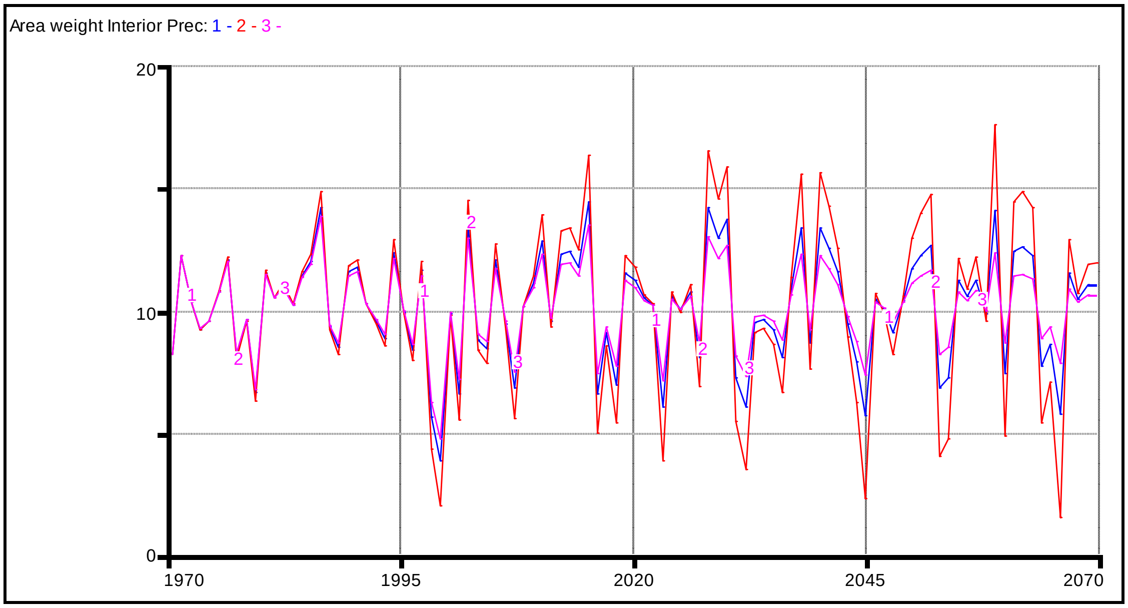


Figure 6.92. Simulated change in area-weighted average precipitation (cm) under three “climate change” scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over 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.

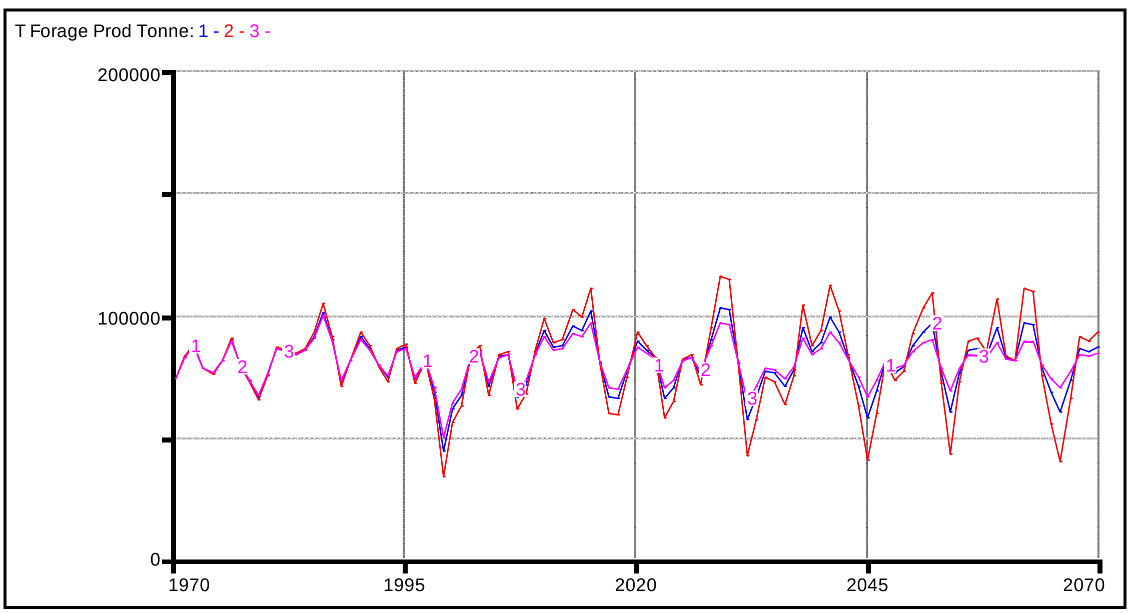


Figure 6.93. Simulated change in forage production (tonne) under three “climate change” scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. 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.

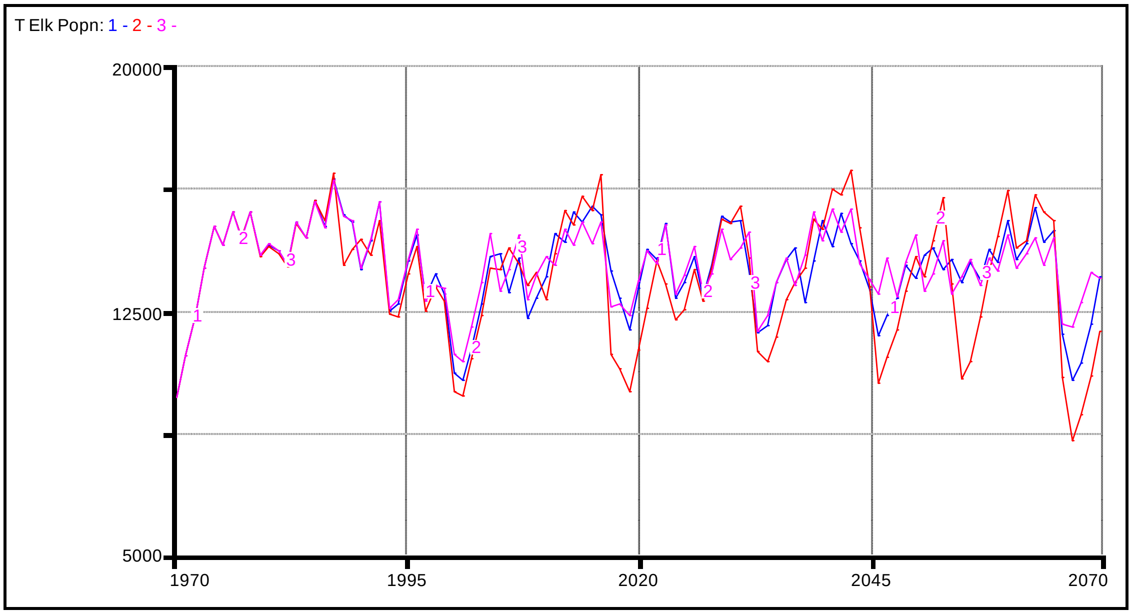


Figure 6.94. Simulated change in total elk populations under three “climate change” scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. 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.

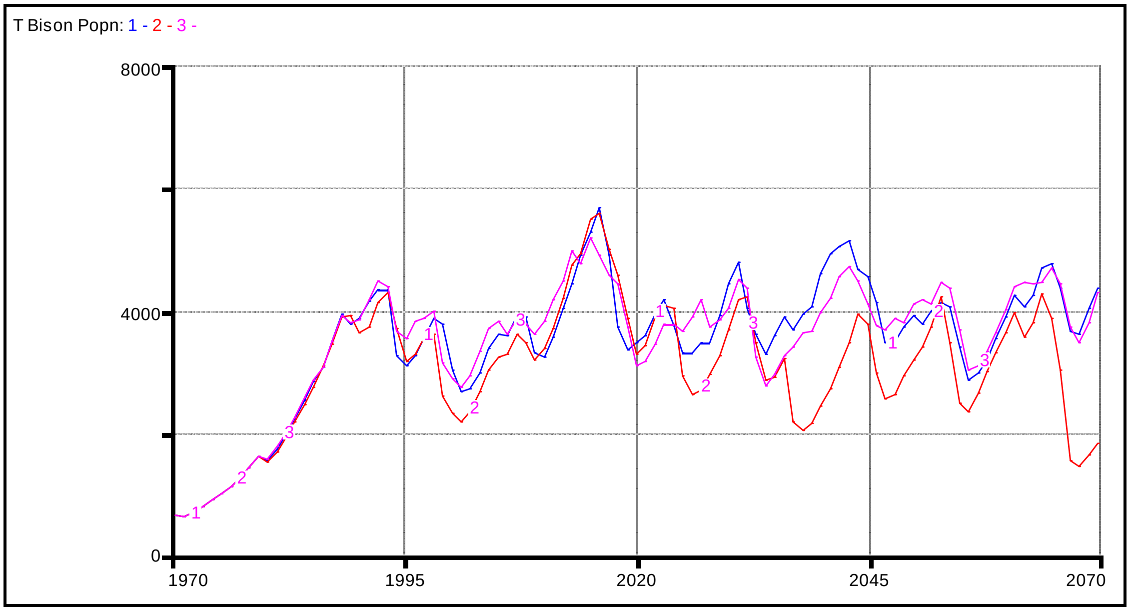


Figure 6.95. Simulated change in bison populations under three “climate change” scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has doubled over a 100 year period. Scenario #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.

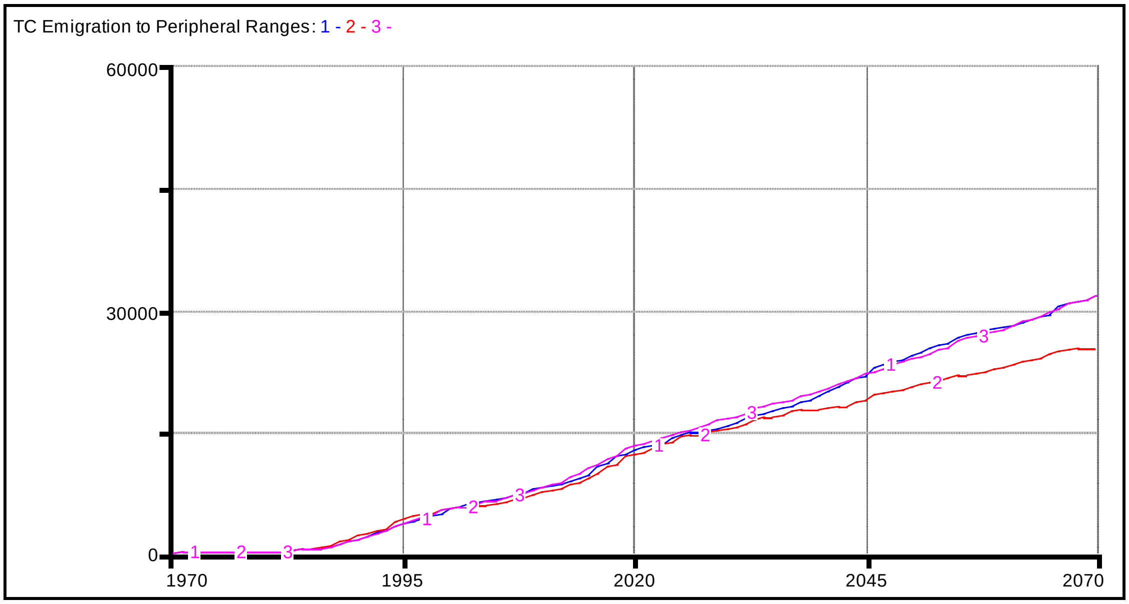


Figure 6.96. Simulated change in total cumulative bison emigration to boundary ranges under three "climate change" scenarios. Scenario #1 reflects current average and variance precipitation levels. Scenario #2 reflects current average levels and incremental increases in variance such that variance has 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.