Project plan: a demographic analysis of the Yellowstone National Park bison (Bison bison) herds from 1901 to 2000.

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Table of Contents

Introduction

Scientists have studied large ungulates worldwide for many decades, searching for mechanisms that drive population dynamics. This research has elucidated many broad patterns of ungulate population regulation and some areas of contention. In some cases, ungulates may be primarily regulated by predation (Messier 1994), but most populations of ungulates appear to be regulated through the interactions of climate and density dependence, as in red deer (Clutton-Brock et al. 1985, Coulson et al. 2000), wildebeest (Sinclair et al. 1985, Mduma et al. 1999), saiga antelope (Coulson et al. 2000), feral donkeys (Choquenot 1991), Svalbard reindeer (Aanes et al 2000), North American elk (Garrott et al. 2003) and many others (Festa-Bianchet et al. 2003, Gaillard et al. 2000, Sæther 1997). The mechanism by which increasing density regulates populations is primarily through food shortages (Caughley 1976), which can be exacerbated by the stochastic effects of climate, such as through droughts or heavy snows (Clutton-Brock et al. 1985, Sæther 1997, Gaillard et al. 2000). Range condition affects the nutrition and body condition of ungulates (Sinclair 1975, DelGiudice et al. 1994), which influences reproductive rates (Gaillard et al. 2000) and survival (Caughley 1970, Mduma et al. 1999). When per capita forage available becomes less plentiful due to increasing ungulate density, ungulate populations may experience an increase in the emigration rate from the effected area, or may expand their range to include new areas (Lemke et al. 1998, Aanes et al. 2000, Larter et al. 2000, Cooch et al. 2001, Ferguson et al. 2001).

If dispersal and range expansion do not alleviate the density-dependent effects, populations may experience changes in vital rates (age-specific survival and fecundity) in accordance to a paradigm for long-lived vertebrates proposed by Eberhardt (1977, 2002) and supported by others (Gaillard et al. 1998, 2000; Coulson et al. 2004). There is an apparent sequence of changes in vital rates as population density increases toward maximal levels, which is: 1) an increase in juvenile mortality, 2) an increase in age at first reproduction, 3) a decrease in reproductive rates of adults, and 4) an increase in adult mortality at the highest densities. Variability in vital rates tends to occur inversely to their sensitivity (Gaillard et al. 1998, Gaillard et al. 2000, Eberhardt 2002): juvenile mortality can often be quite variable between years, but it takes a large change in this rate to affect population growth rates, while adult female mortality is usually very static, and slight changes in this rate greatly influence overall population growth.

Researchers are just beginning to understand how density-dependent factors and density-independent mechanisms interact to affect the variability of vital rates. Currently, many case studies explore these questions, but there are few comprehensive reviews documenting how climate interacts with density to affect vital rates on ungulates in general. Perhaps this is because vital rates of populations of the same species in different climate regimes can vary quite differently. For example, bison in the Mackenzie Bison Sanctuary of the Northwest Territories in Canada experience high variation in juvenile survival over winters and nearly constant reproductive rates (Larter et al. 2000), while bison on Antelope Island, Utah, where winters are milder and warm seasons are drier, experience little variation in juvenile survival but much variation in rates of reproduction (Van Vuren and Bray 1986). Thus, relationships between density-dependent and density-independent drivers on vital rates are key factors in understanding any population’s dynamics, and more research is needed in this regard. Strong evidence of density dependence, however, whether in vital rates or overall population growth rates, may not be readily detectable unless the population is close to its ecological carrying capacity (Fowler 1981, Getz 1996). Therefore, data sets that contain many years of population and climate information are valuable to examine the density-dependent and density-independent mechanisms that affect vital rates.

For this reason, the history of the Yellowstone National Park (hereafter YNP) bison herds will make an excellent case study to examine climate effects and basic population processes. More than 100 years of count and removal information (1902-present) and 34 years of herd composition surveys (1970-present) make this one of the largest, long-term data sets for a large herbivore population. The YNP bison population will provide an excellent natural experiment in density effects: they have been subject to periods of encouraged growth (ie: supplemental feeding), unrestrained growth, and they have been managed around set population levels (Meagher 1973, Meagher 1993, Schullery et al. 1998, NPS 2000). Bison experience negligible predation (Mattson 1997 and Smith et al. 2000), thus are regulated through density-dependent factors, weather effects, and human removals. The many weather stations maintained throughout YNP from the 1930s through present day provide a long-term history of climatic conditions in the area (Farnes et al. 1997), which, combined with long-term count data, should result in excellent power to detect the effects of climate on key population vital rates.

A demographic analysis of the YNP bison will be timely given the increase in public and political attention to the species. Bison are considered by many to be “charismatic megafauna”, and are popular tourist attractions to YNP (NPS 2000). However, bison harbor the disease brucellosis (*Brucella abortus*), which is of concern to livestock-producing states around YNP. Bison are possible, although unproven, vectors of brucellosis to cattle (Cheville et al. 1998), and therefore a potential threat to the brucellosis-free status of Montana. Loss of brucellosis-free status would result in an increased economic burden to livestock producers and to the overall economy of the state (Keiter 1997, Cheville et al. 1998, NPS 2000). In recent years, bison have been leaving YNP boundaries more frequently than they did historically (NPS 2000), with some animals spending part of winter on U.S. Forest Service grazing allotments or on private lands. This behavior worries cattle producers, and has led to considerable debate about why bison are leaving the park now more than in the past. There are two major theories in this regard. First, ungulate range expansion and dispersal or migration from historic ranges can be a natural response to increasing population density (Larter et al. 2000, Bjornlie and Garrott 2001, Ferguson et al. 2001). Alternatively, some researchers believe that dispersal, migration and range expansion are facilitated by the grooming and packing of roads for winter recreational travel that began to occur within YNP in the 1970's (Meagher 1993, Taper et al. 2000). An examination of bison population trends and demographic structure may help clarify the extent to which bison leave the park due to density-dependent pressures. Conversely, density may not be a significant factor, and bison may simply be moving to new areas due to presence of low-energy travel routes.

For my thesis, I plan to conduct a thorough demographic analysis of the YNP bison population in regard to density-dependent and density-independent effects on vital rates and population growth. First, I will estimate the population growth parameter λ (the finite population multiplier) for periods of uninterrupted growth using log-linear trend analysis (Eberhardt 1987, Eberhardt et al. 1999). Next, I will estimate annual λ for periods with major removals. I will use linear regression plots and a model selection approach to examine relationships between climatic variables and changes in reproduction, recruitment and overall population growth using calf/adult ratios, and annual λ estimates for the entire time series where we have weather data. Finally, I will develop Leslie matrix models, or analogous age-specific models, to provide insight to the mechanisms behind population change.

Population Spatial Structure and Management History

The YNP bison population consists of two main herds, here called the northern herd and the central herd. The northern herd primarily ranges between Gardiner and Cooke City through the Blacktail Deer Plateau, the Lamar Valley and the Mirror Plateau: the area commonly referred to as the Northern Range (Houston 1982, Barmore 2003). The central herd ranges from the Pelican Valley in the east through the Hayden and Madison-Firehole Valleys to West Yellowstone (Taper et al. 2000). Estimates of total range size taken from aerial survey units in 1998-2000 is 1,154 km^2 for the central herd and 1,185km^2 for the northern herd (Hess 2002). Bison do occasionally move between herds, but the amount of exchange is thought to be small (Taper et al. 2000). The Northern Range experiences a variety of weather conditions from east to west. Annual precipitation varies from 152cm near Cooke City to just 31cm in the Gardiner area (Farnes et al. 1999). Annual precipitation on the range of the central herd is much less variable, with about 76-102cm throughout the area (Farnes et al. 1999). Winter conditions for the northern herd tend to be less severe than for the central herd, while snows through the Pelican Valley tend to be deeper and frequently crusted (Meagher 1973, Del Giudice 1994, Farnes et al. 1999), although there are likely substantial differences in wind effects on snow among areas for the central herd (White, personal communication). Furthermore, the northern herd is sympatric with a large herd of elk (*Cervus elaphus*), which has varied between 3,000 and >20,000 individuals since the 1930's (White et al. 2003), while the central herd coexists with only 500-600 elk in the winter months (Garrott et al. 2003), resulting in a high potential for inter-specific competition for the northern herd.

The northern and central herds have experienced different management regimes across their histories (see Figure 1). From 1902 through 1938, bison across the park were herded into the Lamar Valley for supplemental feeding, leaving less than 100 bison in the central areas of the park (Meagher 1973). Only after the roundups ceased did the central herd begin to expand, although many animals certainly returned to the Lamar Valley during the winter, as park rangers continued to bait bison to the Northern Range with hay until 1952 (Meagher 1973). From 1929 through 1968, the northern herd experienced periodic removals, while the central herd grew unchecked from 1939 through 1955, when rangers began episodic removals on this herd as well (Meagher 1973). Virtually all removals ceased from 1968 through 1985, when YNP commenced a policy of "natural regulation" (see Cole 1971). During this time, the northern herd grew from 71 to 619 bison, while the central herd increased from 315 to 1415 bison, with a peak of 1752 bison counted in 1981 before the hard winter of 1981-1982. After 1985, bison from both herds began to leave the park more extensively during winter months (Taper et al. 2000) and the National Park Service once again began to manage the herds through removals. In recent years, the northern herd has peaked at 753 animals during 1995, while the central herd reached 3205 in 1997, preceding that year's large winter die-off and the removal of animals outside the park.

The differences in the management histories and environmental conditions experienced by the two herds lead to specific suites of biological hypotheses (see Table 1). The major questions we will ask for all periods are:

1) *Are density-related changes in vital rates evident in the population (or subpopulation)?*
2) *How do density-independent factors interact with density to affect λ and/or vital rates?*
3) *Are there differences in growth rates and/or vital rates between the herds?*
4) *Are there differences in growth rates and/or vital rates within the same herd at different time periods?*

5) How does the abundance of elk affect the growth rates of bison populations?

The 27-year period when the northern herd was fed hay throughout winter (1902-1929) should give insights to the biological potential of the species: during this time, bison likely experienced no food limitation, there was little inter-specific competition, and there were only a few, inconsequential management removals. Comparing and contrasting growth during this period to when both the northern herd and central herd bison herds, as well as the Northern Range elk herd, experienced no reductions (1968-1985, 17 years) will provide information about the growth potential of "released" bison populations given the YNP ecosystem constraints. Further, using these years will allow us to check for effects of density-dependence through changes in the population growth rate and in specific vital rates. Finally, determining yearly growth rates from annual population counts and yearly calf/adult ratios of each population throughout their histories lends itself to regression analysis between population growth parameters and climate variables such as warm season precipitation and snow pack severity. This will describe density-independent effects on population growth parameters. Ultimately, we will evaluate models where density-dependence, in the form of intra- and inter-specific competition interacts with climate variables to detect how these factors combine to effect population demography.

Existing Data and Population Estimates

Before delving further into questions of population demographics, we first have to discuss the existing data and conduct some preliminary analyses to validate the assumptions we will use for the rest of this thesis. We will use 98 years of count information from 1902-2000 as our yearly population abundance index, 30 years of aerial composition surveys from 1970-2000 to determine calf/cow ratios, and 7 years of ground-based herd composition surveys from 1997-

2004 to determine recruitment. Bison counts from 1902-1949 were predominantly ground surveys done once a year during winter months by park rangers on foot or on horseback (Meagher 1973). From 1950-1969, bison counts were done aerially, once a year, during winter time (Meagher 1973). From 1970-1997, flights were conducted multiple times in a year by the same observer (Taper et al. 2000) and from 1998-2000, flights occurred almost monthly by several observers (Hess 2002, NPS unpublished data). Flights from 1970-1997 include calf-adult ratios during all months from calving until early winter, when observers could no longer distinguish calves from cows (Taper et al. 2000). However, ground composition surveys from 1997-2004 include calf-cow ratios from December through early May, providing insight to population recruitment and juvenile survival over winter (Bjornlie and Garrott 2001, Ferrari and Garrott 2002, Bruggeman and Garrott unpublished data).

Working with aerial count data presents its own set of challenges. Specifically, we need to address sightability of animals and possible sex or age class bias. Bison are large-bodied, gregarious herbivores that spend much of the year in open spaces (Meagher 1973), traits that allow aerial surveyors to detect and count bison more easily than other, more solitary ungulates. Researchers on Antelope Island, Utah, aerially surveyed the bison population before a nearly-comprehensive (~98%) roundup. The sighting probability was high (roughly 94%), but calves were “seriously underestimated” (Wolfe and Kimball 1989). Antelope Island is sparsely vegetated, with virtually no tree cover (<1%) (Wolfe and Kimball 1989), so we would expect lower sighting probability in the Yellowstone area due to forested areas and other terrain features that would make bison detection more difficult. Hess (2002) used double-sampling methods to determine the detection probabilities for bison in different group sizes and cover types in YNP. He found that for large group sizes (>20), detection probability for bison in any cover was quite high, over 90%. For smaller group sizes, bison in the forest or in geothermal areas had significantly lower detection probabilities than bison in open areas. Hess (2002) suggested that summertime surveys maximized sighting probability, as most bison congregate in the Hayden and Lamar valleys for the rut. Meagher (1993) believed early winter counts provided the highest detection probability for bison in YNP, and Hess (2002) agreed that bison can be highly detectable in winter as snow provides a good color background, but bison never congregate as highly in winter as they do in summer. Therefore, the aerial surveys that have been performed are likely to be quite good, but may have some inherent biases due to time of year and bison distribution at that season,

To further address these issues, we will conduct a series of analyses for the years where there were multiple flights for bison (1970-2000). We will consider years in terms of the biology of bison, such that a "bison-year" is the time period between the annual birth pulse, or April 1 of one year through March 31 of the next. For these flights, we will determine 1) which month the high count for each herd occurred and 2) the deviance from the high count seen in the other flights of that year. Given that sighting probability of bison is expected to be high (Wolfe and Kimball 1989, Meagher 1993, Taper et al. 2000, Hess 2002), we would expect that all flights within a biological year (censoring years where removals are large and partial or truncated flights) should have similar counts, the variation around the high count of that year should be low, and the high count of the bison-year should be close to biological "truth".

Before proceeding further, we deemed it necessary to run an exploratory analysis to evaluate the quality and consistency of herd composition counts in flight data (1970-1997) to determine whether these data would be usable to estimate reproduction. We graphed the timing of the high calf counts and the calf/adult ratios across the year. Figure 2 indicates that flights in

June and July represent the majority of high calf counts for the northern herd, while July and August represent the high calf counts for the central herd. Figure 3 depicts the calf/adult ratios during April through February, 1970-1997. The high counts and highest calf/adult ratios should biologically occur in April or May when the largest pulse of bison are born, but neonate calves may have lower sightability from the air, as newborn calves are smaller and may be more frequently hiding underneath cows than older calves. In our analysis, both herds show a peak ratio in June, followed by a general decline, as we would expect. Although flights occurring after the birth pulse in April or May will include a substantial mortality component, the consistency of the data indicate we can use calf/adult ratios in the early summer to index reproduction.

Data Analysis

These data span several different management paradigms (Figure 1), and lend themselves to different analysis methods. The specific modeling strategies we will use are: natural-log (ln) transformed linear regression to estimate λ, estimation of annual λ using a ratio method that adjusts for removals, regression models that describe the effects of density-dependent and density-independent factors on herd vital rates, and Leslie style matrix models (or a similar model that analyzes age-specific or stage-specific vital rates). Each technique has its own set of assumptions, and is particularly suited to certain analyses. Running equivalent data through different models will provide credence to observed trends should the outcomes corroborate one another, and will help identify areas that need further investigation should the outcomes be contrary.

Ln-Linear Regression

The first analysis we will perform is to estimate λ using ln-linear regression (Eberhardt 1987) for time periods without (or between) significant removals (Table 1). This method is based on the geometric change model for a population that reproduces once a year:

$$\mathbf{N_t = N_{t-1} * \lambda^t} \quad \text{(eq.1)}$$

Where $\mathbf{N_t}$ = the number in the population at time t, $\mathbf{N_{t-1}}$ = the number in the population at the previous step, and **λ** = the "finite population multiplier", or **λ = 1+r**, where **r** = intrinsic rate of change in the population (Eberhardt 1987). In order to fit eq. 1 to the standard linear regression model **y = a + bx,** one simply takes the natural logarithm of each side of the equation resulting in:

$$\mathbf{\ln(N_t) = \ln(N_{t-1}) + t * \ln(\lambda)} \quad \text{(eq.2)}$$

This technique plots the natural logarithm of count data against time, and fits a regression line using least squares methods. Raising e to the power of the slope of the regression line provides an estimate of λ. The natural logarithm of the count data should increase ln-linearly until it nears K and then begin to plateau (Fowler 1981, Getz 1996). At this plateau, λ = 1. Departure from the regression line at high counts may be an indication of density-dependence.

The advantage of this method is its simplicity: the result of this equation is a linear trend plotted on the natural log scale. It is intuitive to the viewer and easily interpreted. The major assumption of this model is that underlying parameters are constant, but we know that this is not the case for most time series involving large mammals. Stochastic effects of climate, density-related factors, and observational errors will contribute to the variation around the regression line (Eberhardt 1987).

The Ratio Method for Estimation of Annual λ

Ln-linear regression is a preferred method to estimate λ over a time series of similar management regimes, but it does not account for annual variation due to climate, nor can it easily be used during periods when major removals occur regularly (Eberhardt 1987). For these reasons, it is often beneficial to use another method to estimate λ. Eberhardt (1987) demonstrated that a ratio approach, where $\boldsymbol{\lambda} = \mathbf{N_t/N_{t-1}}$, closely approximated estimation of **λ** using least-squares methods. This model can easily be adapted to include removals. In our case, yearly removals happen after the yearly high counts. Thus, we will use the model:

$$\boldsymbol{\lambda} = \mathbf{N_t/(N_{t-1}-K_t)} \qquad \text{(eq. 3)}$$

where removals, $\mathbf{K_t}$, take place after the high count at $\mathbf{N_{t-1}}$, such that the combined effects of reproduction, natural mortality, and observational error are described by λ. This ratio estimator will be used to address how annual λ changes with climate and density. We will approach this analysis by first plotting each independent climate and density variable against the dependent variable, annual λ. These simple regression models will establish presence or absence of basic trends. We will then increase the complexity of our models by adding additive and interactive effects between density-dependent and density-independent variables. Methods for modeling climate interactions are described in detail in the climate section below.

The strengths of using annual λ in analyses are the relative ease in accounting for both regular removals and the yearly effects of climate data. However, the major drawback to this technique is that all estimates of λ are serially correlated, given that the numerator of one ratio becomes the denominator in the next (Eberhardt 1987). As we use this ratio estimator, we will also have to apply the jack-knife technique or another method to address the serial correlation of data and provide variance estimates (Eberhardt 1987).

Estimating Vital Rates

Population vital rates include the overall population growth rate (λ) as well as age-specific survival and reproductive rates (Caughley 1966, 1970). Age-specific survival and fecundity contribute differently to λ. This is a phenomenon that is referred to as elasticity: a proportional change to juvenile survival may not affect λ as much as that proportional change to adult survival. For most large mammals, juvenile survival is one of the most variable vital rates, and has low elasticity compared to adult survival (Gaillard et al. 1998, Eberhardt 2002). Therefore, analyzing the data we have for each vital rate and how vital rates vary with time, density-dependence and density-independent factors will provide insights to the mechanisms behind population change.

We have 7 years of data (1997-2004) on recruitment, the number of calves that survive their first winter to enter the population as yearlings, from Bjornlie and Garrott (2001), Ferrari and Garrott (2002) and Bruggeman and Garrott (unpublished data). These data consist of herd composition surveys from the Madison-Firehole Valleys twice a month from early winter through early spring. We can estimate recruitment into the adult population as a function of the number of year-old calves counted at the end of April. From these data, we can gain an understanding of how climatic and density-related factors effect recruitment, which is a function of both reproduction and juvenile survival.

Reproductive rates of bison are available from several sources. First, pregnancy rates have been assessed in several studies from 1931 through 1997 (Meagher 1973, Kirkpatrick et al. 1996, Aune et al. 1998). Calving rates are published for several other bison herds, including the National Bison Range, Montana (Rutberg 1986), Henry Mountains of Utah (Van Vuren and Bray

1986, Hodson and Karpowitz 1998), Antelope Island, Utah (Wolfe et al. 1999), Badlands National Park, South Dakota (Berger and Cunningham 1994) and Custer State Park in South Dakota (Walker 1998). The average age at first reproduction is provided in most of these reproductive studies. An index of reproduction may be assessed through calf/adult ratios from the flight data of 1970-1997 (Taper et al. 2000) and from flights 1998-2000 (Hess 2002, NPS unpublished data), although these data will include an early-season mortality component.

We currently have little information regarding adult survival rates of the YNP bison population. However, there is a preponderance of literature indicating that, in the absence of hunting and predation, prime-age ungulates rarely die, resulting in annual survival rates of 0.95 or higher for adults (see review in Eberhardt 2002). A study by Berger and Cunningham (1994) for a bison population in South Dakota corroborates this postulate, as they estimated survival rates between 0.968 and 0.995 for adults. Thus, bison have high survival rates, but we need to know about the onset of reproductive senescence, survival senescence and longevity. We can procure this information from various sources. Meagher (1973) used trap records from YNP during the late 1960's to determine that bison rarely reach more than 20 years old, but she based this information on Fuller's work (1959) that lacked known-age animals. Aune (1998) indicated that bison in the age category ">8" experienced reproductive senescence, but this category includes all animals gauged to be over age 8, which does not readily inform us about the age reproductive decline occurs. For a bison population in South Dakota, Berger and Cunningham (1994) document reproductive senescence at ages 14-15. Continued literature searching and an investigation into Department of Livestock records for the bison removals of the 1990's may provide additional data for a further understanding of bison longevity and reproductive senescence.

Incorporating Density-Dependent and Density-Independent Effects

Now that we have described the procedures we will use toward trend analyses, indicators of density-dependence, and estimation of vital rates, the next logical step is to incorporate the climate-induced variation and density-related factors that may affect population growth parameters. Figure 4 (adopted from Garrott et al. 2003) presents a model describing the interactions between climate variation and vital rates for ungulates in northern latitudes. From Figure 4, notice that population density of bison and inter-specific competition are also thought to affect forage availability. We will incorporate bison population numbers in our model suite to search for effects of density-dependence, or intra-specific competition, in both the northern and central herds. However, inter-specific competition with elk may also be an important factor. This is especially relevant to the northern herd, which is almost completely sympatric with a large herd of elk (3,000-19,000) over their shared winter range (Singer and Norland 1994, White et al. 2003). Elk and bison diets can significantly overlap (Singer and Norland 1994), and bison recruitment has been significantly negatively associated with elk numbers in the northern range (Houston 1982). Further, elk populations were released from YNP control in 1968 (Houston 1982), and like the bison herds of this time, experienced a period of rapid growth in the Northern Range. While the northern bison herd may be significantly impacted by the much larger elk population, the central bison herd coexists with just 500-600 elk (Garrott et al. 2003), and so experiences much less inter-specific competition, assuming forage availability and carrying capacity are approximately the same on both ranges. Therefore, it will be informative to assess growth rates and vital rates between the northern and central herds over this time period using elk numbers as a covariate. We will use northern range elk population counts from White et al. (unpublished data) as indicator variables in several models.

Climate Factors

Following Figure 4, we chose to model one warm season and one cold season covariate. We chose the two weather variables based on availability of data, parsimony, and confirmed biological effects in other large ungulate systems. We will use total precipitation during the growing season as the warm season covariate and the accumulated measure of snow water equivalents (SWEacc) during winter as the cold season covariate.

Precipitation during the growing season has a demonstrated effect on ungulate populations across the world, and is simple to measure and understand. Sala et al. (1988) showed that for the central great plains, mean annual precipitation was tightly tied with mean above-ground net primary production, as did Sinclair (1975) for the short and long grasslands of the Serengeti. Further, Van Vuren and Bray (1986) showed a distinct effect of early spring precipitation on bison calves, and Mduma et al. (1999) demonstrated the effect of rainfall on food production in the Serengeti, which then correlated to population processes of the wildebeest. While precipitation alone may be a sufficient metric to use in analysis, the timing of precipitation and its interaction with ambient and soil temperature may affect plant growth through evapotranspiration (Palmer 1968) and the number of growing-degree days (Farnes 1999). These factors are addressed in some drought indices, and it may be informative to explore the relationships between drought measures and bison vital rates. One index in particular would be of interest to us. The Crop Moisture Index (CMI), a derivative of the Palmer Index, uses weekly estimates of mean temperature and total precipitation to index growing conditions amenable to crops over the short term (Palmer 1968). For the sake of parsimony, we will select total precipitation during the growing season as the primary warm-season climate variable in our *a priori* model suite. We will also attempt to explain some of the variation seen in these regression plots by analyzing the effects of the CMI on vital rates in *post posteriori* analyses.

While precipitation during the warm season generally has a positive effect on ungulate populations through enhancing plant growth, precipitation in winter months, in the form of snow, is often an impediment to foraging and locomotion, resulting in a high expenditure of energy and reduced forage availability (Aanes et al. 2002, Garrott et al 2003). Expending energy at this time of year can result in an increase in mortality, especially to juvenile age classes (Larter et al. 2000). We chose to use seasonally accumulated snow water equivalents (SWEacc) to measure winter precipitation for several reasons. First, SWEacc measures the amount of water present in the snowpack. This is more informative than simple snow depth, as dry, powdery snow can be much easier to move through than thick, wet snow of the same depth. Secondly, the cumulative measure of SWEacc across the season is appropriate because each day of snowpack continually draws down ungulate reserves over the whole winter. Finally, SWEacc is a measure already proven to be strongly correlated with ungulate vital rates in YNP (Garrott et al. 2003). We did not consider the effects of temperature during the cold season because bison may have an extremely low thermoneutral zone in part due to their heavy fur and large body size (Christopherson et al. 1979, Schmidt-Nielsen 1997).

We can gather data on SWEacc and precipitation through two main kinds of weather-recording stations across YNP: SNOTEL sites and CLIM sites (Farnes et al. 1999). The SNOTEL sites are automated stations that record daily SWE measurements, temperatures, and precipitation year round. However, they are not of much use because the SNOTEL sites in Yellowstone are either too recently established or they are not in areas of the park central to bison activity. CLIM sites are stations where snow depth, temperature, and precipitation are measured manually every day, year-round. There are two CLIM sites central to bison activity for both the northern and central herd that have been collecting data from 1949 to present: Tower Falls and Lake Yellowstone. We will use these two sites for all analyses because they represent a long time series and should be representative of the conditions experienced by each herd. Because CLIM sites do not record SWE measurements directly, we will use an algorithm formed by Farnes et al. (1999) to convert daily CLIM data into daily SWE, which we will add together to derive SWEacc, our winter-season climate variable.

Model Structure

To evaluate the relationships between density-dependent and density-independent factors on vital rates, we built a set of candidate *a priori* models. We will evaluate each model suite using AICc methods for model selection. The three response variables we will use are recruitment (the number of calves that survived their first winter and entered the population as yearlings), reproductive rates estimated using calf/adult ratios, and annual λ. The indicator variables are total precipitation during the growing season (PREC), accumulated snow-water equivalents through the winter (SWEacc), bison population counts (BISON) and the elk population counts in the Northern Range and Madison/Firehole Valleys (ELK). Recall that we defined the biological year for bison as April 1 through March 31 of the following calendar year. All indicator variables will assessed over the "bison-year". PREC and SWEacc are measured and recorded according to a "water-year" schedule, which runs from October 1 to September 31 of the next calendar year, such that the “bison-year” overlaps two “water-years”: spring precipitation at (t) for the “bison-year” occurs at (t-1) of the “water-year”. To avoid confusion, we will adjust “water-year” data so that precipitation occurring April 1 through October 1 of bison year (t) will be considered PREC(t).

The model suite is listed in Tables 2, 3, and 4. While we only listed linear forms here, we will conduct *a priori* analysis of the relationships between the indicator variables and response variables using quadratic forms as well.

Recruitment (Table 2) is affected by weather throughout time (t): the summer moisture, PREC(t), and winter snowpack severity, SWEacc(t), that affect the calf directly. Forage availability during this time may be effected through the density of the bison herd and the density of the elk herd on the shared winter range. In the case of a high density of large ungulates on the landscape, forage may be depleted, affecting the ability of juveniles to grow and put on fat for winter. Bison recruitment rates have been shown to be negatively correlated with elk numbers in another study (Houston 1982), and so we will create several models that include the covariates ELK and BISON. For our *a priori* analysis, we will only consider the climatic conditions and density effects at (t). However, recruitment can also be affected by condition of the dam during gestation (t-1). Poor body condition in the dam can result in a low birth weight for the offspring, which often results in reduced probability of survival (Clutton-Brock et al. 1987). We have only 7 years of data involving bison recruitment, therefore we will keep our model suite simple, and will not include time interactions. We will explore (t-1) effects in *post posteriori* models to determine if lag effects explain variation around our AICc selected *a priori* model.

We also expect to detect variation in reproductive rates (Table 3). Reproduction biologically occurs at the end of April and early May, but our index occurs during June and July

(Figures 2 and 3). Still, for *a priori* analysis, we will examine only those weather and density-related effects from the year previous to reproduction (t-1) to determine the relationship between environmental effects, conception and the fate of a dam's pregnancy, although reabsorption and abortion rates are thought to be low (Aune et al. 1998). In *post posteriori* analysis, we will also model effects from two years previous, representing the body condition of the dam going into rut. If the winter at (t-2) was severe, perhaps the female did not conceive at (t-1) and therefore did not give birth at (t). Given the large data set, we will be able to model time interactions to some extent.

Finally, we have the most data (47 years: 1953-2000) involving the estimation of annual λ and climate factors after the feeding of the northern herd ceased. Annual λ is the product of the population's vital rates: it incorporates elements of age-specific reproduction and survival. The covariates in this list are reduced to SWEacc(t-1), PREC(t-1) and ELK(t-1). Eberhardt (1970) warns against using covariates involved in generating the response variable, so we will not include BISON as a covariate, as the number of bison in the population at (t) and (t-1) are used to estimate annual λ (eq. 3). Given that the high counts of bison generally occur in summer months (Hess 2002) or early winter (Hess 2002, Meagher 1993), the factors that affect annual λ are most likely those that occurred at (t-1): the precipitation at (t-1) and the winter after the high count of (t-1). Therefore, we will only model (t-1) covariates in our *a priori* model suite. However, given the large data set, we will be able to significantly expand this model list to examine lag effects to attempt to explain the variation we will see around our AICc selected *a priori* model.

Modeling of Age-Specific Vital Rates

Estimation of annual λ and ln-linear trend analysis treat all individuals in the population equally, but we know that different age classes make very different contributions to λ (Eberhardt 2002, Gaillard et al. 2000, Gaillard et al. 1998). For this reason, the use of Leslie matrices can provide insight into the mechanisms behind population changes. Leslie matrices use age-specific survival and reproductive rates to produce an estimate of population growth rate (Leslie 1945). They are tools that can be used to conduct sensitivity analyses, which describe the vital rates most important to population growth; for example, adult survival rates may have a stronger effect on λ than juvenile survival (Caswell 1989). Matrix models are versatile, allowing the researcher to include numerous stochastic effects by using transition matrices and incorporating density dependence (Caswell 1989). This leaves the researcher with the major question of what level of detail to include in their specific population model (Pfister and Stevens 2003).

We will evaluate our available data to determine which age-specific vital rates we can estimate for the YNP bison population. There are some rates we may not be able to establish, and in these cases we will parameterize those matrix elements using data from literature on other herds. Depending on the quality of the input data, we will use the matrix models, or a similar analysis tool, to either 1) corroborate trends seen from earlier analyses or 2) use "best guesses" of vital rates to mimic the trends we saw, and determine how feasible these vital rates are given those seen in other bison populations. In order to corroborate the information we will obtain through our regression analyses, we will require age-specific survival and reproductive rates from the YNP bison herd directly. If matrix inputs are drawn too heavily from other populations and the output of the matrix model does not match our earlier analyses, this could either be because the vital rate data was not truly representative, or that our earlier analyses were incorrect. However, even if we have to draw vital rate information from other sources, we can still perform some important analyses. For example, we can estimate reproductive rate from the period 1902-1932, when bison were supplementally fed and no removals occurred. Here, mortality was likely extremely low for adults, and density-dependence would not be a factor, so we could imitate the λ seen during this period and solve for reproductive rates.

To some extent, we will rely on the previous analyses to help us structure our models in this section. Density-dependent mechanisms may only influence the vital rates of the YNP bison close to their carrying capacity, and if we see no evidence of density-dependence in ln-linear trend analyses, estimation of annual λ, or in the multiple regression models, then we may not incorporate density-dependence into these matrix models. However, we may still have to incorporate a density-dependent mechanism into the model to constrain model dynamics. Similarly, we will use the regression analysis from above to describe the stochastic effects of climate on vital rates. We can incorporate this stochasticity into matrix models by using transition matrices (Caswell 1989). Should the matrix models perform well in this retrogressive analysis, we can create projection models for a variety of scenarios of interest to wildlife managers by altering vital rates to indicate how population growth rates may change under different removal regimes.

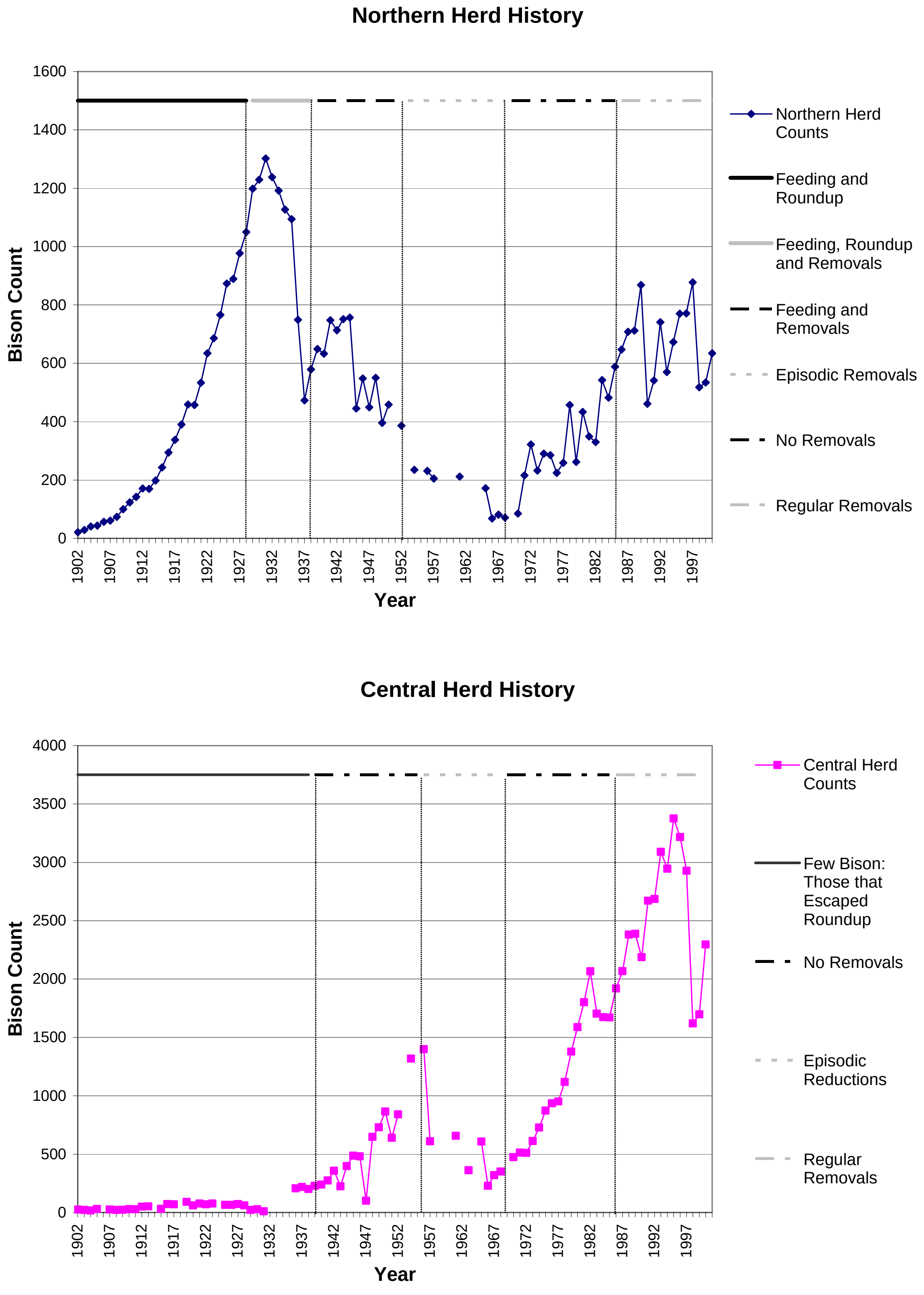


Figure 1: Bison counts by year and the history of herd management from 1902-2000

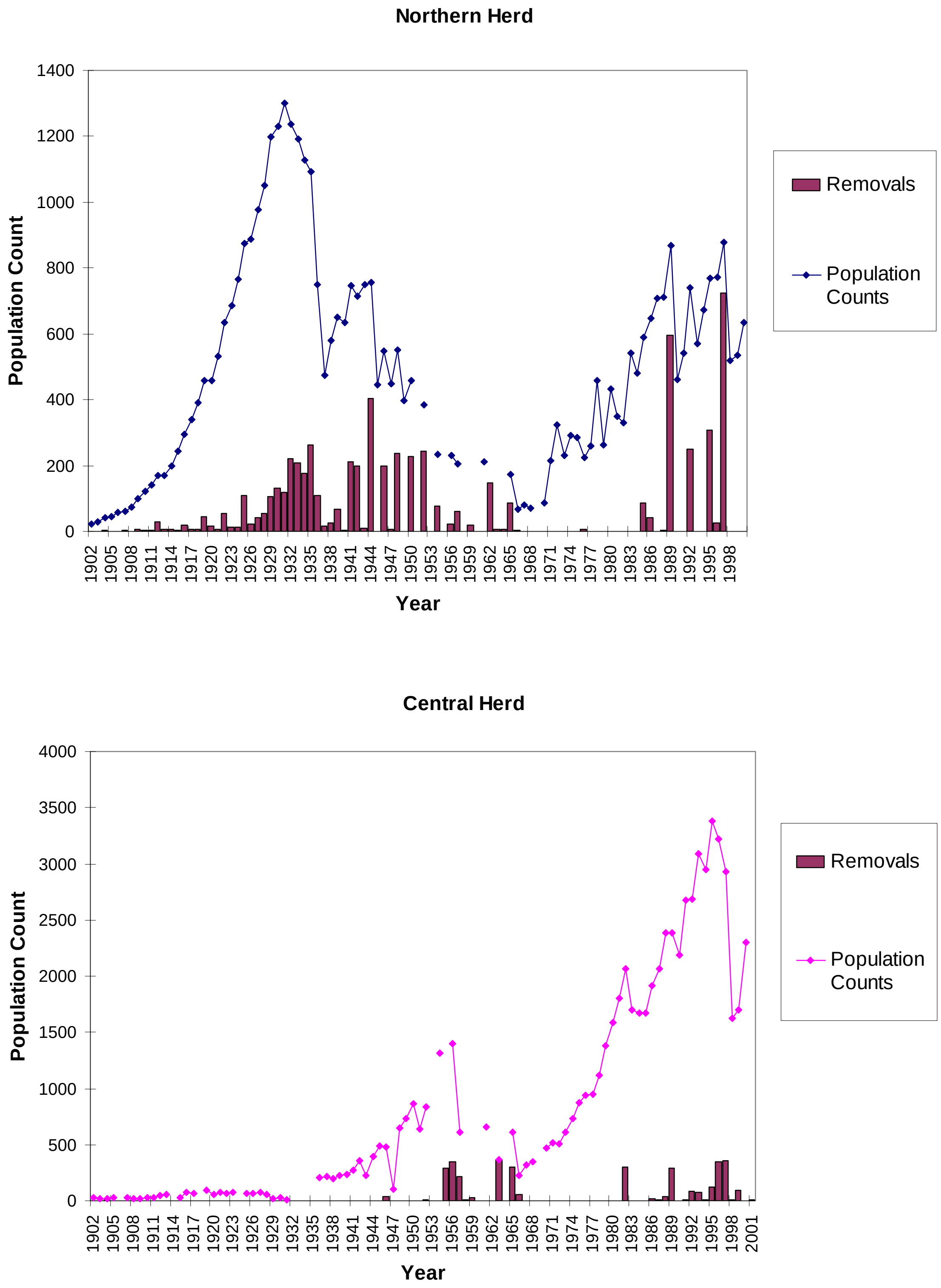


Figure 1a: Bison counts and removals by year from 1902-2000.

Management	Biological Postulates	Analysis Methods
Feeding, roundup, minor removals Northern Herd 1902-1929	1) Growth should occur at nearly biological maximum of the species 2) Does the population show signs of density dependence?	1) Log-linear regression to estimate λ 2) Test for decreasing λ with increasing population
Feeding, roundup, episodic removals Northern Herd 1930-1938	1) Does the population show signs of density dependence?	1a) Estimation of annual λ and piecewise regression between removals to estimate λ 1b) Test for decreasing λ with increasing population
Feeding, episodic removals Northern Herd 1939-1952	1) Does the population show signs of density dependence? 2) Do density independent factors affect annual λ? (post-1949)	1a) Piecewise regression between removals to estimate λ 1b) Test for decreasing λ with increasing population 2a) Estimation of annual λ 2b) Regression of annual λ on climate variables
Episodic removals Northern Herd: 1953-1968 Central Herd: 1956-1968	1) Does either herd show signs of density dependence?	1a) Piecewise regression between removals to estimate λ 1b) Test for decreasing λ with increasing population 1c) Test for differences in λ between herds
No removals Central Herd: 1939-1955 Both Herds: 1969-1985	1) Growth should occur at biological maximum of the species given YNP environment 2) Does either herd show signs of density dependence? 3) Are there differences between growth rates for the Central Herd from 1939-1955 and from 1969-1985? 4) Do elk numbers, which were also released from removals at this time, affect population growth for the bison herds?	1) Use ln-linear regression to estimate λ, compare to estimate from when bison were supplementally fed 2a) Test for decreasing λ with increasing population 2b) Test for differences in λ between herds 3) Test for differences between estimated λ in 1939-1955 and for the Central Herd in 1969-1985. 4) Plot elk numbers against annual growth rates for both bison herds.
Regular removals Both Herds: 1986-2000	1) Does either herd show signs of density dependence?	1a) Estimation of annual λ – adjusted for removals 1b) Test for decreasing λ with increasing population 1c) Test for differences in λ between herds
Post-Feeding Episodic removals in both herds: 1952-2000	1) How do climatic factors affect annual λ? 2) How do climatic factors affect reproduction? (years 1970-2000 only) 3) How do climatic factors affect recruitment? (years 1997-2004 only) 4) How do density-dependent factors interact with density-independent factors to affect population vital rates?	1a) Estimation of annual λ, adjust for removals when necessary. 1b) Regression of annual λ on climate variables 1c) Comparison of regressions between herds 2a) Estimation of reproductive rates using calf/adult ratios from flight data (1970-2000) 2b) Regression of reproductive rates on climate variables 2c) Comparison between herds 3a) Estimation of annual recruitment (1997-2004) 3b) Regression of recruitment rates on climate variables 3c) Comparison between herds 4a) Creation of a suite of interactive effect models between vital rates and climatic variables 4b) Use of information-theoretic methods to determine best model for each herd 4c) Comparison of ß values, analysis of effects

Table 1: An outline of preliminary analysis procedures under each management paradigm

Data constraints:

1) Climate data exist from 1949 to present
2) Calf/adult ratios exist from 1970 to present, we will use 1970-2000 here
3) Recruitment data, in the form of spring calf/adult ratios, exist from 1997-2004, we will use all years

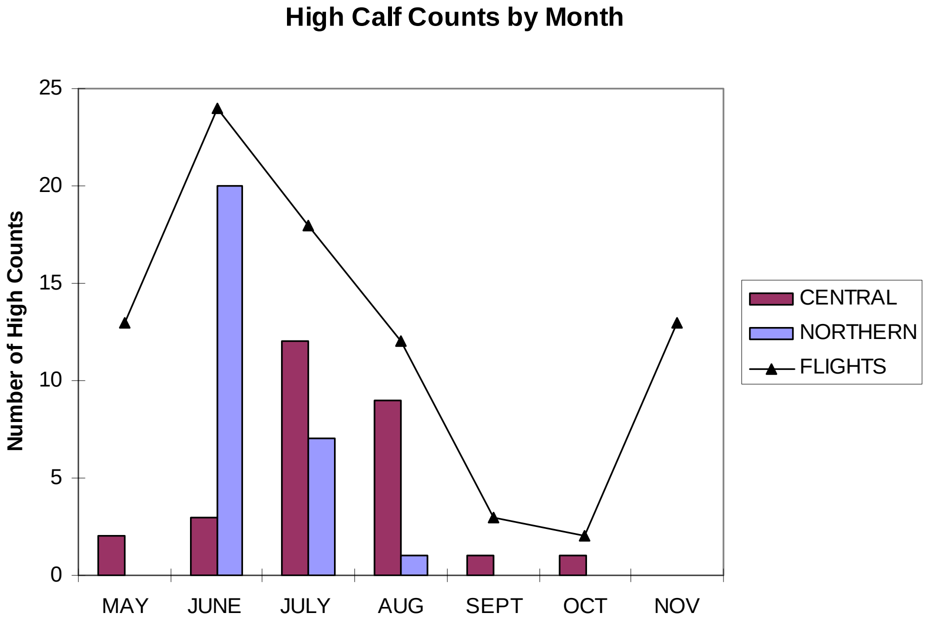
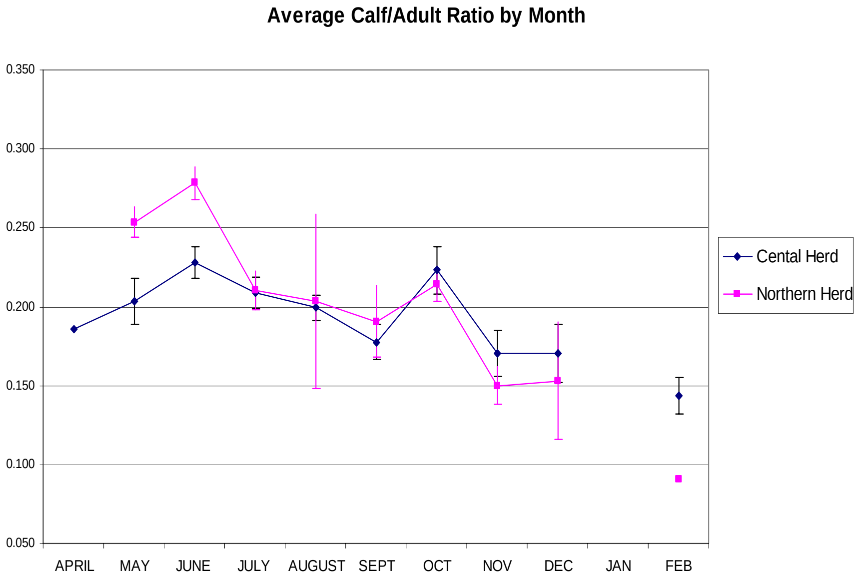


Figure 2: The months where the highest number of calves were counted (1970-1997). The black line indicates the number of flights that occurred in that month over this time span.



Month	Northern Herd Flights	Central Herd Flights
April	0	1
May	13	13
June	24	24
July	18	18
August	12	12
September	3	3
October	2	2
November	13	13
December	8	9
January	0	0
February	3	2

Figure 3: The calf/adult ratio across months for years 1970-1997. The table to the right indicates how many flights that classified calves occurred in each month. Notice the general decline from June's ratio. The exception is October, but only 2 flights occurred in this month during the time period.

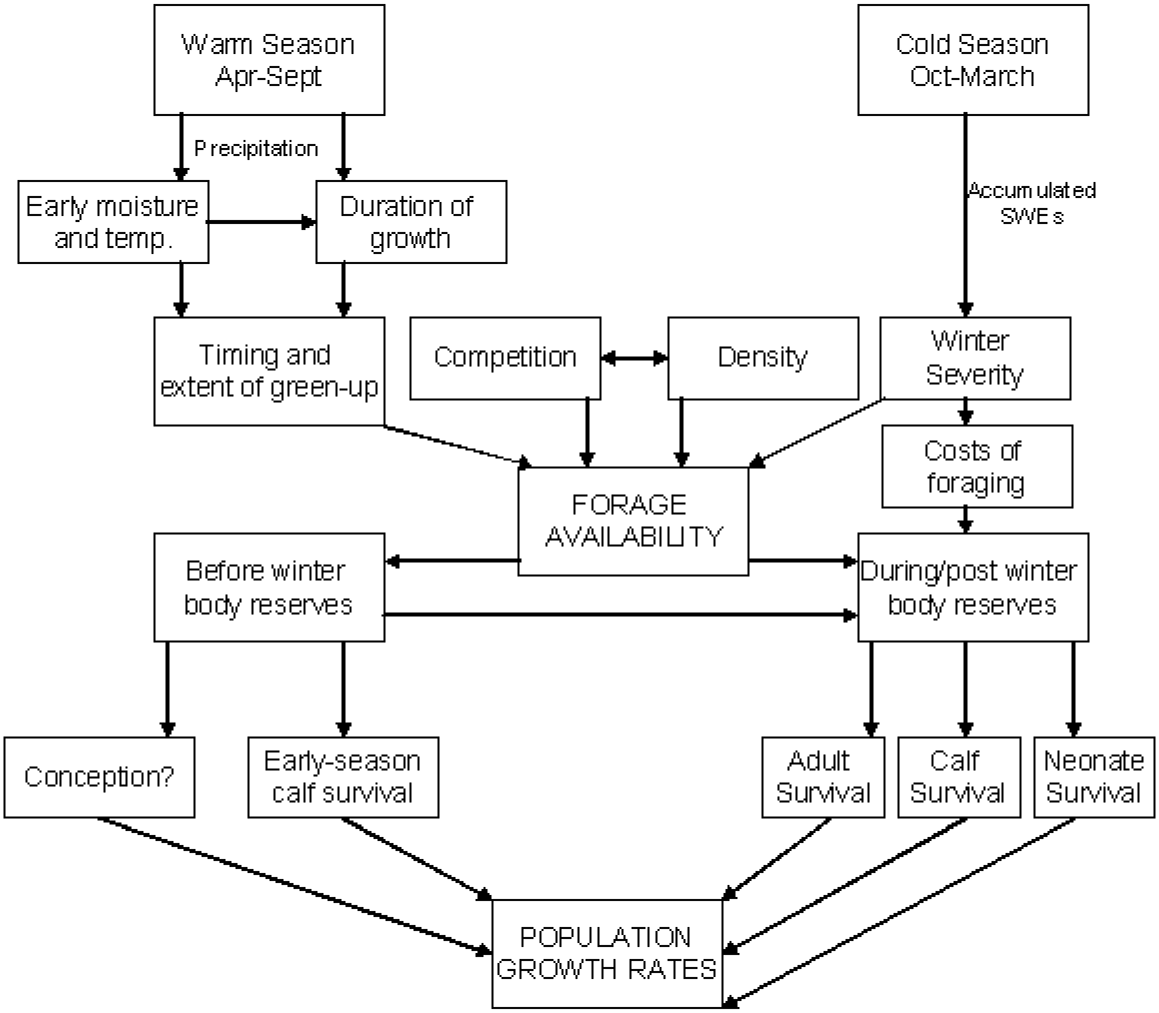


Figure 4: Schematic of climate effects on bison population growth rates. Adopted from Garrott et al. 2003.

RECRUITMENT (t)
Single Main Effects Models
SWEacc(t)
PREC(t) *
BISON(t)
ELK(t)
Paired Main Effects Models
SWEacc(t) + PREC(t)
SWEacc(t) + BISON(t)
SWEacc(t) + ELK(t)
PREC(t) + BISON(t)
PREC(t) + ELK(t)
BISON(t) + ELK(t)
Three Main Effects Models
SWEacc(t) + PREC(t) + BISON(t)
SWEacc(t) + BISON(t)+ ELK(t)
PREC(t) + BISON(t)+ ELK(t)
Four Main Effects Model
SWEacc(t) + PREC(t) + BISON(t) + ELK(t)
Interaction Models
SWEacc(t) * ELK(t)
PREC(t) * ELK(t)
SWEacc(t) * BISON(t)
PREC(t) * BISON(t)

Table 2: A list of *a priori* models for YNP bison recruitment rates. SWEacc(t) = the accumulated measure of snow water equivalents throughout the cold season prior to recruitment, PREC (t) = the total precipitation that fell during the warm season prior to recruitment, BISON(t) = the number of bison in the herd the year of recruitment, and ELK(t) = the estimated number of elk on the shared winter range for the northern herd.

REPRODUCTION
Single Main Effects Models
SWEacc(t-1)
PREC(t-1)
BISON(t-1)
ELK(t-1)
Paired Main Effects Models
SWEacc(t-1) + PREC(t-1)
SWEacc(t-1) + BISON(t-1)
SWEacc(t-1) + ELK(t-1)
PREC(t-1) + BISON(t-1)
PREC(t-1) + ELK(t-1)
BISON(t-1) + ELK(t-1)
Three Main Effects Models
SWEacc(t-1) + PREC(t-1) + BISON(t-1)
SWEacc(t-1) + BISON(t-1)+ ELK(t-1)
PREC(t-1) + BISON(t-1)+ ELK(t-1)
Four Main Effects Model
SWEacc(t-1) + PREC(t-1) + BISON(t-1) + ELK(t-1)
Interaction Models
SWEacc(t-1) * ELK(t-1)
PREC(t-1) * ELK(t-1)
SWEacc(t-1) * BISON(t-1)
PREC(t-1) * BISON(t-1)

Table 3: a list of *a priori* models for YNP bison reproductive rates. Because reproduction is measured early in the bison year, all covariates we use refer to the previous bison year (t-1), events leading up to conception, gestation and birth. SWEacc(t-1) = the accumulated measure of snow water equivalents throughout the cold season during gestation, PREC(t-1) = the total precipitation that fell during the warm season before conception and during early gestation, BISON(t-1) = the number of bison in the herd during gestation, and ELK(t-1) = the estimated number of elk on the shared winter range for the northern herd.

ANNUAL λ
Single Main Effects Models
PREC(t-1)
SWEacc(t-1)
ELK(t-1)
Two Main Effects Models
PREC(t-1) + SWEacc(t-1)
SWEacc(t-1) + ELK(t-1)
Three Main Effects Model
PREC(t-1) + SWEacc(t-1) + ELK(t-1)
Interaction Models
SWEacc(t-1) * ELK(t-1)
PREC(t-1) * ELK(t)

Table 4: a list of *a priori* models for annual λ for bison herds. Because annual λ is generally measured early in the bison year, all covariates we use refer to the previous bison year (t-1), events leading up to the population size at (t). SWEacc(t-1) = the accumulated measure of snow water equivalents throughout the cold season, PREC(t-1) = the total precipitation that fell during the warm season, and ELK(t-1) = the estimated number of elk on the shared winter range for the northern herd.

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