EVALUATION OF MANAGEMENT OPTIONS FOR BISON AND BRUCELLOSIS IN YELLOWSTONE NATIONAL PARK, WYOMING.

A THESIS SUBMITTED TO THE FACULTY OF THE GRADUTE SCHOOL OF THE UNIVERSITY OF MINNESOTA

BY

ROBYN PHYLLIS ANGLISS

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DONALD B. SINIFF, Advisor

January 2003

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ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

University of Minnesota

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Robyn Phyllis Angliss

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Donald B. Siniff

Name of Faculty Advisor

Donald B. Siniff

Signature of Faculty Advisor

7 Jan 03

Date

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FORWARD

This work was funded in part by Yellowstone National Park (YNP). John Mack (Yellowstone National Park; currently at Bandolier National Monument) provided many, many hours of constructive advice and was my constant companion as the models were developed. Mark Boyce (affiliations) provided invaluable insights into the Yellowstone ecosystem. Wayne Brewster (YNP) helped me better understand the culture within which wildlife management operates in the West. Glenn Sargeant (U.S. Geological Survey – Biological Resources Division) assisted by putting my model results into a format which would be easily understood by those digesting the final Environmental Impact Statement and is responsible for suggesting the user-friendly format of the data presented in Figures 17-19.

Completion of this research would not have been possible without the incredible support of several supervisors in the National Marine Fisheries Service (NMFS) who felt strongly that the long term benefits of further graduate work to both me and my agency would outweigh any short term drawbacks caused by my occasional lack of ability to simultaneously juggle all of my professional and academic responsibilities. In particular, Mike Payne and Pat Montanio (Office of Protected Resources, NMFS) allowed me the professional flexibility to participate in NMFS' Advanced Studies Program and attend courses in conservation biology at the University of Minnesota. Doug DeMaster, Sue Moore, and John Bengtson (National Marine Mammal Laboratory, NMFS) allowed me to complete my dissertation on "work time". Particular thanks go to Doug: your friendship and encouragement has helped me negotiate some challenges both academically and professionally, and you have been a terrific role model for years.

Thanks also go to Kristin Laidre, Robert Suydam, and Glenn VanBlaricom for letting me borrow office space at the University of Washington; without this forced solitary confinement, this little project would have taken substantially longer to complete.

As chair of my graduate committee, Don Siniff has proven, yet again, why graduate students in wildlife management have sought his tutorage for decades. Don provided direction when asked, provided criticism without judgment, and was unfailingly kind. Thank you for the opportunity to work with you and to become one of the "Minnesota Marine Mammal Mafia". I also appreciate the time and valuable input provided by the other members of my committee, Dave Smith, Peter Jordan, and Francie Cuthbert, who were there at the end; and Sue Galatowitsch, Karlyn Eckman and Dave Anderson who participated in the beginning.

Finally, I dedicate this dissertation to my family. My parents, Robert and Eleanor Angliss, nurtured my interest in science and provided decades of love and unwavering moral support. My brother, Brian, provided welcome distractions and a constant reminder that there is life outside biology. And although sometimes it may have appeared that I wasn't listening, my grandfather, Edward Bachman, has reminded me kindly for years to "get it done!" To all of you. . .I love you, and I'm done.

And now, finally
My dissertation is done.
What now? Let's go play!

- written on 6/9/02 in gleeful anticipation of the successful completion of my Ph.D.

ABSTRACT

Bison (*Bison bison*) in Yellowstone National Park, Wyoming, have been infected by the disease "brucellosis" since the early 1900's, when bison likely contracted the disease from infected cattle. Brucellosis, which causes abortion in cattle, bison, and elk, has been nearly eradicated from cattle throughout the United States; bison and elk populations in Yellowstone National Park and the surrounding areas are the last remaining wild reservoir of the disease. Although experts agree that the probability that bison will transmit the disease to cattle grazed on lands outside Yellowstone National Park is very low, if transmission does occur, the economic consequences to local ranchers are both certain and significant. In order to efficiently manage the disease transmission risk, it is critical to understand the relative outcomes of different disease and population management tools on the abundance of bison and the disease prevalence in the bison population.

Eight alternative management plans for reducing the risk of transmission from bison to cattle were evaluated using mathematical modeling. Models for nearly all management plans predicted that the bison population would asymptote at a fall population size of approximately 3500-3700 animals. Most models indicated that the management plans were capable of reducing the disease prevalence from 40% to 9-13% by 15 years after the management plan was implemented when the "most plausible" combination of values for percent vaccinated, vaccine efficacy, and reinfection by elk were used; these models also estimated that disease prevalence would be reduced to 2-5% after 25 years. The management plan focused on whole-herd test and slaughter within Yellowstone National Park was estimated to eradicate the disease within 7-15

years. However, all management plans, except whole-herd test and slaughter, rely heavily on the availability of a vaccine against brucellosis. Until a safe, effective vaccine is available for bison, test and slaughter of migrants which carry brucellosis is the only available tool for reducing disease prevalence, and this is not expected to reduce prevalence substantially below the current level.

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INTRODUCTION

In recent years, the impacts of infectious diseases on wildlife populations has been identified repeatedly as a major issue in conservation biology (Daszak et al. 2000; Woodroffe 1999). In addition, many recent papers have evaluated the impacts of disease on wildlife (e.g., Woodroffe 1999) and some have described the results of models developed to evaluate the relative impacts of different wildlife disease management regimes (e.g., Smith et al. 1997; Gross et al. 1998). There have been, however, only a few attempts to actively manage the prevalence of a disease in free-ranging wildlife. Woodroffe (1999) summarized several attempts to manage infectious bacterial, microparasite, and ectoparasie disease in free-ranging, threatened wildlife and noted that no information was available regarding whether the management measures were successful in terms of either seroconversion or a reduction in animal mortality.

One highly-contentious wildlife disease management issue in the U.S. involves bison, a bacteria (*Brucella abortus*) whose eradication has long been a major goal of the U.S. Department of Agriculture (USDA), and the policy of natural regulation established by the U.S. Department of the Interior's (USDI) National Park Service (NPS) in 1967. This combination has resulted in years of negotiations between multiple agencies, affected states, local landowners, and environmental advocates. Several attempts have been made to develop a management plan that reduces the risk of transmission of the disease from bison to cattle, and litigation from a variety of stakeholders is ongoing. The National Environmental Policy Act (NEPA) requires that the environmental impacts of major federal actions be considered before making a decision to commit federal resources to an issue, thus, the negotiated plan for managing bison had to be evaluated objectively in conjunction with alternative management plans. Mathematical models were developed in order to assist in this evaluation, and the results of this evaluation are provided here.

Objectives

The objectives of this project were to 1) develop a model of bison and brucellosis in Yellowstone National Park, 2) use the model to determine the relative outcomes of the bison management plans, 3) identify any implications of having two discrete bison populations within YNP, 4) identify research which could improve our ability to predict the likely outcomes of different management alternatives, and 5) recommend long-term management strategies for maintenance of low levels of *B. abortus* in the YNP bison population.

Bison in Yellowstone National Park

The American bison (*Bison bison*) was nearly extirpated from the western United States in the late 1800's. The bison population in Yellowstone National Park (YNP; Figure 1) increased from under 50 animals in the early 1900's to a maximum of 3956 animals in 1994 (USDI 1998; 2000), and is the largest bison herd occurring on U.S. public lands. As of 1998, there were 2216 bison in the YNP herd (YNP, unpublished data; Figure 2).

Management of the YNP bison population has proceeded through three distinct phases. Between 1901 and 1966, the bison herd was culled almost annually. Culling operations from 1902-1938 focused on removing animals which were crippled, old, diseased, or were otherwise undesirable (Meagher 1973). Between the late 1930's and 1966, bison were culled to maintain a low level recommended by an early range-condition and carrying capacity study (Rush 1932).

In 1967, the NPS initiated a new "natural regulation" policy and began limiting management removals of bison to only those necessary to protect private property (primarily cattle). Because the threat to cattle only occurs when bison migrate out of YNP, only those bison that left YNP were killed. YNP records indicated that between 1966 and 1984, the bison population increased from 397 to 2229 animals, and no more than 8 bison were killed in any one year (USDI 1998, 2000; Figure 2).

The bison population within YNP migrates annually from summer feeding grounds at higher elevations to winter feeding grounds in lower-elevation open valleys, hydrothermal areas, and other areas where winter forage is more available (Figure 1). Because little thought was given to protecting known winter range fcr wildlife when the YNP boundaries were developed, much of the winter range for bison lies outside YNP on public and private land.

Bison migration patterns have changed over the past 50 years as the population has increased; Meagher (1973) provided excellent historical perspectives on the changes. Currently, there are two areas where bison winter; the location and migration rates outside YNP are different for the two groups (Figure 1). Some bison which winter in the Madison Valley/Firehole Valley area (called the "Central" area or group) will migrate outside of YNP to the west along the Madison River and in nearby lowlands. Some bison that winter in the northern portion of YNP (called the Northern Range area or group) commonly migrate down the Yellowstone River valley, past Mammoth Hot

Springs, and outside YNP to the north near Gardner. The rate of interchange between groups is unknown, but analysis of the locations of radio-tagged bison indicates that movement between groups is very infrequent (Gogan pers comm, June 2002). Natural mortality rates, rates of migration outside YNP, and management activities once the bison leave YNP were different for bison on the Northern Range and those wintering in the Central area.

The numbers of bison killed outside YNP has increased dramatically since 1985 as migration outside YNP increased. The first large migration outside YNP occurred during the winter of 1984/85, when 88 bison moved outside YNP and were killed. The largest migration outside YNP occurred during the severe winter of 1996/97, when 1,084 bison were killed (USDI 1998). This policy of intensive management of bison outside or at the boundaries of YNP was developed in order to eliminate any possibility of transmission of a disease, called brucellosis, from bison to cattle.

Brucella abortus and wildlife in Yellowstone National Park

Brucellosis is caused by any of a group of bacteria, *Brucella spp*, which is found in a wide range of species, including goats, swine, sheep, horses, dogs, cattle, Indian buffalo, and camels (see Nicoletti 1980 and Witter 1981 for thorough summaries of the distribution, etiology, and pathology of brucellosis). Recently, many marine mammal species have also been found to test positive for *Brucella* spp, including captive bottlenose dolphins (Miller et al. 1999), a wide variety of pinnipeds and cetaceans in the North Atlantic (Tryland et al. 1999) and South Pacific and the Mediterranean (Van Bressem et al. 2001). The results of infection with *Brucella* spp is dependent on the host species and the *Brucella* spp involved, and range from abscesses (for horses, Witter 1980; bottlenose dolphins, Miller et al. 1999), to abortion (for cattle, Nicoletti 1980 and Witter 1981; bottlenose dolphins, Miller et al. 1999; bison, Rhyan et al. 1994), to chronic undulant fever (for humans; Witter 1981). Humans can be treated with antibiotics to reduce the severity of the disease, but antibiotics cannot be relied upon to eliminate infection (Witter 1980).

The species of *Brucella* which infects domestic cattle is *B. abortus*. As its name implies, *B. abortus* infection in cattle is commonly localized in the reproductive system, and causes cows to abort (Nicoletti 1981). Bison in YNP have been infected with *B. abortus*, since the early 1900's (Mohler 1917; Meagher 1973) when the bison population likely contracted the disease from domestic cattle (Meagher and Meyer 1995). Abortion rates of female bison inoculated experimentally are over 90% in the first year a female is infected (Davis et al. 1990, 1991). During an abortion event, massive numbers of *B. abortus* are expelled in the placental fluids and on the aborted fetus; oral contact with this material by naive individuals represents the major known vector of transmission. Male bison infected with *B. abortus* experience orchitis, epididymitis, and seminal vesiculitis (Rhyan et al. 1997). Infection in bison does not typically cause marked fever, anorexia, or other external signs of disease (NRC 1998).

The eradication of *B. abortus* from cattle herds in the United States has been a primary goal of the U.S. Department of Agriculture (USDA) since 1934 (NRC 1998) because the disease typically causes cows to abort their first calves and because the disease may be passed to humans via ingestion of untreated, contaminated milk or tissue (Witter 1981). Human infection by *B. abortus* remains a health issue in some countries, such as Oman (El-Amin et al. 2001). At this time, the U.S. brucellosis eradication program is lauded as highly successful and nearly all states are now brucellosis-free (USDA 2001). Regulations developed by the USDA's Animal and Plant Health Inspection Service (APHIS) require that livestock producers carry out certain procedures if their herds become infected, and restrict or prohibit interstate movement of infected herds (USDA 1998).

Intensive management of bison at the border of YNP has been deemed necessary by management agencies in recent years because of the potential for bison to transmit brucellosis to cattle. The probability of transmission of *B. abortus* from free-ranging bison to cattle is believed by experts to be very low, but not zero (NRC 1998). However, because of the cattle herd management actions required by the APHIS Uniform Methods and Rules (USDA 1998), such as elimination of the infected herd and possible restrictions on interstate commerce, the economic impact to livestock producers in the Yellowstone area would be both certain and significant if the disease is transmitted from wildlife to cattle (USDI 1998).

Elk in YNP and the surrounding ecosystem are also infected with *B. abortus*. The two elk herds in the area have vastly different seroprevalence rates: the Northern Range elk herd, which overlaps with the YNP bison range, has a very low incidence of disease (< 1%; Aune and Schladweiler 1993), while the Jackson elk herd, which resides in Grand Teton National Park and the surrounding National Forests, averaged 32% seropositive from 1971-1977 and has been known to carry the disease since 1930 (Peterson et al. 1991a citing Thorne et al. 1978; more recent data on the seroprevalence in the Jackson elk herd is compromised because the vaccine currently used on the herd cannot be distinguished from an active infection in standard field tests). Thus, both bison and elk have the potential to transmit *B. abortus* to cattle, and any attempts to evaluate the success of disease management in bison must also include possible reinfection by elk.

Recent bison management history

After a large migration of bison onto private lands in the winter of 1988/89 resulted in an unprecedented number of bison being killed by managers at the border of YNP, the NPS, Montana Department of Fish, Wildlife and Parks, and the U.S. Forest Service (USFS) formally recognized a need for a long-term bison management plan (USDI 1998). These cooperating agencies published a notice of intent in the *Federal Register*, which announced the imminent preparation of an environmental impact statement addressing such a plan. The Montana Department of Livestock (MDOL) and APHIS joined the list of cooperating agencies, and all parties signed a Memorandum of Understanding in 1992 which indicated that they would collaborate to develop a cohesive plan to meet the objectives of all parties.

A series of 4 interim management plans were developed and implemented between 1992 and 1996. In general, the interim management plans involved State of Montana and NPS personnel shooting bison that migrated out of YNP into Montana in order to prevent any physical contact with cattle. In 1997, changes were made to the interim plan that included capture and shipment to slaughter for bison that approached private lands to the north of YNP, and capture, test, and slaughter of seropositive bison and seronegative pregnant females that attempted to migrate onto private lands to the west of YNP (USDI 1998).

In 1998, the NPS, in conjunction with the USFS and the State of Montana, and in cooperation with APHIS, developed a draft Environmental Impact Statement (DEIS) for the Interagency Bison Management Plan for the State of Montana and Yellowstone National Park (USDI 1998). This DEIS described seven management alternatives which ranged from minimal management to aggressive management of brucellosis, and included alternatives that combined several management actions. A simple deterministic model was used to evaluate the likely outcomes of each of the management alternatives in terms of the population size and prevalence of brucellosis in the population. The deterministic models used to develop these estimates used average migration, capture and slaughter rates; environmental stochasticity was incorporated by investigating the fate of bison if there were a high, average, or low migration rate out of YNP in any one year (USDI 1998). While this modeling effort provided a rough estimate of the expected number of bison and reduction in seroprevalence levels, the agencies recognized that a more extensive modeling effort would improve the understanding of the relative outcomes of each management alternative.

This dissertation involved the development of stage-structured models for each of the 7 management alternatives presented in the DEIS and the additional new preferred alternative presented in the final Environmental Impact Statement (FEIS; USDI 2000; Figures 3-10). Both published and unpublished information on bison demography and disease transmission were used to populate the model in order to evaluate the relative effects of each alternative. Each model estimated numerous outputs, including the number of bison killed by management actions, the number of bison vaccinated, the number of bison permitted on public lands outside the park, and the number of bison seropositive for brucellosis. Different vaccine efficacy rates and delivery rates, and three rates of elk:bison transmission were evaluated to bracket the range of likely values. Winter severity was stochastic, and the random value of winter severity selected by the model was used to determine the estimated rate of migration outside the park, the estimated winter mortality rate, and the estimated exchange between areas within the park during the winter. The dynamics of brucellosis in the bison population was modeled using a variation of the susceptible-infected-recovered approach used generally (eg., Heesterbeek and Roberts 1995) and for the Yellowstone bison population (Howe 1998; Dobson and Meagher 1996).

METHODS

Overview

The model developed to examine the population dynamics and disease dynamics of the YNP bison population is a simple stage-structured population model combined with a standard susceptible-infected-recovered-vaccinated model (e.g. Heesterbeek and Roberts 1995; Anderson and May 1982). The fate of individual animals with respect to reproductive success, survival, and disease status was not tracked; rather, the model tracks aggregated changes in the numbers of animals in each stage and disease class. This model included only the dynamics of females because they constitute the reproductive portion of the population. Although male bison may contract brucellosis, they were excluded from the model because they are generally not considered consequential factors in transmission (Peterson et al. 1991).

Slightly different models were developed for each of the eight different management alternatives included in the FEIS (Figures 3-10). This was necessary because the nature and timing of bison and disease management actions differed substantially between each alternative.

General structure and parameterization of the population dynamics model

General structure

The population dynamics model developed for this study was stage structured, as information was available on stage-specific, but not age-specific, demographic rates. Separate models were developed for the Central and Northern Range herds, because there is currently little interchange between herds and because the demographic rates and human-related removal rates from each herd are very different. The model year began in the fall, and the fall population size was used to estimate winter natural mortality and management removals of bison between December and April. A small number of animals were allowed to migrate between wintering areas. The natural mortality rate, the management removals, and migration between herds depended on a random winter severity level selected each model year. In the model, the remaining number of females alive in the spring reproduced. Because the model did not involve any mortality between spring and fall, the fall population size was equivalent to the post-calving spring population size. The parameterization of the model and justifications for assumptions made (e.g., mortality occurs only during the winter) are provided below.

Proportion of bison in each wintering area

Meagher (1973) provides the only published account of the numbers of bison on the Central and Northern Range wintering areas. Between the early 1900's and the early 1930's, the majority of bison in YNP were located on the Northern Range. In 1936, bison from the Lamar Valley were transported and released in the Firehole and Hayden Valleys. After 1936, the proportion of bison in the Central wintering area increased steadily and there was a corresponding decrease in the proportion of bison on the Northern Range (Figure 2; data from Meagher 1973)

In 1944, the proportions of bison in each wintering area were roughly equal, and from 1944-1968 the proportions of bison on the Central and Northern Range averaged 0.7 and 0.3, respectively, although the proportions changed annually due to different mortality rates and management actions carried out in each area.

More recently, an extrapolation from Kirkpatrick et al. (1996) indicates that the proportion of adult female bison on the Central and Northern Range was 0.9 and 0.1, and 0.8 and 0.2, for 1990 and 1991, respectively. An overall distribution between the Central and Northern Range areas of 0.76:0.24 can also be calculated from the numbers provided in the abstract of Kirkpatrick et al. (1996). In addition, recent data on the winter distribution of bison in YNP indicates that the ratio between the number of animals in the Central and Northern Range was 0.75:0.25 in the fall of 1996, 0.81:0.19 in the fall of 1997, and 0.82:0.18 in the fall of 1998 (NPS unpublished data); the unweighted average ratio from 96/97 through 98/99 is 0.79:0.21.

Because a long time-series of data from recent years is not currently available, and because the average proportion of bison on the Central and Northern Range in the 1990's (Kirkpatrick et al. 1996; NPS unpublished data) is not very different from the average proportion of bison in each area calculated based on Meagher (1973), the 70:30 ratio calculated from data for 1944-1968 and provided in Meagher (1973) was used to determine the current proportion of YNP bison in each area.

Sex ratio

There are a variety of sources for information on the sex ratio of the bison population in YNP. According to Pac and Frey (1991), the fetal sex ratio of bison in the harvest of 1988/1989 was 58:42 (female:male) and the overall sex ratio of harvested bison for 1974-1989 was 41:59. Green (1994) found that that the average ratio of adult female to adult male bison carcasses found on transect lines in the Firehole-Gibbon study area between 1985-1990 was 60:40 and that the ratio in 1989 was 58:42. Data collected by the Bear Management Office (BMO; YNP unpublished data) indicate that the average ratio of female to male carcasses observed on transect lines between 1992-1997 was 60:40, and that the ratio in 1997 was 42:58. Although there are considerable differences between the ratios reported for different types of studies (Table 1), when the ratios obtained from studies with sample sizes of greater than 100 bison are averaged, the ratio is approximately 51:49, which is very close to unity. Thus, a 50:50 sex ratio is assumed and is used to calculate the initial population size of females used in the model.

Initial population sizes and stage structure

The initial population size used in the simulations of the management alternatives was 2105, which was the number of bison in YNP counted in fall of 1997 (YNP, unpublished data). The numbers of females in the Northern Range and Central wintering areas was calculated as one-half of the product of the total population size and the proportion of females in each wintering area, which yielded 316 and 737 animals, respectively.

There are four different sources of information on the relative proportions of bison in each stage (Table 2). If we assume that both males and females of all stages are equally likely to be caught or to attempt to move out of YNP in response to severe weather, the stage structure of captured or harvested bison can be used to determine the stage structure of the population. However, it is preferable to use information on bison which remain in YNP as it is not known whether the bison which are captured or harvested are representative of the entire population.

Meagher (1973) indicated that bison captured during the winter of 1964-1965 exhibited a stage structure of 16% calves (9mo old), 11% yearlings (21 mo old), and 73% older adults. Pac and Frey (1991) provided information on stage structure estimated using different methods, and asserted that their best stage structure information was very similar to that observed by Meagher (1973). This model uses the data from Meagher (1973) because they were collected within YNP instead of outside the boundary of YNP, and would better represent the true stage structure if there are any stage-specific differences in the rates of migration out of YNP.

Determining winter severity: Obtaining information on snow water equivalent

Winter severity is measured by snow water equivalent levels, which indicates the amount of water content in the snow at a particular time. Information on the maximum snow water equivalent (SWE) in inches was obtained for the winters of 1934-1997 from the SNOWTEL database run by the National Resource Conservation Service. Data from two sites, Lupine Creek and Lake Camp, were used (Figure 1). The Lupine Creek site is located on the Blacktail Deer Plateau (44° 55', 110° 37'; 2236m), and was used by Farnes (1996) to characterize the winter environment for elk on the Northern Range. The Lake Camp site is located at the northern end of Yellowstone Lake (44° 33', 110° 24', 2358m) and was selected to represent the winter environmental conditions for the bison in the Central wintering area. The maximum SWE was selected from each site for each year to reflect the worst winter conditions experienced by animals during that year; in all cases, the maximum SWE value occurred in March or April. Descriptive statistics for the maximum SWE values at the two sites are provided in Table 3. The variances of the SWE values at the two sites were not significantly different (F-test, $p_{0.05} = 0.19$); the means also were not significantly different (two sample t-test assuming equal variances, $p_{0.05} = 0.58$). Thus, SWE data for each site was averaged for each year and only one SWE value was used to characterize the winter severity in the model.

Natural mortality rates

Sources of natural mortality

Sources of natural mortality for bison include predation, disease, sickness/malnutrition, calving, and accidents. It is reasonable to assume that the vast majority of natural mortality occurs during the winter. Meagher (1973) indicated that most natural mortality occurred in after January and noted that, with the exception of some mortality of new calves near the time of birth, little additional calf mortality occurred over the summer until the following winter.

There is only one species in YNP, the gray wolf (*Canis lupus*), which is known to actively predate on bison. Gray wolves were extirpated from YNP as part of a predator control program; by the time the NPS abandoned their predator control policy in 1933, no wolf packs remained in YNP and individual wolf sightings were very rare (Weaver 1978). Wolves were reintroduced into YNP in 1995 and 1996 (Bangs and Fritts 1996; Bangs et al. 1998). There were 40 wolves in YNP in 1996 and by 2000, the population had increased to over 160 animals and wolf packs were established throughout much of the Greater Yellowstone Ecosystem (Smith et al. 2001). There were no definite or probable predation events on bison in 1995 or 1996 (Phillips and Smith 1997); 2, 5, 14, and 9 definite or probable predation events were noted in 1997-00, respectively (Smith 1998; Smith et al. 1999; Smith et al. 2000a; Smith et al. 2000b; Smith et al. 2001). Predation by grizzly bears (*Ursus arctos*) has been suggested, but has not been observed directly (Meagher 1973). Mattson (1997) confirms that, although bison carrion resulting from winter kill is a major food source for grizzly bears, they have not been observed to take live animals.

Accidents that may cause bison mortality include drowning (Meagher 1973, Berger and Cunningham 1994), contact with hydrothermal pools (Meagher 1973), and presumably rock slides and avalanches that cause mortality in elk (Green 1994). Data from Green (1994) indicated that accidents were the cause of death for 16% of the carcasses found in the Firehole/Gibbon study area from 1985-90.

Meagher (1973) reported that disease-induced mortality was not identified recently in the bison population, although outbreaks of hemorrhagic septicemia caused significant mortality in the early 1900's. Other diseases, such as anthrax and tuberculosis which have caused mortality in other bison populations have not been detected in the YNP population (Meagher 1973).

Green (1994) lists "calving" as a source of mortality for a small (10%) proportion of the adult female bison carcasses found, but does not provide any information regarding how this was identified as the cause of death.

Estimating the magnitude of winter mortality

Most natural mortality occurs during the winter as a result of the combined effects of stress, malnutrition, and physiological condition (Meagher 1973; Green 1994). Data provided in Green (1994) indicated that sickness and malnutrition was the cause of death for 74% of the carcasses found in the Firehole/Gibbon study area for which cause of death could be determined.

The rates of winter natural mortality vary depending on the severity of the winter, and have different levels of impact on different bison stage classes. Meagher (1973) observed that the winter mortality rate was under 1% during mild winters, and that the number of animals that succumbed to winterkill increased during severe winters. Similarly, although only a few years were sampled, Green (1994) found more carcasses per surveyed kilometer during severe winters than during mild winters.

Starting in 1992, the BMO carcass surveys began following protocol developed by Green (1994) and conducted line transect surveys for carcasses in order to determine the amount of carrion available for grizzly bear consumption. The BMO used the same techniques and transects used by Green; thus, their data on the total number of bison carcasses observed each spring can be combined (Table 4). Green (1994) and the BMO collect information on the number of bison carcasses found along transects. Because this sampling method includes only a small proportion of the total winter range, an extrapolation must be made to estimate the total number of bison which died as a result of winterkill each year. There is only one year between 1984/1985 and 1996/1997 for which an independent estimate of mortality was available. At the beginning of 1996/1997, there were approximately 3,500 bison, of which approximately 1,100 were subject to management removals at the border during the winter. The estimated bison population in the spring of 1997 was approximately 2,000 animals; thus, approximately 400 bison must have died due to natural causes during the winter. The ratio of observed carcasses in 1997 (69) to the estimated total winterkill for that year (400) is 5.8. This factor was applied to the number of carcasses in each wintering area to estimate the total number of bison that died of natural causes each winter. This approach requires the assumption that the ratio of the number of carcasses found on transect lines to the total number dead on both winter ranges is the same.

The population model requires estimates of natural mortality for bison in both the Northern Range and the Central wintering areas. The few data available indicate that the natural mortality rate on the Northern Range is low. Even after the Northern Range carcass data is extrapolated using the 5.8 multiplier, the estimated mortality rate only ranges from 0.015 – 0.037. Further, the data are insufficient to determine if there is an increase in natural mortality on the Northern Range in severe winters. The model incorporated a winter mortality rate at random from a uniform distribution between 0.01 and 0.04 for each modeled year.

The natural mortality rate is clearly higher in the Central wintering area during severe winters. Linear regression was used to determine the relationship between the estimated natural mortality rate and the average maximum SWE value (Figure 12); the regression was significant ($F = 5.86$, $p = 0.04$) although the y intercept was not significantly different from zero. Data on the estimated number of bison killed in 1988/1989 was excluded from the regression analysis because it was an outlier. Because the natural mortality rate will vary even for a given winter severity level, a random natural mortality rate for bison in the Central wintering area would be selected using the upper and lower 50% confidence limits for this regression as bounds (Lower limit: $(0.008 * SWE - 0.0449) * 100$, Upper limit: $(0.008 * SWE - 0.0077) * 100$)

Stage-specific natural mortality rates

Both Meagher (1973) and Green (1994) indicate that the natural mortality rate differs for calves, subadult, and adult bison. Meagher (1973) reported that there was considerable mortality among subadults; a loss of 19% between the first and secnd winters, and 31% between the second and third winters was estimated based on the relative numbers of bison in each age class. However, this is not a good way to determine the long-term proportions of animals in each age class unless the intrinsic rate of increase is 0 because otherwise the number of individuals in each age class will be dynamic.

Carcass surveys conducted by Green (1994) and BMO (unpublished data) provide some information on the proportions of bison in each stage class that are subject to winter mortality (Table 5). Green (1994) provides data on calves (assumed to be calves-of-the-year), yearlings, 2-4 year olds, and 5+ year olds. BMO provides data on calves-of-the-year, calves, yearlings, subadults, and adults. Personal communication with staff of the BMO indicated that their designation of "calves" generally means bison that are 9 months old and "yearlings" may include bison of the same age class; thus, for the BMO data "calves" and "yearlings" are pooled. Although no specific range of years is specified for "subadults" in the BMO data, I assumed that the BMO followed the general protocol of Green (1994), and that the subadult and adult designations are roughly comparable. For modeling purposes, I used only calves-of-the-year, yearlings, and adults, which are 9mo, 21mo, and at least 33mo old, respectively, at the beginning of the winter management activities.

The numbers of bison carcasses in each stage class found by Green (1994) and by the BMO are provided in Table 5. The unweighted mean frequency was calculated by dividing the average number of carcasses found in each stage class by the total average number of carcasses found each year. The weighted mean frequency was determined by weighting each observation of the number of carcasses found for each stage class for each year by the total number of carcasses found that year. The weighted mean frequency will be used to determine the proportion of each stage class that is affected by natural mortality each winter. The weighted mean frequency of 0.06 for subadults includes ages 2-4. I assumed that the frequency is evenly distributed between the three stage classes, so the frequency for 2-year olds (21mo old at the beginning of winter management activites) only would be 0.02, and the frequency for adults would be (0.35 + 0.04 = 0.39).

Relationship between SWE, population size and migration

The utility of the development of a mathematical relationship between SWE, population size, and migration rates seems obvious, but very little progress on this task had been made until a NRC report was published in 1998. The NRC (1998) analysis determined that when all data are considered from 1967-1997, none of the weather variables or indices tested were significantly correlated with the number of bison migrating out of YNP and the relationship was solely dependent on the number of bison in YNP. A log transform of the number of bison migrating out of YNP resulted in a significant relationship but the transformation did not communicate the abruptness of the threshold at which bison begin to migrate (NRC 1998). In contrast, when only populations above 3,000 bison are considered, there is a highly significant relationship between snow water equivalent and the number of bison migrating out of YNP. There was no correlation with winter temperature. The analysis demonstrated that bison would only migrate out of YNP if the population size is greater than 3,000 animals and there is more than 17 inches of snow water equivalent. Unfortunately, the results of the NRC analysis could not be incorporated directly into this evaluation of the management alternatives because separate migration rates were not calculated for the Central and Northern Range bison groups.

Relationship between SWE, the number of females in each wintering area, and the proportion of each wintering area that migrates out of YNP

The relationship between SWE, the population size in each wintering area, and the proportion of bison which migrate out of YNP was determined using data from 1967-1997. The number of females in each wintering area was estimated by using the observed total population size and multiplying the proportion of animals in each wintering area (0.7 or 0.3 for the Central and Northern Range wintering areas, respectively) by 0.5 (Table 6). The number of bison migrating out of YNP is assumed to be equivalent to the number of bison removed at the YNP border. Although some bison migrate out of YNP in areas where they are not removed (e.g., up the Hellroaring Creek or Slough Creek drainages), it is generally believed that these groups are typically small and primarily consist of male bison which migrate back into YNP after a short time (J. Mack, personal communication). In addition, a small number of animals migrate to the north onto the Eagle Creek/Bear Creek areas, but the number of migrants into these areas is very small relative to the numbers involved in management actions. The migration rate is calculated by dividing the number of bison removed outside the border of a particular wintering area by the number of bison calculated to be in that wintering area during that year.

There are at least two methods that can be used to describe the relationship between SWE, bison population size, and bison migration rate. The NRC (1998) observed that, below a population size of 3000, few bison migrate outside YNP. However, above a population size of 3000, many bison may migrate out of YNP during winters which are more severe than average. The NRC (1998) used a multiple regression to demonstrate that, above a population size of 3000 animals, the number of bison which migrate out of YNP is strongly related to the SWE.

For this model, a different method was used to describe, in one equation, the migration rates at low, medium, and high population levels for the entire period from 1967/68 – 1996/97. Multiple logistic regression was used to select coefficients for the that would predict the migration rate based on the SWE and the bison population size. The use of the logistic regression ensured that migration rates would always be greater than zero. Although the logistic regression was not significant, likely because of the large proportion of years during which no migration occurred (e.g. between 1967/68 and 1984/85), it did provide coefficients to the logistic equations that result in reasonable estimates of the migration rates. Furthermore, when the bison population is projected from 1967/68 to 1996/97 using the previously discussed natural mortality and fecundity rates, and the results of the logistic regression, the resulting population trajectory is similar to the dynamics observed during that period (Figure 12).

Because the bison migration rates out of the Central and Northern Range wintering areas are different, different equations were used. The proportion of female bison migrating out of the Central wintering area was described as:

$$= \frac{e^{(-11.8265+0.2764*swc+0.00444*N_{Cen})}}{1+e^{(-11.8265+0.2764*swe+0.00444*N_{Cen})}},$$

where "swe" is the maximum snow water equivalent for that year and N_{Cen} is the number of bison in the Central wintering area in the fall. The proportion of female bison migrating out of the NR wintering area was described as:

$$= \frac{e^{(-10.6939+0.35566*swe+0.01025*N_{NR})}}{1+e^{(-10.6939+0.35566*swe+0.01025*N_{NR})}},$$

where "swe" is the maximum snow water equivalent for that year and N_{NR} is the number of bison in the Northern wintering area in the fall. The relationship between bison population size, SWE, and proportion of bison migrating from each wintering area is shown in Figure 13.

Data used to develop above equations were based on total subpopulation sizes of 121 –1147 for the Northern group and 296 – 2808 for the Central group, and SWE values between 5.1 and 17.25. Thus, the relationship may not be valid for population sizes or SWE values outside of these ranges. When a normal distribution is generated with the specified average and standard deviation for observed SWE values, there is a small probability that SWE values both higher and lower than 5.1 and 17.25 will occur. If the model selects a random SWE value larger than 17.25, the proportion of migrants calculated using these equations may or may not reflect the real expected migration rate. For instance, if the random SWE value is 20 and the total size (males + females) of the Central population is 2,500 animals, the equation predicts that ~28% of the population will migrate out of the park, which greatly exceeds the 16% migration rate which occurred during the severe winter of 1996/1997. A similar situation exists for the population size: if the population size is greater than 1147 on the Northern Range, the estimated number of migrants may not accurately reflect the real number of migrants. For instance, if the SWE is 20 and the population size on the Northern Range wintering area is 2000 animals, the equations predict that > 90% of the population in the Northern Range wintering area will migrate out of the park.

There are three methods that could be used to handle population sizes or SWE values which fall outside of the historical range of values: 1) accept extreme values, 2) set limits on the SWE values which can be selected, and 3) set limits on the numbers of migrants based on historical levels. Accepting extreme values is not practical because it occasionally results in unrealistic numbers of migrants. The normal distribution from which random SWE values are selected could be truncated to include only the range of observed values; however, this would not address the issue of extrapolating beyond the range of observed population sizes. Thus, to address the unrealistic scenarios caused by occasional extreme SWE values at high population sizes, the model caps the migration rate out of the Central wintering area at 50%. This cap appears reasonable as it is three times higher than the maximum rate observed at a high population level during the severe winter of 1996/1997.

Migration rates between wintering areas

Although the Central and Northern Range wintering areas are separated by distance and deep snow during the winter, there are some indications that winter migration between wintering areas does occur. During the severe winter of 1996/1997, up to 200 bison (roughly 8% of the Central population) from the Central wintering area moved to the Northern Range; how many of these bison remained on the Northern Range for the remainder of the winter is unknown (YNP unpublished data). In the winter of 1998/1999, which was of average severity, between 20-40 bison (roughly 2% of the Central population) moved from the Norris area to Mammoth and back to Norris (YNP unpublished data). In 1997/1998, one of 10 tagged bison (10%) moved from the Northern Range to the Central wintering area (Gogan pers comm.; Aune et al. 1998). It is believed that movement from the Northern Range to the Central wintering area is more likely to occur during winters that are milder than average. These few observations of bison winter movements suggest that movement from the Central wintering area to the Northern Range is more common than movement from the Northern Range to the Central Wintering area, that movement from the Central wintering area to the Northern Range may be more common in more severe winters, and that movement from the Northern Range to the Central wintering area is possible although it seems to occur less frequently.

Because these few observations are not sufficient to develop a solid relationship between winter severity and winter migration between subpopulations, a simpler method must be used. The migration rate for the Central wintering area to the Northern Range was selected at random from a uniform distribution between 2% and 8% during winters that are worse than average. Similarly, the migration rate for the Northern Range to the Central wintering area will be selected at random from a uniform distribution between 1% and 5% during winters that are milder than average.

Structure and parameterization of the disease model

General structure

A model using the susceptible-infected-recovered (SIR) approach was developed to investigate the dynamics of brucellosis in the modeled bison population. The SIR approach has been widely used to examine the dynamics of disease in humans (Anderson and May 1991) and in wildlife (see reviews by Grenfell and Dobson 1995). The SIR model developed by Dobson and Meagher (1996) was used as a general guide for my model. Most importantly, the Dobson and Meagher (1996) equations were modified to track four classes of animals rather than three: those that are disease-free or "susceptible" to the disease (S), those infected by the disease (I), those recovered from the disease (R), and those that have been vaccinated (V).

The model used by Dobson and Meagher (1996) included some variables, including virulence, increase in mortality rate of infected animals, and vertical transmission, which were not included in the model developed here in order to simplify the equations mathematically and to use only those parameters for which reasonable estimates can be developed. First, I did not incorporate a vertical transmission factor or a increased calf mortality function in the disease equations. The effect of vertical transmission of brucellosis is increased mortality of calves via abortion events. Because the fecundity rate was determined by fitting the model to the annual counts, which occur some months after birth, any prenatal and neonatal calf mortality has already been taken into account and including a separate term for either vertical transmission or increased mortality is unnecessary. Second, because brucellosis is not known to cause increased mortality of the infected host, I did not include this factor in the model.

There is a characteristic of *B. abortus* that relates to the definitions of "infected" and "recovered" as pertains to bison. Bison may be technically "infected" by the disease yet have the disease confined to their lymph nodes, spleen, and other lymphoid organs where it cannot be transmitted to naive animals. Bison that are considered "infectious" are only those with reproductive-tract infections, as they are most likely to transmit the disease to other individuals. Brucellosis infections typically occur in the first two years after the bison was initially exposed to the disease; however, the majority of the abortion events only occur during the first year. In this model, the "infected" state of the classic SIR model is actually defined as those animals that harbor reproductive-tract infections and are thus actively infectious. Similarly, animals which are "recovered" are those which are not infectious; they may harbor the infection in the lymph nodes, spleen, or other non-reproductive organs, but cannot transmit the disease.

The following were the basic equations used to model the dynamics of brucellosis in YNP bison. Slight modifications to the equations were necessary for some management alternatives (e.g., in order to incorporate vaccination of all female bison instead of vaccination of calves only).

$$S_{fallt} = S_{springt} - \frac{\beta . S_{springt} . I_{springt}}{N_{springt}} - Rand(ELK) + C_{springt} - Z_t Ev$$
$$I_{fallt} = I_{springt} + \frac{\beta . S_{springt} . I_{springt}}{N_{springt}} + Rand(ELK) - \gamma I_{springt}$$
$$R_{fallt} = R_{springt} + \gamma I_{springt}$$
$$V_{fallt} = V_{springt} + Z_t Ev$$

Where:

$S_{springt}$ = number of susceptible female bison in the spring of year t

S_{fallt} = the number of susceptible female bison in the fall of year t

$I_{springt}$ = the number of infected female bison in the spring of year t

I_{fallt} = the number of infected female bison in the fall of year t

$R_{springt}$ = the number of recovered/resistant female bison in the spring of year t

R_{fallt} = the number of recovered/resistant female bison in the fall of year t

$V_{springt}$ = the number of vaccinated female bison in the spring of year t

V_{fallt} = the number of vaccinated female bison in the fall of year t

β = transmission rate between bison

γ = rate of recovery per year of infected animals

Rand(ELK) = number of bison infected by elk; this occurs at random with a frequency specified by the user

V = proportion of the stage class(es) which are vaccinated; specified by the user

E = vaccine efficacy; specified by the user

Values used for percent vaccinated, vaccine efficacy, reinfection by elk, and the proportion of bison which could be captured for a whole-herd test and slaughter program are provided in Table 9.

Proportions of animals in each disease class

The initial estimates of susceptible, infected, and recovered/resistant bison include values found in published literature and some unpublished data. Roffe (personal communication, 6/25/98) estimated that the current proportion of bison in YNP which test positive for exposure to brucellosis is 0.4-0.45. The proportion of susceptible bison was calculated to be 0.6 (1 – 0.4 =0.6). James (1992 *in* Meyer and Meagher 1995) reported that 0.1-0.2 of the bison population was infected; Roffe et al. (1999) estimated that 0.46 of seropositive bison were culture positive, which would mean that 0.18 of the bison are infected. For this model, I assumed that the proportion of seropositive animals was 0.4, and the proportion of infectious animals was 0.1 based on the lower estimates provided by James (1992) and Meyer and Meager (1995). Because the proportion of seropositive bison is the sum of the percent of infected bison and the percent of recovered bison, the percent of recovered bison is 0.3.

Recovery rate (γ)

The recovery rate is the rate at which bison recover from the disease and are no longer infected. Peterson et al. (1991) indicated that abortion rates in bison approach zero after the animal has been infected for two years, which is equivalent to a 0.5 recovery rate per year. While Peterson et al. (1991) does not state that the animal technically would not be infected after 2 years, if an infected bison is no longer having abortions it is very unlikely to transmit the disease and can be considered "recovered" for the purposes of this model.

Vaccine efficacy levels (E)

Each model was run using both an upper and lower vaccine efficacy level selected to represent the highest and lowest anticipated efficacy rates. Specifically, vaccine efficacy levels used in the model were 25% and 70%, which were also the levels used in the analysis section of the DEIS (USDI 1998).

The upper and lower limits for vaccine efficacy levels used in this modeling effort are based on the efficacy of Strain 19, which was the vaccine commonly used for domestic cattle until 1996. Strain 19 is 67% effective in preventing infection and abortion when administered to domestic cattle calves (NRC 1998). I elected to use 70% (67% rounded to the nearest 10%) as the upper efficacy level because it represents the likely maximum efficacy rate expected for a vaccine for brucellosis. The lower estimate of the efficacy level is based on information on the efficacy of Strain 19 in bison. Davis et al. (1989 *in* USDI 1998) determined that this vaccine protected 25% of bison vaccinated as calves.

Proportion of the bison that are vaccinated (V)

The proportion of bison that could feasibly be vaccinated is unknown at this time, and will likely depend on some combination of the delivery mechanism for the vaccine (remote delivery via oral vaccine or biobullet; roundup and vaccinate by hand) and environmental conditions (e.g. it may be more difficult to vaccinate a large proportion of bison during certain environmental conditions). Therefore, I assumed that a vaccination program might be able to vaccinate 50%, 75% or 90% of the bison in the age class of interest.

Number of bison infected by elk

Elk in and near Yellowstone National Park and Grand Teton National Park are also infected with *B. abortus*. The Jackson elk herd, which occurs in and near Grand Teton National Park and winters at the National Elk Range (NER), has a seroprevalence level of 0.4 for adult females, and 0.28 overall (Boyce 1989). The northern elk herd, which occurs in the northern portion of the GYE , has a seroprevalence level of 0.017 (NRC 1998:37). There is some evidence that elk may transmit brucellosis to bison (NRC 1998). Specifically, the NRC report indicates that the Jackson bison herd was reportedly brucellosis-free until the herd escaped and began to mingle with infected elk at the feedlines in the NER (M. Meyer, personal communication cited in NRC, 1998). However, the rate of transmission is unknown at this time. In addition, it is unknown whether disease transmission between elk and bison is likely in areas of the GYE where animals are not found in the dense concentrations found on the feedlines. To bracket the range of possible transmission rates, I assumed that a single transmission would occur either once each year, once in 15 years, and once in 100 years for the Northern Range. In recognition of the belief that elk and bison come into contact less on the Central Range, the rate of transmission between elk and bison on the Central Range was higher, at once each year, once in 30 years, and once in 200 years.

Estimation of fecundity and transmission rates

Estimates of fecundity rates or a transmission rates were not available for the YNP bison population. Thus, once the other parameters had been specified, the model was solved iteratively to determine both rates.

Fecundity rates

Because the population model is stage-structured, it was necessary to develop estimates of the fecundity rates for yearlings (21mo) and adults. The fecundity rate for yearlings was based on published literature as described below; the adult fecundity rate was calculated based on the observed population size and estimated mortality rate.

Information on the fecundity rates for yearlings (21mo) are available for the YNP bison herd and for other herds. Green (1990) indicates that 2.5% of females calve successfully at 2 years of age. Meagher (1973) indicates that 0.25% of the 2.5yo bison breed. Aune et al. (1998) indicates that 70% of the 2yo are pregnant. In contrast, Kirkpatrick et al. (1996) states that no animals calve successfully at 2yo. Based on these sources, the percent of females that calve successfully is between 0 and 5%. I used 2% as a reasonable "middle ground" for the fecundity of 2yo bison; the fecundity rate in terms of successful female births would therefore be 1%.

The fecundity rate for adults was determined iteratively by specifying the natural mortality rates and the proportion of bison that are killed when they migrate out of YNP and minimizing the sum of squares of the projected population size and the known population size for the years 1967-97 (Figure 12). The resulting fecundity rate was 0.245 successful female births per female per year, or 0.49 successful births per female per year. This rate is within the range indicated in the literature. For instance, Aune et al. (1998) indicates that the percent of adult females which are pregnant ranges from 0.35-0.88. The most recent estimate of the calving rate (successful pregnancies) is 0.5 (Aune et al. 1998), which would mean a calving rate for females of 0.25, which is nearly identical to the calculated value of 0.245. Because the fecundity rate was determined by fitting the model to the fall counts, the fecundity rate accounts for neonatal mortality and a separate term for this is not necessary.

Transmission rates (β)

No information on the transmission rate between bison exists, so the transmission rate had to be estimated using available data. After estimates for all other parameters were determined, the transmission rate was determined iteratively by selecting the rate that results in a stable, long-term seroprevalence rate of 40% (Figure 14). The calculated transmission rate that results in the specified seroprevalence rate is 1.12. This rate was determined assuming no disease transmission from elk; however, if we assume that elk transmit the disease to bison every 15 years, the rate does not change appreciably although the number of years it takes for the female population to attain a seroprevalence of 40% decreases slightly.

Assumptions required for information used in the model

As indicated in the previous sections describing the types and sources of data used to construct the model, many assumptions were made. Some assumptions are easily validated by the available published or unpublished data, some assumptions are necessary because data are inadequate to make better judgments, and some assumptions are made to facilitate the modeling process. The assumptions identified above are summarized in Table 7 with a brief justification for each assumption.

Detailed model structure

The model is initiated in the late fall/early winter when population counts are made and before winter-severity dependent population changes occur (e.g. winter mortality, migration out of YNP, human-induced mortality of bison outside YNP; Figure 16). Bison in the Central and Northern Range are modeled separately, because the migration rates and winter mortality rates are different for the two areas and because the proposed management at the western and northern borders of YNP is different. Calves born the previous spring are assumed to have survived until the fall. In the model, disease transmission (both bison:bison and elk:bison) and vaccination occurs after calving during the spring, but before winter management actions occur in the next time step.

Before modeling winter removals (from natural mortality or management action), the number of calves born the previous spring is calculated. Numbers of bison susceptible, infected, recovered, and vaccinated is also calculated prior to winter removals from the population. A random snow-water equivalent value is selected from a normal distribution with a mean of 10.32 and a standard deviation of 3.17. The number of bison which die due to natural mortality during the winter is calculated based on the relationship between winter severity and winterkill rates as a proportion of the fall population size. The number of bison which migrate out of YNP is calculated based on the relationship between winter severity and migration rate as a proportion of the fall population size,; the number of migrating bison in each disease class is also tracked.

Once bison migrate out of YNP, different management actions may occur. Depending on the management scenario modeled, management actions may include any or all of the following:

- test and slaughter of animals which are infected and recovered
- allow a specific number of bison to remain on lands outside the park
- hunt bison on lands outside the park
- remove (to quarantine or slaughter) bison regardless of disease status after the hunt if the capacity of the lands outside the park is exceeded.

Finally, bison are allowed to migrate between the Central and Northern Range wintering areas.

After losses to the population from winter natural mortality and winter management actions are calculated, the number of female bison and the number of female bison in each disease class is calculated. The number of calves successfully born to the remaining cows is determined, and the next time step is initiated.

Each management alternative was modeled in a separate Excel workbook. Input variables (proportion of population vaccinated, vaccine efficacy, transmission from elk to bison, proportion of entire population which can be captured, tested, and slaughtered) are entered in tabular form in one spreadsheet. Another spreadsheet includes a vector of 1000 random SWE values with a mean of 10.32 and a standard deviation of 3.17. A visual basic macro inserts a vector of 50 SWE values into the model, the dynamics are calculated for 50 years, and the macro stores key output data in a separate spreadsheet.

For each set of input parameters (vaccination rate, efficacy, reinfection by elk, proportion of bison captured for whole-herd test and slaughter), 100 simulations are run.

The model was run for each management alternative using multiple sets of input parameters (Table 9). Eighteen different sets of input parameters were used for Alternatives 1, 2, 3, 4, and 7; 36 different sets of input parameters were used for Alternative 5 and 6. Each simulation required the projection of the population for 50 years using new values for winter severity for each modeled year.

Management alternatives proposed by Yellowstone National Park

The DEIS (USDI 1998) and subsequent FEIS (USDI 2000) describe 8 alternative management plans, and all (Figures 3-10). The following provides a complete description of each alternative.

Alternative 1: No action – continuation of the current revised interim management plan

Alternative 1, as described in the DEIS, is the "no action" alternative (Figure 3). The current revised interim bison management plan[1] would continue indefinitely with two modifications. First, up to 100 seronegative non-pregnant bison (50 seronegative non-pregnant females; USDI 1998, p. 202) would be allowed on public lands outside the western boundary of YNP. If the number of non-pregnant female migrants exceeds the

[1] REVISED INTERIM BISON MANAGEMENT PLAN: Actions at West Yellowstone: Test/slaughter all seropositive migrants and all seronegative pregnant female migrants. Allow 100 non-pregnant migrants (50 non-pregnant females) on lands at West. If more than 100 bison (50 non-pregnant female bison) migrate out of YNP, additional bison management actions may be necessary to maintain the population size outside YNP at 50 non-pregnant females. Actions outside the Northern Range: Test/slaughter all seropositive migrants (females only for model). Hold seronegative female migrants. If more than 125 bison (63 female migrants) are in the holding facility, additional bison management actions may be necessary.

capacity of the land outside the western boundary, additional management actions may be necessary to maintain the population at 100 bison (50 seronegative non-pregnant females). Secondly, seronegative female bison attempting to migrate out of the Northern Range would be held at a capture facility. If the number of female migrants exceeds the capacity of the holding facility (125 bison; 63 females), additional management actions may be necessary. Remote vaccination of calves would begin in the fall of 2002. Because vaccination would be remote, vaccinated sero-negative animals would be subjected to management actions (eg – holding in capture facilities, management removal if migrant levels exceed the capacity of the holding facility or the lands outside the western boundary of YNP) as vaccinated and non-vaccinated sero-negative calves could not be differentiated.

Alternative 2: Minimal management

Alternative 2 is the "minimal management" alternative (Figure 4) in the DEIS. The goal of this alternative is to restore near-historic migration pathways through minimal management of the population and acquisition of winter range outside YNP. The revised interim bison management plan would be continued through 2004/05, at which point additional lands would have been acquired. Remote vaccination of all calves would begin in 2002/03.

In 2005/06, all test and slaughter operations and all road grooming would cease. Because the effect of cessation of road grooming on bison migration patters was unknown at the time that this alternative was developed (a recent study concluded that road grooming likely does not have any major impacts on bison ecology, and that changes in bison travel patterns during the winter are more likely due to an increased bison population size; Bjornlie and Garrott 2001), the assumption was made that the presumed increased travel cost would eliminate any winter migration between the Central and Northern Range wintering areas. The assumption was also made that the new lands acquired for bison on the western and northern Special Management Areas (SMA) could support 1294 and 725 bison (647 and 363 females), respectively, which is the number of cattle raised in the area (USDI 1998, Table 18). Additional bison above these limits may be subject to unspecified management actions.

Alternative 3: Management with emphasis on public hunting

Alternative 3 focuses on public hunting as a way to regulate bison population numbers (Figure 5). The revised interim bison management plan would be continued through 1999/2000 at the Western boundary, but would be continued through 2000/01 at the northern boundary of YNP.

A public hunt would begin in 2002/03. Thirty hunting permits would be issued between 2002/03 – 2004/05, and 35 permits would be issued each year beginning in 2005/06. We assume that half of the hunted animals are females, that an equal number of yearlings (21 mo) and adults are hunted, and that an equal number of permits are exercised outside the northern and western boundaries of YNP. Bison may only be hunted after they migrate out of YNP; thus, the number of bison hunted is dependent on both the number of permits and the number of bison that migrate out of YNP. In addition, once issuance of hunting permits is begun, the 100-bison (50 females) limit on public lands outside YNP (see below) is a post-hunt limit (e.g. – in any one year, up to 235 bison are allowed on public lands outside YNP; 35 of these would be hunted, thus, the limit on public lands would be 100 animals at North and 100 animals at West). Note that because bison are not tested for brucellosis, some of the hunted bison would be carriers of the disease and some would not be infected.

Test and slaughter would cease at the western boundary in 2000/01, and up to 100 migrants (50 females) would be allowed on public lands outside YNP. Migrants above this limit may be subject to unspecified management actions. Test and slaughter would cease in 2001/02 at the northern boundary, and up to 100 migrants (50 females) would be allowed on public lands outside YNP. Bison above the 100-migrant (50 females) limit would be sent to quarantine. Bison calves would be vaccinated remotely beginning in 2002/03.

Alternative 4: Revised interim management plan with limited public hunting and quarantine

Alternative 4 essentially continues the revised IMP but includes some public hunting and quarantine in order to regulate the size of the bison population (Figure 6). While the revised IMP is followed strictly through 2000/01, some differences from the revised management plan occur beginning in 2001/02. For instance, as of 2001/02, the capture facility at Reese Creek near Gardiner would be disassembled, and bison attempting to migrate onto public lands in that area would be tested, and would be slaughtered if they are seropositive or would be sent to quarantine if they are seronegative. Remote vaccination of all calves would begin in 2002/2003.

Twenty permits would be issued to allow hunting outside the west boundary of YNP. As in other alternatives, I assumed that half of the hunted animals would be females and that an equal number of yearlings (21 mo) and adults would be hunted. Bison attempting to migrate onto public lands along the western boundary would be tested; seropositive bison would be slaughtered, seronegative pregnant females would be sent to slaughter, and all other seronegative bison would be allowed onto public lands until the 100 bison (50 female) limit was reached. Bison above this limit could be subject to additional management actions.

Alternative 5: Aggressive brucellosis control within YNP through capture/test/slaughter

Alternative 5 implements an aggressive test and slaughter program for all bison in YNP (Figure 7). The revised IMP would be continued until 1999/00. As of 2000/01, bison would be rounded up within YNP, seropositive bison would be slaughtered. The model was run using either a 50% capture rate or a 90% capture rate, to simulate the minimum and maximum proportion of bison that could likely be captured in any one year. The test and slaughter program would be discontinued for that season if the population falls below 1160 adult bison (580 adult females; USDI 1998). However, this low population level was never reached in the model, even during the initial years of the test and slaughter program when many bison were removed from the population. All bison attempting to migrate out of YNP would be shot. All stage classes of seronegative bison in the capture facility would be vaccinated beginning in 2002/03. The intensive test and slaughter program would be discontinued when the seroprevalence rate reaches 0.1%. Once that rate is attained, we assume that 4 seropositive bison remain in the population, these animals are found and slaughtered, and the simulation is ended.

Alternative 6: Aggressive brucellosis control within YNP through vaccination

Alternative 6 involves aggressive control of brucellosis through vaccination of seronegative bison (Figure 8). The revised IMP would be continued until 1999/00.

Beginning in 2000/01, all bison attempting to migrate out of YNP at the northern boundary would be removed, and bison above a 100-bison (50 female) limit on public lands outside the west boundary of YNP would be subjected to additional management actions. The aggressive, whole-herd vaccination program would begin in 2000/01. The year at which the seropositive rate stabilizes was determined graphically to be at approximately 17 years after the management program is initiated in 2000/01. After the seropositive rate stabilizes, an aggressive test and slaughter program is initiated in order to find and remove the remaining seropositive animals. The intensive test and slaughter program would be discontinued when the seroprevalence rate reaches 0.1%. Once that rate is attained, we assume that 4 seropositive bison remain in the population, these animals are found and slaughtered, and the simulation is ended.

Alternative 7: Preferred alternative – manage for specific bison population range

Alternative 7 is identified as the preferred alternative in the DEIS (USDI 1998, Figure 9). This alternative uses a combination of all possible management actions (test and slaughter, hunting, and quarantine) to attempt to maintain the population size at or below 2500 animals (1250 females). The revised IMP would be continued until 1999/00 for the Northern Range wintering population, and until 2000/01 for the Central wintering population.

In 2000/01, all bison that attempt to migrate out of YNP along the northern boundary would be slaughtered in order to maintain the population size at 2500 animals (1250 females). Bison migrating out of YNP as of 2001/02 would be tested at the border; seropositive animals would be slaughtered, seronegative bison would be released on SMA's outside YNP until the 100-bison (50 females) limit was reached. However, if the 100-bison (50 female) limit is reached or if the population size exceeds 2500 animals (1250 females) the bison which exceed this limit would be sent to quarantine. Ten permits (5 for females) would be issued to hunt bison on lands outside the park.

New preferred alternative – manage for higher bison population range

The new preferred alternative selected by YNP in their final EIS (USDI 2000, Figure 10) involved managing the population at a higher population size (3000 animals; 1500 females). The revised IMP would be continued until 1999/00. Vaccination of calf and yearling migrants is initiated "in the chute" for one year, then remote vaccination of all calves and yearlings occurs as of 2003/04. When either the caps of 100 bison (50 females) are reached on the SMAs, or if the population size is greater than 3000 animals (1500 females), bison would be tested and slaughtered if seropositive and sent to quarantine if seronegative. A modification of the new preferred alternative was also run to examine the disease dynamics which would occur if no safe, effective vaccine was available for bison.

Assumptions about modeled management actions

There are several different management actions incorporated in the DEIS (USDI 1998) and FEIS (USDI 2000) that have the objective of controlling the transmission of brucellosis from bison to domestic cattle. These management actions include test and slaughter, hunting, quarantine, vaccination, and purchase of land outside YNP to provide for increased winter range for migrating bison. The following assumptions about these management actions were made during model development:

- ✧ There are no stage- or sex-specific differences in the rates of test and slaughter, hunting, quarantine, or migration out of the Park.
- ✧ If an odd number of hunting permits is issued, one more adult than yearling will be hunted. All permits issued are used successfully provided that sufficient bison migrate outside YNP where they can be hunted.
- ✧ The plan described in Alternative 2 allows for substantial numbers of bison to occur on public lands outside YNP. I assumed that the public lands outside YNP could support the same number of bison females as the number of cows which are currently grazed in these areas.

Components of the alternatives not addressed by the model

The models only incorporate those management actions and bison movements that influence the population size or disease prevalence. Thus, there are some aspects of the seven management alternatives that are not addressed by the models. For instance, the models do not include winter migration of bison outside of YNP along Hellroaring Creek or out the east side of YNP; it is assumed that those bison that exit in that manner re-enter YNP in the spring and are subjected to the same natural mortality rate as bison that remained inside YNP. Similarly, the effects of additional road plowing to allow winter access to bison capture facilities is not modeled. It is possible that changes in bison behavior may occur as a result of management actions, and that disease transmission may increase, decrease, or remain constant under a heavily, minimally, or similar management regime. Because these changes are unknown both in terms of magnitude and direction, no attempt is made to model those changes. Finally, if vaccination works to eliminate brucellosis in bison, it is likely that the fecundity rate will increase as the abortion rate declines. This change in bison population dynamics that is likely to occur if the disease is eliminated was not considered.

RESULTS

In order to examine how rates of vaccination, vaccine efficacy, reinfection of bison by elk, and test and slaughter operations affect the disease dynamics and population dynamics of the YNP bison herd, many different combinations of parameters were used in the modeling efforts (Table 9). The following section focuses on how the alternatives differ when three sets of parameters are used: the "most plausible" set of input parameters included a vaccination rate of 0.75, an efficacy level of 0.7, a level of reinfection of 1 bison per 15 years, and a test/slaughter rate of 0.9. The "best case" set of input parameters had the same efficacy level and test/slaughter rate as the "most plausible" case, and included the highest modeled vaccination rate of 0.9 and a reinfection rate of 1 every 100 years. The "worst case" set of input parameters used the lowest values for all input parameters: the vaccination rate was set at 0.5, the efficacy was 0.25, the rate of reinfection was 1 bison every year, and the test/slaughter rate was 0.5. It seemed reasonable to use these cases as a guide for whether major differences between results should be expected when comparing other cases.

Detailed results were generated for the first 18 model years. The model was initiated in 1997, and the new management actions identified in the alternatives were typically implemented in 2000/01, or model year 3. Thus, most results provided reflect the first 15 years of the implementation of each alternative. Some important long term results will be discussed briefly.

General results of each management alternative

Alternative 1: No action – continuation of the current revised interim management plan

The estimated fall population sizes for Alternative 1, or the "no action" alternative", ranged from 3748 to 3822 bison by year 18 (Table 10, Figure 17). The management actions implemented in this alternative included vaccination of calves, holding animals in pens outside YNP, test and slaughter of migrants, and unspecified removals for migrants when the assumed carrying capacity of the lands outside YNP were met. These management actions were estimated to reduce the seroprevalence from 0.4 to 0.07 and 0.09 (83% and 78% decline, respectively; Table 11) for the best and most plausible scenarios, respectively; under the worst case scenario, the seroprevalence would only be reduced to 0.25 (38% decline; Table 11, Figure 18). Cumulative management removals of females from the population over the first 18 years ranged from 2039 to 2129, and were 2544 for the worst case scenario (Table 12, Figure 19)

Alternative 2: Minimal management

This alternative involves the purchase of large quantities of land outside the park to provide winter range for many bison, thus allowing the population to increase. In this management alternative, bison are not hunted, tested and slaughtered, or quarantined; however, "unspecified" management removals occur when the number of migrants exceeds the assumed carrying capacity of the lands outside YNP. At year 18, the model predicted that the seroprevalence would be reduced from 0.4 to 0.12, 0.09, and 0.31 (70%, 78%, and 23% declines, respectively) under the most plausible, best, and worst case scenarios, respectively (Table 11, Figure 18). Because this management alternative assumes that additional lands outside YNP are available as bison winter foraging areas, the bison population increases drastically and asymptotes at approximately 5200 bison in each scenario (Table 10, Figure 17). Cumulative management removals over 18 years are approximately 4000 females, which is substantially higher for this alternative than for other alternatives (Table 12, Figure 19).

Alternative 3: Management with emphasis on public hunting

Alternative 3 includes public hunting (30-35 permits per year) in addition to the vaccination, test and slaughter of migrants, quarantine of migrants, and "unspecified" management removals directed at migrants. The estimated population size at year 18 ranges from 3752 to 3802 (Table 10, Figure 17). At year 18, the seroprevalence levels for the most plausible, best, and worst case scenarios were 0.13, 0.11, and 0.31 (68%, 73%, and 23% declines, respectively; Table 11; Figure 18), respectively, and the cumulative management removals of females range from 2436 to 2692 (Table 12, Figure 19).

Alternative 4: Revised interim management plan with limited public hunting and quarantine

Alternative 4 includes public hunting, but at a lower rate than alternative 3. Test and slaughter and quarantine were employed to manage the bison which are not hunted. The population size at year 18 ranged from approximately 3600-3700 (Table 10, Figure 17), and the seroprevalence levels for the most plausible, best, and worst case scenarios were 0.11, 0.09, and 0.29 (73%, 78%, and 28% declines, respectively; Table 11, Figure 18). The estimated cumulative management removals of females ranged from approximately 2450-2650 over the 18-year period (Table 12, Figure 19).

Alternative 5: Aggressive brucellosis control within YNP through capture/test/slaughter

While alternative 5 includes vaccination of animals in the capture facilities, the primary method of reducing seroprevalence is aggressive test and slaughter within YNP. This approach results in the elimination of brucellosis within a few years of implementing the program for the most plausible, best and worst case scenarios (Table 11, Figure 18). The population size at year 18 ranges from 3555 to 3656 (Table 10, Figure 17); however, due to the test and slaughter program, there is essentially no population growth under this alternative for the first several years. The cumulative management removals, exclusively through test and slaughter, are markedly lower for this alternative than for other alternatives: the removals range from approximately 600 to 736 females (Table 12, Figure 19). However, this result is partially due to the fact that the simulation is ended after the eradication of brucellosis; had the model continued indefinitely, management removals outside YNP would likely have been necessary for population control.

Alternative 6: Aggressive brucellosis control within YNP through vaccination

Alternative 6 employs the use of whole-herd vaccination of female bison within YNP until the seroprevalence stabilizes (assumed to be year 22), after which the final seropositive animals are assumed to be tested and slaughtered. Other management actions implemented include unspecified removals of migrating bison outside YNP once the assumed carrying capacity of the lands outside YNP are exceeded. The estimated population sizes at year 18 are approximately 3700 for all three scenarios (Table 10; Figure 15). By year 18, the estimated seroprevalence for the most plausible, best case, and worst case scenarios were 0.05, 0.05, and 0.12, respectively (88%, 88%, and 70% declines; Table 11, Figure 18). This alternative does result in estimated seroprevalence rates which are substantially lower than those achieved using the management measures implemented in all other alternatives, except alternative 5 which employs an aggressive test and slaughter approach. Cumulative management removals of females by year 18 range are 2442, 1690, and 1640 for the most plausible, best case and worst case scenarios, respectively (Table 12, Figure 19).

Alternative 7: Manage for specific bison population range

Alternative 7 implements vaccination, test and slaughter, limited hunting of migrants, and removal of migrants when the population reaches 2500 animals. The estimated population sizes for year 18 of Alternative 7 range from 3423 to 3640 (Table 10, Figure 17), and the seroprevelance levels attained are 0.13, 0.11, and 0.29 (68%, 73%, and 28% declines, respectively) for the most plausible, best case, and worst case scenarios, respectively (Table 11, Figure 18). The cumulative management removals of females ranged from 2442 to 2670, depending on the scenario considered (Table 12, Figure 19).

New preferred alternative

The new preferred alternative uses vaccination of calves and yearlings, and test and slaughter, to reduce the seroprevalence. In order to reduce the number of migrants, the bison population is managed towards 3000 animals (1500 females) by removing seronegative migrants when the population is higher than this cap. The estimated fall population size for year 18 of the new preferred alternative ranged from 3600 to 3700 animals (Table 10, Figure 17). Although this estimated fall population size is somewhat higher than the management goal of 3000 bison, the average estimated spring population is lower; after 5 complete model runs of 50 years each, the average spring population size was 2966 animals. The seroprevalence levels were 0.11, 0.10, and 0.27 (73%, 75%, and 33% declines, respectively) for the most plausible, best case, and worst case scenario, respectively (Table 11, Figure 18). The cumulative management removals of females over 18 years ranged from 2380 to approximately 2600 (Table 12, Figure 19).

New preferred alternative, without vaccination

Although not evaluated for the DEIS or FEIS, because there is currently no vaccine available for bison which is both safe and efficacious, it seemed reasonable to evaluate the new preferred alternative under the assumption that no vaccine is available. As expected, the population trajectory estimated when the vaccine was eliminated from the model was essentially identical to the trajectory estimated for the model for the new preferred alternative including the vaccine. However, if vaccination is not included, there was almost no reduction in the proportion of seropositive animals in the population (Figure 18A).

Comparisons of population dynamics

The averaged population dynamics for each management alternative for 100 simulations of the most plausible, best case, and worst case scenarios are provided for comparison in Figure 17. The population sizes at year 18 are remarkably similar for most management alternatives and for all three scenarios. The maximum difference between average modeled population sizes within a scenario is less than 175 animals under the most plausible scenario, around 250 animals for the best case scenario, and 160 animals for the worst case scenario. The average population sizes in year 18 are also very similar between most management alternatives. The population trajectory for Alternative 2 shows a substantially higher average population size after year 8 for all scenarios; this difference is due to the fact that this management alternative involves an effective increase in the carrying capacity of YNP by purchasing land adjacent to YNP for bison winter range. The downward spike in the trajectory for alternative 4 early in the model indicates the initiation of a quarantine program for all bison which migrate out of YNP along the northern border. The whole-herd, within-YNP test and slaughter program is responsible for the lower population trajectory for alternative 5; although the disease modeling was discontinued when this test and slaughter program resulted in eradication (seroprevalence $<= 0.001$ for two consecutive years), the model indicates that the population would attain roughly 3600 animals by year 18.

Although short-term information is most interesting to managers who hope to see definitive positive results of their management, it can also be useful to evaluate more long-term results. Table 12 shows the estimated population sizes in year 25. For all alternatives, the estimated population sizes at year 25 are quite similar to those in year 18.

Comparisons of seroprevalence levels

The averaged seroprevalence for each year for 100 simulations of each management alternative for the most plausible, best case, and worst case scenarios are provided in Figure 18. In all three scenarios, the whole-herd, within-Park test and slaughter program results in the lowest seroprevalence rates. In fact, the test and slaughter program was estimated to eliminate brucellosis within 4 years after the initiation of the program for the most plausible and best case scenarios (although elimination would not occur for the worst case scenario due to the combination of frequent reinfection by elk and the low proportion of the population captured). The changes in seroprevalence for each management alternative during the first 18 modeled years are similar for the most plausible and best case scenarios; the changes are quite different for the worst case scenario.

When a vaccination rate of 75% and 90%, an efficacy level of 70%, and a reinfection rate of 1 per 100 years are used in the model, management alternatives 1, 2, 3, 4, 7 and the "new preferred" all result in seroprevalence levels at year 18 between 0.09 and 0.13 for the most plausible scenario (Table 11, Figure 18A) and between 0.07 and 0.11 for the best case scenario (Table 11, Figure 18B).

The estimated seroprevalence levels in year 25 were also determined for all alternatives considered by the management agencies (Table 13). In particular, because the within-Park test and slaughter program is not instigated until year 22 of the model the estimated seroprevalence for Alternative 6 in year 25 is more relevant than the estimate for year 18; in year 25, the estimated seroprevalence is zero. For all other alternatives, the seroprevalence declined an additional 45-81% between years 18 and 25.

Comparisons of cumulative numbers of bison removed

Each alternative management plan included the removal of bison migrants from the population by managers in order to achieve at least one of the following: reduce the seroprevalence, reduce the probability of bison coming into contact with cattle, or reduce the size of the population. For some alternatives, management removals were clearly identified as test/slaughter or test/slaughter/quarantine operations; for other alternatives, the management action was unspecified. The cumulative numbers of bison removed by any management action provide an indication of the level of effort which would be required to manage both the disease and the population for the first 18 modeled years.

There are substantial differences between the cumulative numbers of female bison which the model predicts must be removed (Table 12, Figure 19). The numbers of females which must be removed is highest for alternative 2 because the increased winter range led to a substantially higher proportion of predicted migrants in both winter ranges that must be removed once the capacity of the new winter range is reached. The numbers of females which must be removed is lowest for alternative 5 because, once the within-Park, whole-herd test and slaughter program is complete, the modeled population size is low and the seroprevalence is zero, and few animals must be removed for the remainder of the time frame considered. With these exceptions, the cumulative management removals of females for all other alternatives are quite similar for the most plausible, best case, and worst case scenarios both between and within scenarios.

Relative impacts of management on the Northern Range and Central groups

The management agencies were focused solely on evaluating the relative impacts of the management alternatives of the YNP bison population as a whole. However, the actual degree of interchange between the bison on the Northern Range and those in the Central area is unknown at this time, so it is prudent to also examine the relative impacts of the management regimes on the two groups of animals in the event that interchange is limited.

Figure 20 provides sample population dynamics of the bison groups from the two wintering areas. Clearly, the estimated population dynamics of both the Northern Range and Central groups vary with winter severity. Over the full 50 years modeled, the estimated average fall population size for the new preferred alternative was 2589 for the Central group and 975 for the Northern Range group; the average minimum and maximum estimated population sizes for the Central and Northern Range were 1437 and 3641, and 587 and 1248, respectively. The minimum estimated population sizes for both groups was only slightly lower than the initial population sizes used for year 1 of the model.

There are differences in how the seroprevalence levels for bison on the Northern and Central Ranges change over time in response to management measures implemented in each alternative (Figure 21). These differences primarily occur during the earlier years of the model. However, there appear to be no substantial differences in the estimated seroprevalence levels between the bison groups in the two areas by model year 18.

DISCUSSION

One objective of this research was to determine the relative outcomes of the different management alternatives for bison and brucellosis considered by the management agencies. As previously stated, the number of scenarios examined was very large, but since few differences were noted between many of the scenarios, this dissertation focuses on differences and similarities between what was considered to be the most plausible, best case, and worst case scenarios. The following discussion focuses first on the implications of the initial population sizes used for the model, the lack of a safe, effective vaccine for bison, and new information published since these models were originally developed and parameterized. I close with a comparison of my model results with those of other researchers, and discuss the approaches, limitations, and new modeling directions which may be useful to pursue in the future.

The implications of the initial population size

Management removals of a large proportion of bison during the winters of 1994/95-1996/97 resulted in a substantial decline in the bison population (Figure 2); by the end of this period, the bison count was 2108, which was well below the average count of 3275 for the previous 10 years. The first year of the modeled population used the 1997/98 population count of 2105 as the initial population size[2]. At this low population level,

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[2] Although the FEIS (2000) indicated that 2108 was the population count in 1997/98, an earlier document provided by the YNP indicated that the population count for that year was 2105; the latter estimate was used as the initial population size in the model. Because the two numbers differ by only

there is little migration of bison out of the Central or Northern Range wintering areas even during winters that are more severe than average, and thus few bison are killed outside YNP. Even under consistently mild winter conditions, the model estimates that it would takes 5-7 years for the Central group to attain a population size where there would be a 10% migration rate even for an average winter, and 3-4 years for the Northern Range group to reach a population size where 15% of the population migrates. Thus, because at a low population size there is little migration, and thus little mortality outside YNP, the rate of increase of the bison population is constant and high for the first few years of the model for all trajectories (Figure 17).

In addition, because of the difference in the relationship between winter severity and winter migration rates in the two wintering areas, management of significant numbers of bison outside YNP, including removals of seropositive animals in the modeled population happens sooner for the Northern Range population than for the Central population. Thus, one potential reason for the lower seroprevalence on the Northern Range during the early years of the model is that the higher migration rate allows increased numbers of seropositive bison to be preferentially removed from the Northern Range group during years prior to when the Central group is sufficiently large to experience even a low migration rate outside YNP.

It is clear that some management tools, specifically vaccination, will not be available for use on bison in YNP for some time (see section below). By the time this tool can be used, the population size might be drastically different. Thus, it seems

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three animals, and this is assumed to make no measurable difference in the population dynamics, the models were not re-run to include the slightly higher population size.

prudent to conduct some exploratory evaluations to determine how the model results may be affected if a higher initial population size is used.

The new preferred alternative was re-run using two higher population sizes: the count of 2414 for 1999/00 and the average count of 3274 for the 10 years prior to the high management removals in 1994/95. Results confirm that the initial increase seen for all other population trajectories is due to the low initial population size used for the models. However, the estimated fall population sizes for year 18 of 3615 and 3702 for the 1999/2000 and the average high counts, respectively, are within the range of the estimated population sizes of the other models at year 18. The seroprevalence levels at year 18 are 0.07 when either new population size is used as an initial condition. This level is identical to that reported for the new preferred alternative when the initial population size is substantially lower.

Implications of restricting most management actions to locations outside YNP

Most management alternatives considered included both a within-Park vaccination program and a test and slaughter program which would be implemented outside the Park. Any management action which can occur only outside YNP, including test and slaughter, vaccination of seronegative animals "in the chute", quarantine, or monitoring whether any of the above successfully reduces the seroprevalence in the population, will be limited to those animals which elect to migrate outside YNP during the winter.

For the alternatives modeled during this project, the estimated average migration rate over 50 years for Alternatives 1, 3, 4, 7, and the new preferred alternative was between 0.06-0.08 for the Central wintering area, and between 0.16-0.23 for the Northern Range wintering area[3]. Assuming that the ratio of bison in both wintering areas remains approximately the same, on average, approximately 100-200 bison per year from the Central area will be available for management outside YNP, and approximately 100-250 bison from the Northern Range population will be available for management. Applying a test and slaughter program only to this small proportion of the population is unlikely to result in a significant reduction in seroprevalence over a meaningful time period. In addition, if vaccination opportunities are limited to animals that migrate out of YNP because of either available delivery options or policy, this will also limit any reduction in seroprevalence. Clearly, the development of disease management, such as remote vaccination, which can be implemented within YNP, becomes even more crucial if the goal of brucellosis reduction is to be met.

Vaccination: A critical need

At the time the models for this dissertation were developed in 1998-early 2000, management agencies anticipated that a safe, efficacious vaccine to prevent abortions caused by brucellosis would be available for bison by the winter of 2002/2003. However, as of June 2002 no vaccine is available.

In 1996, the USDA-APHIS approved RB51 for use as a calfhood vaccine in cattle. One major benefit of this vaccine over the only other vaccine approved for cattle, Strain 19, is that RB51 vaccinates do not register as "seropositive" in standard tests for either cattle or bison (Lord et al. 1998; Stevens et al. 1994 *in* Olsen et al. 1998).

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[3] Calculations not done for Alternatives 5 and 6 since the modeling ceases once eradication is successful; Alternative 2 not included because it seems unlikely under current management policies that

Evaluation of the use of RB51 in bison started almost immediately (Olsen et al. 1998; 1999). While RB51 does show that the vaccine protects cattle against abortion and infection after challenge doses are administered (Elzer et al. 1998), there is no published information which indicates whether RB51 provides similar protection for bison. Given the importance of this information, publications addressing this issue are likely to be forthcoming. Searches for an oral vaccine for brucellosis in bison are also ongoing (Ribeiro et al. 2002).

The lack of a safe and effective vaccine for bison is the Achilles heel for all management alternatives modeled during this effort. The model for the new preferred alternative was run assuming no vaccination took place; although the population trajectory was indistinguishable from the trajectory when vaccination was included, there was effectively no reduction in seroprevalence by year 18 (Figure 18A). Although test and slaughter of seropositive animals is implemented outside YNP and a slight reduction in seroprevalence can be seen when the population is small, once the population increases above 3000 bison, the management plan calls for the removal of both seropostive and seronegative animals to reduce the population size, and the seroprevalence level promptly returns to 0.4. The importance of developing a safe, effective vaccine cannot be overemphasized: without this disease management tool, management of brucellosis will have to rely solely on test and slaughter.

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the population will attain the high population sizes modeled.

Seroprevalence, "infected", and what constitutes "recovered"

As indicated in the introduction, the proportion of seropositive animals, or "seroprevalence", reflects the proportion of animals in a population which test positive for a disease. Because blood from infected and recovered bison both respond to the field tests for brucellosis, the proportion of animals which are seropositive includes both infected and recovered animals. Although there seems to be general consensus that abortion events from infected females are the primary vector of transmission, there is serious debate regarding whether animals truly "recover"; studies of cattle do document that small amounts of brucellosis can be "shed" after the initial infected period has passed. Because of this debate, my approach to parameterizing and reporting the data from the modeling is slightly inconsistent. Throughout this effort, I have assumed that the most important vector of bison:bison transmission involves abortive events; thus, the recovery rate should reflect that an infected female will cease to have abortions in 2 years (or alpha = 0.5). Because no abortive events occur after a female recovers, they are no longer able to transmit the disease to cattle. To be truly internally consistent, it would be best to evaluate the relative success of management programs based on the proportion of infected bison instead of the proportion of bison which are seropositive (infected plus recovered). However, because of ongoing debate about the possibility that bison may "shed" the bacteria even after the first two years of clinical infection, management agencies are most interested in evaluating potential management actions based on the seroprevalence levels.

Consideration of recent information

The models developed for this project were completed and parameterized in 1998; since that time, new information relevant to the modeling effort has been published. The following provides a summary of the new information and the potential ramifications of this information on the model or the interpretation of the model results.

Predation by wolves

Gray wolves were introduced into YNP in 1995 and 1996 (Fritts et al. 1997). At the time the models were developed, no wolf predation on bison had been reported, thus none was modeled. Wolf predation occurred in YNP first in 1995, and has involved 14 known kills between 1995-99 (Smith et al. 2000a; also see section on natural mortality in this dissertation). However, Smith et al. (2000a) indicated that all predation events on bison occurred in late winter when bison were vulnerable because of poor condition or were directed at bison which were injured or young. Thus, it seems reasonable that mortality due to wolves would be compensatory, and no changes would be necessary because the models already incorporate winter mortality due to natural causes.

Migration between wintering areas

One key component of Alternative 2 is the cessation of road grooming, which has long been believed to greatly alter the migration of bison within YNP (Meagher 1973). To include this component in the model for Alternative 2, winter migration, which would otherwise result in a net movement of approximately 3% of bison from the Central to the Northern Range herd each year, was eliminated. However, a recent study showed that use of roads by bison during the winter was negatively correlated with road grooming, and concluded that road grooming had no major impacts on bison travel patterns and that changes in travel patterns were likely due to the increasing bison population (Bjornlie and Garrott 2001). Thus, the entire premise of Alternative 2 (that fewer bison will migrate if roads are not groomed) is probably not realistic.

Recent information from tagged bison (Gogan pers comm 2002) indicates that little or no migration of animals occurs between Central and Northern Range herds. Thus, management actions in one area may have a disproportional affect on one bison group. To investigate the impacts of removing this movement, I eliminated the migration between areas in the model for the new preferred alternative, and looked at the change in the average minimum number of bison in the population in any one year. When migration was included in the new preferred alternative, the average population in the Central and Northern Range wintering areas was 2356 and 968, respectively (averaged over 18 years for 10 model runs). When the low net migration rate from Central to Northern was eliminated, the average estimated population size was 2588 and 883, respectively, which indicates a slight increase for the Central group and a slight decrease for the Northern Range group relative to the results when the model included migration between areas. Clearly, whether there are two separate herds of bison in YNP should be investigated further, as the impacts of management actions on separate, smaller bison groups, will likely be different than the impacts of management on a population of 3500.

Comparisons between this model and those developed in other studies

Peterson et al. (1991a, b) described the results of the his modeling of the bison:brucellosis system in two papers and followed those with a discussion of the management of bison and brucellosis (Peterson 1991). Major differences between my modeling efforts and Peterson's efforts are described as follows.

Peterson et al (1991a) modeled the dynamics of bison and brucellosis in Grand Teton National Park (GTNP) when calves were vaccinated; Peterson et al (1991b) expanded on his earlier paper and examined the dynamics if vaccination of all females was practicable and used in combination with test and slaughter operations. Some major differences between my model and the Peterson et al. (1991a, b) model result from the fact that slightly different parameters are appropriate for the GTNP population than for the YNP population. For instance, the bison herd in GTNP has a much higher seroprevalence level (69% - Peterson et al. 1991a; vs 40% for YNP), which is likely due to contact with infected elk on the Jackson Hole feed lots during the winter. In addition, Peterson et al. (1991a, b) used the same transmission rate from elk to bison as from bison to bison. Again, this might be reasonable for the GTNP population, but is likely to overestimate the interspecies transmission rate for the YNP population because feed lots are not used anywhere within the range of YNP bison.

There are some differences in model and parameter selection which were not due to differences in population parameters, but were differences in model development or interpretation of data available in published literature. Peterson et al (1991a, b) used age-specific demographic rates from a well-known commercial bison herd to parameterize the "STELLA" model, which is a population dynamics model commonly used in the early 1990s, to generate the dynamics of bison and brucellosis. In contrast, the model developed for the YNP bison was stage structured, separated into two discrete groups, and many parameters (e.g., migration rates, fecundity, transmission rates) were estimated from data collected on the YNP population.

Some differences in parameter selection are worth noting. Peterson et al (1991a, b) incorporated an abortion rate for infected females in both years 1 and 2 of the infection (rates of 90% and 20%; cited Davis et al. 1990, 1991 as the source) and a subsequent high probability that calf born in year 2 would be infected with brucellosis (vertical transmission) and would likely die as a result of this infection. In addition, he incorporated a decrease in fecundity for young females. In contrast, I assumed that the high rate of abortion in year 1, and the low rate of abortion in year 2 combined with a high rate of infected calf mortality essentially amounted to complete reproductive failure in both years 1 and 2.

Peterson et al (1991a) concluded that implementing a full-scale calfhood vaccination program using a vaccine which is 65% efficacious will reduce the seroprevalence from 69% to approximately 10% (a decline of 86%), but that vaccination would not eliminate brucellosis from YNP within 20 years. My model results for Alternative 2 are similar: under the best case scenario where 90% of calves can be vaccinated with a vaccine which is 70% effective, it is possible to reduce the prevalence using vaccination to under 10% in 20 years (a decline of 78%). However, the graph in Peterson et al (1991a) demonstrates that the success of the vaccination program asymptotes; thus, complete elimination of brucellosis from the GTNP system is not likely. In contrast, the results for Alternative 2 show elimination of the disease is possible using calfhood vaccination. This difference is likely due the substantially different elk-bison transmission rates used in the models.

Peterson et al. (1991b) incorporated vaccination of all females in the population, and concluded that the most optimistic vaccine efficacy level of 65% would result in a seroprevalence level of 18%, or a reduction of 70% from the initial seroprevalence level. Alternative 6 in this effort also incorporates vaccination of all females; my results indicate that this approach can reduce the seroprevalence by 70-88%, depending on assumptions regarding vaccination rate and vaccine efficacy.

Dobson and Meagher (1996) also modeled the dynamics of bison and brucellosis in YNP, and some of our parameters are nearly identical (e.g., seroprevalence rates). The basic dynamics of the establishment of the disease are also identical (compare Figure 5B in Dobson and Meagher, 1996 to Figure 15 in this dissertation[4]). However, there are also some key differences between their approach and the approach taken for this project. Dobson and Meagher (1996), like Peterson et al. (1991a, b), included both vertical transmission and mortality of infected calves; the model developed for this project did not include either parameter for reasons discussed previously. The Dobson and Meagher (1996) approach also required an estimate of the carrying capacity within YNP, which was assumed to be 4000 bison, while the population modeled in this project was regulated by winter mortality rates and management actions outside YNP.

Dobson and Meagher (1996) point out that, from a theoretical standpoint, slightly more than 50% of the bison would have to be effectively inoculated to eradicate brucellosis by vaccination (cites Anderson and May 1982, 1985 for the theoretical framework). This is roughly consistent with the results described in this dissertation: the low vaccination rate for the "worst case" scenario fails to eradicate the disease in all

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[4] Note that the captions for Figures 5A and 5B in Dobson and Meagher (1996) are reversed.

situations, while the higher vaccination rates of 63% and 53% for the "best case" and "most plausible" scenarios, respectively, nearly eliminate the disease by model year 25 (Table 13).

Dobson and Meagher (1996) further suggests that if seropositive and seronegative animals cannot be identified in the field, a test and slaughter program would have to nearly eliminate bison before the disease would be eradicated. In contrast, my model assumes that it is possible to distinguish between seropositive and seronegative animals, which greatly increases the effectiveness of a test and slaughter program. The results of Alternative 5 suggest that if 90% of the population can be captured for a within-Park test and slaughter program, the disease can be eradicated and the lowest estimated population size would only be approximately 2000 animals (Figure 15A). If only 50% of the population can be captured, then the lowest population size would be slightly larger but it would take more years to eliminate the disease (Figure 15C).

Gross et al. (1998) developed an individual-based model of brucellosis in bison and elk in the Greater Yellowstone Ecosystem, and their simulations indicated that a calfhood innoculation rate approaching 60% would be necessary to eradicate brucellosis. Figure 11 (graph "VR") in Gross et al. (1998) indicates that eradication would be achieved within approximately 20 years. This result is reasonably consistent with the results of simulations carried out in this exercise, where a vaccination rate of either 0.75 or 0.9, combined with a vaccine efficacy level of 0.7 (which yields innoculation rates of 53% and 63%, respectively) results in substantial reductions in seroprevalence 15 years after the initiation of vaccination (Figure 16) and a seroprevalence level of under 0.03 within 25 years (Table 13).

Model approaches, limitations, and future directions

Models developed to explain aspects of wildlife biology, wildlife disease, or wildlife management may be constructed to address many objectives. The objectives of Peterson et al. (1991a, b), Dobson and Meagher (1996), and Gross et al. (1998) were to develop models which would evaluate, in a general sense, the relative impacts of two different management options, test and slaughter or vaccination, either separately or in combination. The approaches used by each author to achieve these objectives have been incredibly varied, and have included off-the-shelf STELLA software (Peterson et al. 1991a, b), a more theoretical approach using "classic" difference equations (Dobson and Meagher 1996), and a computationally complex individual based model of each elk and bison in the Greater Yellowstone Ecosystem (Gross et al. 1998).

The main objective of my modeling project was to determine the relative outcomes of very specific measures proposed by management agencies to reduce the disease prevalence and to manage the population size. The management alternatives I modeled were developed by the management agencies after consultation with stakeholders. The management alternatives developed included many minor variations in how test and slaughter would operate, dual, and sometimes competing management objectives of disease reduction and population regulation, differences in when each management tool was applied, and differences in the numbers of bison which would be tolerated outside YNP before management measures were to be applied. The myriad of conditions modeled for this project makes direct comparisons between the results of my modeling efforts to results from general models slightly challenging. In making the comparisons discussed previously, I was careful to focus on those alternatives which focused on the management option of primary interest; for instance, after the first few modeled years, Alternatives 2, 5 and 6 focus exclusively on calfhood vaccination, whole-herd test and slaughter, and all-female vaccination, respectively, and thus comparisons between model results from these alternatives and model reported by other researchers should be generally comparable.

Because the management alternatives modeled in this dissertation include site-specific actions, it was necessary to consider whether there were different demographic rates in different parts of the bison wintering range in YNP. In some cases, data on which to establish a important demographic rate initially appeared sufficient, but were later found to be somewhat less than adequate. For instance, I had optimistically anticipated that the significant relationship found between population size, winter severity, and numbers of migrants for the entire population (NRC 1998) prophesized a similarly significant relationship between wintering area population sizes, winter severity, and migration rates out of different wintering areas. Unfortunately, a significant relationship at the smaller scale was not found; whether this was a result of the timeframe considered, the method used to determine the population size on each winter range, or some other factor is unknown. However, modeling the management alternatives required estimates of this and similar rates, and although "the best available" data were used, in some cases the "best available" data left much to be desired.

While the objectives of this modeling approach were to evaluate a variety of very specific management measures after the measures have been identified, and the objectives of prior modeling efforts were to evaluate general impacts of management measures before the measures are identified, there are two additional modeling approaches which have not yet been attempted and which may be useful as management agencies work towards managing bison and brucellosis in YNP. First, an evaluation of actual risk of brucellosis transmission from bison (or elk) to cattle should be pursued. Such an evaluation should incorporate both population-specific management measures and a spatial component so that seasonal occupation of lands by bison and cattle outside YNP can be incorporated. Should such an effort be pursued, substantial new information will be needed regarding population-specific fecundity, mortality, and migration rates, and the seasonal and temporal overlap of bison, elk and cattle outside YNP.

Second, modeling of management alternatives could be attempted while managers and stakeholders are actively negotiating a management plan designed to achieve some specific, measurable threshold. The bison management situation seems well-suited for this approach, as a measurable goal has been identified (elimination of risk of transmission), sufficient information exists to construct useful models, and new demographic and disease informaticn is constantly being collected and can be integrated into the modeling efforts. Integrating a modeling effort with negotiations about management plans may move management agencies beyond selecting a management plan based on consensus and evaluating the success of the plan only after agreement has been reached, to selecting a management plan which has both constituent buy-in and is likely to meet stated conservation goals.

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TABLE 1: Summary of sex ratio information from different sources.

Source	Ratio (Female:Male)	Comments
Pac and Frey (1991)	58:42	Fetal sex ratio (n=52)
Pac and Frey (1991)	43:57	1988-89 harvested animals (n = 522)
Green (1994)	60:40	1985-1990 adult carcasses (n = 114)
Green (1994)	58:42	1989 adult carcasses (n = 62)
Bear Management Office, unpublished data	60:40	1992-1997 carcasses (n = 82)
Bear Management Office, unpublished data	42:58	1997 carcasses (n = 69)
Gogan, unpublished data	51:49	1997 harvest (n = 721)
Average, harvested only	**47:53**	
Average, carcass data	**60:40**	
Average, sample size > 100	**51:49**	

- **TABLE 2**: Summary of information on the proportion of animals in each stage class.

Source	9-12 mo calves	21 mo juveniles	Adults	Comments
Meagher (1973)	0.16	0.11	0.16	
Pac and Frey (1991)	0.17	0.15	0.68	Field method
Pac and Frey (1991)	0.14	0.14	0.72	Modified method
Gogan, unpublished data	0.16	0.16	0.69	Calves of the year not included in the calculation of proportions
Average				

TABLE 3: Descriptive statistics for the maximum SWE values for Lupine Creek and Lake Camp, and the averaged values. The value of 17.25 was used for the maximum value, as this was the actual maximum value observed during the winter of 1997.

	Lupine Creek (Northern Range)	Lake Camp (Central range)	Average
Mean	10.47	10.13	10.32
Standard error	0.41	0.44	0.41
Standard deviation	3.14	3.53	3.17
Variance	9.88	12.46	10.07
Minimum	5.2	4.5	5.1
Maximum	17	20.5	17.25

TABLE 4: Number of bison carcasses observed on transect lines in the Central and Northern Range wintering areas, 1984/1985-1989/1990 and 1991/1992–1996/1997.

			Bison carcasses observed NS = not surveyed NO = area surveyed; none observed		
Year (fall/ winter)	**Average maximum SWE**	**# of bison in the fall**	**Firehole/ Madison**	**Northern Range**	**Source**
84/85	9.7	2114	27	NS	Green 1994 (Table 22)
85/86	12.85	2291	28	NS	Green 1994 (Table 22)
86/87	5.15	2643	12	5	Green 1994 (Tables 5, 22)
87/88	6.35	2644	22	5	Green 1994 (Tables 5, 22)
88/89	12.75	3159	138	6	Green 1994 (Tables 5, 22)
89/90	8.65	2606	7	2	Green 1994 (Tables 5, 22)
91/92	7.5	3426	20	NO	unpublished data from YNP/BMO
92/93	10.15	3304	13	NO	unpublished data from YNP/BMO
93/94	7.5	3551	5	NO	unpublished data from YNP/BMO
94/95	13.25	3956	16	NO	unpublished data from YNP/BMO
95/96	12.85	3398	22	NO	unpublished data from YNP/BMO
96/97	17.25	3436	69 (400)	1	unpublished data from YNP/BMO; estimate of 400 killed in the Central wintering area from 3500 in population – 1100 shot at border – spring population size = 400 animals

TABLE 5: Numbers and frequencies of bison carcasses identified as calves, adults, and adults from Green (1994) and from BMO (unpublished data).

	Year												Mean frequency	
	85	**86**	**87**	**88**	**89**	**90**	**92**	**93**	**94**	**95**	**96**	**97**	**Unw.**	**Weighted**
Calves (9mo old)	12	19	2	7	72	0	5	4	2	5	8	41	0.53	0.59
Subadults (2-4yo)	1	1	1	2	9	2	2	1	0	0	1	0	0.06	0.06
Adults	0	6	9	10	37	3	9	7	3	8	13	29	0.40	0.35
Total	13	26	12	19	118	5	16	12	5	13	22	70		

TABLE 6: Maximum SWE in inches, and estimated number of bison and migration rate for the Central and Northern Range wintering areas, 1967/1968–1996/1997. Data from 1976/1977–1980/1981 were eliminated because information on the number of bison killed at the YNP border was not collected.

			Central		Northern Range	
Year	**SWE**	**Total bison**	**Estimated # of bison**	**Migration rate**	**Estimated # of bison**	**Migration rate**
1967/1968	9.85	418	292.6	0	125.4	0
1968/1969	13.15	556	389.2	0	166.8	0
1969/1970	12.35	592	414.4	0	177.6	0
1970/1971	15.15	565	395.5	0	169.5	0
1971/1972	13.7	713	499.1	0	213.9	0
1972/1973	7.65	837	585.9	0	251.1	0
1973/1974	14.85	873	611.1	0	261.9	0
1974/1975	11.85	1068	747.6	0	320.4	0
1975/1976	13.6	1125	787.5	0	337.5	0
1981/1982	11.65	2239	1567.3	0	671.7	0
1982/1983	9.45	2160	1512	0	648	0
1983/1984	7.9	2229	1560.3	0	668.7	0
1984/1985	9.7	2114	1479.8	0	634.2	0.139
1985/1986	12.85	2291	1603.7	0.060	687.3	0.010
1986/1987	5.15	2433	1703.1	0.004	729.9	0
1987/1988	6.35	2644	1850.8	0.020	793.2	0.003
1988/1989	12.75	3159	2211.3	0.001	947.7	0.598
1989/1990	8.65	2606	1824.2	0.002	781.8	0.001
1990/1991	8.05	3178	2224.6	0.006	953.4	0
1991/1992	7.5	3426	2398.2	0.009	1027.8	0.242
1992/1993	10.15	3304	2312.8	0.034	991.2	0
1993/1994	7.5	3551	2485.7	0.002	1065.3	0
1994/1995	13.25	3956	2769.2	0.043	1186.8	0.257
1995/1996	12.85	3398	2378.6	0.165	1019.4	0.032
1996/1997	17.25	3436	2405.2	0.149	1030.8	0.704

TABLE 7: Summary of assumptions regarding initial model conditions and parameter estimates.

Type of data	Assumption(s)	Brief justification
Natural mortality	Winterkill is the predominant source of natural mortality	Supported by published literature
	Natural mortality during the summer is negligible relative to natural mortality during the winter.	Supported by published literature
Numbers of bison on each winter range	The average proportion of bison on the Central and Northern Range wintering ranges has remained relatively constant over time.	Hypothesis; data from 1944-1968 shows a proportion similar to the one used for the model
Proportion of winterkilled bison observed on carcass transect.	The ratio between the number of carcasses found and the actual number of bison winterkilled is relatively constant at 5.8.	Hypothesis; better data not available.
Sex ratio	The sex ratio in the population is 1:1 for all stage classes.	Made to simplify modeling; no strong evidence to the contrary. Largest data sets support assumption (e.g. Gogan unpublished data)
	The sex ratio of bison that die due to natural mortality, are hunted, or are removed by management measures is 1:1.	Made to simplify modeling; no strong evidence to the contrary.
Migration rate	The migration rate of bison out of YNP is not stage specific (e.g., if the combination of population size and winter severity cause 50% of the bison on a particular winter range to migrate, 50% of each stage class will migrate)	Made to simplify modeling; no strong evidence to the contrary.

Type of data	Assumption(s)	Brief justification
Timing of birth	Birth occurs in the spring after all management actions take place.	Median birth date in the southern GYE is ~May 22; 95% of births occur between 4/29 and 6/28 in GYE; most severe winter conditions (i.e. – highest SWE values) and presumably most mortality & most migration outside YNP occurs by March/April
Disease-induced mortality	With the exception of neonatal mortality, brucellosis does not cause increased mortality of any bison age class.	There is no evidence in the literature that brucellosis causes increased mortality of any bison stage class in Yellowstone.
Natural resistance to brucellosis	Bison have no natural resistance to brucellosis.	Although there has been one abstract that suggests that bison may have some natural resistance to brucellosis (Templeton et al. 1994), directed studies have not yet occurred. Thus, bison are assumed to not have natural resistance.
Bison-bison disease transmission	Bison do not become re-infectious once they have the disease for two years	There is little information on the length of time that infected female bison remain infectious. However, Peterson et al. (1991b) indicated that abortion rates approached zero after the animal had been infected for 2 years.

Type of data	Assumption(s)	Brief justification
Bison-bison disease transmission	The primary vector of transmission is from infected female to infected female	While the role of male bison in disease transmission is unclear, it is very unlikely that transmission from males is a significant factor relative to transmission from females. This is consistent with Peterson et al. (1991a) and NRC (1998), both of whom indicated that although male bison may carry the disease, they are generally believed to be an insignificant source of transmission.
Vaccination	Vaccination has no deleterious effects on any vaccinated stage class of bison	Although this assumption is not valid for either strain 19 or RB51, the assumption is included based on the belief that a vaccine would not be used on bison in YNP if deleterious effects occurred in the targeted stage class.
Field differentiation of seropositive bison versus vaccinated bison	Unless otherwise stated, assume that field tests can differentiate between seropositive bison and bison that have been vaccinated	This assumption is not valid for Strain 19 but is valid for RB51, and is presumed to be valid for whichever vaccine is approved for use in the YNP bison population
Sensitivity of the serology test	Assume that the sensitivity of the test used to identify seropositive animals is 100%	

TABLE 8: Summary of assumptions regarding management actions.

Management action	Assumption(s)
Test and slaughter	There are no stage-specific differences in the rate of test and slaughter.
Hunting	Hunting is not stage specific with respect to yearlings and adults; calves are not hunted.
	Hunting is not sex specific.
	If an odd number of permits is issued, one more adult than yearling bison is hunted.
	All permits issued are used successfully provided that sufficient numbers of bison migrate outside YNP
Quarantine	There are no stage-or sex specific differences in which bison are sent to quarantine.
Migration out of YNP	Migration rates do not differ between stage classes.
Allowing bison on public lands outside YNP	Alternative 2, management allows for substantial numbers of bison to occur on public lands outside YNP. We assumed that the public lands outside YNP could support the same number of bison females as the number of cows which are currently grazed in those areas.

TABLE 9: Combinations of input parameters used for model simulations and identification of the best case, worst case, and most plausible scenarios presented in detail.

Cases used for comparisons	Vaccination	Vaccine efficacy	Reinfection by elk	Proportion captured in whole-herd test/slaughter
		Alternatives 1, 2, 3, 4, 7		
Worst case	50	25	1	
	50	70	1	
	50	25	15	
	50	70	15	
	50	25	100	
	50	70	100	
	75	25	1	
	75	70	1	
	75	25	15	
Most plausible	75	70	15	
	75	25	100	
	75	70	100	
	90	25	1	
	90	70	1	
	90	25	15	
	90	70	15	
	90	25	100	
Best case	90	70	100	
		Alternatives 5, 6		
Worst case	50	25	1	50
	50	70	1	50
	50	25	15	50
	50	70	15	50
	50	25	100	50
	50	70	100	50
	75	25	1	50
	75	70	1	50
	75	25	15	50
	75	70	15	50
	75	25	100	50
	75	70	100	50
	90	25	1	50
	90	70	1	50
	90	25	15	50
	90	70	15	50

Cases used for comparisons	**Vaccination**	**Vaccine efficacy**	**Reinfection by elk**	**Proportion captured in whole-herd test/slaughter**
	90	25	100	50
	90	70	100	50
	50	25	1	90
	50	70	1	90
	50	25	15	90
	50	70	15	90
	50	25	100	90
	50	70	100	90
	75	25	1	90
	75	70	1	90
	75	25	15	90
Most plausible	75	70	15	90
	75	25	100	90
	75	70	100	90
	90	25	1	90
	90	70	1	90
	90	25	15	90
	90	70	15	90
	90	25	100	90
Best case	90	70	100	90

TABLE 10: Estimated population sizes at 18 years for the most plausible, best case, and worst case scenarios. Standard deviations are provided in parentheses.

Alternative	Most plausible	Best case	Worst case
1	3748 (644)	3816 (702)	3822 (660)
2	5247 (446)	5238 (541)	5233 (519)
3	3752 (667)	3792 (597)	3802 (632)
4	3716 (567)	3608 (650)	3626 (589)
5	3578 (571)	3656 (565)	3555 (546)
6	3751 (612)	3704 (571)	3653 (622)
7	3640 (568)	3663 (559)	3423 (598)
New	3703 (502)	3627 (461)	3607 (517)

TABLE 11: Estimated seroprevalence at 18 years for the most plausible, best case, and worst case scenarios. Standard deviations are provided in parentheses.

Alternative	Most plausible	Best case	Worst case
1	0.09 (0.01)	0.07 (0.01)	0.25 (0.01)
2	0.12 (0.01)	0.09 (0.01)	0.31 (0.01)
3	0.13 (0.01)	0.11 (0.01)	0.31 (0.01)
4	0.11 (0.01)	0.09 (0.01)	0.29 (0.01)
5	0 (0)	0 (0)	0.002 (0)
6	0.05 (0.01)	0.05 (0.01)	0.12 (0.01)
7	0.13 (0.01)	0.11 (0.01)	0.29 (0.01)
New	0.11 (0.01)	0.10 (0.01)	0.27 (0.01)

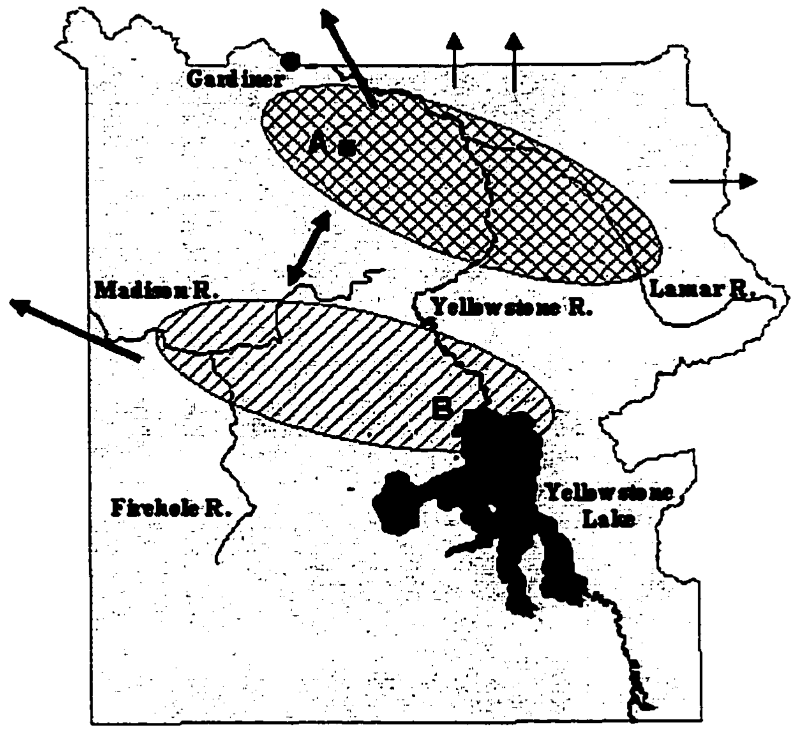
TABLE 12: Estimated cumulative management removals of females after 18 years for the most plausible, best case, and worst case scenarios. Types of management removals differ for each alternative; refer to the descriptions of each alternative in "Results".

Alternative	Most plausible	Best case	Worst case
1	2126	2039	2544
2	4092	3996	4000
3	2642	2436	2692
4	2073	1842	2236
5	598	597	736
6	2173	1690	1640
7	2442	2573	2670
New	2380	2591	2543

TABLE 13: Results of the estimated population size and proportion of bison seropositive for the most plausible, best case, and worst case scenarios after 25 years. Standard deviations are provided in parentheses.

	Most plausible		Best case		Worst case	
Alternative	**Est. size**	**Prop. sero+**	**Est. size**	**Prop. sero+**	**Est. size**	**Prop. sero+**
1	3971 (647)	0.02 (0.005)	3809 (662)	0.02 (0.002)	3816 (599)	0.22 (0.001)
2	5465 (456)	0.05 (0.003)	5441 (519)	0.03 (0.005)	5443 (447)	0.29 (0.004)
3	3686 (626)	0.05 (0.003)	3807 (642)	0.03 (0.001)	3694 (628)	0.27 (0.005)
4	3632 (639)	0.04 (0.005)	3606 (657)	0.03 (0.005)	3735 (607)	0.25 (0.008)
5	3513 (573)	0 (0)	3596 (591)	0 (0)	3528 (512)	0.002 (0.001)
6	3649 (684)	0 (0)	3682 (681)	0 (0)	3772 (549)	0.005 (0.005)
7	3513 (551)	0.04 (0.003)	3532 (612)	0.03 (0)	3593 (538)	0.27 (0.004)
New	3553 (540)	0.03 (0.003)	3661 (521)	0.03 (0.002)	3408 (520)	0.22 (0.011)

FIGURE 1: Map of Yellowstone National Park. The single hatched area is the Central wintering area; the crosshatched area is the Northern Range wintering area. A and B identify the SNOTEL sites "Lupine Creek" and "Lake Camp", respectively, which were used to determine winter severity. Heavy arrows indicate winter bison movements out of Yellowstone National Park that were included in the model; light arrows indicate bison movements which were not modeled.



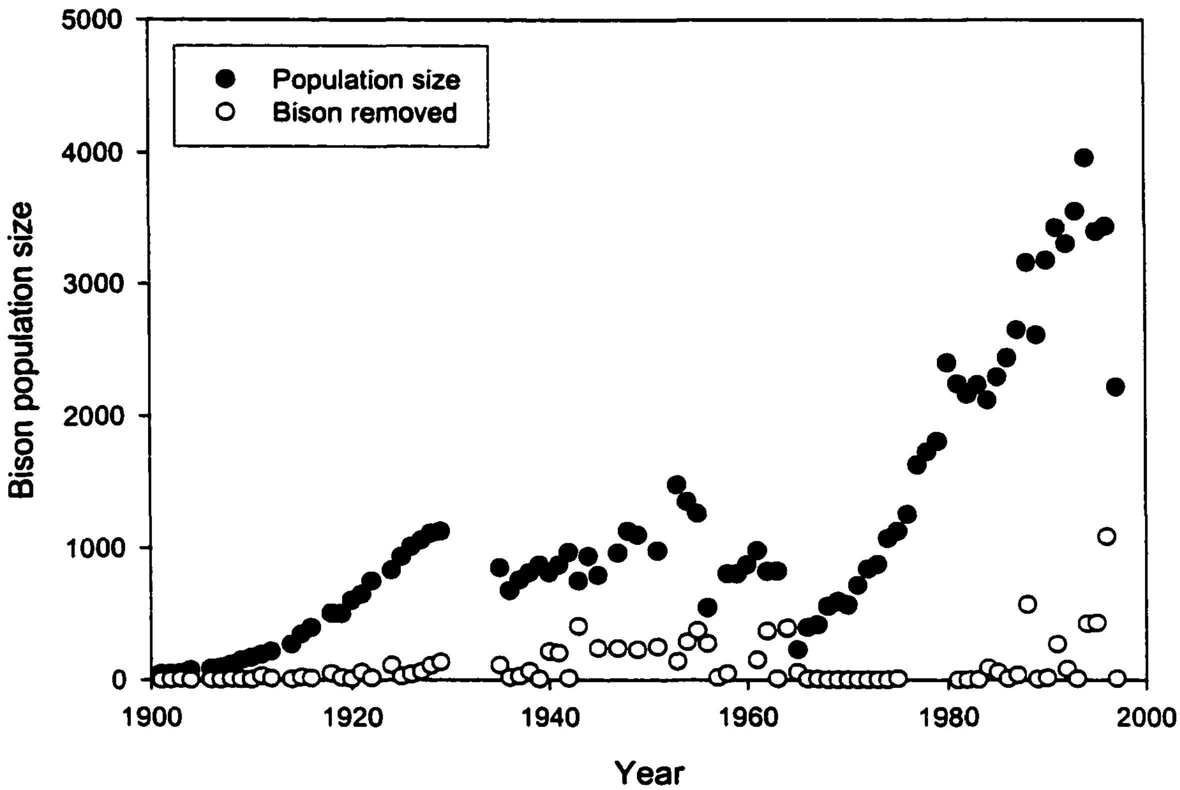


FIGURE 2: Bison population counts and numbers of bison removed by management actions, 1901/02 to 1997/98.

FIGURE 3: Alternative 1 – No action, continuation of the current revised interim management plan.

YEAR

97/98 98/99 99/00 00/01 01/02 02/03 03/04 04/05 05/06 06/07 07/08 08/09 09/10

Revised IMP:
Central: **T/S** sero+ female migrants and sero - pregnant female migrants
NR: **T/S** sero+ female migrants; hold sero- female migrants
IF # of sero- migrants exceeds the capacity of the holding facility (125 bison; 63 female), **additional bison may be subject to management actions**

Vaccinate (50/75/90%) of calves remotely

SMA on West: **Cap** bison at 100 migrants (50 females) (will all be sero- non-pregnant females)
IF migrants at Central > 100 migrants (50 females), **additional bison may be subject to management actions**

FIGURE 4: Alternative 2 – Minimal management.

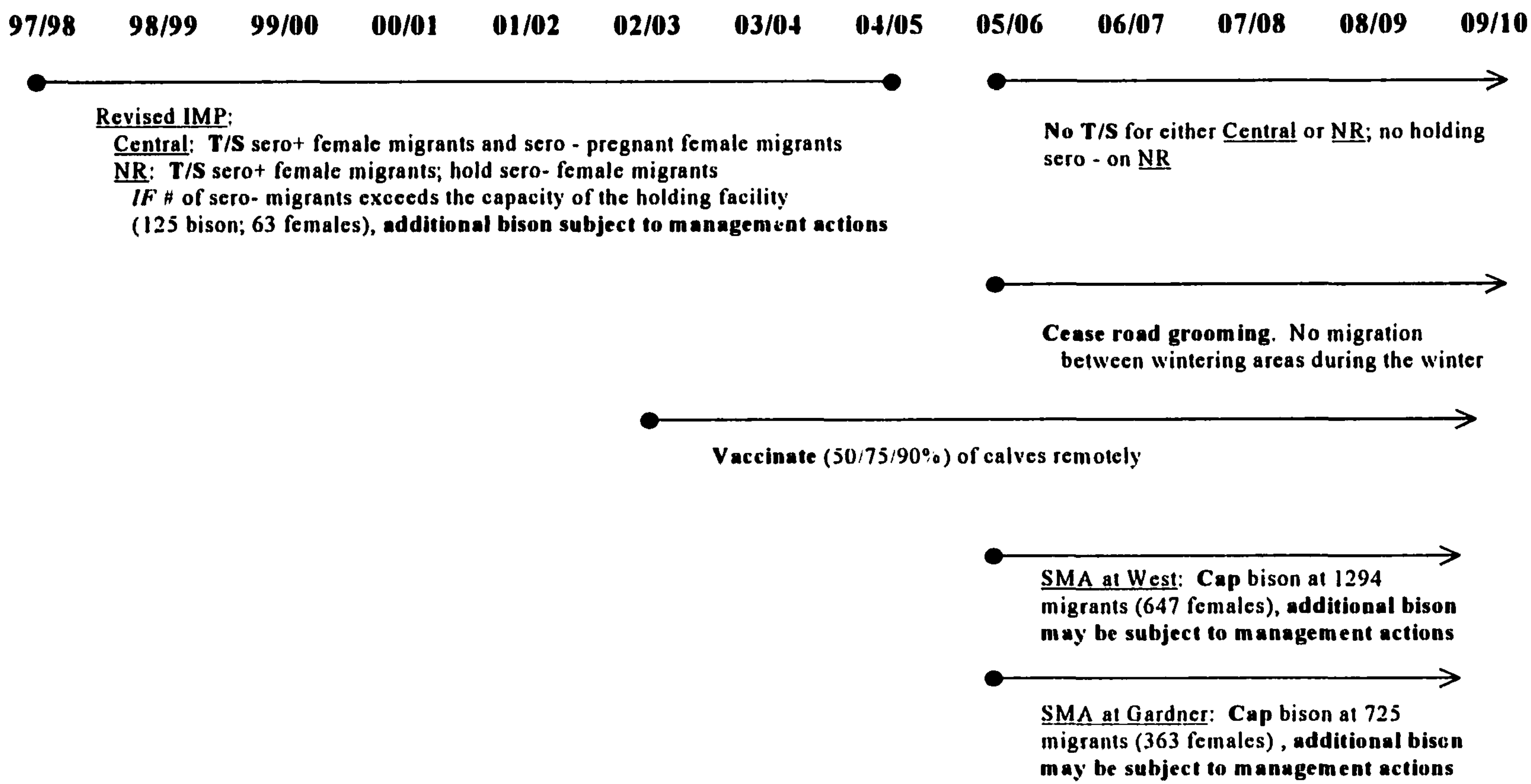


FIGURE 5: Alternative 3 – Management with emphasis on public hunting.

YEAR

97/98 98/99 99/00 00/01 01/02 02/03 03/04 04/05 05/06 06/07 07/08 08/09 09/10

Revised IMP:
Central: **T/S** sero+ female migrants and sero- pregnant female migrants

No T/S for Central, allow migrants outside YNP until limit reached

Revised IMP:
NR: **T/S** sero+ female migrants; hold sero- female migrants
IF # of sero- migrants exceeds the capacity of the holding facility (125 bison; 63 females), **additional bison may be subject to management actions**

T/S/Quarantine on NR if the number of post-hunt migrants > 100 bison (50 females)

Public hunt (1/2 female, distributed evenly between subadults & adults):
30 permits from 02/03 - 04/05
35 permits after 05/06

Vaccinate (50/75/90%) of calves remotely

SMA at West: **Cap** bison migrants at 100 bison (50 females) post-hunt; **additional bison subject to management actions**

SMA at North: **Cap** bison at 100 migrants (50 females) post-hunt; **additional bison subject to T/S/Quarantine**

FIGURE 6: Alternative 4 – Revised interim management plan with limited public hunting and quarantine.

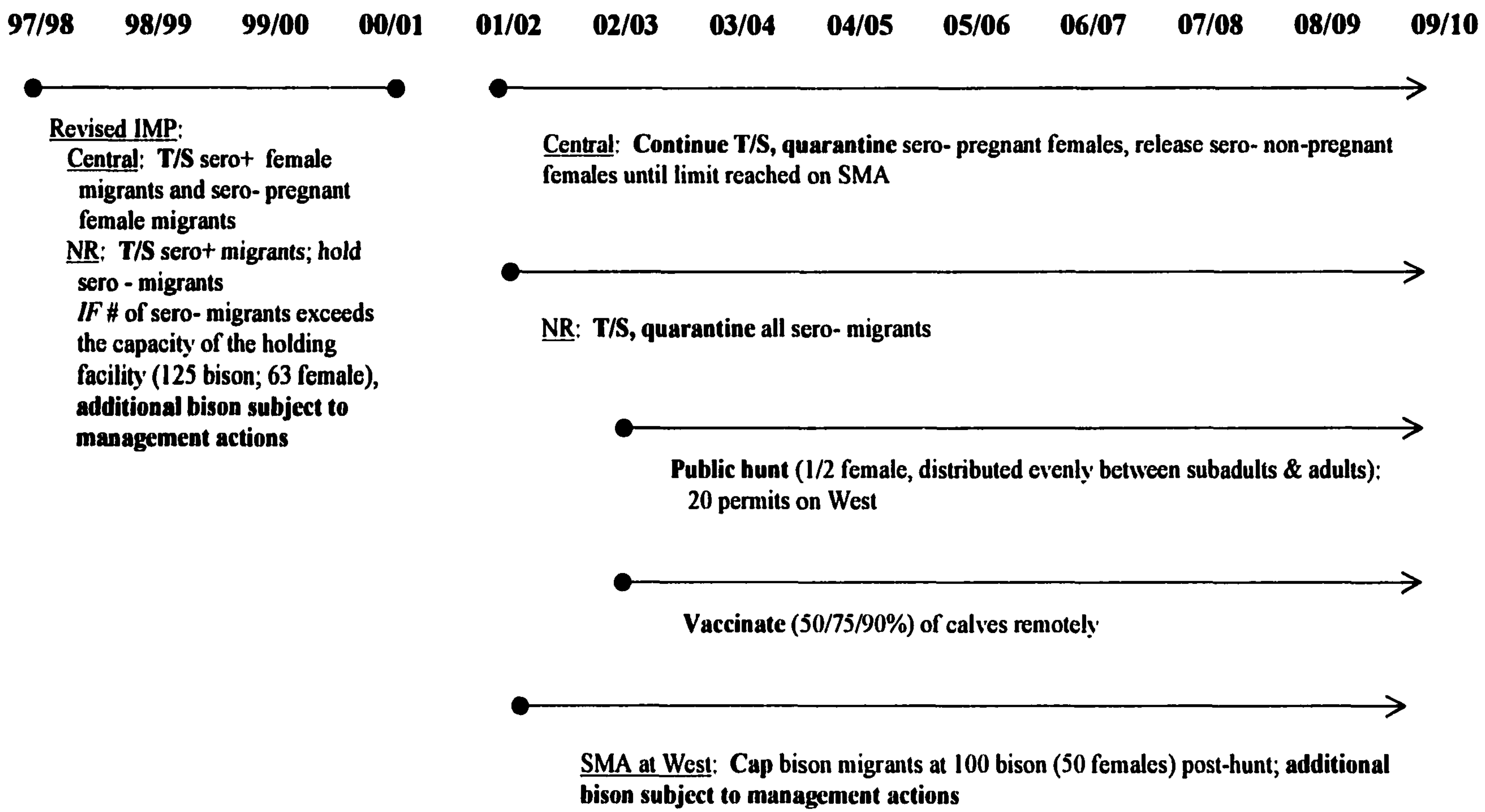


FIGURE 7: Alternative 5 – Aggressive brucellosis control within YNP through capture/test/slaughter.

97/98 98/99 99/00 00/01 01/02 02/03 03/04 04/05 X1/X2 X2/X3 X3/X4 X4/X5

97/98 – 99/00:

Revised IMP:
- Central: **T/S sero+ female migrants and sero- pregnant female migrants**
- NR: **T/S sero+ female migrants; hold sero - female migrants**
- *IF* **# of sero- migrants exceeds the capacity of the holding facility (125 bison; 63 females), additional bison may be subject to management actions**

00/01 – 04/05:

T/S all (50/90% annually) sero+ until the proportion of sero+ bison is 0.1%. DO NOT test/slaughter if the population is below 580 adult females (84 adult females on NR, 206 adult females on Central). When the sero+ level reaches 0.1%, shoot the number of bison that would be expected to still be infected (4). END SIMULATION after shooting the last infected bison.

00/01 – 04/05:

Shoot all migrants on NR and Central

02/03 – X4/X5:

Vaccinate all sero- female bison in the capture facility

FIGURE 8: Alternative 6 – Aggressive brucellosis control within YNP through vaccination.

97/98 98/99 99/00 00/01 01/02 02/03 03/04 04/05 X1/X2 X2/X3 X3/X4 X4/X5

97/98 – 99/00:
Revised IMP:
Central: **T/S** sero+ female migrantsand sero- pregnant female migrants
NR: **T/S** sero+ female migrants; hold sero- migrants *IF* # of sero- migrants exceeds the capacity of the holding facility (125 bison), **additional bison may be subject to management actions**

02/03 – 04/05 →:
Remote vaccination of entire bison herd (50/75/90%) until sero+ stabilizes (determine graphically)

00/01 – 04/05 →

X1/X2 – X4/X5 →:
T/S all (50/90% annually) sero+ until the proportion of sero+ bison is 0.1%. **DO NOT** T/S if the population is below 580 adult females (84 adult females on NR, 206 adult females on Central). When the sero+ level reaches 0.1%, **shoot** the number of bison that would be expected to still be infected (4). **END SIMULATION** after shooting the last infected bison.

X1/X2 – X4/X5 →:
Vaccinate all sero- bison in the capture facility

00/01 – X4/X5 →:
SMA on West: allow only sero-, maximum of 100 bison (50 females); **additional bison may be subject to management actions**

00/01 – X4/X5 →:
Slaughter all migrating bison on NR

FIGURE 9: Alternative 7 – Manage for specific bison population size.

97/98 98/99 99/00 00/01 01/02 02/03 03/04 04/05 05/06 06/07 07/08 08/09 09/10

Revised IMP:
Central: **T/S** sero+ female migrants and sero- pregnant female migrants

Central: **T/S** sero+, **quarantine** sero- pregnant females, allow sero- non-pregant females on SMA, if the number of migrants >100 (50 females), or if the total population size > 2500 (1250 females) **additional bison may be subject to management actions**

SMA on West: limited to 100 (50 female) sero- bison, if the number of migrants is > 100 (50 females) or if the total population size > 2500 (1250 females) after 00/01, **additional bison may be subject to management actions.**

Revised IMP:
NR: **T/S** sero+ female migrants; hold sero- migrants *IF* # of sero- female migrants exceeds the capacity of the holding facility (125 bison; 63 females), **additional bison may be subject to management actions**

A B

NR: **T/S** sero+females, release sero- females on SMA. **Quarantine** sero- female if the number of migrants >100 (50 females) or if the total population size > 2500 (1250 females)

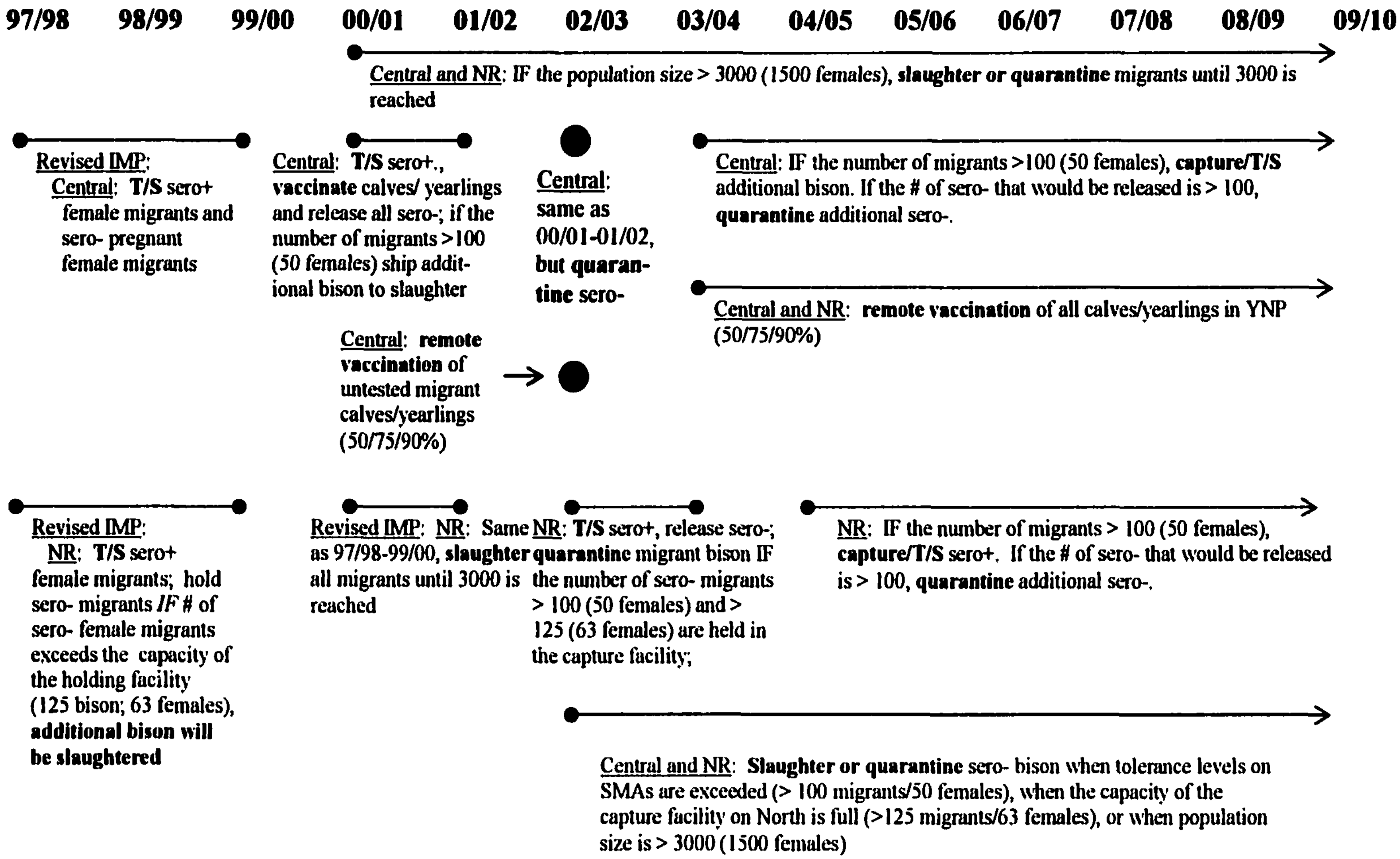
SMA on NR: limited to 100 sero- bison

A: NR - **slaughter** all sero- to maintain 2500 (1250 females) in population if necessary
B: NR - **T/S** sero+, quarantine all sero- migrants

Vaccinate (50/75/90%) calves remotely

Public hunt: 10 permits on West (50% female, distribute evenly between adults/sub-adults)

FIGURE 10: New preferred alternative – manage for bison population size of 3000



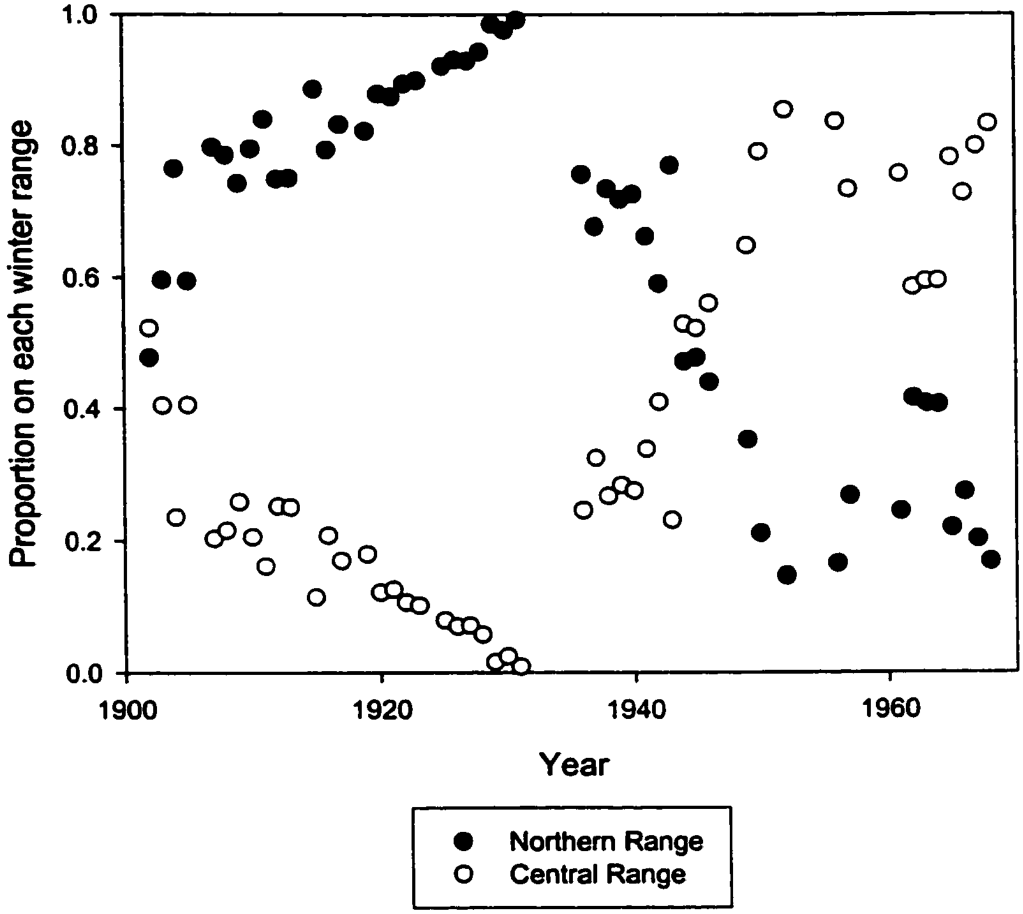


FIGURE 11: Proportion of bison counted on the Northern and Central ranges of YNP, 1901/02 – 1968/69 (from Meagher 1973).

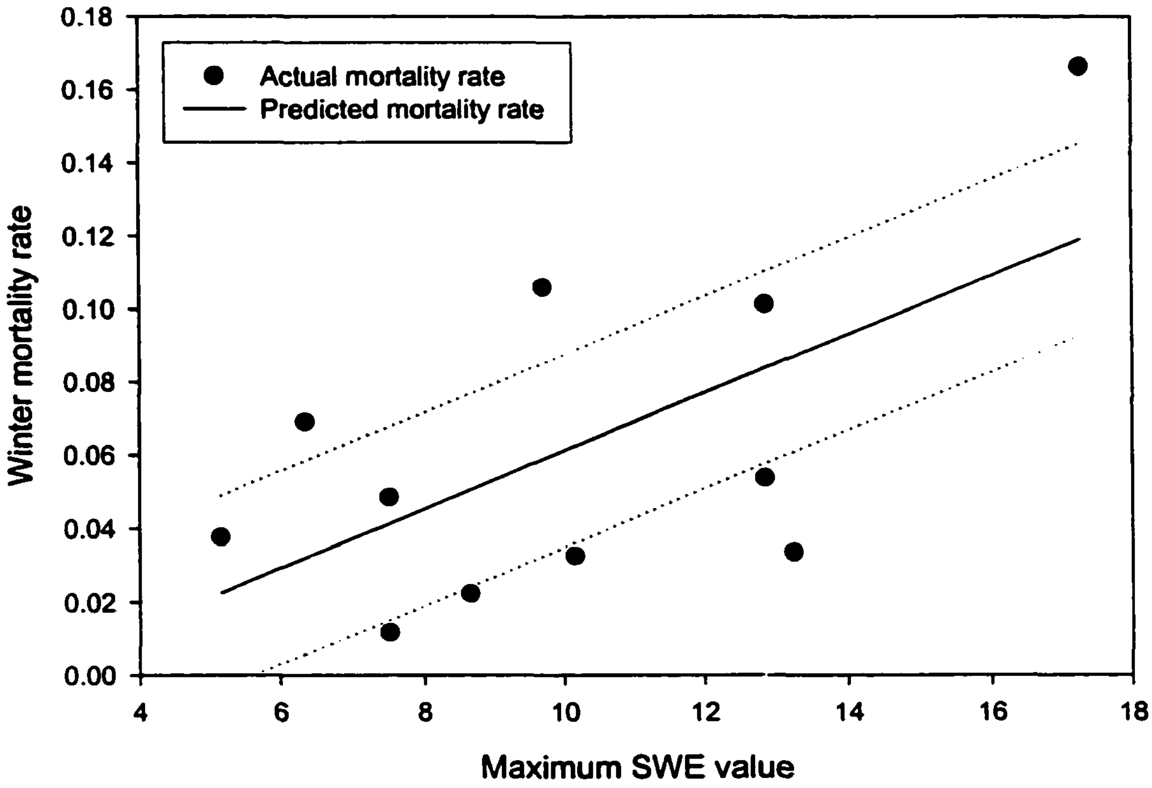


FIGURE 12: Increase in natural mortality rate with increasing winter severity on the Central range.

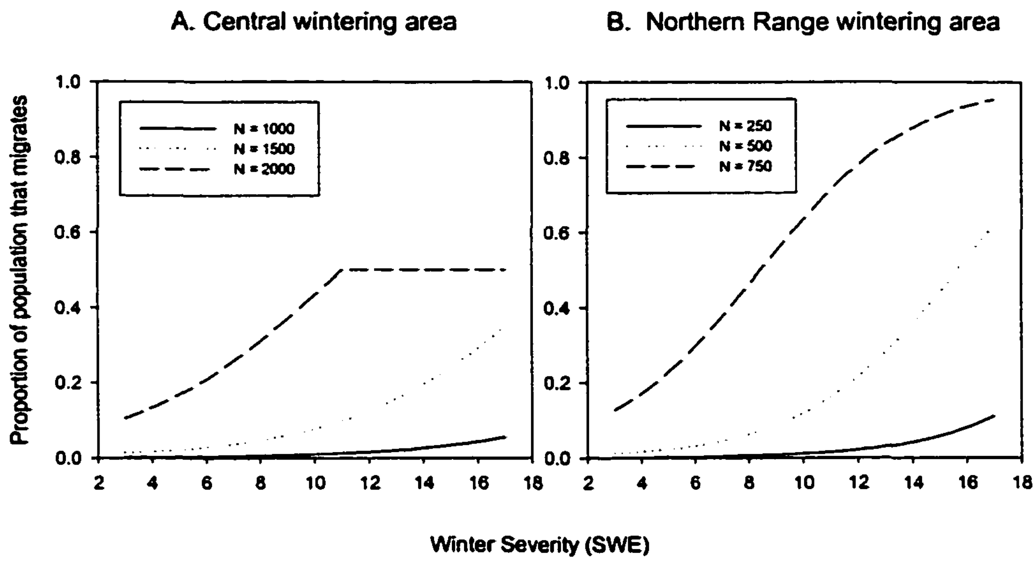


FIGURE 13: Relationship between the population sizes, winter severity measured by the snow water equivalent (SWE), and migration rates for the Central and Northern Range bison groups. The relationship is illustrated for three different population sizes (N) in each wintering area.

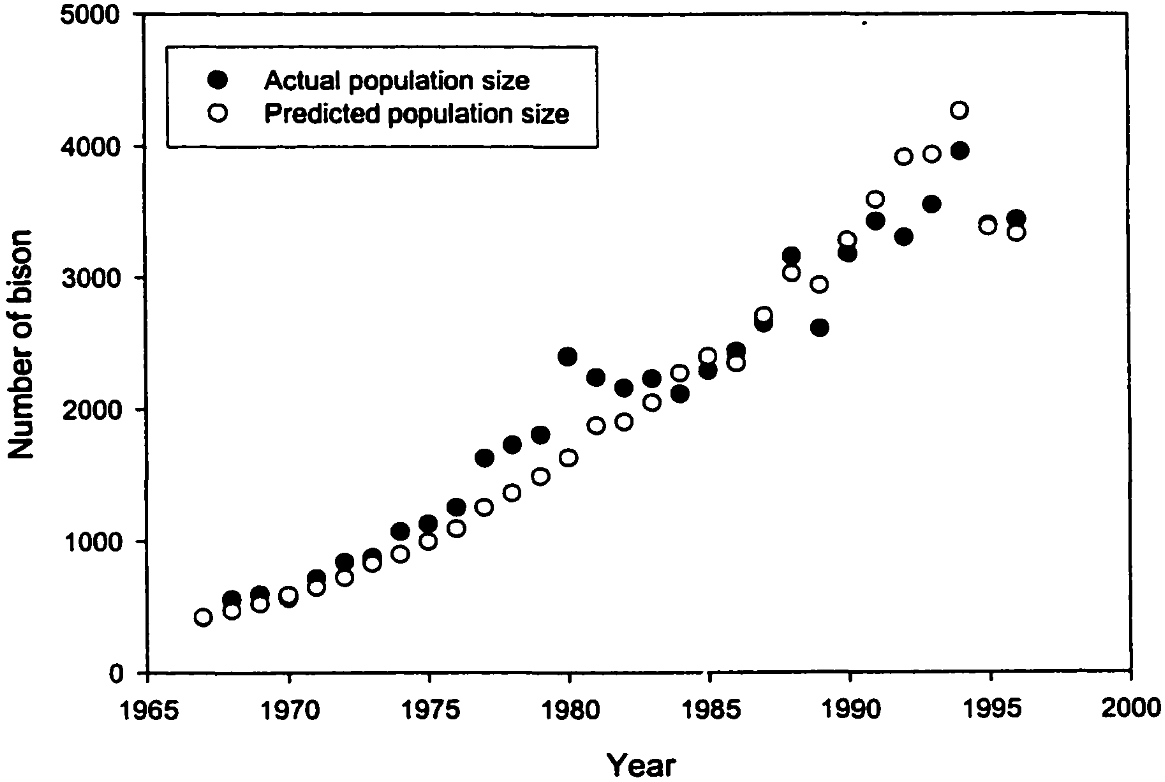


FIGURE 14: Actual and modeled total bison population size, 1967/1968 –1996/1997.

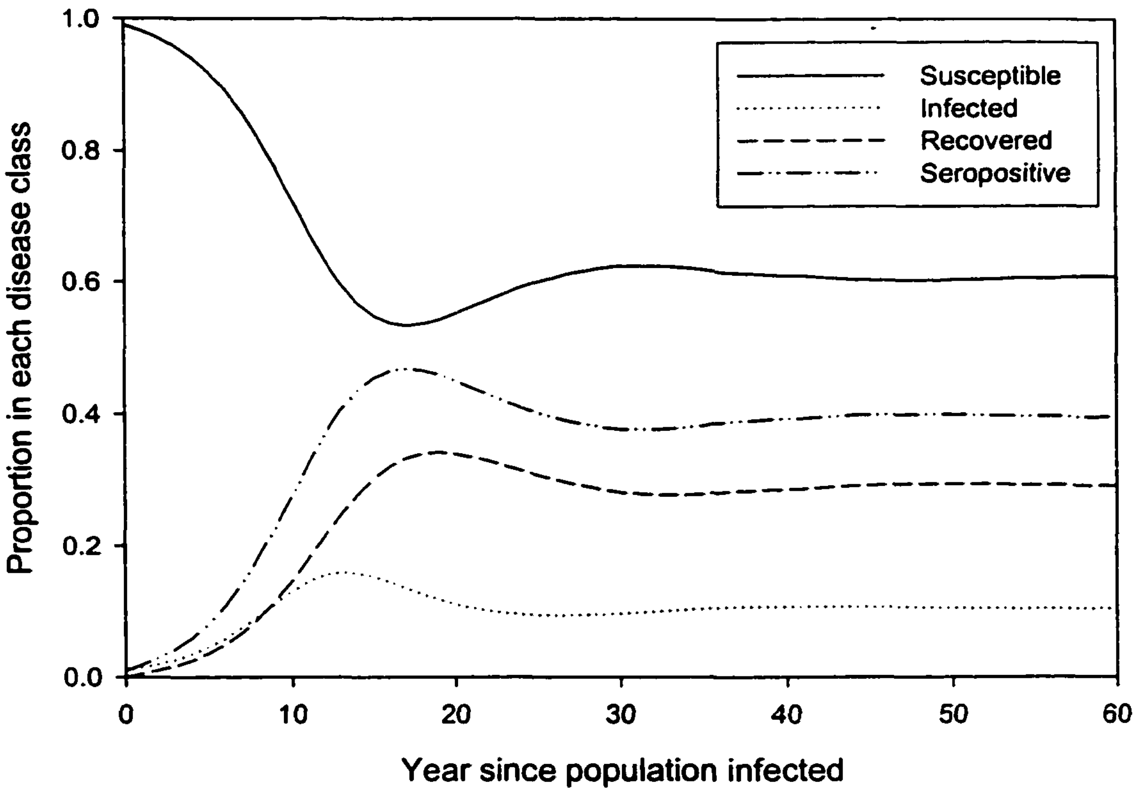


FIGURE 15: Change in proportions of bison susceptible, infected, recovered, and seropositive over time, given an initial proportion of 0.01 infected, a transmission rate of 1.15, and a recovery rate of 0.5. This simulates the dynamics of brucellosis as it became established in the Yellowstone National Park bison herd.

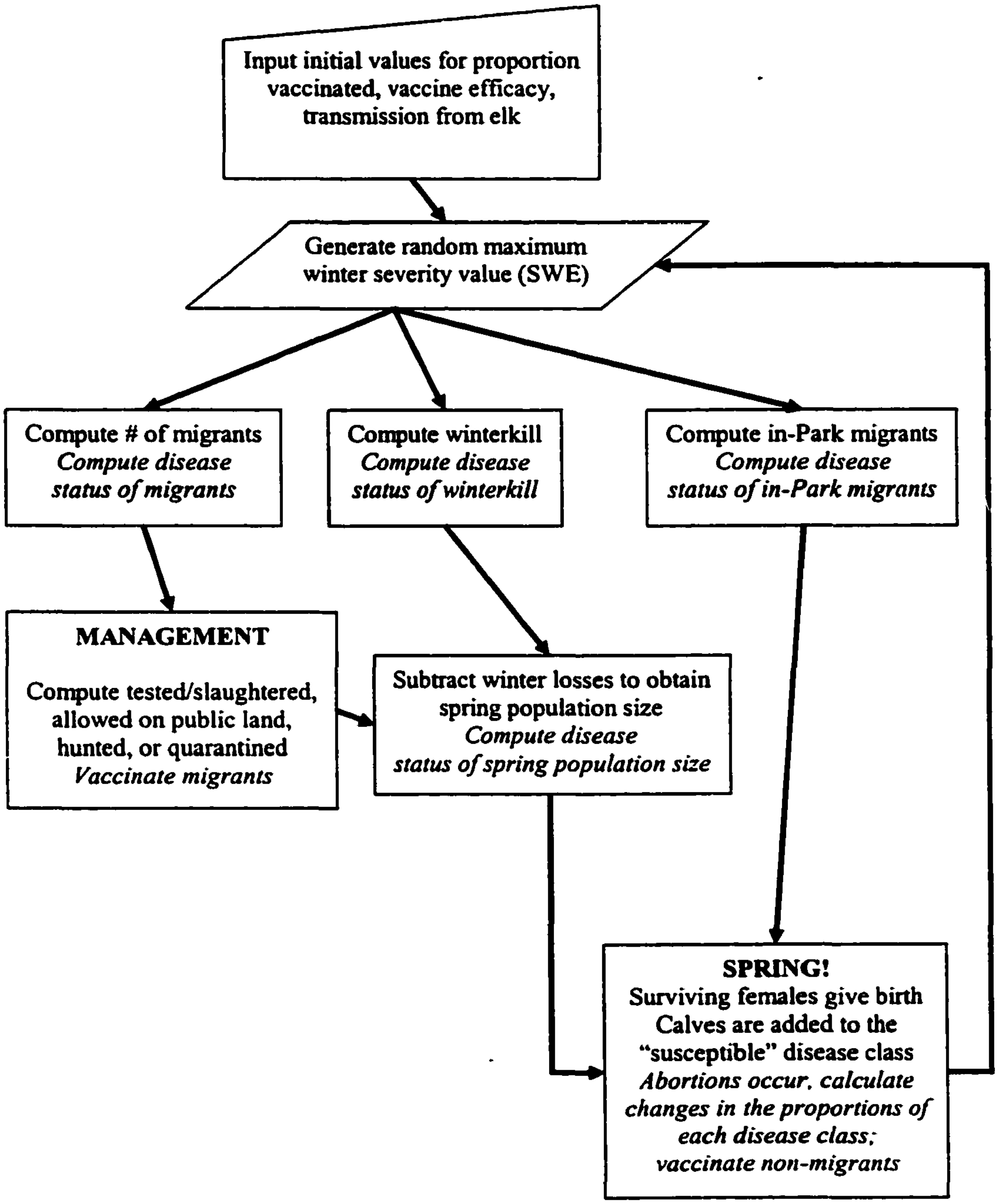


FIGURE 16: Basic structure of the population model. Plain text indicates steps taken in the population dynamics model; italicized text indicates steps taken in the disease model.

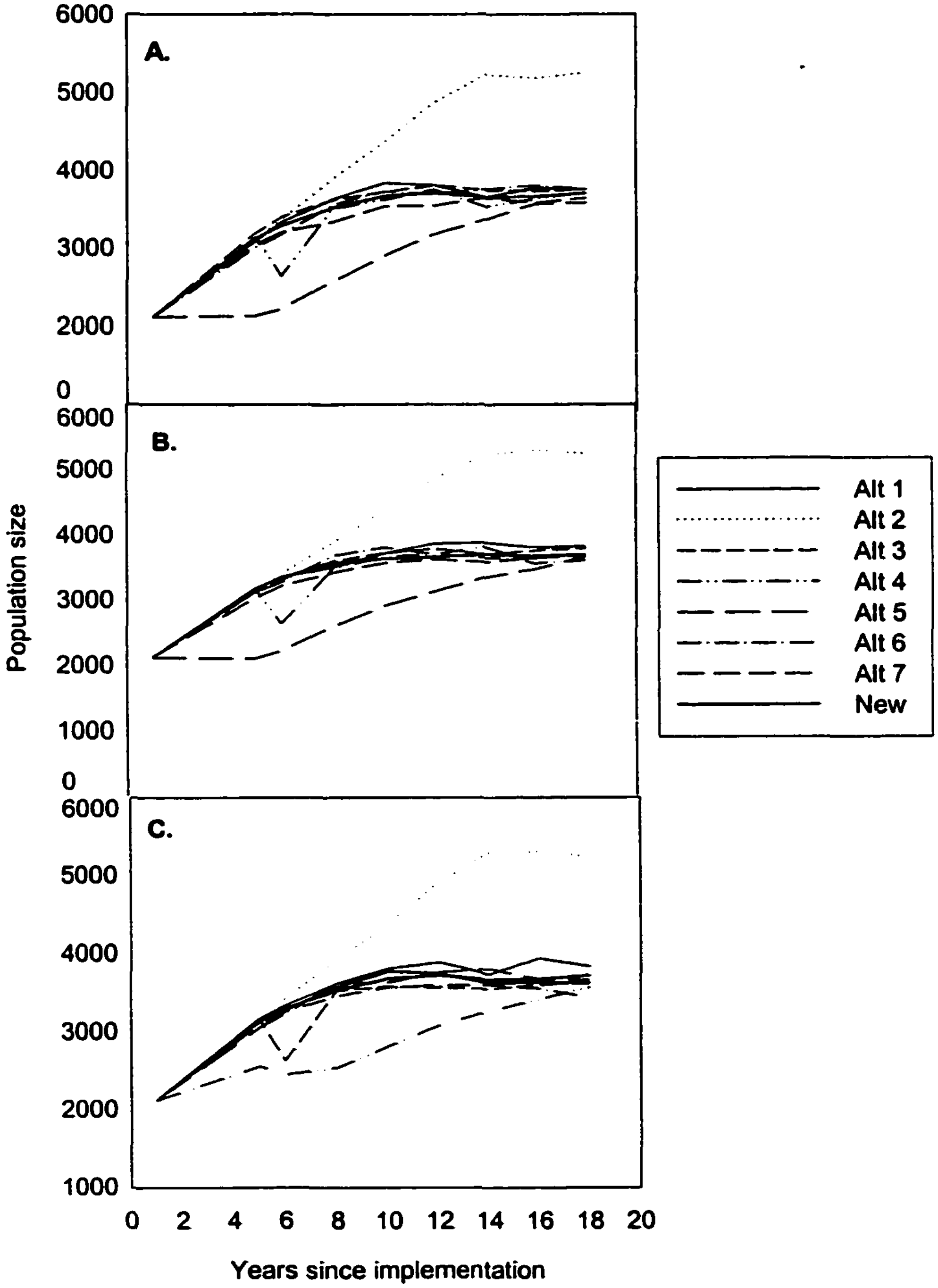


FIGURE 17: Population trajectories for all alternatives and three key sets of disease management parameters. A. The "most plausible" disease management scenario; B. The "best case" disease management scenario; C. The "worst case" disease management scenario. All trajectories represent fall counts and include calves born the previous spring.

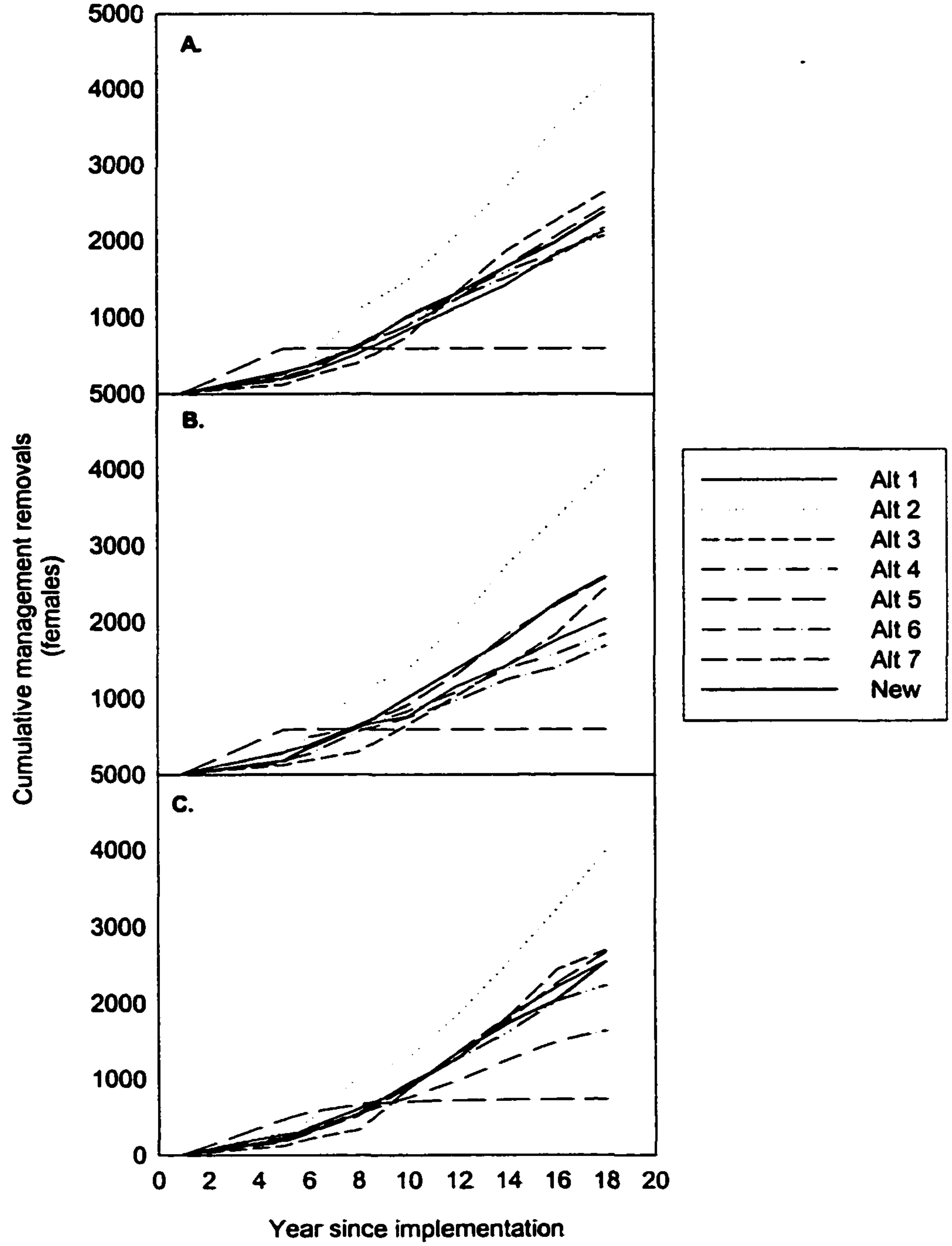


FIGURE 18: Changes in seroprevalence for all alternatives and three key sets of disease management parameters. A. The "most plausible" disease management scenario; B. The "best case" disease management scenario; C. The "worst case" disease management scenario. Plots of the new preferred alternative modified to eliminate vaccination is provided for the best case scenario for comparison.

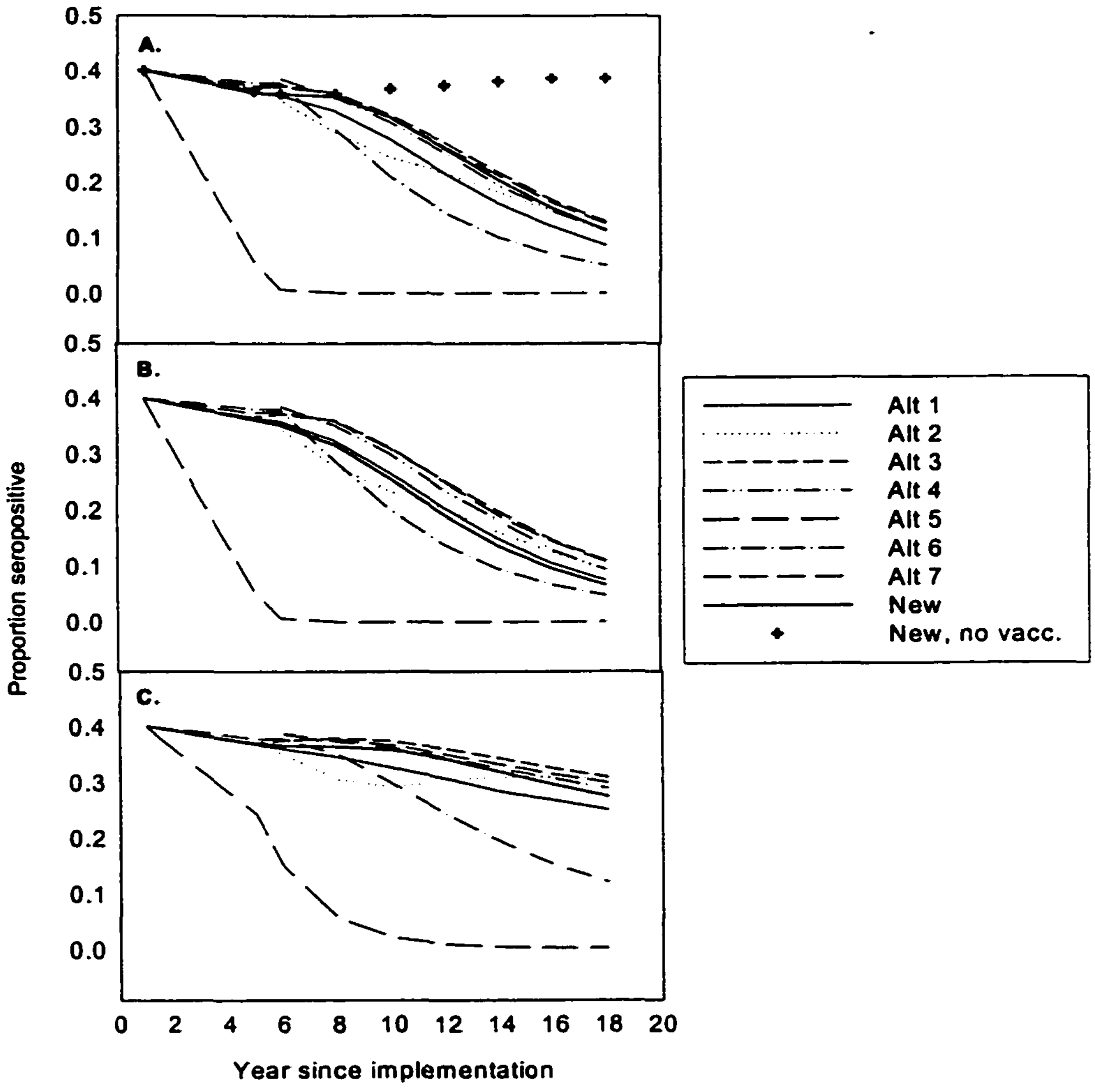


FIGURE 19: Cumulative management removals of females for all alternatives and three key sets of disease management parameters. Management removals for each alternative may include test and slaughter, public hunting, quarantine, or "other"; refer to the descriptions of each alternative and Figures 3-10 for details. A. The "most plausible" disease management scenario; B. The "best case" disease management scenario; C. The "worst case" disease management scenario.

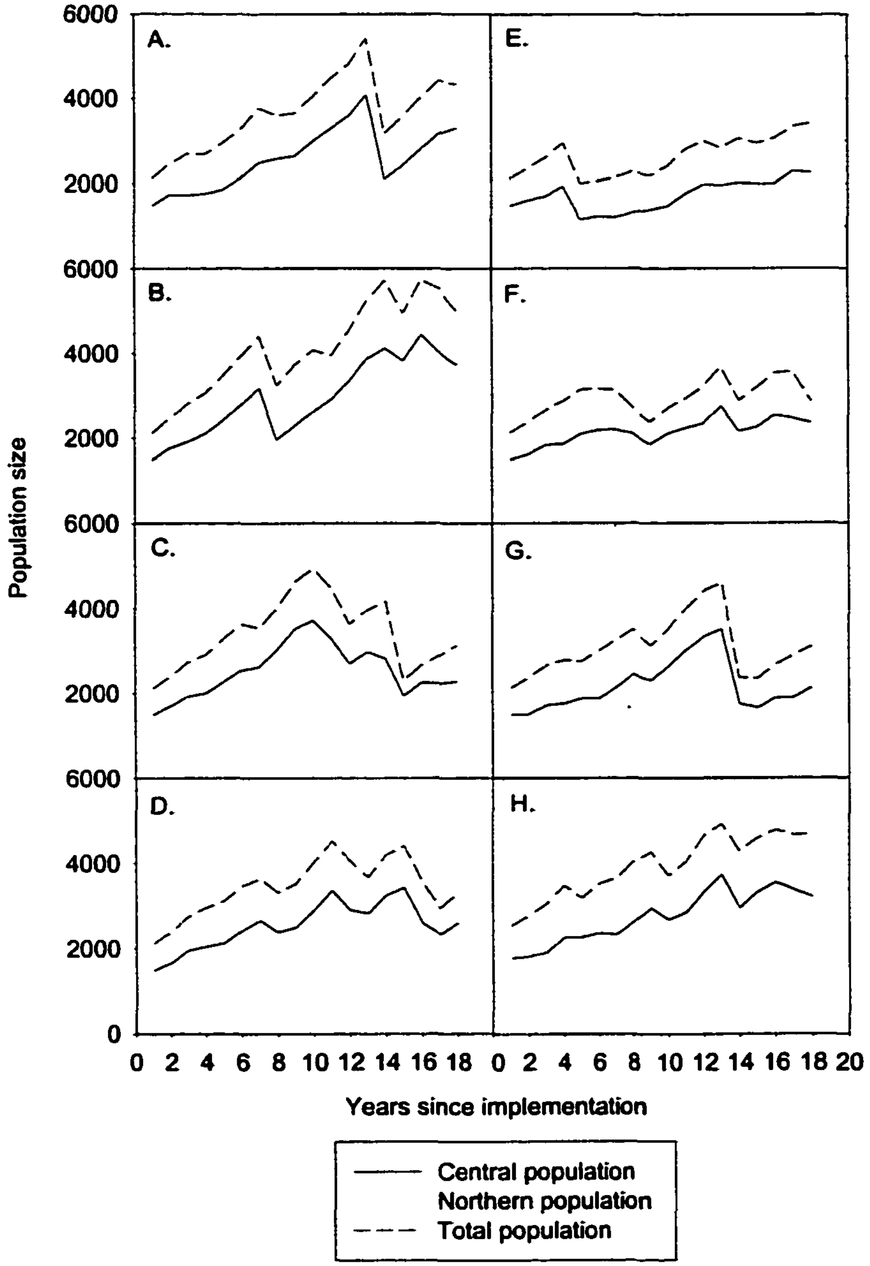


FIGURE 20: Examples of population trajectories for bison in the Central and Northern Range wintering areas. A. Alternative 1, B. Alternative 2, C. Alternative 3, D. Alternative 4, E. Alternative 5, F. Alternative 6, G. Alternative 7. For all results illustrated above, the vaccination rate was 75%, the efficacy was 70%, elk were assumed to re-infect bison ever 15 years, and aggressive test and slaughter programs were directed at 90% of the bison.

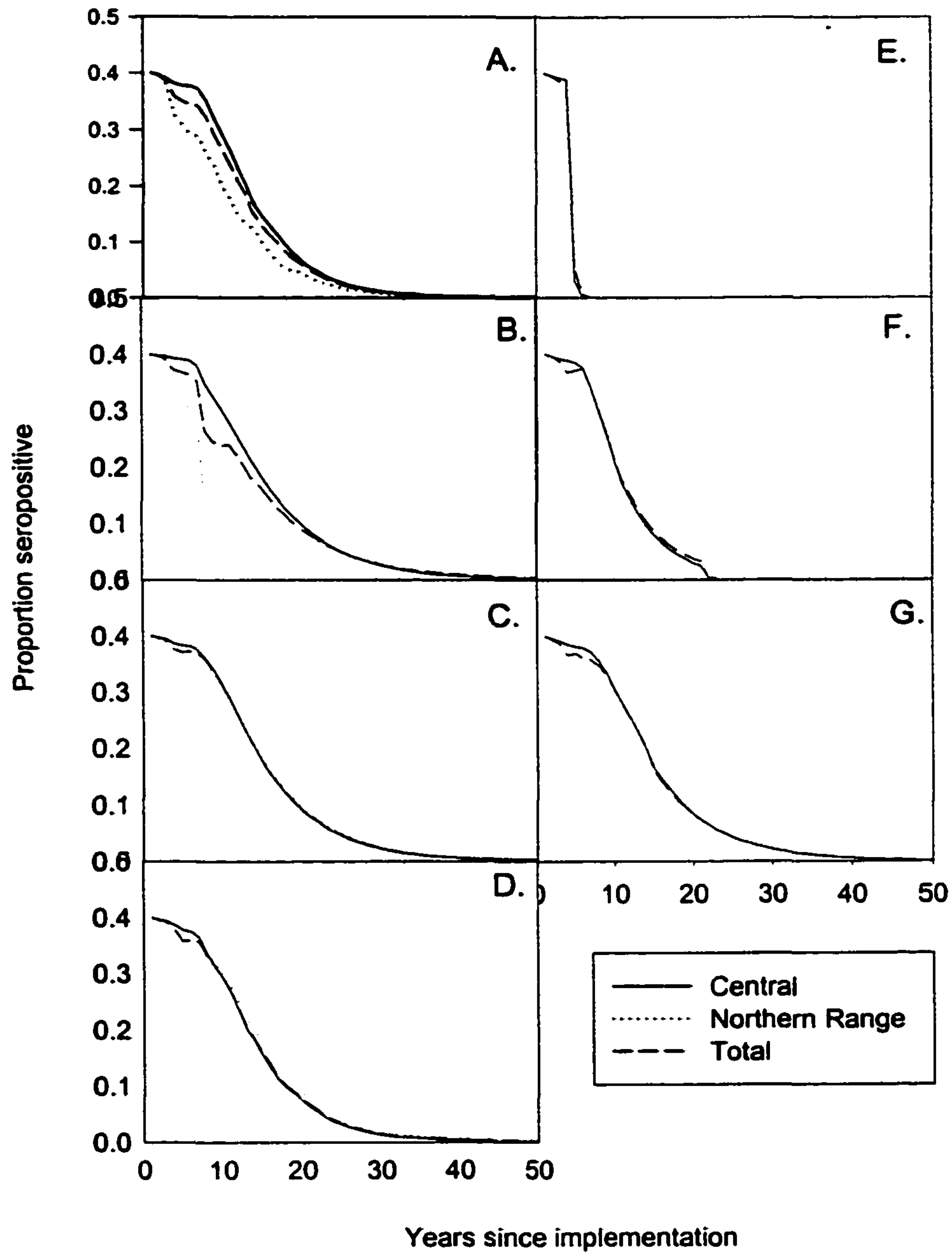


FIGURE 21: Estimated average reduction in seroprevalence based on five model runs for bison in the Central and Northern Range wintering areas for A. Alternative 1, B. Alternative 2, C. Alternative 3, D. Alternative 4, E. Alternative 5, F. Alternative 6, G. Alternative 7. For all results illustrated above, the vaccination rate was 75%, the efficacy was 70%, elk were assumed to re-infect bison ever 15 years, and aggressive test and slaughter programs were directed at 90% of the bison

APPENDIX 1: Example of model in Excel

The models developed to simulate each management alternative are each included in separate Excel spreadsheets. Each spreadsheet for each management alternative includes the following worksheets:

"Model": This worksheet includes all the mathematics necessary to project the bison population and the disease dynamics of that population. Bison dynamics are in black text; disease dynamics are in blue text. Each column, G-AZ, includes one modeled year. Successive sets of rows calculates the following for each year: Number of females in the fall, winterkill (natural mortality), migrants out of YNP, animals tested/slaughtered/quarantined, remaining migrants quarantined to meet population targets, migrants to the other wintering area, and number of females remaining alive in the spring. Winterkill and number of migrants are both based on a function of the winter severity level, which is located at the top of the worksheet, and fall population size, which is calculated at the top of the sections for each population.

Key population parameter values are included on the left hand side of the worksheet. Cells for reinfection by elk, proportion vaccinated, and vaccine efficacy refer to data included in the "Inputs&Graphs" spreadsheet.

Certain columns and rows are colored to aid the user in following the logic of the spreadsheet. The Central population and disease dynamics have an orange column to the left of the labels while the Northern Range population and disease dynamics are identified with a green column. Summary data at the bottom of the worksheet is identified by a pink column. Sometimes, the columns for the early years of the model are colored to show when management actions change. Similarly, rows may be shaded to identify calculations that are of particular interest. There are differences in shading between spreadsheets, so a common pattern should not be sought other than the shading that identifies the Central population, the Northern Range population, and the summary data.

"Inputs&Graphs": This worksheet provides a place to input information on stage structure, reproductive rate, harvest levels, and other demographic information. Graphs of the population and disease dynamics are linked to the "Model" worksheet, so the user can modify the demographic rates and see how the dynamics of the population change. This worksheet also includes a summary of the following key output data:

Total population size, spring
Total population size, fall
Female bison migrating out of Central
Female bison migration out of Northern Range
Total number of female bison migrating
Female bison tested/slaughtered/quarantined from Central, if applicable

Female bison tested/slaughtered/quarantined from Northern Range, if applicable
Total number of female bison tested/slaughtered/quarantined
Female bison slaughtered on Central
Female bison slaughtered on Northern Range
Additional number of female bison subject to management actions on Central
Additional number of female bison subject to management actions on Northern Range
Total additional number of female bison subject to management actions
Female bison remaining outside YNP at North
Female bison remaining outside YNP at Central
Total number of female bison remaining outside YNP
Total female bison held in capture facilities
Total females successfully vaccinated
Proportion susceptible
Proportion infected
Proportion recovered
Proportion vaccinated
Proportion seropositive

"Input": The user enters a series of input parameters here for frequency of reinfection by elk, vaccination rate, and efficacy rate. The macro "SimB" copies these scenarios into the spreadsheet "Inputs&Graphs" for use in the "Model" (printout not provided).

	A	B	C	D	E	F	G	H	I	J	K
1						FALL OF	1997	1998	1999	2000	2001
2	Average	Min	Max			Winter Severity					
3	2554.598902	1454.559498	3758.031282			SWE	12.54511753	12.67453	6.890612	14.60476685	10.12953172
4	948.327981	174.0492377	636.4949685			TOTAL FALL POPULATION SIZE				1441.491234	1329.745686
5						IS TOTAL FALL POPULATION SIZE > 3000?				1441.491234	1329.745686
6											
7	Population parameter values					Dynamics					
8	Central subpopulation			Pop size in 2027		Central population					
9	Stage class	Proportion of animals affected by natural mortality	Fecundity (successful female births)	3779.8138		MANAGEMENT	Revised interim management plan			1st year of in-chute vaccination of c/y; vaccinates don't show up until	
10	New calves	0	0	1253.4119							
11	Yearlings (9-12 months)	0.59	0	636.49497		Proportion of females that die from winterkill	0.06	0.09	0.04	0.09	0.05
12	Two year olds	0.02	0.01								
13	Sexually mature	0.39	0.24			Proportion of females in Central that migrate out of the park	0.005488178	0.005917	0.001388	0.01942714	0.006182078
14				Pop size in 2010			0.064363793				
15				200.7679							
16							1	2	3	4	5
17											
18	Disease parameter values					NUMBER OF FEMALES IN THE FALL	Initial population distribution				
19		Initial prop. susceptibl	0.6			New calves as of spring	0	114.8984	120.474	140.3575863	141.4396279
20		Initial prop. infected	0.1			9 mo old calves, fall	118	114.8984	120.474	140.3575863	141.4396279
21		Initial prop. resistant/r	0.3			21 mo old	81	82.21116	70.40874	106.0290207	84.45994292
22						Sexually mature adults	538	549.1352	576.1324	654.451102	683.5516994
23		Transmission rate BE	1.12			Fall of:	1997	1998	1999	2000	2001
24		Elk infect bison with b	15			Modeled number of females	737	746.2448	767.0152	900.837709	909.4512702
25		Rate at which infected	0.5								
26		Proportion of calves v	0.75			Modeled annual rate of increase		0.012466	0.027453	0.160818553	0.0095163
27		Vaccine efficacy	0.7								
28											
29	Hunt -- West Yellowstone										
30	9 mo olds	0				Disease dynamics					
31	21 mo olds	2				Susceptible	442.2	451.9436	469.3378	555.5070204	565.3445122
32	Adults	3				Infected	73.7	73.87987	75.29581	88.39393228	88.91574904
33						Recovered/resistant	221.1	220.4213	222.3815	256.9367563	253.1248345
34						Vaccinated					2.066174475
35						Total	737	746.2448	767.0152	900.837709	909.4512702
36											
37						CHECK	0	0	0	0	0
38	OUTPUT FOR CENTRAL POPULATION										
39						Central proportion susceptible	0.6	0.605624	0.611902	0.616656047	0.62163255
40		Modeled values	Values from the literature			Central proportion infected	0.1	0.099002	0.098167	0.098124148	0.097768569
41	Predicted # of animals in fa	1435.891269	1219.78			Central proportion recovered/resistant	0.3	0.295374	0.289931	0.285219806	0.27832699
42						Central proportion vaccinated	0	0	0	0	0.002271891

	A	B	C	D	E	F	G	H	I	J	K
43						Central proportion seropositive	0.4	0.394376	0.388098	0.383343953	0.376095559
44	Average percent 9 mo old c	0.152138126	14.5% of population (Gogan unpublished)				1	1	1	1	1
45	Average percent adults in fa	0.723380127	59-64% of population (Gogan unpublished)								
46						Transmission from elk?	0	0	0	0	0
47	Percent 9mo old calves in 97										
48											
49											
50						**WINTERKILL**	=proportion of females that die from winterkill * total number of animals * distribution				
51											
52						9 mo old calves, fall	26.0898	39.6256	18.10156	47.83448235	26.82881247
53						21 mo old	0.8844	1.343241	0.613612	1.621507876	0.90945127
54						Sexually mature adults	17.2458	26.19319	11.96544	31.61940359	17.73429977
55						Total number of animals	44.22	67.16203	30.68061	81.07539381	45.47256351
56											
57						**Number of diseased animals in winterkill**					
58						Susceptible	26.532	40.67492	18.77351	49.99563184	28.26722561
59						Infected	4.422	6.649188	3.011832	7.955453905	4.445787452
60						Recovered/resistant	13.266	19.83792	8.89526	23.12430807	12.65624172
61						Vaccinated	0	0	0	0	0.103308724
62						Total number of animals	44.22	67.16203	30.68061	81.07539381	45.47256351
63											
64						**CHECK**					
65											
66						**# MIGRATING OUT OF THE PARK**	f the park during a particular winter * proportio/n of calves in the fall population (# of				
67											
68						**Total # migrating out of Central**				**17.50069992**	**5.622298544**
69											
70											
71						9 mo old calves, fall	0.647605062	0.679844	0.167235	2.726746422	0.87439079
72						21 mo old	0.444542458	0.486437	0.097737	2.059840586	0.522137941
73						Sexually mature adults	2.952640027	3.249188	0.799751	12.71411291	4.225769813
74						Total number of animals	4.044787546	4.415469	1.064723	17.50069992	5.622298544
75											
76						**Diseased animals migrating out of YNP**					
77											
78						Susceptible 9mo olds	0.388563037	0.41173	0.102331	1.681464669	0.543549776
79						Susceptible two year olds (21 mo)	0.266725475	0.294598	0.059805	1.270213153	0.32457794
80						Susceptible adults	1.771584016	1.967786	0.489369	7.840234607	2.626876065
81						Pregnant 21 mo = 0.01*2*2yo	0.005334509	0.005892	0.001196	0.025404263	0.006491559
82						Pregnant adults = birth rate*2 *adults	0.850360328	0.944537	0.234897	3.763312611	1.260900511
83						Total susceptible	2.426872528	2.674113	0.651506	10.79191243	3.495003781
84											
85											
86						Infected 9 mo olds	0.064760506	0.067306	0.016417	0.267559668	0.085487936
87						Infected 21 mo olds	0.044454246	0.048158	0.009595	0.202120102	0.051048679
88						Infected adults	0.295264003	0.321677	0.078509	1.247561492	0.413147466
89						*Total infected*	0.404478755	0.437141	0.104521	1.717241261	0.549684082
90											
91											
92						Recovered 9 mo olds	0.194281518	0.200808	0.048486	0.777722085	0.243366556
93						Recovered 21 mo olds	0.133362737	0.143681	0.028337	0.587507332	0.145325082

	A	B	C	D	E	F	G	H	I	J	K
94						Recovered adults	0.885792008	0.959726	0.231873	3.626316815	1.176145792
95						Total recovered	1.213436264	1.304215	0.308696	4.991546231	1.56483743
96											
97						Vaccinated 9 mo olds	0	0	0	0	0.001986521
98						Vaccinated 21 mo olds	0	0	0	0	0.001186241
99						Vaccinated adults	0	0	0	0	0.00960049
100						Total vaccinated	0	0	0	0	0.012773251
101						TOTAL:	4.044787546	4.415469	1.064723	17.50069992	5.622298544
102								0	0	0	0
103						**CHECK**	0	0	0	stop	stop
104											
105						**SLAUGHTERED OR QUARANTINED TO MAINTAIN POPULATION LIMIT**					
106											
107						9 mo old calves, fall				0	0
108						21 mo old				0	0
109						Sexually mature adults				0	0
110						Total number of animals				0	0
111											
112						**Disease status of animals slaughtered or quarantined to maintain population limit**					
113											
114						Susceptible 9mo olds				0	0
115						Susceptible two year olds (21 mo)				0	0
116						Susceptible adults				0	0
117						Total susceptible				0	0
118											
119											
120						Infected 9 mo olds				0	0
121						Infected 21 mo olds				0	0
122						Infected adults				0	0
123						Total infected				0	0
124											
125											
126						Recovered 9 mo olds				0	0
127						Recovered 21 mo olds				0	0
128						Recovered adults				0	0
129						Total recovered				0	0
130											
131						Vaccinated 9 mo olds					0
132						Vaccinated 21 mo olds					0
133						Vaccinated adults					0
134						Total vaccinated					0
135						TOTAL:				0	0
136											
137						**REMAINING MIGRANTS AFTER POPULATION LIMIT MET**					
138											
139						9 mo old calves, fall				2.726746422	0.87439079
140						21 mo old				2.059840586	0.522137941
141						Sexually mature adults				12.71411291	4.225769813

	A	B	C	D	E	F	G	H	I	J	K
142						Total number of animals				17.50069992	5.622298544
143											
144						**Disease status of remaining migrants**					
145											
146						Susceptible 9mo olds				1.681464669	0.543549776
147						Susceptible two year olds (21 mo)				1.270213153	0.32457794
148						Susceptible adults				7.840234607	2.626876065
149						Total susceptible				10.79191243	3.495003781
150											
151											
152						Infected 9 mo olds				0.267559668	0.085487936
153						Infected 21 mo olds				0.202120102	0.051048679
154						Infected adults				1.247561492	0.413147466
155						Total infected				1.717241261	0.549684082
156											
157											
158						Recovered 9 mo olds				0.777722085	0.243366556
159						Recovered 21 mo olds				0.587507332	0.145325082
160						Recovered adults				3.626316815	1.176145792
161						Total recovered				4.991546231	1.56483743
162											
163						Vaccinated 9 mo olds					0.001986521
164						Vaccinated 21 mo olds					0.001186241
165						Vaccinated adults					0.00960049
166						Total vaccinated					0.012773251
167						TOTAL				17.50069992	5.622298544
168											
169											
170						**# OF REMAINING MIGRANTS TESTED/SLAUGHTERED OR SENT TO QUARANTINE**					
171						9 mo old calves, fall	0.259042025	0.268114	0.064903	1.045281753	0.328854492
172						21 mo old	0.183151493	0.197731	0.039128	0.789627433	0.196373761
173						Sexually mature adults	2.031416338	2.22594	0.545279	4.873878306	1.589293258
174						Total number of animals	2.473609856	2.691785	0.64931	6.708787493	2.114521512
175											
176						**Disease status of remaining migrants tested/slaughtered or sent to quarantine**					As of 2001, have to te
177											
178						Susceptible 9mo olds				0	0
179						Susceptible two year olds (21 mo)				0	0
180						Susceptible adults				0	0
181						Pregnant 21 mo = 0.01*2*2yo	0.005334509	0.005892	0.001196		
182						Pregnant adults = 0.2589*2 *adults	0.850360328	0.944537	0.234897		
183						Total susceptible	0.855694837	0.950429	0.236093	0	0
184											
185						Infected 9 mo olds	0.064760506	0.067306	0.016417	0.267559668	0.085487936
186						Infected 21 mo olds	0.044454246	0.048158	0.009595	0.202120102	0.051048679
187						Infected adults	0.295264003	0.321677	0.078509	1.247561492	0.413147466
188						Total infected	0.404478755	0.437141	0.104521	1.717241261	0.549684082
189											
190						Recovered 9 mo olds	0.194281518	0.200808	0.048486	0.777722085	0.243366556

	A	B	C	D	E	F	G	H	I	J	K
191						Recovered 21 mo olds	0.133362737	0.143681	0.028337	0.587507332	0.145325082
192						Recovered adults	0.885792008	0.959726	0.231873	3.626316815	1.176145792
193						Total recovered	1.213436264	1.304215	0.308696	4.991546231	1.56483743
194											
195						Vaccinated 9 mo olds					0
196						Vaccinated 21 mo olds					0
197						Vaccinated adults					0
198						Total vaccinated					0
199						TOTAL:	2.473609856	2.691785	0.64931	6.708787493	2.114521512
200											
201											
202						**REMAINING NUMBER OF MIGRATING BISON POST T/S**					
203											
204						**Tolerance threshold reached?**					
205											
206						9 mo old calves, fall	0.388563037	0.41173	0.102331	1.681464669	0.545536297
207						21 mo old	0.261390965	0.288706	0.058609	1.270213153	0.325764181
208						Sexually mature adults	0.921223688	1.023249	0.254472	7.840234607	2.636476555
209						Total number of animals	1.57117769	1.723684	0.415412	10.79191243	3.507777032
210											
211						**Remaining number of animals**					
212											
213						Susceptible 9mo olds	0.388563037	0.41173	0.102331	1.681464669	0.543549776
214						Susceptible two year olds (21 mo)	0.261390965	0.288706	0.058609	1.270213153	0.32457794
215						Susceptible nonpregnant adults	0.921223688	1.023249	0.254472	7.840234607	2.626876065
216						Pregnant 21 mo = 0.01*2*2yo					
217						Pregnant adults = 0.2589*2 *adults					
218						Total susceptible	1.57117769	1.723684	0.415412	10.79191243	3.495003781
219											
220						Infected 9 mo olds					
221						Infected 21 mo olds					
222						Infected adults					
223						Total infected					
224											
225						Recovered 9 mo olds					
226						Recovered 21 mo olds					
227						Recovered adults					
228						Total recovered					
229											
230						Vaccinated 9 mo olds	0	0	0	0	0.001986521
231						Vaccinated 21 mo olds	0	0	0	0	0.001186241
232						Vaccinated adults	0	0	0	0	0.00960049
233						Total vaccinated	0	0	0	0	0.012773251
234						TOTAL:	1.57117769	1.723684	0.415412	10.79191243	3.507777032
235											
236											
237											
238						**# OF MIGRATING BISON ALLOWED ON ADJACENT LANDS**				**SAME AS REMAINING # OF MIGRATING BIS**	

	A	B	C	D	E	F	G	H	I	J	K
239						9 mo old calves, fall	0.388563037	0.41173	0.102331	1.681464669	0.545536297
240						21 mo old	0.261390965	0.288706	0.058609	1.270213153	0.325764181
241						Sexually mature adults	0.921223688	1.023249	0.254472	7.840234607	2.636476555
242						Total number of animals	1.57117769	1.723684	0.415412	10.79191243	3.507777032
243											
244						**Disease status of remaining bison allowed on public land**					
245											
246						Susceptible 9mo olds	0.388563037	0.41173	0.102331	1.681464669	0.543549776
247						Susceptible two year olds (21 mo)	0.261390965	0.288706	0.058609	1.270213153	0.32457794
248						Susceptible adults	0.921223688	1.023249	0.254472	7.840234607	2.626876065
249						Total susceptible	1.57117769	1.723684	0.415412	10.79191243	3.495003781
250											
251											
252						Vaccinated 9 mo olds					0.001986521
253						Vaccinated 21 mo olds					0.001186241
254						Vaccinated adults					0.00960049
255						Total vaccinated					0.012773251
256						TOTAL:					3.507777032
257											
258											
259							[redacted]				
260											
261											
262						**ADDITIONAL BISON AVAILABLE FOR SLAUGHTER/QUARANTINE**					
263											
264						9 mo old calves, fall	0	0	0		
265						21 mo old	0	0	0		
266						Sexually mature adults	0	0	0		
267						Total number of animals	0	0	0		
268											
269						**Disease status of bison available for slaughter/quarantine**					
270											
271						Susceptible 9mo olds	0	0	0		
272						Susceptible two year olds (21 mo)	0	0	0		
273						Susceptible adults	0	0	0		
274						Total susceptible	0	0	0		
275											
276											
277						Vaccinated 9 mo olds					
278						Vaccinated 21 mo olds					
279						Vaccinated adults					
280						Total vaccinated					
281						TOTAL.					
282											
283											
284											
285											

	A	B	C	D	E	F	G	H	I	J	K
286						**# MIGRATING OUT OF CENTRAL TO NR**					
287											
288						**Rate of migration from Central**	0.08	0.04	0	0.05	0
289											
290											
291						9 mo old calves, fall	9.44	4.595936	0	7.017879317	0
292						21 mo old	6.48	3.288446	0	5.301451035	0
293						Sexually mature adults	43.04	21.96541	0	32.7225551	0
294						Total number of animals	58.96	29.84979	0	45.04188545	0
295											
296						**Diseased animals migrating from Central to NR**					
297											
298						Susceptible 9mo olds	5.664	2.783408	0	4.327617716	0
299						Susceptible (21 mo olds	3.888	1.991561	0	3.269171837	0
300						Susceptible adults	25.824	13.30277	0	20.17856147	0
301											
302											
303						Infected 9 mo olds	0.944	0.455008	0	0.688623426	0
304						Infected 21 mo olds	0.648	0.325563	0	0.520200364	0
305						Infected adults	4.304	2.174624	0	3.210872825	0
306											
307											
308						Recovered 9 mo olds	2.832	1.35752	0	2.001638175	0
309						Recovered 21 mo olds	1.944	0.971322	0	1.512078834	0
310						Recovered adults	12.912	6.488011	0	9.333120807	0
311											
312						Vaccinated 9 mo olds	0	0	0	0	0
313						Vaccinated 21 mo olds	0	0	0	0	0
314						Vaccinated adults	0	0	0	0	0
315						Total vaccinated					
316						TOTAL:	58.96	29.84979	0	45.04188545	0
317											
318						**NUMBER ALIVE IN SPRING IN CENTRAL WINTERING AREA**					
319											
320						9 mo old calves, spring	82.21115798	70.40874	106.029	84.45994292	115.5587403
321						21 mo old	73.45244851	77.38174	72.65512	98.31643436	84.29314602
322						Sexually mature adults	475.6827837	498.7507	581.796	585.235265	670.4181872
323						Total number of animals	631.3463901	646.5412	760.4801	768.0116423	870.2700735
324											
325						Fall pop/Spring pop		1.181989	1.186336	1.184564438	1.18416339
326						Nt/Nt+1		1.027833	1.174472	1.009561724	1.134764889
327											

	A	B	C	D	E	F	G	H	I	J	K
328						**Diseased animals at end of spring management actions (does not account for vaccination; see beginning of next time interval for actual values)**					
329						Susceptible	379.4363052	392.2405	466.3013	477.7360376	542.7161093
330						Infected	62.97752125	63.83834	74.48423	74.3015405	84.64168907
331						Recovered	188.9325637	190.4623	219.6946	215.9740642	240.7073253
332						Vaccinated					2.204949849
333						**Total**	631.3463901	646.5412	760.4801	768.0116423	870.2700735
334											
335	[redacted]									0	0
336						**FALL OF**	**1997**	**1998**	**1999**	**2000**	**2001**
337	**Parameter values**					**Dynamics**					
338	**Northern Range subpopulation**					**Northern Range population**					
339	**Stage class**	**Proportion of animals affected by natural mortality**	**Fecundity (successful female births)**								
340	Calves	0	0								
341	Yearlings	0.59	0			**Proportion of females that die from winterkill**	0.02	0.03	0.01	0.03	0.01
342	Two year olds	0.02	0.01								
343	Sexually mature	0.39	0.24			**Proportion of females in NR that migrate out of the park**	0.048206534	0.14199	0.04069	0.510530944	0.058238085
344		1	0.335								
345											
346											
347	**Disease parameter values**						**Revised interim management plan**				
348						**NUMBER OF FEMALES IN THE FALL**	Initial population distribution				
349		Initial prop. susceptibl	0.6			New calves as of spring	0	64.51393	74.42997	81.68898941	63.83896603
350		Initial prop. infected	0.1			9 mo old calves, fall	51	64.51393	74.42997	81.68898941	63.83896603
351		Initial prop. resistant/r	0.3			21 mo old	35	55.71599	57.98235	66.70513832	46.95140652
352						Sexually mature adults	231	307.7914	363.4853	392.259397	309.5040435
353		*Transmission rate BET*	*0*			*Fall of:*	1997	1998	1999	2000	2001
354		Elk infect bison with b	0			Modeled number of females	317	428.0213	495.8976	540.6535248	420.294416
355		Rate at which infected	0								
356		Proportion of calves v	0			Modeled annual rate of increase		0.300271	0.147196	0.086409171	-0.251823183
357		Vaccine efficacy	0								
358						**CHECK**	0	0	0	0	STOP
359							0	0	0	0	0
360						Disease dynamics					
361						Susceptible	190 2	262.074	319.4604	351.6042584	281.9411339
362						Infected	31.7	41.92888	46.09548	51.10453135	36.07057859
363						Recovered/resistant	95.1	124.0185	130.3418	137.944735	90.17849865
364						Vaccinated					12.10420488
365						Total	317	428 0213	495.8976	540 6535248	420.294416
366											
367						NR proportion susceptible	0 6	0.612292	0.644206	0.650331945	0.670818177

	A	B	C	D	E	F	G	H	I	J	K
368					[redacted]	NR proportion infected	0.1	0.09796	0.092954	0.094523626	0.085822169
369					[redacted]	NR proportion recovered/resistant	0.3	0.289748	0.26284	0.255144429	0.214560306
370					[redacted]	Vaccinated					0.028799347
371					[redacted]	NR proportion seropositive	0.4	0.387708	0.355794	0.349668055	0.300382476
372					[redacted]						
373					[redacted]	Transmission from elk?	0	0	0	0	1
374					[redacted]						
375					[redacted]						
376					[redacted]	**WINTERKILL**					
377					[redacted]						
378					[redacted]	9 mo old calves, fall	3.7406	7.575978	2.925796	9.569567388	2.479737055
379					[redacted]	21 mo old	0.1268	0.256813	0.09918	0.324392115	0.084058883
380					[redacted]	Sexually mature adults	2.4726	5.00785	1.934001	6.32564624	1.639148223
381					[redacted]	Total number of animals	6.34	12.84064	4.958976	16.21960574	4.20294416
382					[redacted]						
383					[redacted]	**Number of diseased animals in winterkill**					
384					[redacted]	Susceptible	3.804	7.862219	3.194604	10.54812775	2.819411339
385					[redacted]	Infected	0.634	1.257866	0.460955	1.53313594	0.360705786
386					[redacted]	Recovered/resistant	1.902	3.720555	1.303418	4.13834205	0.901784987
387					[redacted]	Vaccinated					0.121042049
388					[redacted]	Total	6.34	12.84064	4.958976	16.21960574	4.20294416
389					[redacted]						
390					[redacted]	**# MIGRATING OUT OF THE PARK**					
391					[redacted]						
392					[redacted]	9 mo old calves, fall	2.458533218	9.16033	3.028548	41.70475689	3.717859104
393					[redacted]	21 mo old	1.687228679	7.91111	2.359297	34.05503724	2.734359985
394					[redacted]	Sexually mature adults	11.13570928	43.70329	14.79018	200.2605603	18.02492267
395					[redacted]	Total number of animals	15.28147118	60.77473	20.17803	276.0203545	24.47714176
396					[redacted]						
397	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	***Diseased animals migrating out of YNP***					
398	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]						
399	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	Susceptible 9mo olds	1.475119931	5.608795	1.95101	27.12193567	2.494007466
400	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	Susceptible 21 mo olds	1.012337208	4.843908	1.519874	22.14707861	1.83425838
401					[redacted]	Susceptible adults	6.68142557	26.75917	9.527928	130.2358397	12.09144576
402					[redacted]						
403					[redacted]	Infected 9 mo olds	0.245853322	0.897344	0.281515	3.942084826	0.319074734
404					[redacted]	Infected 21 mo olds	0.168722868	0.774971	0.219305	3.21900559	0.234668706
405					[redacted]	Infected adults	1.113570928	4.281165	1.374801	18.92935422	1.546937967
406					[redacted]	Total infected	1.528147118	5.95348	1.875621	26.09044464	2.100681407
407					[redacted]						
408					[redacted]	Recovered 9 mo olds	0.737559965	2.654191	0.796024	10.64073639	0.797704988
409					[redacted]	Recovered 21 mo olds	0.506168604	2.292231	0.620118	8.68895304	0.586685116
410					[redacted]	Recovered adults	3.340712785	12.66296	3.887453	51.09536636	3.867432929
411					[redacted]	Total recovered	4.584441354	17.60938	5.303594	70.4250558	5.251823033
412					[redacted]						
413					[redacted]	Vaccinated 9 mo olds					0.107071916
414					[redacted]	Vaccinated 21 mo olds					0.078747783
415					[redacted]	Vaccinated adults					0.519106009
416					[redacted]	Total vaccinated					0.704925708
417					[redacted]	TOTAL:	15.28147118	60.77473	20.17803	276.0203545	24.47714176
418					[redacted]						
419					[redacted]	**CHECK**	0	0	0	0	0
420					[redacted]						

	A	B	C	D	E	F	G	H	I	J	K
421						**SLAUGHTERED OR QUARANTINED TO MAINTAIN POPULATION LIMIT**					
422											
423						9 mo old calves, fall				0	0
424						21 mo old				0	0
425						Sexually mature adults				0	0
426						Total number of animals				0	0
427											
428						**Disease status of animals slaughtered or quarantined to maintain population limit**					
429											
430						Susceptible 9mo olds				0	0
431						Susceptible two year olds (21 mo)				0	0
432						Susceptible adults				0	0
433						Total susceptible				0	0
434											
435						Infected 9 mo olds				0	0
436						Infected 21 mo olds				0	0
437						Infected adults				0	0
438						Total infected				0	0
439											
440											
441						Recovered 9 mo olds				0	0
442						Recovered 21 mo olds				0	0
443						Recovered adults				0	0
444						Total recovered				0	0
445											
446						Vaccinated 9 mo olds					0
447						Vaccinated 21 mo olds					0
448						Vaccinated adults					0
449						Total vaccinated					0
450						TOTAL:				0	0
451										1441.491234	1329.745686
452						**REMAINING MIGRANTS AFTER POPULATION LIMIT MET**					
453											
454						9 mo old calves, fall				41.70475689	3.717859104
455						21 mo old				34.05503724	2.734359985
456						Sexually mature adults				200.2605603	18.02492267
457						Total number of animals				276.0203545	24.47714176
458											
459						**Disease status of remaining migrants**					
460											
461						Susceptible 9mo olds				27.12193567	2.494007466
462						Susceptible two year olds (21 mo)				22.14707861	1.83425838
463						Susceptible adults				130.2358397	12.09144576
464						Total susceptible				179.504854	16.41971161
465											
466											
467						Infected 9 mo olds				3.942084826	0.319074734

	A	B	C	D	E	F	G	H	I	J	K
468						Infected 21 mo olds				3.21900559	0.234668706
469						Infected adults				18.92935422	1.546937967
470						Total infected				26.09044464	2.100681407
471											
472											
473						Recovered 9 mo olds				10.64073639	0.797704988
474						Recovered 21 mo olds				8.68895304	0.586685116
475						Recovered adults				51.09536636	3.867432929
476						Total recovered				70.4250558	5.251823033
477											
478						Vaccinated 9 mo olds					0.107071916
479						Vaccinated 21 mo olds					0.078747783
480						Vaccinated adults					0.519106009
481						Total vaccinated					0.704925708
482						TOTAL:				276.0203545	24.47714176
483											
484						**# OF REMAINING MIGRANTS TESTED/SLAUGHTERED/ QUARANTINED**					
485											
486						9 mo old calves, fall	0.983413287	3.551535	1.077539	32.18589481	1.116779722
487						21 mo old	0.674891472	3.067202	0.839423	26.28217806	0.821353822
488						Sexually mature adults	4.454283713	16.94412	5.262254	154.5522816	5.414370896
489						Total number of animals	6.112588472	23.56286	7.179215	213.0203545	7.352504441
490											
491						**Disease status of remaining bison tested/ slaughtered/quarantined**					Test if susc + vaccina
492											
493						Susceptible 9mo olds				17.6030736	0
494						Susceptible two year olds (21 mo)				14.37421943	0
495						Susceptible adults				84.52756099	0
496						Total susceptible				116.504854	0
497											
498											
499						Infected 9 mo olds	0.245853322	0.897344	0.281515	3.942084826	0.319074734
500						Infected 21 mo olds	0.168722868	0.774971	0.219305	3.21900559	0.234668706
501						Infected adults	1.113570928	4.281165	1.374801	18.92935422	1.546937967
502						Total infected	1.528147118	5.95348	1.875621	26.09044464	2.100681407
503											
504											
505						Recovered 9 mo olds	0.737559965	2.654191	0.796024	10.64073639	0.797704988
506						Recovered 21 mo olds	0.506168604	2.292231	0.620118	8.68895304	0.586685116
507						Recovered adults	3.340712785	12.66296	3.887453	51.09536636	3.867432929
508						Total recovered	4.584441354	17.60938	5.303554	70.4250558	5.251823033
509											
510						Vaccinated 9 mo olds					0
511						Vaccinated 21 mo olds					0
512						Vaccinated adults					0
513						Total vaccinated					0
514						TOTAL				213.0203545	7.352504441
515											

	A	B	C	D	E	F	G	H	I	J	K
516						**REMAINING NUMBER OF MIGRATING BISON POST T/S**					
517											
518						9 mo old calves, fall	1.475119931	5.608795	1.95101	9.518862076	2.601079382
519						21 mo old	1.012337208	4.843908	1.519874	7.772859181	1.913006163
520						Sexually mature adults	6.68142557	26.75917	9.527928	45.70827874	12.61055177
521						Total number of animals	9.168882708	37.21187	12.99881	63	17.12463732
522											
523						**Remaining number of bison**					
524											
525						Susceptible 9mo olds				9.518862076	2.494007466
526						Susceptible 21 mo olds				7.772859181	1.83425838
527						Susceptible adults				45.70827874	12.09144576
528						Total susceptible				63	16.41971161
529											
530											
531						Infected 9 mo olds	0	0	0		
532						Infected 21 mo olds	0	0	0		
533						Infected adults	0	0	0		
534						Total infected	0	0	0		
535											
536											
537						Recovered 9 mo olds	0	0	0		
538						Recovered 21 mo olds	0	0	0		
539						Recovered adults	0	0	0		
540						Total recovered	0	0	0		
541											
542						Vaccinated 9 mo olds	0	0	0		0.107071916
543						Vaccinated 21 mo olds	0	0	0		0.078747783
544						Vaccinated adults	0	0	0		0.519106009
545						Total vaccinated					0.704925708
546						TOTAL:				63	17.12463732
547											
548											
561											
562						**# OF MIGRATING BISON IN CAPTURE FACILITY**					
563											
564						9 mo old calves, fall	1.475119931	5.608795	1.95101	9.518862076	2.601079382
565						21 mo old	1.012337208	4.843908	1.519874	7.772859181	1.913006163
566						Sexually mature adults	6.68142557	26.75917	9.527928	45.70827874	12.61055177
567						Total number of animals	9.168882708	37.21187	12.99881	63	17.12463732
568											
569						**# OF MIGRATING BISON ALLOWED ON ADJACENT LANDS**	none - all bison captured or t/s/q	same	same	same	same
570						9 mo old calves, fall					

	A	B	C	D	E	F	G	H	I	J	K
571						*21 mo old*					
572						Sexually mature adults					
573						Total number of animals					
574											
575						**Disease status of remaining bison allowed on public land**					
576											
577						Susceptible 9mo olds					
578						Susceptible two year olds (21 mo)					
579						Susceptible adults					
580						Total susceptible					
581											
582						Infected 9 mo olds					
583						Infected 21 mo olds					
584						Infected adults					
585						Total infected					
586											
587											
588						Recovered 9 mo olds					
589						Recovered 21 mo olds					
590						Recovered adults					
591						Total recovered					
592											
593						Vaccinated 9 mo olds					
594						Vaccinated 21 mo olds					
595						*Vaccinated adults*					
596						Total vaccinated					
597						TOTAL:					
598											
599											
600											
601						**# OF ADDITIONAL BISON WHICH MUST BE REMOVED DUE TO BEING ABOVE THE MAX ALLOWED ON ADJACENT LANDS**	none - all bison captured or t/s/q	same	same	same	same
602											
603						9 mo old calves, fall					
604						21 mo old					
605						Sexually mature adults					
606						Total number of animals					
607											
608						**Disease status of additional bison which must be removed**					
609											
610						Susceptible 9mo olds					
611						Susceptible 21 mo olds					
612						Susceptible adults					
613						Total					
614											
615						Vaccinated 9 mo olds					
616						Vaccinated 21 mo olds					
617						Vaccinated adults					
618						Total vaccinated					

	A	B	C	D	E	F	G	H	I	J	K
619						TOTAL					
620											
621											
622						**# OF ADDITIONAL BISON SENT TO QUARANTINE**					
623											
624						9 mo old calves, fall					
625						21 mo old					
626						Sexually mature adults					
627						Total number of animals					
628											
629						**Disease status of bison sent to quarantine**					
630											
631						Susceptible 9mo olds					
632						Susceptible two year olds (21 mo)					
633			Average % calves	0.1542725		Susceptible adults					
634			Average % yearlings	0.1105599		Total susceptible					
635											
636						Vaccinated 9 mo olds					
637						Vaccinated 21 mo olds					
638						Vaccinated adults					
639						Total vaccinated					
640						TOTAL					
641			Average % adults	0.7351676							
642											
643						**PROPORTION MIGRATING FROM NR TO CENTRAL**					
644							0	0	0.05	0	0.02
645											
646						**# MIGRATING OUT OF NR TO CENTRAL**					
647											
648						9 mo old calves, fall	0	0	3.721499	0	1.276779321
649						21 mo old	0	0	2.899118	0	0.93902813
650						Sexually mature adults	0	0	18.17426	0	6.19008087
651						*Total number of animals*	0	0	24.79488	0	8.405888321
652											
653						**Diseased animals migrating from NR to Central**					
654											
655						Susceptible 9mo olds	0	0	2.397413	0	0.856486776
656						*Susceptible (21 mo olds*	0	0	1.86763	0	0.629917139
657						Susceptible adults	0	0	11.70798	0	4.152418764
658							0	0	15.97302	0	5.638822678
659											
660						Infected 9 mo olds	0	0	0.345927	0	0.109575971
661						Infected 21 mo olds	0	0	0.269484	0	0.080589431
662						Infected adults	0	0	1.689364	0	0.531246169
663											0.721411572
664											
665						Recovered 9 mo olds	0	0	0.978159	0	0.273946162
666						Recovered 21 mo olds	0	0	0.762004	0	0.201478163

	A	B	C	D	E	F	G	H	I	J	K
667						Recovered adults	0	0	4.776925	0	1.328145648
668						Total					1.803569973
669											
670						Vaccinated 9 mo olds					0.036770411
671						Vaccinated 21 mo olds					0.027043397
672						Vaccinated adults					0.178270289
673						Total					0.242084098
674						TOTAL					8.405888321
675											
676						**NUMBER ALIVE IN SPRING IN NORTHERN RANGE WINTERING AREA**					
677											
678						9 mo old calves, fall	55.71598671	57.98235	66.70514	46.95140652	58.96566993
679						21 mo old	40.67830853	55.68042	54.14463	45.40001917	45.10696569
680						Sexually mature adults	267.1131163	307.8049	338.1148	264.1040243	296.2604435
681						Total number of animals	363.5074115	421.4676	458.9645	356.45545	400.3330791
682											
683											
684						**Diseased animals at end of spring (does not account for vaccination; see top of next time step for calculation)**					
685						Susceptible	221.772	272.2895	300.2927	252.3266277	273.4828999
686						Infected	35.43385288	37.67273	41.45413	27.90064738	32.88777983
687						Recovered	106.3015586	111.5054	117.2177	76.22817496	82.22132066
688						Vaccinated					11.74107673
689							363.5074115	421.4676	458.9645	356.45545	400.3330791
690							0	0	0	0	0
691											
692						Fall pop/Spring pop		1.177476	1.176597	1.177985407	1.179093814
693						Nt/Nt+1		1.158581	1.090252	0.777382181	1.122752616
694											
695											
696						**SUMMARY POPULATION INFORMATION**	**1989.7076**	**2136.02**	**2438.89**	**2248.934185**	**2541.206305**
697						Year (fall)	1997	1998	1999	2000	2001
698						Modeled # calves	169	179.4123	194.904	222.0465758	205.278594
699						Modeled # yearlings	116	137.9271	128.3911	172.734159	131.4113494
700						Modeled # adults	769	856.9267	939.6177	1046.710499	993.0557428
701						Modeled # of females (fall)	1054	1174.266	1262.913	1441.491234	1329.745686
702						Modeled total population size (fall)	2108	2348.532	2525.826	2882.982468	2659.491373
703						Modeled total population size (spring)	1989.707603	2136.018	2438.889	2248.934185	2541.206305
704							1	2	3	4	5
705						Modeled rate of increase		0.108051	0.072777	0.132257385	-0.080690446
706											
707						Modeled # of migrants	19.32625873	65.1902	21.24275	293.5210544	30.0994403
708						Actual # of migrants					
709											
710											
711											

	A	B	C	D	E	F	G	H	I	J	K
712					[redacted]	% calves	0.160341556	0.152787	0.154329	0.154039491	0.154374326
713						% yearlings	0.110056926	0.117458	0.101663	0.119830183	0.098824422
714						% adults	0.729601518	0.729755	0.744008	0.726130326	0.746801252
715						% on Central	0.699240987	0.635499	0.607338	0.624934573	0.683928724
716						% on NR	0.300759013	0.364501	0.392662	0.375065427	0.316071276
717											
718						Disease dynamics	1	2	3	4	5
719						Summed susceptible	632.4	714.0176	788.7982	907.1112788	847.2856462
720						Summed infected	105.4	115.8087	121.3913	139.4984636	124.9863276
721						Summed recovered/resistant	316.2	344.4398	352.7233	394.8814913	343.3033331
722						Summed vaccinated (first vaccinates don't appear until spring of the 1st year - included in next fall's dynamics)	0	0	0	0	14.17037936
723						Total	1054	1174.266	1262.913	1441.491234	1329.745686
724							1	2	3	4	5
725						Proportion summed susceptible	0.6	0.608054	0.624586	0.629286712	0.637178714
726						Proportion summed infected	0.1	0.098622	0.09612	0.096773716	0.093992655
727						Proportion summed recovered/resistant	0.3	0.293323	0.279293	0.273939572	0.258172173
728						Proportion summed vaccinated	0	0	0	0	0.010656458
729						Proportion summed seropositive	0.4	0.391946	0.375414	0.370713288	0.352164828
730											
731						**Total population size**	2108	2348.532	2525.826	2882.982468	2659.491373
732						**Total population size, spring**				2248.934185	2541.206305
733						**Female bison migrating out of Central**	4.044787546	4.415469	1.064723	17.50069992	5.622298544
734						**Females bison migrating out of NR**	15.28147118	60.77473	20.17803	276.0203545	24.47714176
735						**Total female bison migrating out of YNP**	19.32625873	65.1902	21.24275	293.5210544	30.0994403
736						**Female bison from Central tested/slaughtered, or quarantined if available**	2.473609856	2.691785	0.64931	6.708787493	2.114521512
737						**Female bison from NR tested/slaughtered, or quarantined if available**	6.112588472	23.56286	7.179215	213.0203545	7.352504441
738						**Total female bison sent to test/slaughter, or quarantine if available**	8.586198328	26.25464	7.828525	219.7291419	9.467025952
739						**Female bison slaughtered on Central**	see t/s/q, if av:	see t/s/q, if	see t/s/q, if	see t/s/q, if available	see t/s/q, if available
740						**Female bison slaughtered on NR**	see t/s/q, if av:	see t/s/q, if	see t/s/q, if	see t/s/q, if available	see t/s/q, if available
741						**Total female bison slaughtered**	see t/s/q, if av:	see t/s/q, if	see t/s/q, if	see t/s/q, if available	see t/s/q, if available
742						**Additional female bison which may be subject to management action on Central**	see t/s/q, if av:	see t/s/q, if	see t/s/q, if	see t/s/q, if available	see t/s/q, if available
743						**Additional female bison which may be subject to management action on NR**	see t/s/q, if av:	see t/s/q, if	see t/s/q, if	see t/s/q, if available	see t/s/q, if available

	A	B	C	D	E	F	G	H	I	J	K
744						Total additional female bison which may be subject to management action	see t/s/q, if av:	see t/s/q, if	see t/s/q, if	see t/s/q, if available	see t/s/q, if available
745						Female bison remaining outside YNP at West	1.57117769	1.723684	0.415412	10.79191243	3.507777032
746						Female bison remaining outside YNP at North	None	None	None	None	None
747						Total female bison remaining outside YNP	1.57117769	1.723684	0.415412	10.79191243	3.507777032
748						Total female bison held in capture facilities	9.168882708	37.21187	12.99881	63	17.12463732
749						Female calves and yearlings successfully vaccinated	None	None	None	Vaccinations done, sho	14.17037936
750						Total females successfully vaccinated	NA	NA	NA	NA	NA
751						Proportion susceptible	0.6	0.608054	0.624586	0.629286712	0.637178714
752						Proportion infected	0.1	0.098622	0.09612	0.096773716	0.093992655
753						Proportion recovered	0.3	0.293323	0.279293	0.273939572	0.258172173
754						Proportion vaccinated	0	0	0	0	0.010656458
755						Proportion seropositive	0.40	0.39	0.38	0.37	0.35

APPENDIX 2: VisualBasic macro used to run population simulations.

The mathematics of the bison and brucellosis model are all included in the Excel spreadsheet. This macro copies initial values from one Excel worksheet into the main worksheet where the population projections occur. The macro then selects 100 sets of random winter severity data, pastes the data into the main projection worksheet, and then copies the resulting output into a new worksheet.

Sub SimB()

```
' SimB Macro
' Macro originally recorded 11/9/98 by Robyn P. Angliss
' Copied on 4/28/99 10:35am from SimA - use this module to try to run all 12
simulations
' in sequence
' If it doesn't work, go back to SimA!
' Simulation that copies SWE into the model, then copies key
' results (number of animals, proportion infected, proportion
' seropositive) at 1, 5, 6, 8, 10, 12, 14, 16, 18 years into the Results
' sheet.
'
'  Updated for new preferred alternative on 1/12/00 - used simB from Alt 5 as example

' There are a total of 36 simulations the new preferred alternative - see sheet "Inputs"

' Becaue the offset command adds 1, have to use 0 as the first simulation
' Can do up to 9 simulations in one spreadsheet

For s = 0 To 0

' Copy input values from Inputs sheet into Inputs&Graph sheet

    Sheets("Input").Select
    Range("A1").Select
    ActiveCell.Offset(s + 1, 1).Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Inputs&graphs").Select
    Range("C16").Select
    ActiveSheet.Paste
    Sheets("Input").Select
    Range("A1").Select
    ActiveCell.Offset(s + 1, 2).Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Inputs&graphs").Select
    Range("C14").Select
    ActiveSheet.Paste
    Sheets("Input").Select
    Range("A1").Select
    ActiveCell.Offset(s + 1, 3).Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Inputs&graphs").Select
```

```
    Range("C17").Select
    ActiveSheet.Paste
    Sheets("Input").Select
    Range("A1").Select

' Insert labels onto results worksheet

For i = 0 To 24

    Sheets("Inputs&graphs").Select
    Range("W1").Select
    ActiveCell.Offset(i + 1, 0).Select
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(0, 10 * i).Range("a1").Select
    ActiveSheet.Paste
    Range("A2").Select
    ActiveCell.FormulaR1C1 = "1"
    Range("B2").Select
    ActiveCell.FormulaR1C1 = "5"
    Range("C2").Select
    ActiveCell.FormulaR1C1 = "6"
    Range("D2").Select
    ActiveCell.FormulaR1C1 = "8"
    Range("E2").Select
    ActiveCell.FormulaR1C1 = "10"
    Range("F2").Select
    ActiveCell.FormulaR1C1 = "12"
    Range("G2").Select
    ActiveCell.FormulaR1C1 = "14"
    Range("h2").Select
    ActiveCell.FormulaR1C1 = "16"
    Range("i2").Select
    ActiveCell.FormulaR1C1 = "18"

Next

' Copy and paste the years across the worksheet

For p = 1 To 24

    Range("a2:j2").Select
    Selection.Copy
    Range("a1").Select
    ActiveCell.Offset(0, 10 * p).Range("a2").Select
```

```
   ActiveSheet.Paste
Next

' Generate 100 simulations & paste results in the spreadsheet
' For testing purposes, set i = 0 to 19

Let i = 0

For i = 0 To 99

Let j = i

' Get new SWE values

   Sheets("SWE").Select
   Calculate
   Columns("A:B").Select
   Range("A31").Activate
   Selection.Sort Key1:=Range("A2"), Order1:=xlAscending, Header:=xlGuess, _
      OrderCustom:=1, MatchCase:=False, Orientation:=xlTopToBottom
   Range("B2:B20").Select
   Selection.Copy

' Paste new SWE values into model

   Sheets("Model").Select
   Range("G3").Select
   Selection.PasteSpecial Paste:=xlAll, Operation:=xlNone, SkipBlanks:=False _
      , Transpose:=True

' Check to see if population sizes are reasonable

'   Calculate
'   Sheets("Inputs&graphs").Select
'   Range("ad2").Select
'   If ActiveCell < 0 Then
'      Msg = "The population is negative!"
'      Style = vbOKOnly
'      Title = "What went wrong?"
'      Response = MsgBox(Msg, Style, Title)
'      If Response = vbOKOnly Then
'         Exit Sub
'      Else
'         Exit Sub
'      End If
'   End If
```

```
'
'  If ActiveCell > 10000 Then
'     Msg = "The population is unrealistically huge!"
'     Style = vbOKOnly
'     Title = "What went wrong?"
'     Response = MsgBox(Msg, Style, Title)
'     If Response = vbOKOnly Then
'        Exit Sub
'     Else
'        Exit Sub
'     End If
'   End If
'
' Copy total population size, fall

    Sheets("Inputs&graphs").Select
    Range("x2:ag2").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("a2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
       False, Transpose:=False

' Copy total population size, spring

    Sheets("Inputs&graphs").Select
    Range("x3:ag3").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("k2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
       False, Transpose:=False

' Copy # of female bison migrating out of Central

    Sheets("Inputs&graphs").Select
    Range("x4:ag4").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("u2").Select
```

```
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy total # of female bison migrating out of Northern Range

    Sheets("Inputs&graphs").Select
    Range("x5:ag5").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("ae2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy total # of female bison migrating

    Sheets("Inputs&graphs").Select
    Range("x6:ag6").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("ao2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy # of female bison t/s/quarantined from Central, if available

    Sheets("Inputs&graphs").Select
    Range("x7:ag7").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("ay2").Select
    Selection:PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy total number of female bison t/s/quarantined from NR, if available

    Sheets("Inputs&graphs").Select
    Range("x8:ag8").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
```

```
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("bi2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy total # of female t/s/quarantined, if available

    Sheets("Inputs&graphs").Select
    Range("x9:ag9").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("bs2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy # of female bison slaughtered on Central

    Sheets("Inputs&graphs").Select
    Range("x10:ag10").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("cc2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy # of female bison slaughtered on NR

    Sheets("Inputs&graphs").Select
    Range("x11:ag11").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("cm2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy total # of female bison slaughtered

    Sheets("Inputs&graphs").Select
    Range("x12:ag12").Select
    Application.CutCopyMode = False
```

```
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("cw2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy additional # of female bison whcih may be subject to management action on Central

    Sheets("Inputs&graphs").Select
    Range("x13:ag13").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("dg2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy additional # of female bison whcih may be subject to management action on NR

    Sheets("Inputs&graphs").Select
    Range("x14:ag14").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("dq2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy total additional # of female bison whcih may be subject to management action

    Sheets("Inputs&graphs").Select
    Range("x15:ag15").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("ea2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy # of female bison remaining outside YNP at West
```

```
    Sheets("Inputs&graphs").Select
    Range("x16:ag16").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("ek2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy # of female bison remaining outside YNP at North

    Sheets("Inputs&graphs").Select
    Range("x17:ag17").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("eu2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy total # of female bison remaining outside YNP

    Sheets("Inputs&graphs").Select
    Range("x18:ag18").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("fe2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy total female bison held in capture facilities

    Sheets("Inputs&graphs").Select
    Range("x19:ag19").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("fo2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False
```

```
' Copy female calves & yearlings successfully vaccinated

    Sheets("Inputs&graphs").Select
    Range("x20:ag20").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("fy2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy total females successfully vaccinated

    Sheets("Inputs&graphs").Select
    Range("x21:ag21").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("gi2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy proportion susceptible

    Sheets("Inputs&graphs").Select
    Range("x22:ag22").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("gs2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=False

' Copy proportion infected

    Sheets("Inputs&graphs").Select
    Range("x23:ag23").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("hc2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
```

```
      False, Transpose:=False

' Copy proportion recovered

    Sheets("Inputs&graphs").Select
    Range("x24:ag24").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("hm2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy proportion vaccinated

    Sheets("Inputs&graphs").Select
    Range("x25:ag25").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("hw2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

' Copy proportion seropositive

    Sheets("Inputs&graphs").Select
    Range("x26:ag26").Select
    Application.CutCopyMode = False
    Selection.Copy
    Sheets("Results").Select
    Range("A1").Select
    ActiveCell.Offset(j + 1, 0).Range("ig2").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

'---------------------

' Copy 5 population trajectories into Results sheet (includes males & females)

    If j <= 4 Then
      Sheets("Model").Select
      Range("G702:ag702").Select
      Selection.Copy
```

```
      Sheets("Results").Select
      Range("A1").Select
      ActiveCell.Offset(1, j + 1).Range("a150").Select
      Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=True
    End If

' Copy 10 serology trajetories into Results sheet

    If j = 0 Then
      Sheets("Model").Select
      Range("g751:ag755").Select
      Selection.Copy
      Sheets("Results").Select
      Range("a1").Select
      ActiveCell.Offset(1, j * 5).Range("l150").Select
      Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
        False, Transpose:=True
    End If

Next i

' ADD A HEADER TO THE RESULTS SHEET

'   Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False

    Rows("1:1").Select
    Selection.Insert Shift:=xlDown
    Selection.RowHeight = 42.75
    Range("A1").Select
    ActiveCell.FormulaR1C1 = "SIMULATION FOR:"
    Range("B1").Select
    ActiveCell.FormulaR1C1 = "PROPORTION VACCINATED = "
'   Range("F1").Select

'   Copy and paste current proportion vaccinated value in results sheet

    Sheets("Inputs&graphs").Select
    Range("C16").Select
    Selection.Copy
    Sheets("Results").Select
    Range("F1").Select
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
      False, Transpose:=False
```

```
' Copy and paste current efficacy value in results sheet
  Rows("2:2").Select
  Selection.Insert Shift:=xlDown
  Range("B2").Select
  ActiveCell.FormulaR1C1 = "VACCINE EFFICACY ="
  Sheets("inputs&graphs").Select
  Range("C17").Select
  Selection.Copy
  Sheets("Results").Select
  Range("F2").Select
  Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
    False, Transpose:=False

' Copy and paste current reinfection by elk value in results sheet
  Rows("3:3").Select
  Selection.Insert Shift:=xlDown
  Range("B3").Select
  ActiveCell.FormulaR1C1 = "REINFECTION BY ELK HAPPENS ONCE EVERY X
YEARS:"
  Range("B3:E3").Select
  With Selection
    .HorizontalAlignment = xlCenter
    .VerticalAlignment = xlBottom
    .WrapText = False
    .Orientation = 0
    .ShrinkToFit = False
    .MergeCells = False
  End With
  Selection.Merge
  With Selection
    .HorizontalAlignment = xlCenter
    .VerticalAlignment = xlBottom
    .WrapText = True
    .Orientation = 0
    .ShrinkToFit = False
    .MergeCells = True
  End With

  Sheets("inputs&graphs").Select
  Range("C14").Select
  Selection.Copy
  Sheets("Results").Select
  Range("F3").Select
  Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:= _
    False, Transpose:=False
```

```
' Format header

    Range("A1:F4").Select
    Range("F3").Activate
    Selection.Font.Bold = True
    With Selection.Font
        .Name = "Arial"
        .Size = 12
        .Strikethrough = False
        .Superscript = False
        .Subscript = False
        .OutlineFont = False
        .Shadow = False
        .Underline = xlUnderlineStyleNone
        .ColorIndex = xlAutomatic
    End With

' ADD SUMMARY STATISTICS TO THE BOTTOM OF THE SHEET

    Range("A4:A106").Select
    Selection.Insert Shift:=xlToRight
    Range("A107").Select
    ActiveCell.FormulaR1C1 = "Average"
    Range("A108").Select
    ActiveCell.FormulaR1C1 = "Standard deviation"
    Range("A109").Select
    ActiveCell.FormulaR1C1 = "Minimum"
    Range("A110").Select
    ActiveCell.FormulaR1C1 = "Maximum"
    Range("A111").Select
    ActiveCell.FormulaR1C1 = "90% confidence"
    Range("A112").Select
    ActiveCell.FormulaR1C1 = "95% confidence"
    Range("A113").Select
    ActiveCell.FormulaR1C1 = "90% ci: lower"
    Range("A114").Select
    ActiveCell.FormulaR1C1 = "90% ci: upper"
    Range("A115").Select
    ActiveCell.FormulaR1C1 = "95% ci: lower"
    Range("A116").Select
    ActiveCell.FormulaR1C1 = "95% ci: upper"
    Range("B107").Select
    ActiveCell.FormulaR1C1 = "=AVERAGE(R[-101]C:R[-1]C)"
    Range("B108").Select
    ActiveCell.FormulaR1C1 = "=STDEV(R[-102]C:R[-2]C)"
    Range("B109").Select
```

```
    ActiveCell.FormulaR1C1 = "=MIN(R[-103]C:R[-3]C)"
    Range("B110").Select
    ActiveCell.FormulaR1C1 = "=MAX(R[-104]C:R[-4]C)"
    Range("B111").Select
    ActiveCell.FormulaR1C1 = "=CONFIDENCE(0.1,R[-3]C,100)"
    Range("B112").Select
    ActiveCell.FormulaR1C1 = "=CONFIDENCE(0.5,R[-4]C,100)"
    Range("B113").Select
    ActiveCell.FormulaR1C1 = "=R[-6]C-R[-2]C"
    Range("B114").Select
    ActiveCell.FormulaR1C1 = "=R[-7]C+R[-3]C"
    Range("B115").Select
    ActiveCell.FormulaR1C1 = "=R[-8]C-R[-3]C"
    Range("B116").Select
    ActiveCell.FormulaR1C1 = "=R[-9]C+R[-4]C"
    Range("B107:B116").Select
    Selection.AutoFill Destination:=Range("B107:FT116"), Type:=xlFillDefault
    Range("B107:FT116").Select
    Calculate

'   ADD GRAPHS TO SHEET

'   Input years in column for sample population trajectories

    Range("a155").Select
    ActiveCell.FormulaR1C1 = "1997"
    Range("a156").Select
    ActiveCell.FormulaR1C1 = "1998"
    Range("a155:a156").Select
    Selection.AutoFill Destination:=Range("a155:a172"), Type:=xlFillDefault

'   Add graph for sample population trajectories

    Range("a172").Activate
       Charts.Add
    ActiveChart.ChartType = xlXYScatterLinesNoMarkers
    ActiveChart.SetSourceData Source:=Sheets("Results").Range("a155:f172"), _
       PlotBy:=xlColumns
    ActiveChart.Location Where:=xlLocationAsObject, Name:="Results"
    With ActiveChart
       .HasTitle = True
       .ChartTitle.Characters.Text = "Five sample population trajectories"

       .Axes(xlCategory, xlPrimary).HasTitle = True
       .Axes(xlCategory, xlPrimary).AxisTitle.Characters.Text = "Year"
       .Axes(xlValue, xlPrimary).HasTitle = True
```

```
        .Axes(xlValue, xlPrimary).AxisTitle.Characters.Text = _
        "Total number of bison"
        Selection.Interior.ColorIndex = x1None
    End With

'   Delete legend

    ActiveChart.Legend.Select
    Selection.Delete

'   Change plot format

    ActiveChart.PlotArea.Select
    Selection.Interior.ColorIndex = x1None

'   Change format for lines

    ActiveChart.SeriesCollection(2).Select
    With Selection
        .MarkerBackgroundColorIndex = xlNone
        .MarkerForegroundColorIndex = xlNone
        .MarkerStyle = xlNone
        .Smooth = False
        .MarkerSize = 3
        .Shadow = False
    End With
    ActiveChart.SeriesCollection(4).Select
    With Selection.Border
        .ColorIndex = 1
        .Weight = xlThin
        .LineStyle = xlDot
    End With
    With Selection
        .MarkerBackgroundColorIndex = xlNone
        .MarkerForegroundColorIndex = xlNone
        .MarkerStyle = xlNone
        .Smooth = False
        .MarkerSize = 3
        .Shadow = False
    End With
    ActiveChart.SeriesCollection(1).Select
    With Selection.Border
        .ColorIndex = 1
        .Weight = xlThin
        .LineStyle = xlDashDot
    End With
```

```
With Selection
   .MarkerBackgroundColorIndex = xlNone
   .MarkerForegroundColorIndex = xlNone
   .MarkerStyle = xlNone
   .Smooth = False
   .MarkerSize = 3
   .Shadow = False
End With
ActiveChart.SeriesCollection(3).Select
With Selection.Border
   .ColorIndex = 1
   .Weight = xlThin
   .LineStyle = xlDash
End With
With Selection
   .MarkerBackgroundColorIndex = xlNone
   .MarkerForegroundColorIndex = xlNone
   .MarkerStyle = xlNone
   .Smooth = False
   .MarkerSize = 3
   .Shadow = False
End With
ActiveChart.SeriesCollection(5).Select
With Selection.Border
   .ColorIndex = 1
   .Weight = xlThin
   .LineStyle = xlDashDotDot
End With
With Selection
   .MarkerBackgroundColorIndex = xlNone
   .MarkerForegroundColorIndex = xlNone
   .MarkerStyle = xlNone
   .Smooth = False
   .MarkerSize = 3
   .Shadow = False
End With

' Make chart for disease dynamics

Range("k155").Select
ActiveCell.FormulaR1C1 = "1997"
Range("k156").Select
ActiveCell.FormulaR1C1 = "1998"
Range("k155:k156").Select
Selection.AutoFill Destination:=Range("k155:k172"), Type:=xlFillDefault
```

```
' Insert labels

  Range("l154").Select
  ActiveCell.FormulaR1C1 = "Susceptible"
  Range("m154").Select
  ActiveCell.FormulaR1C1 = "Infected"
  Range("n154").Select
  ActiveCell.FormulaR1C1 = "Recovered"
  Range("o154").Select
  ActiveCell.FormulaR1C1 = "Vaccinated"
  Range("p154").Select
  ActiveCell.FormulaR1C1 = "Seropositive"

' Make chart

  Range("l154:p172").Select
  Range("p172").Activate
  Charts.Add
  ActiveChart.ChartType = xlXYScatterLinesNoMarkers
  ActiveChart.SetSourceData Source:=Sheets("Results").Range("k154:p172"), _
     PlotBy:=xlColumns
  ActiveChart.Location Where:=xlLocationAsObject, Name:="Results"
  With ActiveChart
     .HasTitle = True
     .ChartTitle.Characters.Text = "Sample disease dynamics"
     .Axes(xlCategory, xlPrimary).HasTitle = True
     .Axes(xlCategory, xlPrimary).AxisTitle.Characters.Text = "Year"
     .Axes(xlValue, xlPrimary).HasTitle = True
     .Axes(xlValue, xlPrimary).AxisTitle.Characters.Text = _
     "Proportion of bison in each disease category"
  End With

' Change plot format

  ActiveChart.PlotArea.Select
  Selection.Interior.ColorIndex = xlNone
  ActiveChart.ChartArea.Select
  ActiveChart.Axes(xlCategory).Select

' Change plot scale

  With ActiveChart.Axes(xlCategory)
     .MinimumScale = 1995
     .MaximumScale = 2015
     .MinorUnitIsAuto = True
     .MajorUnit = 5
```

```
        .Crosses = xlCustom
        .CrossesAt = 1995
        .ReversePlotOrder = False
        .ScaleType = xlLinear
    End With

'   Change line characteristics

    ActiveChart.SeriesCollection(3).Select
    With Selection.Border
        .ColorIndex = 1
        .Weight = xlThin
        .LineStyle = xlDot
    End With
    With Selection
        .MarkerBackgroundColorIndex = xlNone
        .MarkerForegroundColorIndex = xlNone
        .MarkerStyle = xlNone
        .Smooth = False
        .MarkerSize = 3
        .Shadow = False
    End With
    ActiveChart.SeriesCollection(4).Select
    With Selection.Border
        .ColorIndex = 1
        .Weight = xlThin
        .LineStyle = xlDash
    End With
    With Selection
        .MarkerBackgroundColorIndex = xlNone
        .MarkerForegroundColorIndex = xlNone
        .MarkerStyle = xlNone
        .Smooth = False
        .MarkerSize = 3
        .Shadow = False
    End With
    ActiveChart.SeriesCollection(2).Select
    With Selection.Border
        .ColorIndex = 1
        .Weight = xlThin
        .LineStyle = xlDashDotDot
    End With
    With Selection
        .MarkerBackgroundColorIndex = xlNone
        .MarkerForegroundColorIndex = xlNone
        .MarkerStyle = xlNone
```

```
      .Smooth = False
      .MarkerSize = 3
      .Shadow = False
   End With
   ActiveChart.SeriesCollection(5).Select
   With Selection.Border
      .ColorIndex = 48
      .Weight = xlMedium
      .LineStyle = xlContinuous
   End With
   With Selection
      .MarkerBackgroundColorIndex = xlNone
      .MarkerForegroundColorIndex = xlNone
      .MarkerStyle = xlNone
      .Smooth = False
      .MarkerSize = 3
      .Shadow = False
   End With

'  Copy results into new sheet

   Windows("newalt5-31-02.xls").Activate
   Cells.Select
   Selection.Cut
   Sheets.Add
   ActiveSheet.Paste


Next s

Beep

End Sub
```