

# A REVIEW OF AMERICAN BISON (*Bos bison*) DEMOGRAPHY AND POPULATION DYNAMICS

By Jedediah F. Brodie

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# PART I: INTRODUCTION

American bison numbered in the tens of millions prior to European settlement, then declined catastrophically in the late 1800s to the brink of extinction (Roe 1951). Conservation efforts for the species have been very successful, and today there are over 500,000 bison in North America (Boyd 2003, Freese et al. 2007). Yet the vast majority of these animals exist in carefully-managed captive herds, divorced from the ecological processes that would influence their demographics and population structure in nature (Boyd 2003, Freese et al. 2007, Sanderson et al. 2008). Biologists and managers are increasingly interested in re-establishing bison populations in areas from which they have been extirpated, and in managing herds to mimic natural age and sex structure (Harper et al. 2000). All of these goals will be more attainable with a detailed understanding of bison demography and population dynamics.

In this review, I compile what is known of the demographic rates, population structure, intrinsic and extrinsic regulating forces, and overall population growth rate of American bison across their range. My goal is to assemble the information needed to construct accurate and detailed matrix projection models for bison populations. These models can be used in population viability analysis, assessment of the effects of alternative management strategies, or to predict equilibrium age and sex ratios. Much of the information compiled here could be used in other types of models, such as difference or differential equation-based models, or individual-based simulations. Yet matrix models are likely to be the most useful quantitative tools to address most of the questions posed by bison managers, and they are very straightforward to use. I refer readers to Morris and Doak (2002) for an excellent and simple introduction to the use of matrix models in conservation biology, and Caswell (2001) as a complementary reference. While various pre-packaged software applications exist to assist in matrix-based population viability analysis (e.g. VORTEX, RAMAS), I do not advocate the use of these programs due to their black-box approach; data is input and results churned out without the user knowing quite what went on. Instead I suggest that managers use the POPTOOLS add-in for Microsoft Excel to do simple exercises with matrices, and use the transparent MATLAB codes in Morris and Doak (2002) to address more advanced questions.

Part I of this review introduces the issue, and Part II covers the vital rates of individuals, in particular age- and sex-specific survivorship and fecundity, the temporal variation in each, and factors known to influence these rates. Part III expands the scale to the population level; here I review what is known about

age and sex structures, and the capacity for increase or decrease in different herds. Part IV assesses the large-scale drivers of population dynamics such as density dependence and the various forms of extrinsic regulation (e.g. predators, disease, climate). I also include brief sections on inbreeding and spatial dispersal; while much has been written on these subjects (indeed they could be topics for completely separate reviews), here I am solely concerned with how each might affect demographic vital rates or population dynamics. Finally, Part V combines data from the previous sections to ask what structured population models for different bison herds might look like, and what they can tell us.

It is important to note that all of the information presented here must be evaluated critically. There is little detailed information on the demographics, population structure, and population growth rates of bison under truly “natural” conditions (Millspaugh et al. 2005). All bison herds today are managed by humans in some form or another, with varying impacts on vital rates and population processes. Many managers use culling programs to achieve their population structure targets; often management seeks to avoid high rates of natural mortality and limit the presence of older males that can be difficult to handle (R. Wallen, pers. comm.). Many herds are artificially maintained at sizes where density dependence is unlikely to be strongly expressed, and selective culling can importantly influence sex ratios and age structures. Management actions such as culling and removals for translocation make it difficult to assess vital rates such as survivorship. Supplemental feeding can affect survivorship as well as reproduction. Table 1 lists the bison herds covered in this review, and gives an overview of the major human influences on each.

It is my hope that this review will assist managers in the further re-introduction of bison across their former range.

# PART II: INDIVIDUAL DEMOGRAPHICS

## Survivorship

Calf survival rates vary quite dramatically across populations. Annual calf survival in the Slave River Lowlands from 1975-1979 (calculated from data in Van Camp and Calef 1987) averaged 25.7% (temporal standard deviation = SD = 9.0%), ranging from 6-30% (Calef 1984). Average annual calf survival in the Mary Mountain and Northern Range sub-populations of Yellowstone National Park were 61.1% and 76%, respectively, from 1990-1992 (Kirkpatrick et al. 1996). In the small, closed population of the Texas State Bison Herd (Halbert et al. 2005a), annual calf survival ranged from 25-75% ( $\bar{x}$  = 46.07%, SD = 23.0%). Over-winter calf survival in the Mackenzie Bison Sanctuary from 1984-1998 (calculated from data in Larter et al. 2000) averaged 54.3% (SD = 20.8%). In the Henry Mountains, average annual calf survival from 1977-1983 (Van Vuren and Bray 1986) was 95.5% (SD = 5.0%). On Catalina Island, Lott and Galland (1985: 301) report that, “First year survival is nearly 100% in this population.”

Adult survival rates are generally higher than those of calves, and less variable. Bison in the wild occasionally live up to 20+ years (Meagher 1973); a captive individual reached age 41 (Reynolds et al. 1982). Annual adult survival in the Mackenzie Bison Sanctuary from 1986-1991 (Larter et al. 2000) was ~96% (SD = 0.3%). Annual adult survival in the Texas State Bison Herd (Halbert et al. 2005a) was 94.6% (SD = 5.5%), and in Yellowstone National Park was 91-93% from 1995-2001 (Fuller et al. 2007b). Survival of adults in Badlands National Park was 96.8-99.5%, while survival of juveniles (subadults + calves) was 95.8-97.5% (Berger and Cunningham 1994).

Survival may be slightly higher for females than males. In Wood Buffalo National Park, annual adult survival for females and males (with one or no diseases) was 94.6% (SD = 1.5%) and 92.6% (SD = 1.5%), respectively (Joly 2001). In the Henry Mountains, average annual survival (excluding mortality from hunting) of females and males was 95.2% (SD = 4.5%) and 95.2% (SD = 6.2%), respectively (Van Vuren and Bray 1986). Table 2 shows age-structured survivorship for bison. Note that variation in sample size (and other factors) across ages can make the estimates of survival discontinuous, which likely does



not accurately reflect the underlying biology. Thus it is generally more desirable to fit a smooth curve to the data and use the predicted survival for each age in matrix projection models (Morris and Doak 2002). For example, Shull and Tipton (1987) present survival and sample size data for bison in the Wichita Mountains Wildlife Reserve. Figure 1 shows the discontinuous survivorship estimates for each age and sex (from Shull and Tipton 1987), overlain with logistic survival functions. For females, the model fit is improved by adding a quadratic term to the simple logistic function ( $\Delta AIC_c = -27.050$ ), suggesting that the annual probability of survival increases from calves to young adults, then declines as adults senesce. This incorporation of senescence is important since the high survivorship rates reported for many adult bison very likely decline at advanced ages (J. Gross, pers. comm.).

Survival rates may be affected by climate. The lower calf survival rate of the Mary Mountain population in Yellowstone (reported above), as compared to the Northern Range population, was attributed by Kirkpatrick et al. (1996) to the former site receiving about 10cm more snowfall per year. Annual precipitation had no effect on calf survival in the Henry Mountains (calculated from data in Van Vuren and Bray 1986), possibly because rainfall varies positively with elevation, and bison can migrate up- or down-slope to find suitable forage (Van Vuren and Bray 1986). Harsh winters are often an important cause of mortality, especially for calves (Fuller 1962, Van Camp 1975, Barmore 2003) or calves and yearlings (Meagher 1973).

Survival rates are also influenced by natural and anthropogenic predation as well as disease. Hunting in the Henry Mountains reduced average calf survival (“natural” levels given above) to 92.8% (SD = 4.9%), a decline of 2.8% (from data in Van Vuren and Bray 1986). Figure 2 shows the effects of hunting on adult male and female survival in this population; assuming that hunting-induced mortality is additive, hunting reduces average annual male and female survival by 17.2% and 5.6%, respectively. Poaching in the Mackenzie Bison Sanctuary (Larter et al. 2000) accounted for 25% of adult male mortality, though the sample size was low (1 individual of 4 killed from a total population of 36 collared males). Wolf predation in Wood Buffalo National Park accounted for 52.6-75% of total mortality in the Delta Herd (Joly 2001), and survival of adult bison in this sub-population was 15.6-22% lower than in two other sub-populations with negligible wolf predation. As with hunting by humans, however, it is difficult to assess how much of the wolf predation is additive versus compensatory; the lower survival of the Delta Herd could be due to other factors as well as wolves (Joly 2001). However, calf survival in the presence of wolf predation seems to be much lower (<50%) than in areas lacking intense wolf predation (Calef 1984). In Wood Buffalo National Park, the combination of tuberculosis and *Brucella* infection reduces adult survival by 10% (from data in Wilson et al. 1995, Joly 2001, Joly and Messier 2004, Bradley and Wilmshurst 2005; also see Figure 2). Sometimes the effects of management actions on survival can be difficult to assess from published studies. For example, the mortality rates calculated for the Wichita Mountains Wildlife Reserve (Shull and Tipton 1987) include both natural deaths and auction sales combined, but not separately. But in Badlands National Park from 1985 to 1989 we can partition the sources of mortality; poaching accounted for an aver-

age of 4.3% of the total deaths per year ( $SD = 7.2\%$ ,  $N = 62$  deaths over the five years), while “corral-related” mortality accounted for an average of 26.8% of deaths ( $SD = 22.3\%$ ) (Berger and Cunningham 1994: 102).

## Reproduction

### Female reproductive output

Compared to males, reproductive output in females is less variable (in terms of the number of calves produced per year or throughout the lifetime), longer in duration (2-20 years), and more constant over the course of an individual's life (Wilson et al. 2002). Table 3 shows mean pregnancy rates of adult females across different populations, which range considerably from 37-89%. There can even be substantial variation among studies on the same population that differ in survey methodology and study duration; pregnancy rates in Yellowstone range from 37-54% (Kirkpatrick et al. 1996) to 78.5% (Aune et al. 1998). Table 4 shows the mean percentage of females that calve each year.

Age is an important determinant of female reproductive rates. Female bison rarely breed as yearlings (Halloran 1968, Meagher 1973, Shaw and Carter 1989), and the proportion of 2 year olds in a herd that calves is usually low (Halloran 1968, Shaw and Carter 1989, Wilson et al. 2002). Reproductive output generally peaks later (McHugh 1958, Halloran 1968, Shaw and Carter 1989, Green and Rothstein 1991, Aune et al. 1998). Figure 3 and Table 5 show age-related variation in pregnancy and calving rates across different populations. Several studies (e.g. Wilson et al. 2002) have noted negative linear relationships between female age and reproductive success (Wilson et al. 2002 linear regression:  $R^2 = 0.329$ ). Yet this negative linear relationship may be overly simplistic. I used the data in Wilson et al.'s (2002) figure 2 to calculate the proportion of females at each age that bred successfully. Adding a quadratic term for age substantially improves the model fit ( $R^2 = 0.827$ ,  $\Delta AIC_c = -28.520$ ). Thus age affects reproductive success non-linearly; reproductive success increases with age initially and then declines as the individual senesces (see Berger and Cunningham 1994). In Wood Buffalo National Park, pregnancy rates were highest in “young adults” ( $\bar{x} = 61.63\%$ ,  $SD = 17.2\%$ ,  $N = 324$ ), lower in “adults” ( $\bar{x} = 43.19\%$ ,  $SD = 24.0\%$ ,  $N = 432$ ), and still lower among the “aged” ( $\bar{x} = 38.01\%$ ,  $SD = 32.1\%$ ,  $N = 127$ ) (Carbyn et al. 1993: 121). However, in Yellowstone National Park, Fuller et al. (2007b) found no effects of senescence on female pregnancy or calving rates, and Meagher (1973: 54) found that pregnancy rates increased from “young adults” ( $\bar{x} = 50\%$ ,  $N = 6$ ) to “adults” ( $\bar{x} = 57\%$ ,  $N = 23$ ) to “aged” ( $\bar{x} = 75\%$ ,  $N = 17$ ).

Reproductive success among young (2-8 years old) female bison may increase with age in part because of a corresponding increase in social dominance. This relationship has been noted at the National Bison Range (Rutberg 1983, 1986b) and Wind Cave National Park (Green 1987), but not at Badlands National Park (Berger and Cunningham 1994), possibly due to higher interchange of individuals among groups at the latter site. Dominant individuals may enjoy greater access to food (Rutberg 1986a, Kojola 1989). However, there is a trade-off between growth and reproduction for adult female bison (Halloran 1968, Green and Rothstein 1991); thus dominant females may have access to more

resources, but “choose” to invest them in reproduction rather than growth. Older females have been shown to nurse their calves more than younger females, though this did not lead to noticeable differences in calf survival (Green 1986). Several studies have found no relationship between reproduction rates and body mass (Green and Rothstein 1991, Berger and Cunningham 1994). Yet by grazing near their mothers (Green et al. 1989), calves of dominant females may have access to greater food resources and achieve higher dominance status, size, or reproductive output (Berger 1979, Green and Berger 1990).

Female reproductive output may be affected by disease (Joly 2001) and nutritional status (Verme 1969, White et al. 1989). Females in good body condition at Badlands National Park were better able to synchronize their parturition with the rest of the herd (Berger 1992), which may help in avoiding predators (Gates and Larter 1990). Average birth rates for 3 year old Yellowstone National Park bison with and without brucellosis were 40% and 63%, respectively (Fuller et al. 2007b). Pregnancy rates in Wood Buffalo National Park declined from 0.78 in individuals with “good” body condition to 0.68 in “poor” body condition, but otherwise healthy, females (Joly and Messier 2004). In addition, body condition may interact synergistically with disease. The difference in pregnancy rates between animals in good and poor body condition (0.73 and 0.62, respectively) was slightly greater in individuals with tuberculosis and *Brucella* bacteria than in healthy animals (Joly and Messier 2004). *Brucella* infection alone did not significantly affect pregnancy rates in WBNP, though tuberculosis reduced the latter by ~33% (Joly 2001). The interaction between the two diseases may also be important; individuals with both ailments had ~12% lower pregnancy rates than those with neither or only one disease (Joly 2001).

### Calving sequence

Female bison have been thought to reproduce roughly every other year (Halloran 1968) or 2 out of every 3 years (Soper 1941, Fuller 1961), but actually display substantial variation among individuals in terms of how often they calve (Lott and Galland 1985, Shaw and Carter 1989). Some of this variation may be due to reproductive rates being affected by an interaction between body condition and age (Green and Rothstein 1991, Kirkpatrick et al. 1996) or dominance (Green and Rothstein 1991). Reproduction incurs long-term costs in terms of reduced growth and lower offspring quality in years following calf production (Halloran 1968, Green and Rothstein 1991). By following individual females and dividing the number of calves produced in a given time period by the number of years surveyed, estimates of mean annual per-capita production can be generated. These range from 0.64 calves/year (SD = 0.3%) in Elk Island National Park (recalculated from Wilson et al. 2002), to 0.66 calves/year (SD = 0.2%) in Wichita Mountains Wildlife Reserve (Shaw and Carter 1989), to 0.71 calves/year (SD = 0.2%) on Catalina Island, California (recalculated from Lott and Galland 1985).

Bison nearly always bear a single calf at a time. Twinning is often reported to be very rare (Halloran 1968, Meagher 1986, Rutberg 1986b, Shaw and Carter 1989, Novak 1999), but it is difficult to find actual estimates of its frequency. Only one set of twins was born out of 5633 births (twinning rate  $\approx$  0.02%) over 58 years in the Wichita Mountains Wildlife Reserve (Halloran

1968). McHugh (1958) recorded one set of twins as well, but did not report the total number of births observed. It is also uncommon for females to have more than one estrus in a given year; only 3 of 154 pregnant females (1.9%) killed in Fort Niobrara Wildlife Reserve and Wind Cave National Park were found with two corpora lutea (Haugen 1974).

### **Male reproductive output**

Few studies have assessed how age affects reproductive effort in males as compared to females. As in most mammals, reproductive success is much more variable amongst individuals in male bison than in females (Berger and Cunningham 1994, Wilson et al. 2002). In a 4-year period in Elk Island National Park, the number of calves produced per female ranged from 0-4 whereas the number produced per male ranged from 0-24 (Wilson et al. 2002). In a 4-year period in Badlands National Park, the range in number of calves produced per female and per male was 0-4 ( $\bar{x} = 2.43$ ,  $SD = 1.2\%$ ) and 0-16+ (Berger and Cunningham 1994). In a 3-year period at Hook Lake, the number of calves produced per male ranged from 0-30 (Wilson et al. 2005). Age is related to dominance (Roden et al. 2005), though these effects may be non-linear, with the dominance peaking at approximately 9-11 years (Wolff 1998). Although age is clearly an important determinant of male reproductive success, this is apparently not due to an increase in body mass with age; most studies find no relationship between male mass and reproductive success (e.g. Wolff 1998). In contrast, Wilson et al. (2002) did find an effect of body mass on male reproductive success, but they used post-rut weight measurements which may be biased in that mature males lose more weight over the course of the rut than non-mating males (Wolff 1998). Berger and Cunningham (1994) also found a strong correlation between age and body weight in males ( $R = 0.78$ ) at Badlands National Park, though at Fort Niobrara, the National Bison Range, and the Wichita Mountains Wildlife Reserve weight increased with age only until age 7-9, at which point the relationship flattened out (Berger and Peacock 1988).

Male reproductive output is more sharply peaked than in females, with a greater difference between productivity at the optimum age versus older or younger individuals (Wilson et al. 2002). Males may occasionally reach sexual maturity as yearlings (Fuller 1962), but this is likely quite rare (Halloran 1968). Though most males may reach physiological maturity by 2-3 years old, the presence of older dominant bulls generally delays mating until about 5-6 (Maher and Byers 1987, Wilson et al. 2002); thus the age structure of the herd importantly affects mating opportunities of bulls at different ages (Komers et al. 1994). The onset of the rut at Fort Niobrara Wildlife Refuge led to no discernible change in the proportion of time spent active for 1-5 year old males (Maher and Byers 1987). Four year olds actually spent more time grazing after the rut began than they had before (Maher and Byers 1987). In contrast, males 6 years and older became more active and grazed less after the onset of the rut; this was particularly marked for the 9-12 year olds (12 years was the maximum age surveyed in this study) (Maher and Byers 1987). Among wood bison in Elk Island National Park, siring of calves (using genetic markers to assign paternity) started at age 5, peaked at ages 8-14, and was last recorded at age 14 (the maximum age surveyed was 18, though there were only four individuals between

ages 14-18; see Figure 4) (Wilson et al. 2002). However this relatively crude metric of male reproductive output only measured annual reproductive success as a binary variable; there could plausibly be important, untested, effects of age on the number of calves sired per year. Lott (1981) noted a positive relationship between male dominance status and the number of cows bred on the National Bison Range.

Genetic techniques offer a promising tool to assess male reproductive output (Roden et al. 2002). Molecular assignments of bison calf paternity in Elk Island National Park (Wilson et al. 2002) and Hook Lake (Wilson et al. 2005) generated measurements of the average number of calves sired by successful bulls of 1.96 (SD = 1.4) and 3.87 (SD = 5.2), respectively. These estimates are lower than those generated by studies that measure male reproductive success by observed copulations (e.g. Wolff 1998) because not all copulations lead to pregnancy. An important, and untested, question concerns how the number of calves sired per bull varies with male density. As the proportion of males to females in the population declines, we might expect the reproductive success rate of a given individual male to increase. But given the paucity of data that allow us to estimate even static measures of male reproductive success, it will be very difficult indeed to assess variation in success as a function of male density. An analysis of data presented in Wilson et al. (2002) shows no relationship between the number of calves sired per successful male and either a) the total number of successful males (linear regression:  $F_{1,2} = 0.000$ ,  $p = 0.990$ ) or b) the total number of mature males in the herd ( $F_{1,2} = 0.110$ ,  $p = 0.772$ ), though the short timeseries (4 years) severely limits the power of these tests.

# PART III: POPULATION STRUCTURE AND GROWTH RATE

## Sex structure

In many mammals, *in utero* sex ratios are slightly skewed towards males (Fuller 1962). Bison appear to follow this pattern; Haugen (1974), Fuller (1962), and Rutberg (1986b) all report that >50% of fetuses were male (see Table 6). Yet the evidence for this pattern persisting after birth is equivocal; Table 6 shows high variation among populations in terms of calf sex ratios after birth, ranging from 46-54% male. Sex ratios may change across age classes due to differential survival between the sexes. McHugh (1958) reports exact parity among 5-8 month old calves ( $N = 1465$ ). Van Vuren and Bray (1986) show a 42-50% male rate among 14-16 month old yearlings from 1977-1983 ( $N = 192$ ).

There is some evidence that offspring sex may partly be determined by maternal condition. Trivers and Willard (1973) suggested that mothers in good condition should preferentially produce sons in species with a) small litter size, b) male-male competition (where reproductive success is strongly influenced by body condition), and c) strong correlation between maternal and offspring condition. Put another way, female reproductive success is less variable than that of males, and less strongly dependent on good body condition; therefore females would maximize their own fitness by having daughters when they are in poor condition and sons when they are in good condition and can pass on the extra resources to their offspring. Bison satisfy the above conditions. Rutberg (Rutberg 1986b) found that the offspring sex ratio of lactating (presumably resource-stressed) females on the NBR was near parity (49.1% male), while the offspring sex ratio of non-lactating (less resource-stressed) females was highly male skewed (86.2% male). However, Shaw and Carter (1989) found no significant differences in the offspring sex ratios of lactating and non-lactating females in the Wichita Mountains Wildlife Reserve. Likewise, females in Elk Island National Park that did not produce calves one year (and should therefore have been in better condition than those that did produce) were no more likely to have male offspring the next year than females who had calved the first year (Wilson et al. 2002).

It is difficult to assess “natural” sex ratios among adult bison, given the very different (but often intensive) management and culling regimes of different herds. Among wood bison adults ( $\geq 2$  yrs) in the Mackenzie Bison Sanctuary, the male percentage ranged from 40.9% to 44.6% across 3 years ( $N = 1941$ ) (Gates and Larter 1990). In the declining population of the Slave River Lowlands (1974-1983), Van Camp and Calef (1987: 21) reported a “skewed adult sex ratio” of 24.2% males. In the hunted population of the Henry Mountains, adult sex ratio ranged from 34-41% male between 1977 and 1983 (Van Vuren and Bray 1986). The Etthithun population in British Columbia had an adult sex ratio of 23.7% male in 2006, though this is likely a legacy of the heavily female-biased introduction in 2000 (Rowe and Backmeyer 2006). In Yellowstone National Park from 1964-66, the percentages of trapped individuals that were male were 57% ( $N = 71$ ) for calves, 51% ( $N = 47$ ) for yearlings, 52% ( $N = 24$ ) for 2 year olds, 37% ( $N = 16$ ) for 3 year olds, and 64% ( $N = 159$ ) for adults (Meagher 1973). However, it should be noted that gender differences in dispersal and capture probability may bias these assessments of Yellowstone sex ratios.

### Age structure

The proportion of the population made up of calves and yearlings varies substantially across populations, as well as over time within populations. These proportions are usually measured as the number of calves or yearlings per 100 adult females; the former also serves as an important metric of herd productivity. Since the calf to adult female ratio integrates across actual reproductive rates as well as calf survival until the census, the measurements can be utilized in birth-pulse matrix models (see Morris and Doak 2002, chapter 6). Temporal variance in the measure over time can also be used to incorporate environmental stochasticity into the population model (see Morris and Doak 2002, chapter 8). Figure 5 shows trends in calf:cow ratios for 4 populations. Mean calf per 100 cow ratios vary from 31 ( $\sigma^2 = 30.2$ ) in Wood Buffalo National Park (Bradley and Wilmshurst 2005) and 34 in the Etthihun bison herd (Rowe and Backmeyer 2006), to 50.7 ( $\sigma^2 = 329.4$ ) in the Henry Mountains (Van Vuren and Bray 1986). In addition to the data presented in Figure 5, Van Camp and Calef (1987) report an average of 35 calves per 100 cows in the Slave River Lowlands. Calf percentages in the Henry Mountains were positively, non-linearly related to pre-conception precipitation levels (Van Vuren and Bray 1986). Likewise, calf ratios in Yellowstone from 1995-2001 were negatively related to winter snow-water-equivalent and positively related to the Palmer Drought Severity Index (a measure of the wetness of a given year), indicating that harsh winters and summer droughts are detrimental to reproduction and/or calf survival (Fuller et al. 2007b). It should be noted, however, that some of the variation in calf:cow ratios among herds may be due to different interpretations of the age at which females are considered “adults” (J. Berger, pers. comm.).

The proportion of yearlings in the population also show considerable variation. Figure 6 shows the number of yearlings per 100 cows across 3 populations, ranging from 10 (SD = 5.9) in Wood Buffalo National Park (Bradley and Wilmshurst 2005) to 42 (SD = 15.8) in the Henry Mountains (Van Vuren and

Bray 1986). The late winter yearling ratio in the Etthithun bison herd was 19:100 cows (Rowe and Backmeyer 2006). Figure 7 shows the age structure of adult females and males.

## Population growth rate

Bison populations have the ability to increase or decrease quite rapidly, depending on a variety of conditions. Table 7 shows the estimated population growth rates for a variety of populations. In 1963, 18 bison were re-introduced to the Mackenzie Bison Sanctuary and increased at an average of 22.3% per year over the next 26 years, at which point population growth declined (calculated from data in Larter et al. 2000). The bison population in the nearby Slave River Lowlands grew at an average of 25.4% per year from 1948-1957, then declined at 7.2% per year until 1983 (calculated from data in Van Camp and Calef 1987). The 39 bison in the National Bison Range in 1909 expanded to a population of 554 by 1922 (22.1% annual increase), at which point yearly removals were instigated (reducing the 1909-1928 growth rate to 15.3% per year) (Gross et al. 1973, Fredin 1984). Though the population growth rate in the Henry Mountains estimated from long-term index data (1949-1982) was 3.8% per year, actual population counts from 1977-1983 show an increase of 9.2% per year (Van Vuren and Bray 1986). Note in Figure 7 that the overall Wood Buffalo National Park population declined from 1971-1999 (Bradley and Wilmshurst 2005), driven by a decline in the two largest of the five sub-populations (Joly and Messier 2004).

Managers may be acutely interested in how quickly their bison herds can increase or decrease. Several studies provide time-series of annual counts, which can be used to estimate population growth rate. The stochastic log growth rate ( $\mu$ ) for a given population can be estimated from the regression procedure of Dennis et al. (1991) (also see Morris and Doak 2002). Specifically, the natural log of the incremental change in population size (e.g. from one population count to the next) is divided by the square root of the time increments (between counts) to generate an array of independent variables ( $y$ ):

$$y_t = \frac{\log_e \left( \frac{N_{t+1}}{N_t} \right)}{\sqrt{t_{t+1} - t_t}}$$

where  $N_t$  and  $t_t$  are the population count and year, respectively, in year  $t$ . The  $y$  array is regressed, with the intercept forced through 0, against an array of independent variables ( $x$ ), where:

$$x_t = \sqrt{t_{t+1} - t_t}$$

The slope of this regression is an estimate of  $\mu$ , and the 95% confidence limits of  $\hat{\mu}$  are:

$$\left( \hat{\mu} - \left( t_{0.05, q-1} \times SE[\hat{\mu}] \right), \hat{\mu} + \left( t_{0.05, q-1} \times SE[\hat{\mu}] \right) \right)$$



where  $SE [\hat{\mu}]$  is the standard error of the regression slope and  $t_{0.05,q-1}$  is two-tailed Student's  $t$  distribution critical value with  $\alpha = 0.05$  and degrees of freedom equal to the number of transitions in the time-series ( $q$ ) minus 1. Finally, the stochastic log growth rate estimates are converted into measures of discrete population growth:

$$\hat{\lambda} = e^{\hat{\mu}}$$

where  $\hat{\lambda} = 1$  indicates a population not growing over the long term, while  $\hat{\lambda} < 1$  and  $\hat{\lambda} > 1$  indicate declining and increasing populations, respectively.

# PART IV: POPULATION REGULATION

## Density dependence

Population growth is often affected, at least in part, by population density, though density dependence is often obscured or precluded by extrinsic regulating factors, and may or may not be detectable in natural populations (Saether 1997, Singer et al. 1998, Gaillard et al. 2000). An understanding of how density affects different vital rates (e.g. survival or reproduction) or overall population growth is critical for accurately predicting bison population dynamics.

Very few studies have explicitly examined density dependence in bison. Berger and Cunningham (1994) found few detectable effects of density on vital rates, except for a positive relationship between density and natural mortality. Fuller (2006) and Fuller et al. (2007a) found evidence of density dependence in both the northern and central herds in Yellowstone National Park, though the effects were stronger in the former, particularly from 1970-1981, when bison were not culled from the population (Treanor et al. 2007). Density regulation of growth rate in the central herd may have been less noticeable than in the northern herd because of density-induced emigration from the central to northern ranges (Fuller et al. 2007a). The number of young produced per year among 3 year old females on the National Bison Range dropped from ~0.7 at a population size of 100-200 to ~0.3 at a population size of 500 (Gross et al. 1973, Fredin 1984).

But even in studies that do not explicitly assess density dependence, we can sometimes extract information from existing data to test for its effects. We can use time-series of bison counts for “first-pass” assessments of density dependence, following the methods of Morris and Doak (2002; chapter 4). Here we fit three models to the time-series data, and compare them using information criteria. The simplest of the three is the straightforward exponential growth, or density independent, model. The most complex is the theta logistic, where log annual population growth ( $Y_t$ ) is given by:

$$Y_t = \log_e \left( \frac{N_{t+1}}{N_t} \right) = r \left( 1 - \left( \frac{N_t}{K} \right)^\theta \right)$$

where  $N_t$  is abundance in year  $t$ ,  $r$  is the intrinsic rate of increase,  $K$  is the “carrying capacity,” or the maximum number of individuals the environment is able to support before population growth becomes negative, and  $\theta$  is a parameter controlling the shape of the density dependence function. The final model is the Ricker model, where log population growth rate declines linearly with population density (Morris and Doak 2002); this is mathematically equivalent to the theta logistic equation with  $\theta$  set equal to 1 (Morris and Doak 2002). In the Mackenzie Bison Sanctuary (data analyzed from Larter et al. 2000), the population is best fit by a Ricker density dependence model, though the evidence is equivocal (Akaike weights:  $\omega_{\text{Ricker}} = 0.51$ ,  $\omega_{\text{exponential}} = 0.41$ ). This population provides an interesting illustration of density dependence in bison, where abundance rapidly but sigmoidally increases for about the first three decades, at which point it begins to fluctuate. These fluctuations are approximately around the carrying capacity ( $\hat{K} = 2035$ ) predicted by an allometric relationship between herbivore body mass and population density (Nudds 1992). Larter et al. (2000) speculate the population growth was limited either by a reduction in the availability of high quality forage or increased predation by wolves on bison calves. A more recently formed sub-population (at Mink Lake) has better quality forage, and higher levels of adult female reproduction and calf over-winter survival (Larter et al. 2000). In Wood Buffalo National Park (data analyzed from Bradley and Wilmschurst 2005), the evidence for density dependence is similarly equivocal ( $\omega_{\text{exponential}} = 0.54$ ,  $\omega_{\text{Ricker}} = 0.44$ ). The Henry Mountains population (data analyzed from Van Vuren and Bray 1986) demonstrates a similar situation, ( $\omega_{\text{exponential}} = 0.54$ ,  $\omega_{\text{Ricker}} = 0.37$ ). In all of these cases, model averaging (see Burnham and Anderson 2002) could be used to input the best-supported density dependence information into population models.

The first-pass assessment of density dependence above, using time-series of abundance, can be useful for un-structured population models (i.e. those that treat all individuals the same, regardless of age or sex). However, bison managers will likely more often be interested in structured models (e.g., projection matrices) to more accurately predict population dynamics as well as track changes in age and sex structure. To incorporate density dependence into matrix models, we need to know which vital rates in particular (e.g., juvenile survival, age at maturity for females, etc.) are affected by density, as well as which measure of density matters (e.g. just adults or the whole population). With time-series of density (or its surrogate, abundance) and annual measures of vital rates, we can assess particular levels of density dependence with the Ricker function. For example we might measure the effects of density on adult survival ( $S_t$ ) as:

$$S_t = S_0 \times e^{-\beta D_t}$$

where  $S_0$  is survival when density approaches zero,  $D_t$  is density at time  $t$ , and  $\beta$  is a fitted parameter. In practice this model is easily fit with a linear regression of the natural log of survival versus density; the slope of the regression is  $-\beta$  and the intercept is the natural log of  $S_0$  (Morris and Doak 2002). Unfortunately, it is rare to find all of these data for a given population. In one case where they

do exist, total bison abundance in Wood Buffalo National Park (data analyzed from Bradley and Wilmshurst 2005) shows no effect on juvenile survival ( $R^2 = 0.120$ ,  $p = 0.189$ ), adult male survival ( $R^2 = 0.013$ ,  $p = 0.675$ ), or adult female survival ( $R^2 = 0.013$ ,  $p = 0.675$ ). In another case, the expected total abundance of adults in the Mackenzie Bison Sanctuary (from a logistic model fitted to data in Larter et al. 2000) shows a marginally significant effect on over-winter calf survival ( $\beta = -0.001$ ,  $R^2 = 0.242$ ,  $p = 0.074$ ). This may partially explain the density dependence observed in the overall population dynamics of this herd that was detected using the count-based analysis above.

## **Dispersal and colonization**

Certain bison populations consist of several sub-populations with dispersal among them. In these cases we can model the overall population dynamics by accounting for the internal demographics of each sub-population as well as dispersal amongst them. Dispersal of adult bison in the Mackenzie Bison Sanctuary was said to be “innate” (i.e. genetically determined, density independent) for males and driven by “pressure” (i.e. density dependence) in females (Gates and Larter 1990, Larter et al. 2000). Gates and Larter (1990: 236) report that:

“Expansion of the Mackenzie population was density dependent; major shifts occurred when a critical density threshold of 0.5-0.8 bison  $\text{km}^{-2}$  was reached. The most parsimonious explanation for the observed pattern of range expansion is an adaptation to avoid a high level of resource limitation.”

Similarly, rising density in the central herd of Yellowstone National Park likely led to substantial emigration to the northern range of the park. The carrying capacity for bison in Yellowstone was estimated at 2800-3200 (Taper et al. 2000); density-induced emigration from the northern range of the park led to culling as individuals left the national park (Gates et al. 2005, Fuller et al. 2007a, Treanor et al. 2007). Exchange of individuals between these herds was estimated at 4.85-5.83% annually (Olexa and Gogan 2007), and may be facilitated by road grooming during winter (Meagher 1993, Taper et al. 2000, Bruggeman et al. 2007). Movement between sub-populations may be episodic rather than continuous; Fuller et al. (2007a) estimate that an important flux of individuals from the central range to the northern range occurred during the winter of 1982. Likewise, dispersal across the Peace River in Wood Buffalo National Park may, “...vary considerably depending on such factors as flooding and predator activities” (Carbyn et al. 1993: 108). Population density in Badlands National Park was positively correlated with the number of animals found outside the park, suggesting density-induced emigration or range expansion (Berger and Cunningham 1994).

## **Inbreeding**

Conservation genetics are of huge concern for the management of small populations, and much work has dealt with this issue explicitly in bison (Halbert et al. 2005a, Halbert et al. 2005b, Halbert and Derr 2007). For the purpose of this review, I focus solely on how genetics may affect bison demography.

Most bison herds today are small and closed, introducing the possibility that inbreeding could affect vital rates or population growth (Wilson et al. 2005). Acute inbreeding (as opposed to chronic inbreeding) occurs when once large populations are quickly and drastically reduced in size. Acute inbreeding is often a critical problem, and may occur in certain American bison populations (Freese et al. 2007). Bison socioecology suggests that the species may be adapted to be outbred (Lott 1991). Indeed, the effective population sizes of bison at the Wichita Mountains Wildlife Refuge (Shull and Tipton 1987) and Badlands National Park (Berger and Cunningham 1994) were only 8.4-29.6% and 37.4-42.7%, respectively, of the total population sizes. Though many studies have looked at bison genetics and assessed heterozygosity, few have asked how this in turn might influence demography or abundance. Inbred bison in the Badlands National Park had lower pre-winter body weights than their less inbred counterparts (Berger and Peacock 1988), which could importantly affect over-winter survival (DelGiudice et al. 1994). Halbert et al. (2005a: 263) estimated that genetic variation in the Texas State Bison Herd was being lost, "... at a staggering rate of 30-40% within the next 50 years," and that this led to a 51-year extinction probability of 99%. Inbreeding in small herds should, however, be relatively easy to ameliorate. Halbert et al. (2005a) suggest that the introduction of new, unrelated bulls could lower the 51-year extinction probability to ~0%. Even in larger, free-ranging populations, care must be taken to ensure that management activities such as culling do not degrade genetic diversity (Gross et al. 2004).

### **Extrinsic population regulation**

In addition to the "self-limitation" of population size via density dependence and inbreeding, many external factors can affect bison abundance. The effects of disease, wolf predation, hunting by humans, and climate on individual vital rates have been discussed above (see Part II). But the impacts of these factors on overall population dynamics for bison remain under-studied and, in some cases, controversial. Simulation models suggest that bison population growth rates can be limited by disease (Peterson et al. 1991b). Fuller et al. (2007b) suggest that brucellosis vaccination in Yellowstone National Park could raise the bison population growth rate (but see Tunnicliff and Marsh 1935, Meagher 1973). Bison abundance in the Mackenzie Bison Sanctuary may be limited by internal density dependence and external wolf predation (Gates and Larter 1990). The bison population crash in the Slave River Lowlands from 1974-1983 has been attributed to a combination of disease and predation by humans and wolves (Van Camp 1987, Van Camp and Calef 1987). Wolves in Wood Buffalo National Park appear to exhibit a Type II functional response, in that their per capita kill rates are positively, but asymptotically, related to bison density (Joly 2001). In such situations, especially where wolf numerical responses are limited by their own territorial behavior (Messier 1994, Messier and Joly 2000), bison populations that grow large enough can escape from regulation of their abundance by predators. But Joly and Messier (2004) argue that tuberculosis and brucellosis limit bison populations enough so that predator regulation can occur, and that this synergy explains a long-term decline in bison abundance

in Wood Buffalo National Park. Moreover, anthrax may have been responsible for massive bison die-offs in the mid-1800s in what is now Wood Buffalo National Park (Ferguson and Laviolette 1992), though anthrax continued to be present from 1962-1991, only killing 0-0.9% of the population per year (Carbyn et al. 1993). Hemorrhagic septicemia also led to “considerable mortality” in the introduced herd of the Lamar Valley (Yellowstone National Park) during the early 1900s (Meagher 1973: 70). Bradley and Wilmshurst (2005) dispute the “disease-predation” hypothesis for Wood Buffalo National Park and show that bison populations there have recently started increasing rapidly despite constant levels of disease and predation. Bison populations can also be limited by mortality induced by vehicle collisions on large roads; this is thought to be a more important population regulation mechanism than wolf predation in Nordquist, British Columbia, bison (Rowe 2007).

Climate can also importantly affect bison vital rates and population structure. The proportion of calves in the Henry Mountains herd increased asymptotically with pre-conception precipitation (Van Vuren and Bray 1986). Population growth rate and calf recruitment in the central herd of Yellowstone National Park were negatively correlated with snow pack (Fuller 2006, Fuller et al. 2007b). Extracting data from other published studies, I assessed climate impacts on populations in other locations using autoregressive techniques widely applied to other species (Stenseth et al. 1999, Forchhammer and Post 2004, Post 2005). I generated time-series of winter snowpack in the Northwest Territories (Canada) by taking the December-March average for all weather stations in the territory from Environment Canada ([http://www.climate.weatheroffice.ec.gc.ca/climateData/canada\\_e.html](http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html)), and compared these to corresponding vital rate and abundance time-series for Wood Buffalo National Park (from Bradley and Wilmshurst 2005) and the Mackenzie Bison Sanctuary (from Larter et al. 2000). Juvenile survival rates (natural log transformed) in Wood Buffalo National Park were marginally significantly related to winter snowpack levels ( $\beta = -0.025$ ,  $R^2 = 0.218$ ,  $p = 0.068$ ). To assess the population-level impacts of climate, I used an autoregressive time-series model (c.f. Post 2005):

$$\hat{X}_t = \beta_0 + (1 + \beta_1)X_{t-1} + \sum_{i=2}^3(\beta_{t-i})X_{t-i} + \sum_{j=0}^2(\beta_{t-j})C_{t-j}$$

where  $X_t$  is the natural log of abundance in year  $t$ ,  $C_t$  is the climate measure (e.g. annual snowfall) in year  $t$ ,  $i$  and  $j$  are time lags for the effects of density and climate, respectively,  $\beta_0$  is the regression intercept, and  $\beta_h$  (for  $h = 1-6$ ) are parameter coefficients. Following the methods outlined in Post (2005), I first used maximum likelihood techniques to determine the most parsimonious autoregressive dimension, then added climate terms at different time lags to see if model fit was improved. The most parsimonious autoregressive dimension was 1 (thus the model included  $X_{t-1}$ ) and I tested the eight possible combinations of climate lags. The most parsimonious population model for the bison of Wood Buffalo National Park includes a term for snowfall at a 3-year lag ( $\beta = -0.01$ ,  $R^2 = 0.94$ , Akaike weight compared to 7 other models = 0.40). The time lag suggests that the influence of winter conditions on the population dynamics of this herd could be felt through impacts on body condition (see DelGiudice et al. 2001) that translate into differential reproduction or survival.

# PART V: POPULATION MODELS AND OUTPUT

## Existing population models for bison

Compared to many mammals, the demography of bison is relatively well researched. Different studies have employed a variety of population models for this species, generally to address two questions: the interplay of disease and demography, and the interplay of genetics and demography. Halbert et al. (2005b) used stochastic simulations to test the degradation of genetic diversity in a small, enclosed herd, and to ask how importation of animals would rectify the issue. Gross et al. (2006) used an individual-based model that combined demography and population genetics, to assess how different management strategies affected the maintenance of genetic diversity. Several models have been used to assess disease transmission rates. Peterson et al. (Peterson et al. 1991b, a) used age-structured, yearly time-step models to predict *Brucella* infection rates and the efficacy of vaccination programs in the National Bison Range and Grand Teton National Park. The *Brucella*-transmission issue has also been approached in Yellowstone with models that pooled individuals of all ages, and grouped them into “infected,” “susceptible,” and “recovered” (Dobson and Meagher 1996), and by stage-structured stochastic models (National Park Service 2000, Angliss 2003). Individual-based models have also been employed to account for stochasticity in the transmission behavior of individuals (Gross et al. 1998, Gross et al. 2002). Such individual-based models are well suited for assessing the effects of rare, highly variable, and stochastic events such as disease transmission (Gross et al. 1998). However, they generally rely on very simple, stage-structured models and are therefore not ideal for detailed demographic analyses. The simultaneous effects of disease and wolf predation have been examined with age-structured, discrete models (Joly and Messier 2004), and age-structured stochastic simulations (Bradley and Wilmshurst 2005).

## A sample population model for bison

The construction and use of matrix projection models is covered in detail in Morris and Doak (2002) and Caswell (2001). As an example of some of the ways in which they can be used, I built a series of models for a hypothetical bison herd, based on vital rates extracted from different populations. Age-

based male and female survivorship values came from Grand Teton National Park (Peterson et al. 1991b), age-based female reproduction from Wilson et al. (2002), and age-based male reproduction from Berger and Cunningham (1994). Smoothed values from logistic, linear, or quadratic functions were used rather than observed values (see Figures 1, 3, and 4), to avoid discontinuous jumps in vital rates across ages. See Table 8 for details of the model structure. The left eigenvector of the resulting deterministic matrix represents the stable age distribution, or proportion of the individuals in each age class once the population reaches equilibrium. The right eigenvector represents the reproductive value of each age class, or its relative importance to population growth. The stable age distributions for males and females are similar (Figure 8A), with inverse relationships between age and abundance in the population. The reproductive values differ between the sexes however (Figure 8B), peaking at ages 5-7 for females and 8-10 for males.

Projection matrices can also be used in “sensitivity analysis” to assess the impact of different management options on population growth rate. For example we might measure how much population growth rate changes due to small changes in various vital rates, which allows us to explore the management implications of altering those rates. The elasticity, or proportional sensitivity (Caswell 2001), of age- and sex-specific survival and reproduction rates are shown in Figure 9. As in nearly all long-lived animals (Pfister 1998), survival rates in bison have higher elasticities than reproductive rates. Commensurate with the delayed peak in male reproductive value, the reproductive elasticities peak at later ages in males than in females.

Simulations with matrix models also allow us to test the effects of different types of density dependence on population growth. In a density-independent, female-based model described using the vital rates described above, the population grows exponentially at a discrete rate of  $\lambda = 1.12$  (Figure 10). Note that the growth rate of this hypothetical population differs from those observed in actual bison populations (Table 7) since it draws on vital rates from a variety of populations. Nevertheless the estimated growth rate is close to the average growth rate among all the populations presented in Table 7. Incorporating the density-dependent calf mortality detected in the Mackenzie Bison Sanctuary (see “Density Dependence” section above) into the general bison population model described above restricts the population growth trajectory to sigmoidal over a 100-year time frame. Adding the more severe effects of density on total natural mortality detected by Berger and Cunningham (1994) in Badlands National Park restricts the growth rate and equilibrium population size substantially more.

We can also use the matrix models to assess the impact of anthropogenic influences on bison population dynamics. For each of 10,000 stochastic simulations, I iterated the population size at each year for 100 years, where each vital rate in each year was randomly drawn from a beta distribution characterized by the mean vital rate as above (in the deterministic models) and assuming 10% temporal variance. I then calculated the mean stochastic growth rate, and its confidence intervals, across several alternative management regimes. Diseases and hunting have been shown to affect bison survival rates (see Figure 2), but with the matrix models we can assess their impact on overall population growth

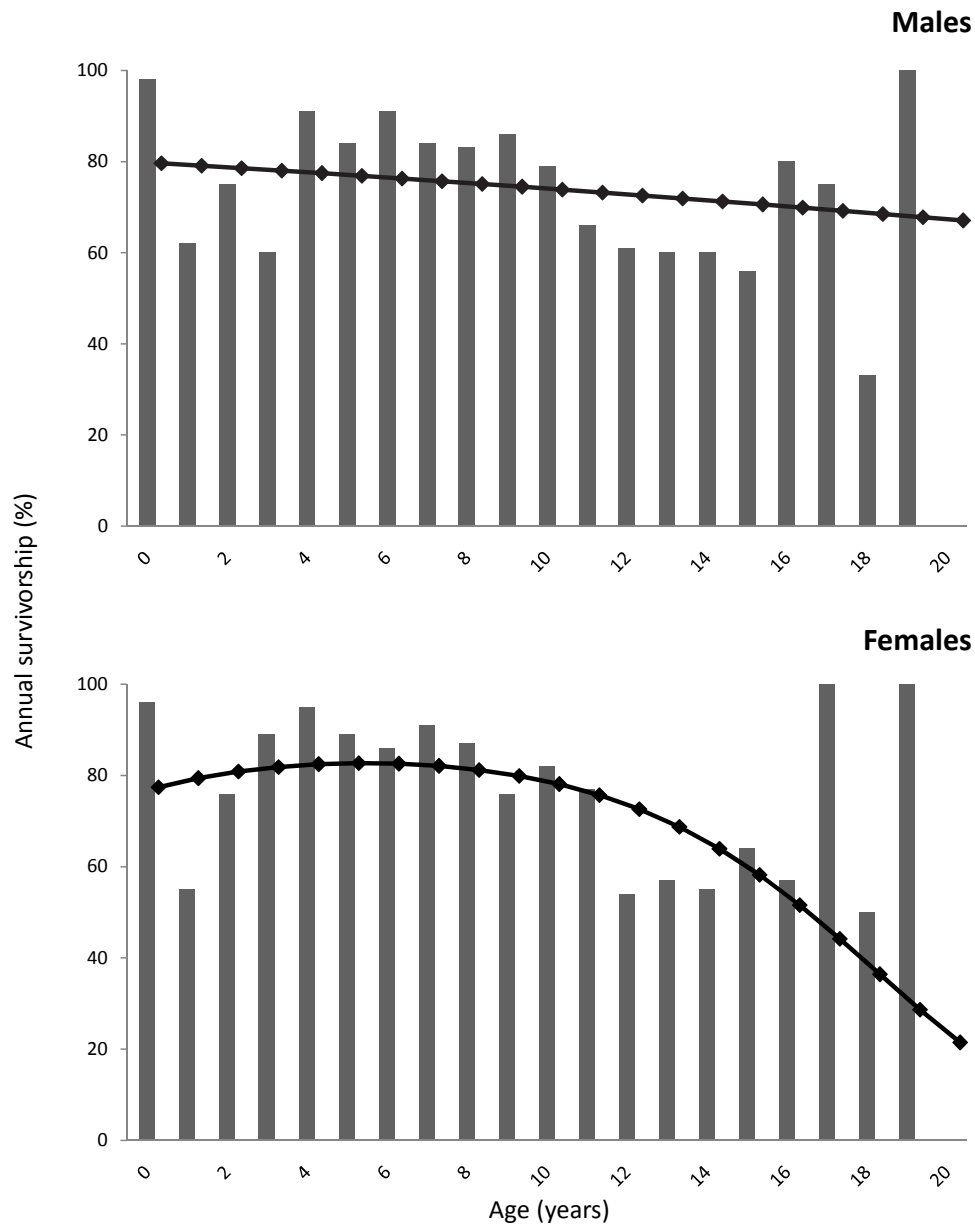


rates (Figure 11). The lowered survival rate of bison in Wood Buffalo National Park with both tuberculosis and brucellosis reduced the stochastic, density dependent growth rate by an average of 7.9%, while the lowered survival of bison in the Henry Mountains from hunting reduced the population growth rate by an average of 5.6%.

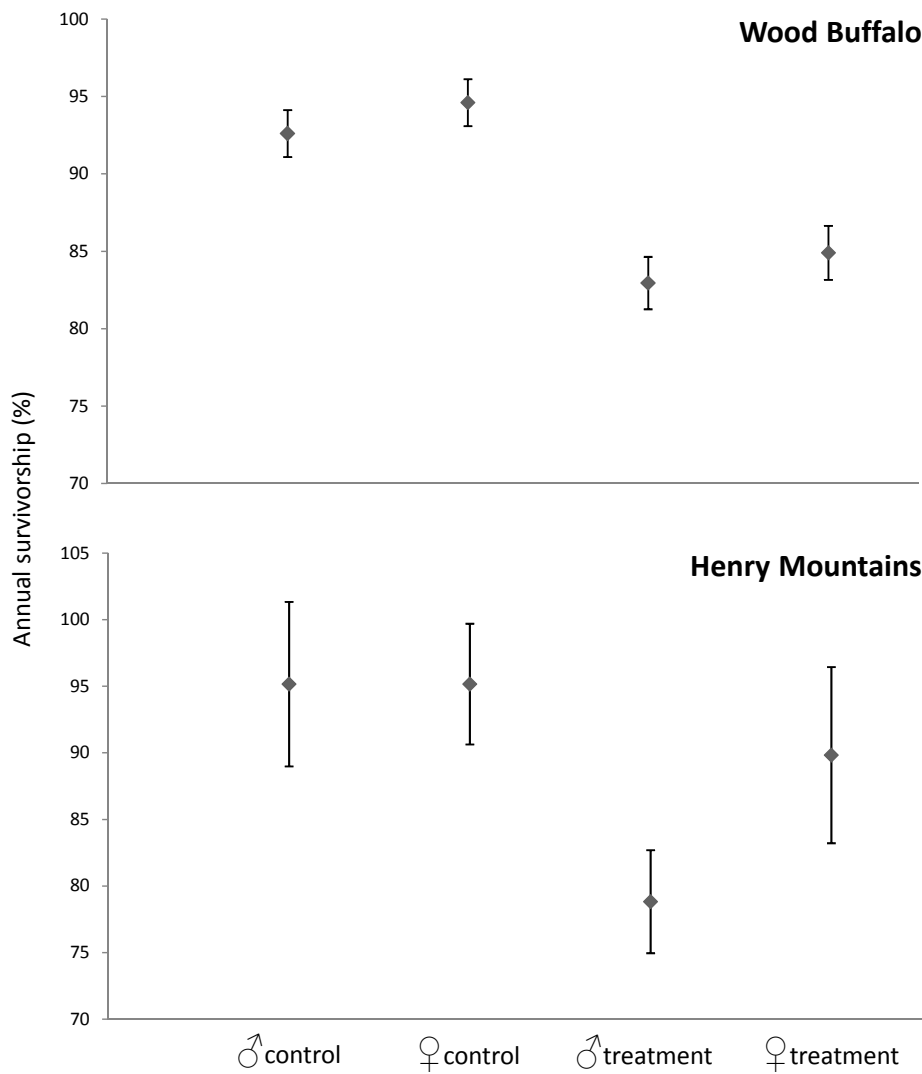
### **Sex ratio and population growth**

As noted above (see “Sex structure”), it is very difficult to determine what “natural” sex and age structures might be for bison. There is substantial variation in sex structure among extant herds, probably largely due to their different management and harvest regimes. “Natural” sex ratios may be approximately 50-60 bulls to 100 cows: 33-38% males (P. Gogan, pers. comm.). Sex structure is a relatively easy factor for bison managers to manipulate and can have important effects on population growth; thus it can serve as a useful tool for regulating herd size. I assessed how sex structure affects population growth with simulations. I assumed that managers would cull or remove calves from the herd, as these would constitute the easiest life stage to transport. I started with a two-sex model based on the sample above, and varied the calf sex ratio from 0-100% male. Assuming that at least one adult male remains in the herd that can fertilize all of the adult females, then the more the calf ratio is skewed towards females the faster the population will grow. The decline in growth rate as the percent of calves that are male goes from 0 to 90 is fairly slow and linear; above 90% male the population growth rate declines quickly (see Figure 12). Thus the manipulation of calf sex ratio can importantly affect population growth rate. However, care must usually be taken that culling and removal programs do not contribute to a loss of genetic variability in the herd (Gross et al. 2006). In a series of simulations, Gross et al. (2006) tested how well various population control options maintained genetic diversity in bison herds, and concluded that, “...strategies that increase generation time, such as removal or contraception of young animals, most effectively retain genetic variation” (Gross et al. 2006: 3).

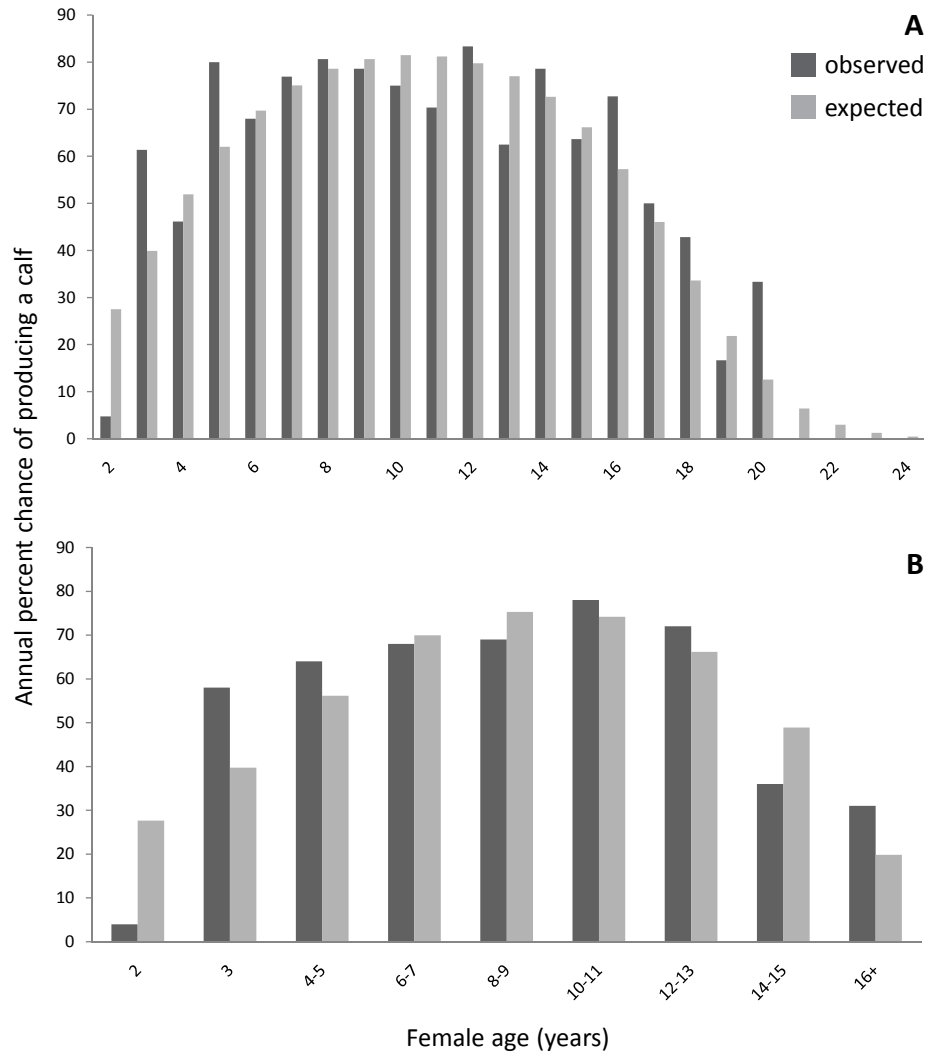
**Figure 1:** Average survivorship for each age (gray bars) from the Wichita Mountains Wildlife Reserve (Shull and Tipton 1987), overlain with fitted logistic functions (black lines) where, for males,  $\hat{y} = \frac{e^{1.396-0.033x}}{1+e^{1.396-0.033x}}$  and for females,  $\hat{y} = \frac{e^{1.291+0.134x-0.013x^2}}{1+e^{1.291+0.134x-0.013x^2}}$



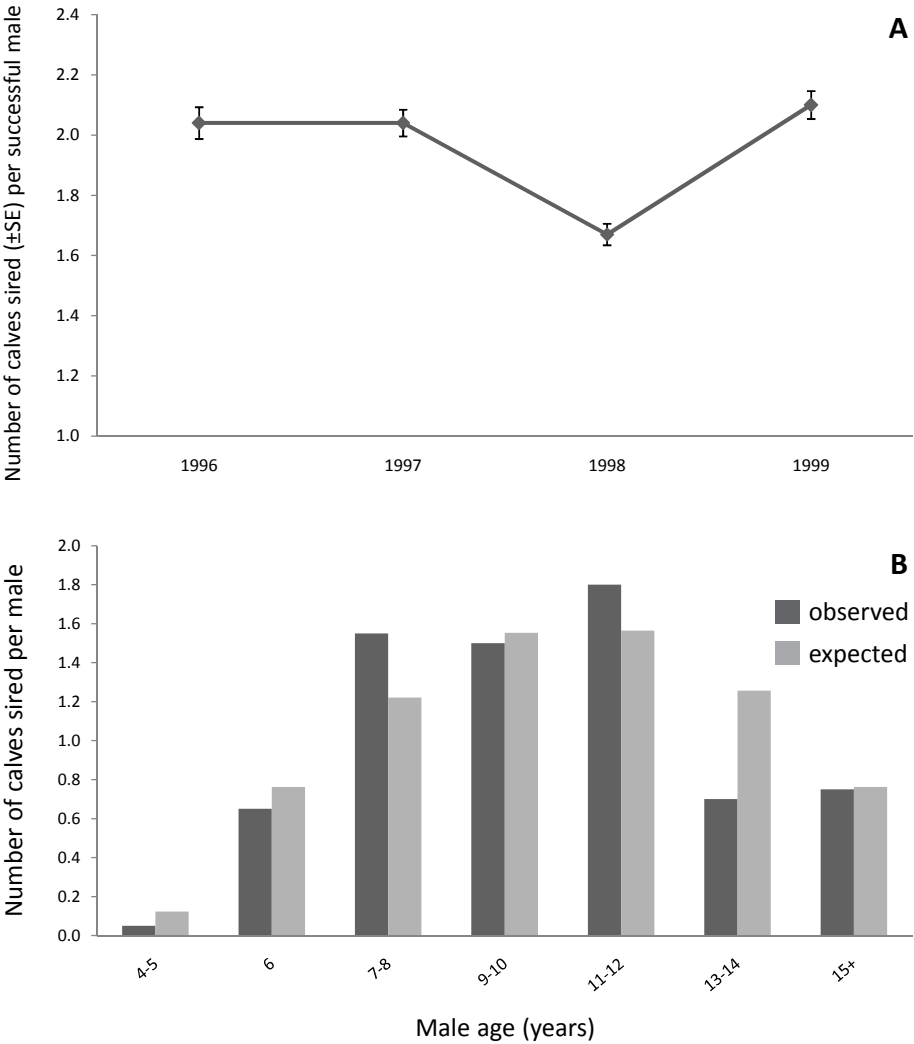
**Figure 2:** Adult survivorship by sex in Wood Buffalo National Park (“control” = 0-1 diseases, “treatment” = tuberculosis + brucellosis) (Bradley and Wilmschurst 2005) and the Henry Mountains (“treatment” = hunting) (Van Vuren and Bray 1986). Error bars show temporal standard deviation.



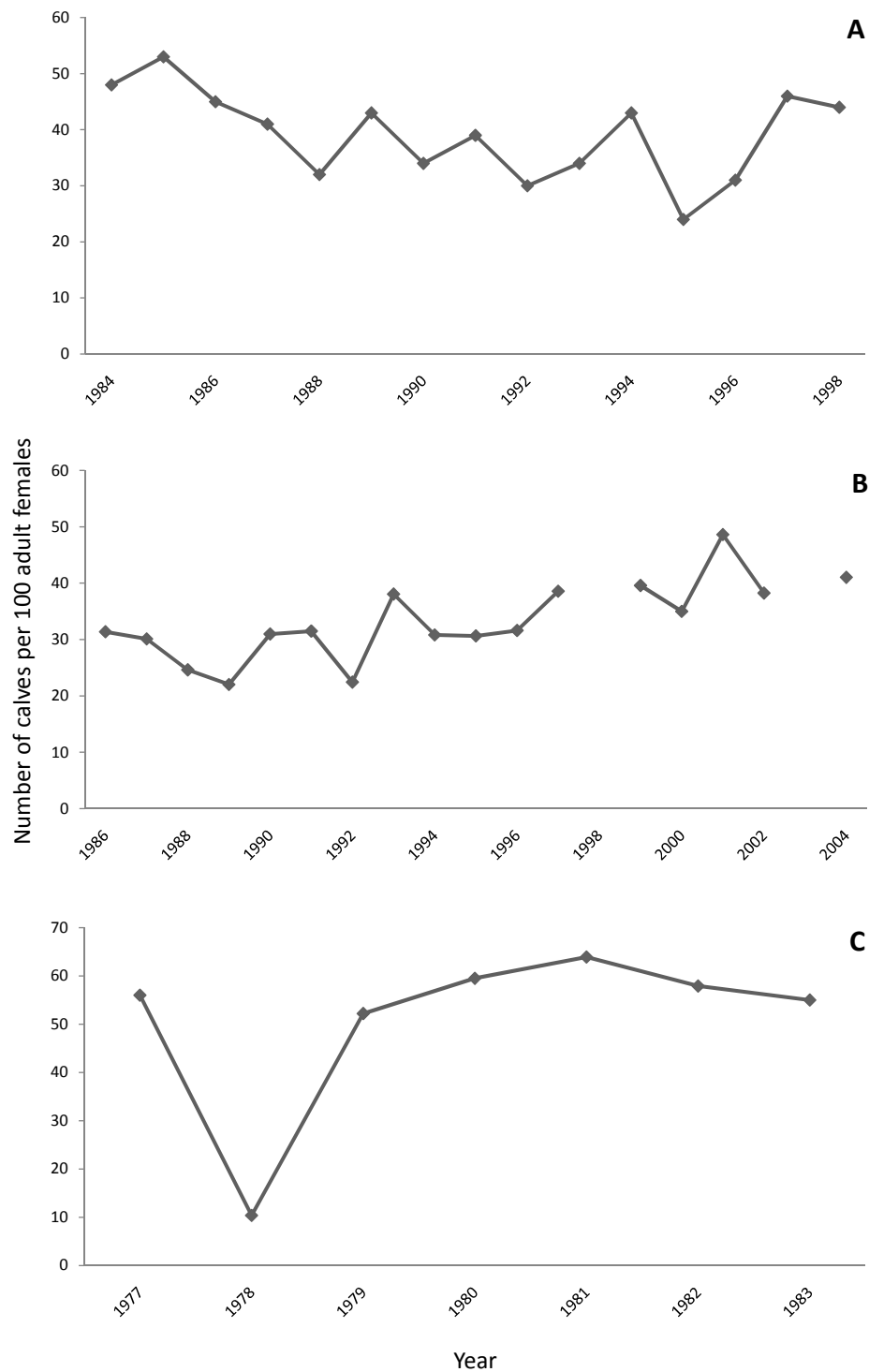
**Figure 3:** Observed annual female reproduction by age (gray bars) and expected reproduction (black bars) from a fitted logistic function A) in Elk Island National Park (Wilson et al. 2002) where  $\hat{y} = \frac{e^{-2.300+0.738x-0.036x^2}}{1 + e^{-2.300+0.738x-0.036x^2}}$  (log likelihood: LL = -246.47,  $p < 0.001$ ), and B) in Badlands National Park (Berger and Cunningham 1994) where  $\hat{y} = \frac{e^{-2.298+0.750x-0.041x^2}}{1 + e^{-2.298+0.750x-0.041x^2}}$  (LL = -188.31,  $p < 0.001$ ).

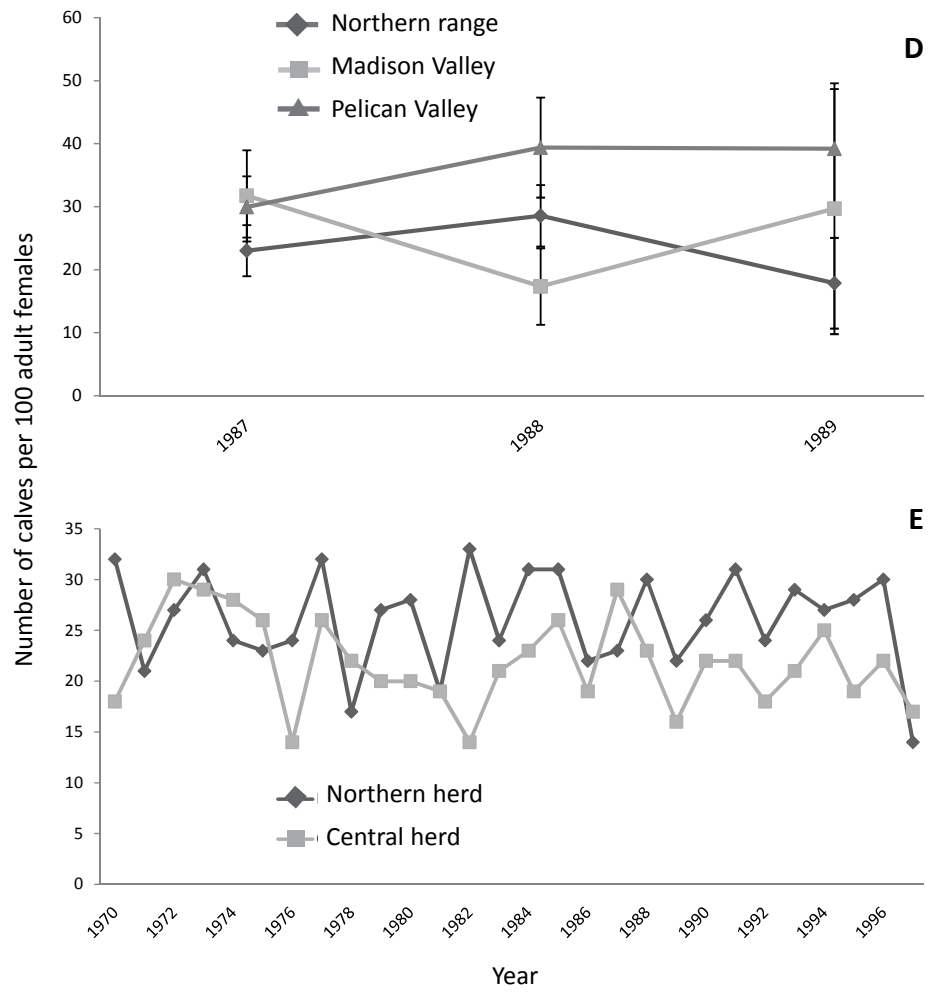


**Figure 4:** A) Annual male reproduction over 4 years in Elk Island National Park (Wilson et al. 2002). B) Observed annual male reproduction (gray bars) across age classes in Badlands National Park (Berger and Cunningham 1994) and expected reproduction (black bars) from a fitted function ( $F_{2,188} = 343.2$ ,  $R^2 = 0.785$ ,  $p < 0.001$ ), where  $\hat{y} = -2.874 + 0.846x - 0.040x^2$

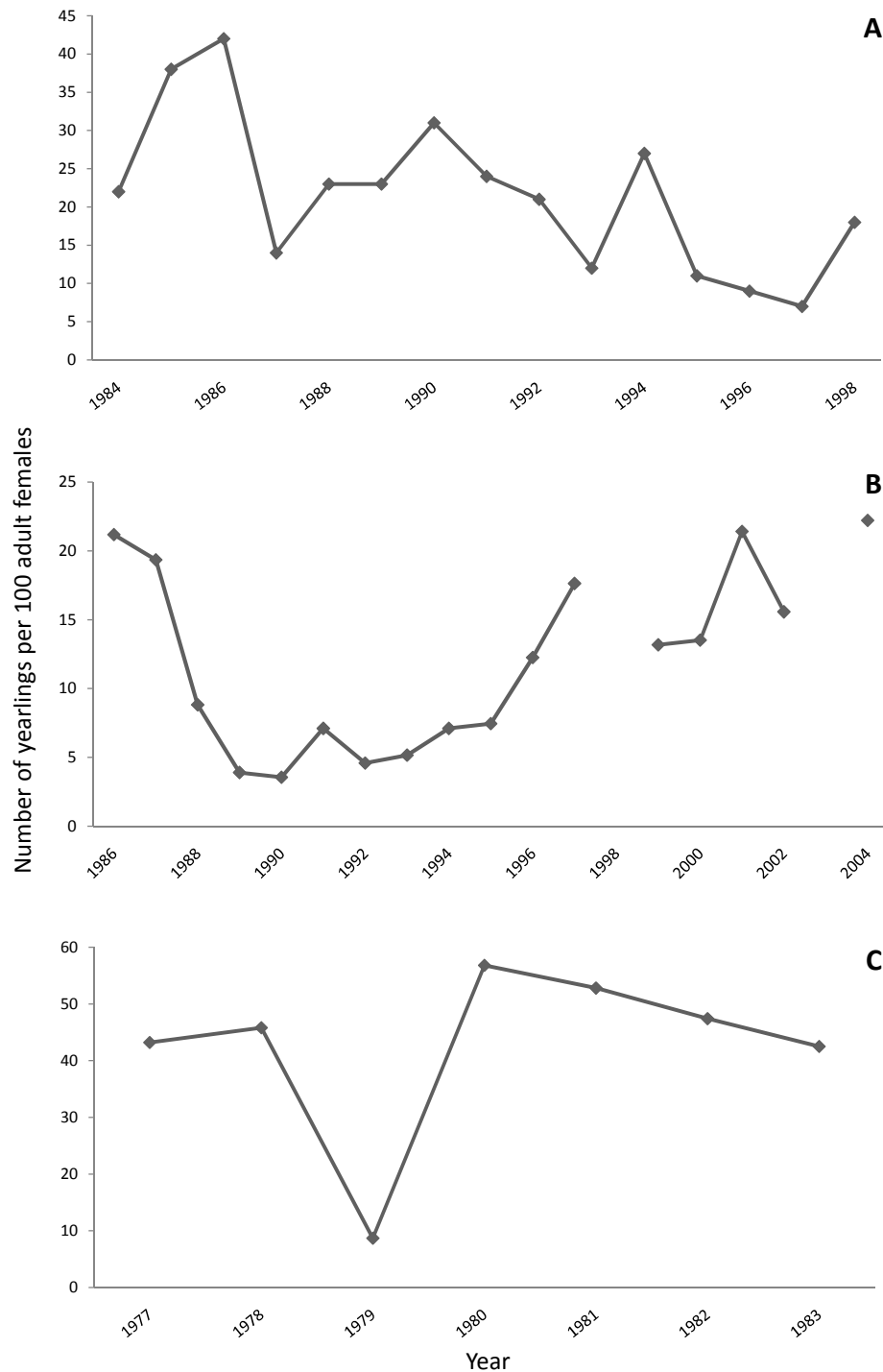


**Figure 5:** Calf:cow ratios over time in A) the Mackenzie Bison Sanctuary (Larter et al. 2000), B) Wood Buffalo National Park (Bradley and Wilmshurst 2005), C) the Henry Mountains (Van Vuren and Bray 1986), D) Yellowstone National Park (DelGiudice et al. 2001) and E) Yellowstone National Park (Fuller et al. 2007b).



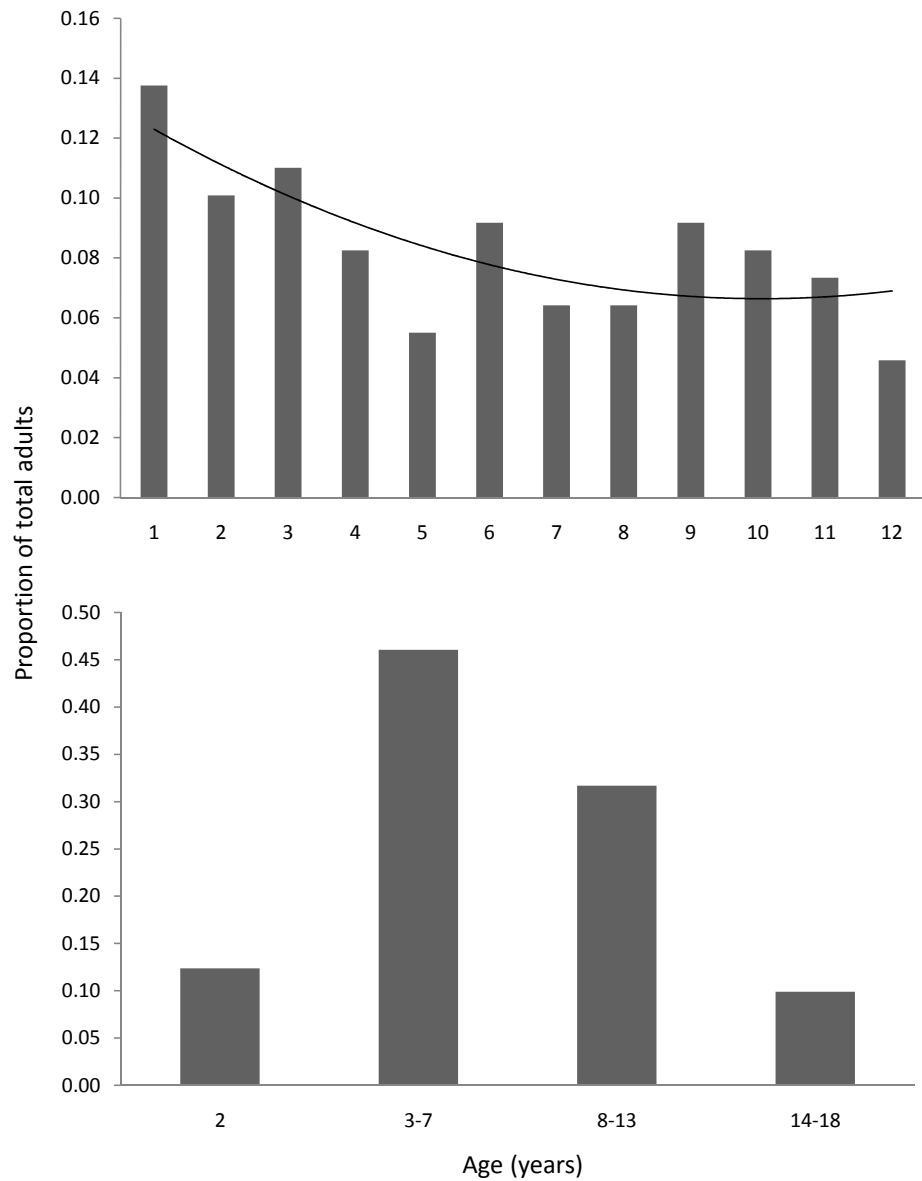


**Figure 6:** Yearling:cow ratios over time in A) the Mackenzie Bison Sanctuary (Larter et al. 2000), B) Wood Buffalo National Park (Bradley and Wilmschurst 2005), and C) the Henry Mountains (Van Vuren and Bray 1986).

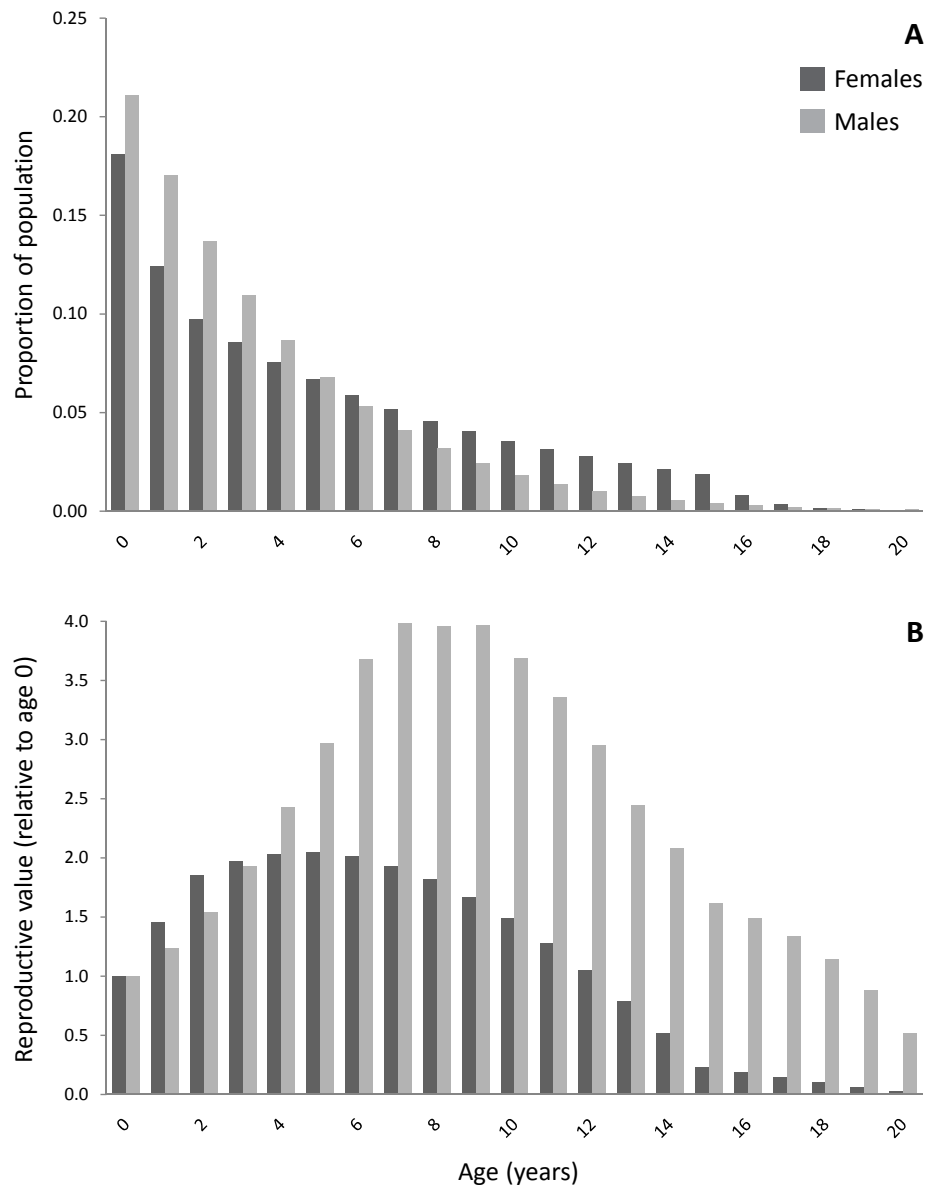




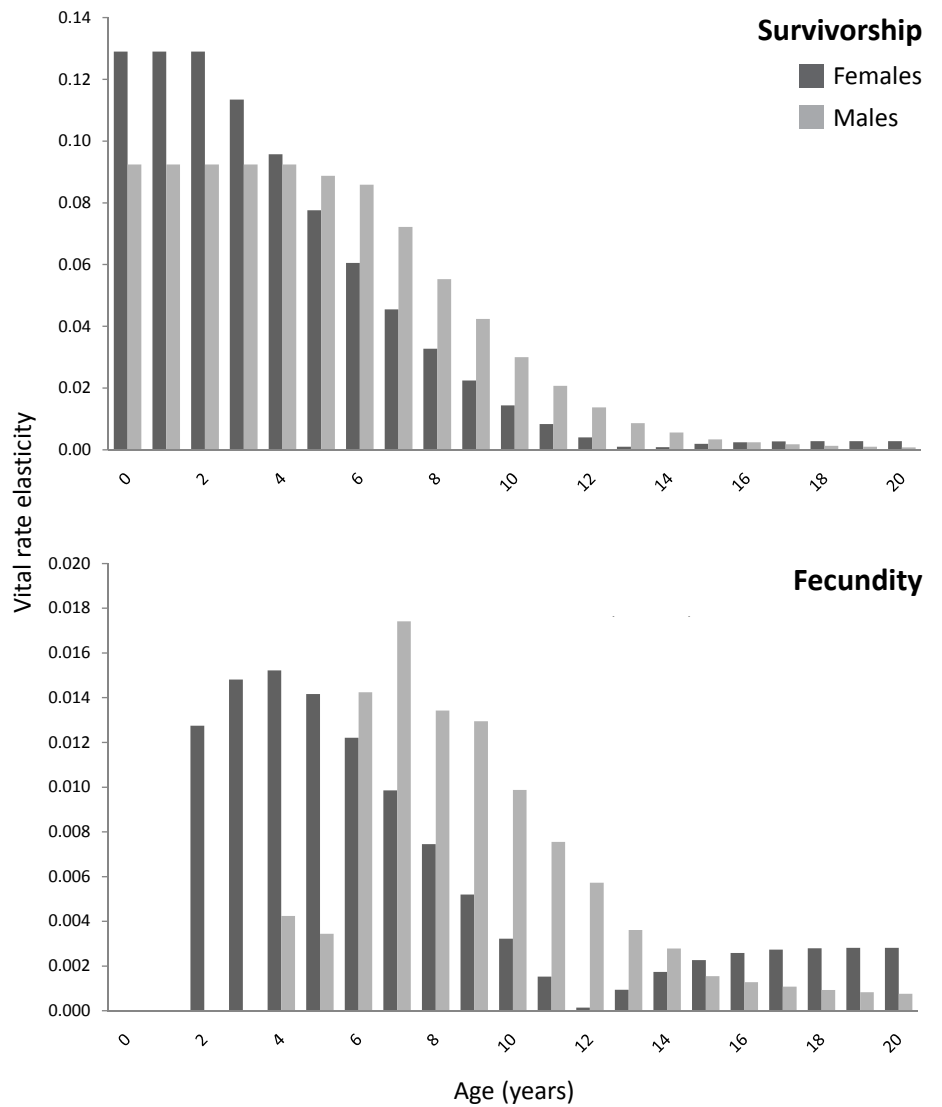
**Figure 7:** Age structure of A) adult males in the Fort Niobrara Wildlife Reserve (Maher and Byers 1987) overlain with polynomial trend line where  $\hat{y} = 0.136 - 0.014x + 0.001x^2$ , and B) adult females in the Wichita Mountains Wildlife Reserve (Shaw and Carter 1989).



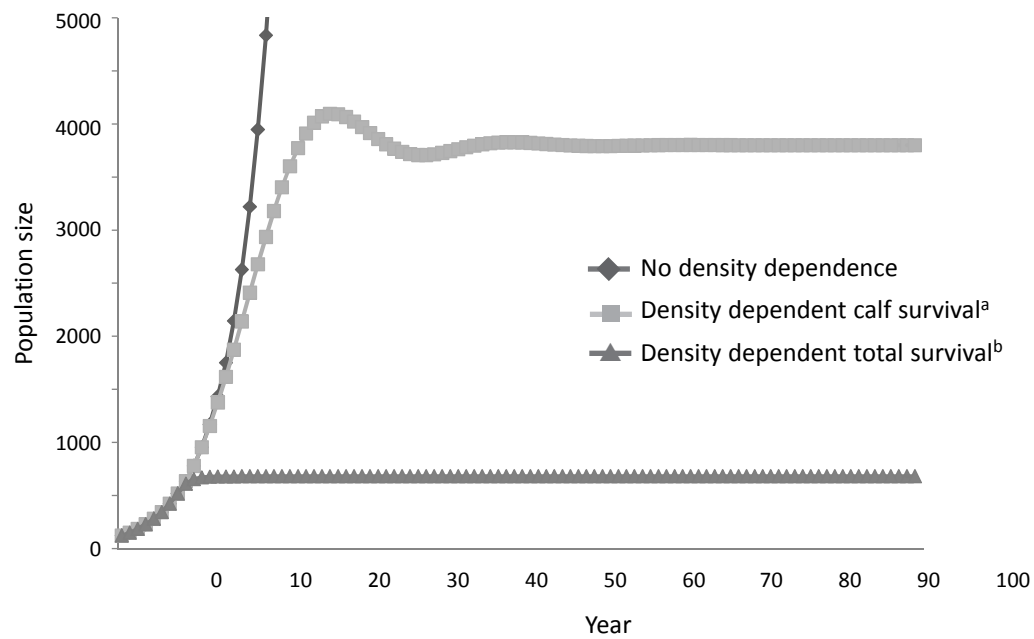
**Figure 8:** Stable age distribution (A) and age-specific reproductive values (B) from the deterministic matrix projection models described in Part V.



**Figure 9:** Elasticities of survivorship and fecundity vital rates from the deterministic matrix projection models described in Part V.



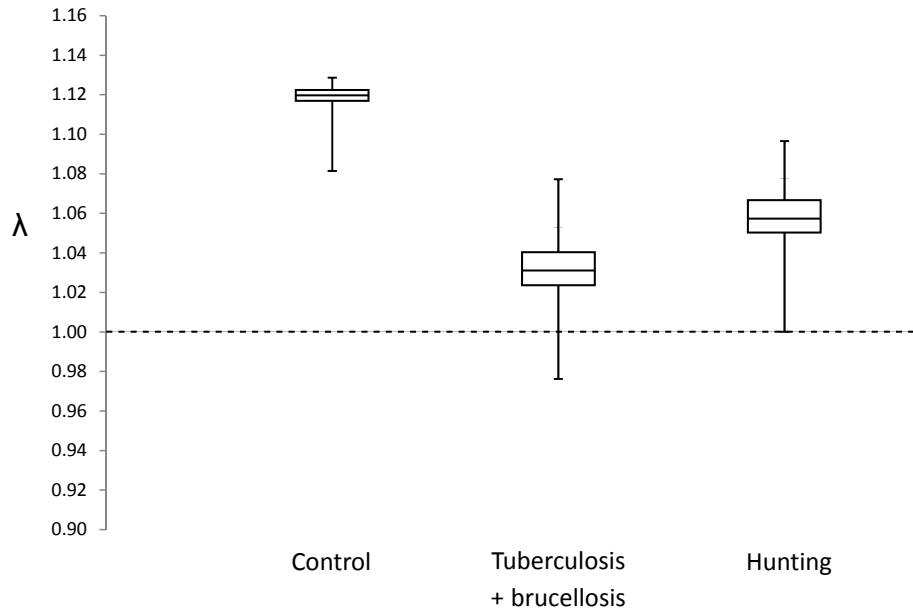
**Figure 10:** Effects of population density on population growth, from deterministic matrix projection models described in Part V.



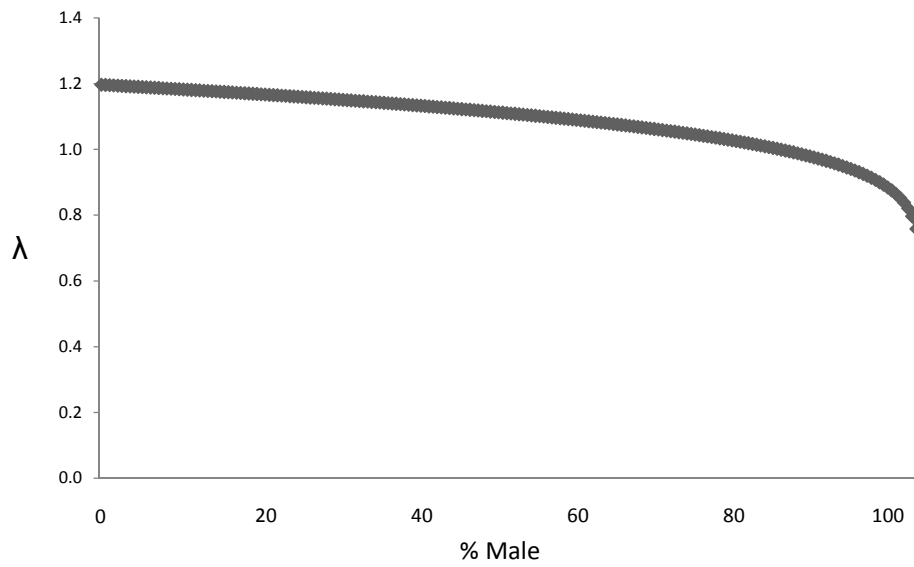
<sup>a</sup> Data analyzed from Larter et al. (2000)

<sup>b</sup> From Berger and Cunningham (1994)

**Figure 11:** Effects of tuberculosis + brucellosis (from July 2001) and hunting (from Van Vuren and Bray 1986) on the density-dependent, stochastic population growth rate of bison, from matrix projection models described in Part V. Horizontal lines and boxes show mean population growth rate ( $\lambda$ ) and 25% confidence intervals, respectively; error bars show 90% confidence intervals.



**Figure 12:** Population growth rate ( $\lambda$ ) as a function of the percent of total calves that are male, assuming that enough adult bulls remain in the herd to fertilize all of the adult females.



**Table 1:** Bison herds for which published demographic data is currently available, and the history and major anthropogenic influences on each.

Bison herd	Acronym	Location	Management and major anthropogenic influences
Badlands National Park	BNP	South Dakota (USA)	Plains bison introduced in 1963. Annual removals of individuals except from 1985-1989 (during the Berger and Cunningham [1994] study), though some poaching continued during this time. Fenced.
Etthithun Bison Herd	EBH	British Columbia (Canada)	43 wood bison introduced in 2000, heavily female-biased.
Elk Island National Park	EINP	Alberta (Canada)	Wood bison introduced in the 1960s from WBNP. Area fenced, herd "semi-wild." Bison removed annually. Likely free of brucellosis and tuberculosis.
Fort Niobrara Wildlife Reserve	FNWR	Nebraska (USA)	Plains bison introduced in 1913; animals removed annually. Fenced.
Grand Teton National Park	GTNP	Wyoming (USA)	Herd formed from enclosure escapees in 1968, roams into the Jackson Hole (Wyoming) area and the National Elk Refuge, at the latter they may receive supplemental feeding. Hunting and some culling.
Henry Mountains	HM	Utah (USA)	Plains bison introduced in 1941; hunted through present.
Hook Lake	HL	Northwest Territories (Canada)	Brucellosis- and tuberculosis-free bison introduced from WBNP in 1996-98. Small, fenced herds.
Mackenzie Bison Sanctuary	MBS	Northwest Territories (Canada)	Brucellosis- and tuberculosis-free bison introduced from WBNP in 1963.
National Bison Range	NBR	Montana (USA)	Bison introduced in 1910, culled annually since the 1920s. Area fenced.
Slave River Lowlands	SRL	Northwest Territories (Canada)	Wood bison never extirpated, mixed with wood-plains hybrids expanding from WBNP since the late 1920s. Free-roaming.
Texas State Bison Herd	TSBH	Texas (USA)	Herd descended from 5 calves captured from the wild in the 1880s. Heavily managed, including supplemental feed and vaccinations. Likely disease-free.
Wichita Mountains Wildlife Reserve	WMWR	Oklahoma (USA)	Plains bison introduced in 1907. Area fenced; animals removed annually.
Wind Cave National Park	WCNP	South Dakota (USA)	Bison free-ranging; animals removed annually. Fenced.
Wood Buffalo National Park	WBNP	Northwest Territories (Canada)	Wood bison never exterminated, plains bison introduced in 1925-26, along with brucellosis and tuberculosis. Vaccinations and culling occurred until 1972.
Yellowstone National Park	YNP	Wyoming, Montana, Idaho (USA)	Plains bison never extirpated, but individuals added to population in early 1900s. Some food and penning in the decades thereafter; since 1968 the population has been left to "natural regulation" in the park itself, though individuals that leave the park are killed. From 1985-2005, an average of 6.4% of the herd ( $SD = 7.98$ ) has been culled annually (Treanor et al. 2007).

**Table 2:** Survivorship across different studies, stratified by age and gender. Sample sizes (where available) in parentheses. See Table 1 for interpretation of location acronyms.

Age	♀ Survival (%)			♂ Survival (%)
	NBR <sup>a</sup>	GTNP <sup>a</sup>	WMWR <sup>b</sup>	WMWR <sup>b</sup>
0	94	77	96 (655)	98 (681)
1	98	88	55 (632)	62 (665)
2	99	99	76 (350)	75 (414)
3	99	99	89 (265)	60 (311)
4	99	99	95 (235)	91 (186)
5	99	99	89 (224)	84 (170)
6	99	99	86 (200)	91 (143)
7	99	99	91 (171)	84 (130)
8	99	99	87 (155)	83 (109)
9	99	99	76 (135)	86 (91)
10	99	99	82 (103)	79 (78)
11	99	99	77 (84)	66 (62)
12	99	99	54 (65)	61 (41)
13	98	98	57 (35)	60 (25)
14	98	98	55 (20)	60 (15)
15	50	50	64 (11)	56 (9)
16			57 (7)	80 (5)
17			100 (4)	75 (4)
18			50 (4)	33 (3)
19			100 (2)	100 (1)
20	?	?	0 (2)	0 (1)

<sup>a</sup> Flocchini, unpub. data; cited in Peterson et al. 1991

<sup>b</sup> Shull and Tipton 1987



**Table 3:** Female pregnancy rates across different studies. See Table 1 for interpretation of location acronyms.

Location	Years studied	Percent adult cows pregnant	Reference
YNP –Lamar Valley	1931-32	65	Meagher 1973
YNP –Lamar Valley	1940-50	81.9	Meagher 1973
YNP	1964-66	52	Meagher 1973
YNP -Mary Mountain	1990-92	37-45 <sup>a</sup>	Kirkpatrick et al. 1996
YNP -Northern Range	1990-92	49-54 <sup>a</sup>	Kirkpatrick et al. 1996
YNP	1996-97	78.5 <sup>b</sup>	Aune et al. 1998
YNP	1995-2001	88 <sup>c,d</sup>	Fuller et al. 2007b
NBR	1957-67	86 <sup>e</sup>	Rutberg 1986
EINP	1996-99	50-70 <sup>f</sup>	Wilson et al. 2002
MBS	1984-88	70 <sup>c,e</sup>	Gates & Larter 1990
WBNP	1952-74	47 <sup>e</sup>	Carbyn et al. 1993g
WBNP -Hay Camp & Delta	1998-99	62-72 <sup>c</sup>	Joly 2001
WBNP -Nyarling River	1998-99	54-89 <sup>c</sup>	Joly 2001

<sup>a</sup> Based on urinary & fecal steroid analysis

<sup>b</sup> Based on ovarian analysis

<sup>c</sup> Based on blood hormone assays

<sup>d</sup> Based on ultrasound

<sup>e</sup> Based on autopsies

<sup>f</sup> Based on genetic assignment

<sup>g</sup> Including references therein

**Table 4:** Female calving percentages across different studies. See Table 1 for interpretation of location acronyms.

Location	Percent adult cows that calve per year	Reference
SRL	<50	Van Camp and Calef 1987
YNP	52	Meagher 1973
NBR	88	Rutberg 1986
WMWR	67	Halloran 1968
FNWR & WCNP	78	Haughen 1974
TSBH	19.0-73.3	Halbert et al. 2005

**Table 5:** Female pregnancy rates across different studies, stratified by age or age class. Sample sizes (where available) in parentheses. See Table 1 for interpretation of location acronyms.

	Pregnancy percentage					Calving percentage			
Age	YNP <sup>1</sup>	YNP <sup>2</sup>	WMWR <sup>3</sup>	NBR <sup>4</sup>	WBNP <sup>5</sup>	EINP <sup>6</sup>	NBR <sup>7</sup>		BNP <sup>8</sup>
2	14 (7)	70 (10)	8		37 (317)	5 (42)	12 (25)		4 (24)
3	27 (11)	70 (10)	75	80 (20)	55 (303)	61 (44)	71 (93)		58 (26)
4	71 (7)	95 (19)	93	88 (75)	60 (246)	46 (39)			64 (48)
5	63 (46)		93		61 (324)	80 (35)			
6			93			68 (25)			68 (41)
7		92 (12)	93			77 (26)			
8			93			81 (31)	81 (64)		69 (44)
9		50 (8)	92			79 (28)			
10			92			75 (28)			78 (48)
11			92			70 (27)			
12			92			83 (18)			72 (30)
13			92			63 (16)			
14			80			79 (14)	45 (20)		36 (23)
15			80			64 (11)			
16						73 (11)			31 (24)
17						50 (8)			
18						43 (7)			
19						17 (6)			
20	?	?		?	?	33 (3)			?

<sup>1</sup> Meagher 1973; study: 1964-1966

<sup>2</sup> Aune et al. 1998; study: 1995-1997

<sup>3</sup> Shaw and Carter 1989; study: 1981-1988

<sup>4</sup> Flocchini, unpub. data; cited in Peterson et al. 1991

<sup>5</sup> Carbyn et al. 1990 and references therein

<sup>6</sup> Wilson et al. 2002; study: 1996-1999

<sup>7</sup> Rutberg 1986

<sup>8</sup> Berger and Cunningham 1994

**Table 6:** Calf sex ratios before and after birth across different studies. Sample sizes (where available) in parentheses. See Table 1 for interpretation of location acronyms.

Location	Percent of calves that were male	Reference
NBR	62.2 (82) <sup>a</sup>	Rutberg 1986
YNP	56.6 (921) <sup>a</sup>	Meagher 1973
FNWR & WCNP	54.5 (101) <sup>a</sup>	Haugen 1974
WBNP	53 (472) <sup>a</sup>	Fuller 1962
BNP	50.6 (397) <sup>b</sup>	Berger and Cunningham 1994
WMWR	51 (5633) <sup>b</sup>	Halloran 1968
WMWR	45.9 (122) <sup>b</sup>	Shaw and Carter 1989
EINP	54.4 (215) <sup>b</sup>	Wilson et al. 2002
FNWR	41.9 (205) <sup>b</sup>	Wolff 1998

<sup>a</sup> Calves in utero

<sup>b</sup> Calves born

**Table 7:** Estimated mean population growth rate ( $\lambda$ ) across different studies. See Table 1 for interpretation of location acronyms.

Location	Years studied	$\lambda$ (95% C.I.)	Reference
TSBH	1997-2002	1.021 (0.904, 1.154) <sup>a</sup>	Halbert et al. 2005
HM	1949-1982	1.038 (0.925, 1.164) <sup>a</sup>	Van Vuren and Bray 1986
NBR	1909-1922	1.221 (1.179, 1.266) <sup>a</sup>	Fredin 1984
YNP	1970-2005	1.07 <sup>b</sup>	Fuller et al. 2007b
YNP –Northern	1970-1990	1.047 (0.897, 1.222) <sup>a</sup>	Fuller et al. 2007b
YNP –Northern	1970-1997	1.018 (0.885, 1.171) <sup>a</sup>	Fuller et al. 2007b
YNP –Central	1970-1990	1.087 (1.034, 1.141) <sup>a</sup>	Fuller et al. 2007b
YNP –Central	1970-1997	1.048 (0.987, 1.113) <sup>a</sup>	Fuller et al. 2007b
BNP	1964-1972	1.108 <sup>c</sup>	Berger and Cunningham 1994
BNP	1985-1989	1.167 <sup>c</sup>	Berger and Cunningham 1994
MBS	1963-1989	1.223 (1.135, 1.317) <sup>a</sup>	Larter et al. 2000
MBS	1963-1998	1.151 (1.068, 1.242) <sup>a</sup>	Larter et al. 2000
SRL	1948-1983	1.003 (0.898, 1.120) <sup>a</sup>	Van Camp and Calef 1987
EBH	2000-2006	1.19 <sup>c</sup>	Rowe and Backmeyer 2006
WBNP -Delta	1970-1999	0.914 (0.896, 0.932) <sup>c</sup>	Joly and Messier 2004
WBNP -Hay Camp	1970-1999	0.970 (0.942, 0.980) <sup>c</sup>	Joly and Messier 2004
WBNP -Garden River	1970-1999	1.020 (0.990, 1.062) <sup>c</sup>	Joly and Messier 2004
WBNP -Little Buffalo	1970-1999	1.030 (0.905, 1.062) <sup>c</sup>	Joly and Messier 2004
WBNP -Nyarling River	1970-1999	1.139 (1.041, 1.246) <sup>c</sup>	Joly and Messier 2004
WBNP -all 5 populations	1971-1999	0.950 (0.912, 0.990) <sup>a</sup>	Bradley and Wilmshurst 2005
WBNP -all 5 populations	2000-2003	1.089 (0.778, 1.523) <sup>a</sup>	Bradley and Wilmshurst 2005

<sup>a</sup> Population growth rate calculated by author from data in study

<sup>b</sup> Population growth rate presented in study, calculated from matrix model

<sup>c</sup> Population growth rate presented in study

**Table 8:** Structure of the sample deterministic, female-based matrix projection model for bison described in Part V.

Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
0	0	0	0.136	0.198	0.257	0.307	0.345	0.372	0.389	0.399	0.403	0.402	0.395	0.377	0.356	0.166	0.143	0.115	0.084	0.055	0.032
0.770	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.880	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0.990	0	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.990	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.980	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.980	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.500	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.500	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.500	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.500	0

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