POPULATION DEMOGRAPHY OF THE YELLOWSTONE NATIONAL PARK BISON HERDS

by

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ABSTRACT

The bison population of Yellowstone National Park (YNP) represents an outstanding conservation success story, as their numbers have increased from just 46 in 1902 to >4,000 today. Bison are keystone herbivores in YNP, and are central to several management controversies due to their infection with brucellosis. I integrated 100 years of historical count data with 7 years of recent vital rate data, and parameterized a matrix model using these vital rates to validate population growth estimates and to project future management scenarios involving disease control through vaccination and/or culling programs. From count data, I determined that historical population growth rates were heavily influenced by supplemental feeding, resulting in high population growth rates ($\lambda = 1.17$). I found evidence for density dependence in two subpopulations, the northern and central herds. The herds displayed divergent population dynamics over 1970-1981 and 1982-2000, as density dependence weakened in the northern herd and increased in the central herd, and herd growth rates were negatively correlated after 1982 (R^2=0.40, P<0.01) I postulate the severe winter of 1982 catalyzed emigration from the central herd to the northern herd. Survival and birth rates did not differ between the herds 1995-2001, and calf-adult ratios did not differ between the herds or the periods. I found that snow pack was negatively associated with the central herd population growth rates, and with spring calf ratios and recruitment (R^2=0.26–0.60, P<0.05). Birth rates were not variable with density-dependent or density-independent factors, but did vary according to serological status for brucellosis and with age structure, as primiparous bison had lower birth rates than adults. I did not detect reproductive or survival senescence. Adult survival rates were high and static (0.92). Integrating these vital rates into a matrix model resulted in a population growth rate estimate of λ=1.07, which closely corroborated an estimate of λ from count data during 1990-2000 (λ=1.05). Simulating the effects of brucellosis eradication through vaccination programs resulted in $\lambda = 1.09$, roughly a 29% increase. I concluded brucellosis eradication could further increase bison population growth rates, exacerbating conflicts outside YNP.

CHAPTER 1

A CENTURY OF DEMOGRAPHIC CHANGE IN YELLOWSTONE'S BISON HERDS

Abstract

Understanding the relative importance of density-dependent and density-independent feedback on population growth is essential for developing management strategies to conserve wildlife. I examined a 99-year time series of annual counts and removals for two bison (*Bison bison*) herds occupying Yellowstone National Park in the western United States. Aggressive management intervention was effective at recovering bison from 46 animals in 1902 to >1,500 animals in 1954. Supplemental feeding of the northern herd facilitated rapid growth ($r = 0.16$) during 1902-1952. Augmentation of the central herd with 71 animals also led to rapid growth over 1936-1954 ($r = 0.10$). Manipulative management ceased in the park during 1969, and I detected evidence of density-dependent changes in population growth rates for both herds during 1970-2000 as numbers increased to >3,000 animals. The central herd showed evidence of density dependence over 1970-2000. In contrast, density dependence had a stronger effect on the northern herd's growth rate during 1970-1981 than during 1982-2000. I found evidence to suggest these trends resulted from pulses of emigration from the central herd to the northern range beginning in 1982 in response to resource limitation generated by an interaction between density and severe snows. Corroborative evidence supporting this interpretation included: 1) the annual growth of the central herd was negatively correlated with snow pack but the northern herd was not; 2) growth rates of the central and northern herds were uncorrelated during 1970 to 1981, but significantly and negatively correlated during 1982-2000; and 3) the northern herd could not have sustained the high removals during 1984-2000 without immigration. Density-related emigration from the central herd to the northern range has important implications for managers tasked with conserving bison, while reducing the potential risk of brucellosis transmission outside the park.

Introduction

Processes that regulate the abundance of wildlife are of basic interest to ecologists. It is widely accepted that increasing density regulates ungulate populations through declining forage quality and quantity, negatively influencing nutrition and body condition and decreasing survival and reproductive rates (Sinclair 1975, Caughley 1976, Eberhardt 2002). Stochastic effects of climate, such as droughts or heavy snows, can exacerbate these effects by further reducing the availability of forage and/or increasing energetic costs of foraging and locomotion (Clutton-Brock et al. 1985, Sæther 1997, Gaillard et al. 2000). Most recent reviews of large herbivore dynamics focused on density-related effects on survival and reproduction, but few studies have considered the possibility of spatial responses to increasing density, which may be equally plausible (Sæther et al. 1999, Amarasekare 2004). Emigration and range expansion have been documented in several large ungulate populations when forage quantity or quality decreased due to density-dependent resource consumption (Lemke et al. 1998, Aanes et al. 2000, Larter et al. 2000, Ferguson et al. 2001).

The mechanisms underlying density-dependent feedbacks on population growth of bison (*Bison bison*) in Yellowstone National Park are of special interest to ecologists and park managers. As bison numbers increased from 46 animals in 1902 to nearly 5,000 animals in 2005, bison expanded their range and began crossing the park boundary into adjacent areas of Montana (Gates et al. 2005). Range expansion was likely a natural response to increasing population density (Bjornlie and Garrott 2001, Gates et al. 2005).

However, the increase in abundance and egress may have been facilitated by the presence of mechanically snow-packed roads for snowmobiles in the central and western areas of Yellowstone that provided energy-efficient travel routes to lower-elevation areas where forage was more readily-available, thereby lessening winter mortality and resulting in increased population growth (Meagher 1993). Regardless of the underlying cause, range expansion is of great interest because bison are possible, though unproven, vectors of brucellosis (*Brucella abortus*) to cattle and a perceived threat to the brucellosis-free status of Montana (Cheville et al. 1998, National Park Service 2000).

Understanding the population demography of Yellowstone bison is essential for developing feasible management strategies for their conservation and addressing controversies over how and why bison leave Yellowstone. Fortunately, there is an unusually long time series of count and removal data spanning 99 years as management efforts shifted from intensive husbandry to "natural regulation" whereby bison numbers were allowed to fluctuate without any direct manipulations within the park (Leopold 1963, Cole 1971, Meagher 1973). I took advantage of this unique time series to analyze how bison responded to differing management actions during the first half of the 20th century and to evaluate the strength of relationships between density and weather covariates during the second half of the century by evaluating multiple competing model formulations of population dynamics (Zeng et al. 1998).

Study Area

Yellowstone National Park encompassed 9,018 km^2 in the western United States, including portions of Wyoming, Montana, and Idaho. The bison population existed almost entirely within the boundaries of the Park and consisted of the central and northern herds. These herds were spatially distinct before the 1980s, but recent information suggests interchange may be occurring (Hess 2002, Gates et al. 2005). Present-day ranges of the central and northern herds were comparable in size (1200 km^2; Hess 2002); but the herds existed with different plant communities, precipitation patterns, and competition potential with other large ungulates. The range of the northern herd encompassed a decreasing elevation gradient extending approximately 90 km between Cooke City and Gardiner, Montana (Houston 1982, Barmore 2003). The northern range was drier and warmer than the rest of the park, with mean annual precipitation decreasing from 35-25 cm along the elevation gradient (Houston 1982, Farnes et al. 1999, Barmore 2003). Average snow-water equivalents ranged from 29.5 cm to 2.0 cm in the higher- and lower-elevation portions of the range, respectively (Farnes et al. 1999). Upland grasses comprised the majority of forage in the northern range, followed by sedges (*Carex spp.*) and rushes (*Juncus spp.*; Barmore 2003). Bison shared this range with a large elk herd, which increased from approximately 3200 to >19000 counted individuals during 1968-1994, and then decreased to approximately 12000 counted individuals by 2002 (White and Garrott 2005).

The range of the central herd extended from the Hayden and Pelican Valleys in the east to the lower-elevation Madison-Firehole Valley in the west (Hess 2002). Winter conditions were severe, with snow-water equivalents averaging 35.1 cm and temperatures reaching -42 C (Meagher 1973, Farnes et al. 1999). Windswept areas in the upper portions of the Hayden Valley and snow-free geothermal areas throughout the range provided some relief from deep snows and facilitated access to forage (Kittams 1949, Craighead et al. 1973, Gates et al. 2005). The central range included a higher proportion of mesic meadows than the northern range, which contained grasses, sedges (*Carex* spp.), and willows (*Salix* spp.), with upland grasses in the drier areas (Craighead et al. 1973). The central herd coexisted with 400-600 elk during winter (Garrott et al. 2003).

Management actions to conserve Yellowstone bison changed adaptively as their abundance increased. The northern herd was subject to intense animal husbandry during 1902-1938 to increase their remnant numbers. Park managers rounded up northern herd bison from their summer ranges, confined them, and fed them hay throughout winter in the Lamar Valley (Cahalane 1944). Roundups and confinement ceased in 1938, but bison were still baited into the northern range and fed through winter until 1952 (Meagher 1973). Periodic removals were implemented during 1925-1968 to limit the growth of the bison population (Meagher 1973). The central herd was not subject to intense animal husbandry, and remained <100 bison through the mid-1930's. To stimulate population growth, the central herd was augmented with 71 bison from the northern herd in 1936 (Cahalane 1944). Periodic culling was instituted to limit bison numbers in the central herd during 1954-1968 (Meagher 1973).

A new management policy was initiated by Yellowstone National Park in 1969 (Cole 1971). Bison herds were allowed to fluctuate without any direct manipulations (e.g., culling) within the park; allowing a combination of weather, predators, and resource limitation to influence bison numbers. However, the State of Montana removed more than 3,000 bison that emigrated from the park during 1984-2000 to prevent the possible transmission of brucellosis from bison to cattle (National Park Service 2000). A cooperative Bison Management Plan between the State of Montana and Yellowstone National Park (National Park Service 2000) allowed continued culling of bison emigrating from the park from 1984 until present.

Methods

Data Collection Methods: Population Counts and Removals

The time series of count and removal data for Yellowstone bison consisted of two periods when bison were counted regularly: 1902-1954 and 1970-2000 (Figures 1 and 2; Appendix A). Counts during 1902-1954 were predominantly made from horseback, foot, or skis, although airplanes were also used after 1949 (Meagher 1973). Aerial counts continued during 1970-2000, with 2-18 counts per year (Dobson and Meagher 1996, Hess 2002). For each year during 1970-2000, I used the bison count taken during summer months (June through August), a time when bison were highly detectable due to gregarious behavior during the rut (Hess 2002). If multiple counts occurred during a given summer, then I used the single highest count during June through August. These counts occurred after the birth pulse in each year, but before any management removals.

Management removals of bison from the northern herd were sporadic and consisted of 1-6% of counted animals per year during 1902-1925. However, larger removals (≤50% of counted bison) occurred every 1-2 years during 1926-1968 (Figure 2, Appendix A). There were no significant removals from the central herd until the late 1950's, after which yearly removals of 20-50% occurred sporadically. After 1968, the northern herd grew without removals until 1984, when the State of Montana and the National Park Service began to cull animals attempting to emigrate from the park along the northwestern boundary. The central herd began to emigrate out of the park at the west-central boundary after 1994, and several culling events were imposed on this herd as well. There was no bison hunting except during 1985-1989 when 668 bison were harvested outside the park by hunters and game wardens (State of Montana 1990). I analyzed data from the central and northern herds separately because they were exposed to different habitat factors, environmental conditions, and management actions (Meagher 1973, Gates et al. 2005).

Population Models – 1902-1954

I did not evaluate density-dependent models for this period because density-related suppression of growth was highly unlikely for either herd. The northern herd received supplemental feeding throughout winter and was periodically culled to keep it at low abundance (Meagher 1973). The central herd began this period at 25 bison and only increased to 61 bison by 1928. There was an 8-year gap in the time series from 1928 to 1936, when the herd was augmented with 71 bison. After augmentation, the herd began

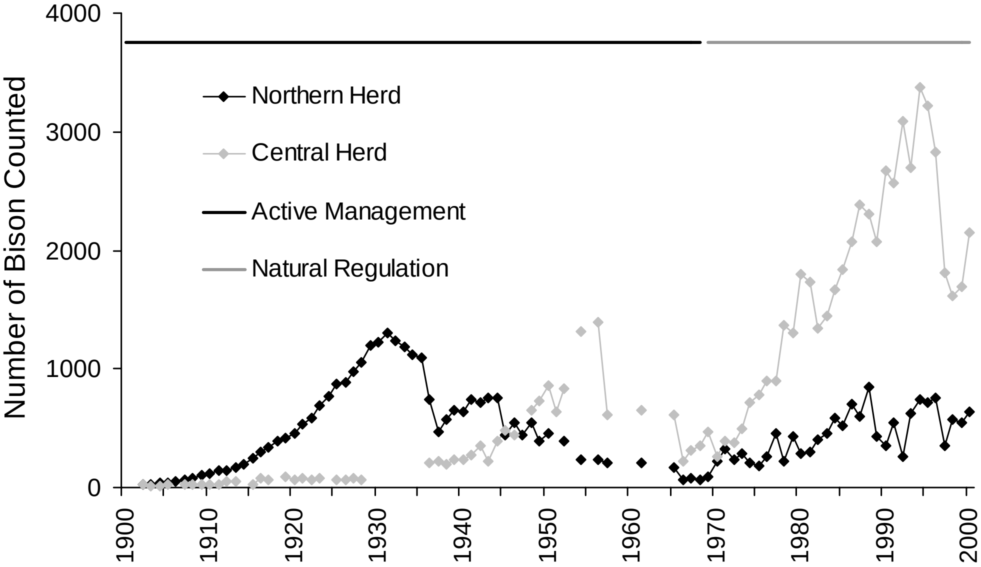

Figure 1. Population counts for the northern and central bison herds of Yellowstone National Park, Montana and Wyoming, during 1902-2000. Ground surveys were conducted during 1902-1949. Aerial surveys began in 1950, and multiple counts were conducted each year after 1970. Data were coalesced from historic records (Cahalane, 1944 Kittams 1949, Barmore 1968, Meagher 1973) and 1970-2000 counts taken from summer time aerial surveys (Dobson and Meagher 1996, Hess 2002)

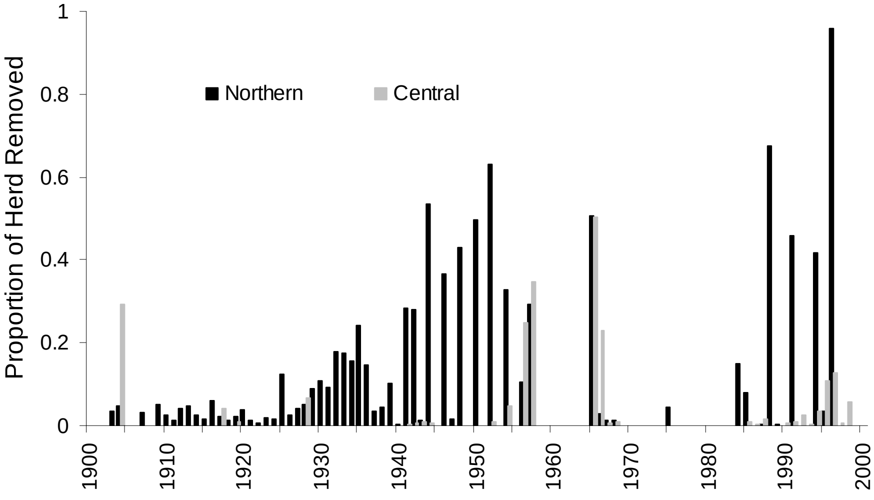

Figure 2. The proportion of bison removed each year from the central and northern herds of Yellowstone National Park, Montana and Wyoming, during 1902-2000. Data were coalesced from historic records (Cahalane, 1944 Kittams 1949, Barmore 1968, Meagher 1973) and NPS reports.

to grow rapidly, but densities remained much lower than those eventually reached in the 1990's when the population exceeded 3000. Thus, I assumed bison were not resource limited during 1902-1954 and used simple exponential growth models to estimate the growth rates for each herd before and after significant management actions (e.g., intensive husbandry, supplemental feeding, selective culling, augmentation). I calculated the annual, relative change in the total size of each herd (r_t) as

$$r_t = \log_e(n_t) - \log_e(n_{t-1}) \tag{1}$$

where n refers to the number of counted individuals and the annual index $t = (1, 2, \ldots, N-1)$ (Eberhardt 1987). The 1926-1950 time series of northern herd data was complicated by frequent and extensive removals. I accounted for removals with the modification:

$$r_t = \log_e(n_t) - \log_e(n_{t-1} - R_{t-1}) \tag{2}$$

where R_{t-1} represents removals taken after the count at n_{t-1} (Eberhardt 1987). I estimated growth rate and 95% confidence intervals using an equation describing perturbed exponential growth:

$$r_t = a + \varepsilon \tag{3}$$

where a represents the growth rate in the absence of density dependence and ε represents the stochastic contribution from noise and unmodeled processes (Zeng et al. 1998, Jacobson et al. 2004). For the northern herd, I compared the simple model estimating a single growth rate from the entire time series of r_t values (1902-1952) with a 2-period model that estimated a separate growth rate for the pre-culling (1902-1925) and culling (1926-1952) periods by including an indicator variable in equation 3 to designate the two periods. I then compared 1- and 2-period models using AIC_c for model selection (Burnham and Anderson 1998).

I handled the analysis for the central herd differently. Count data for the central herd were uncomplicated by removals over 1902-1954, and I expected there could be differences between the pre-augmentation (1902-1928) and post-augmentation (1936-1954) periods. I tested for differences in these periods using a piecewise $\log_e$-linear regression (Eberhardt 1987, Morris and Doak 2000) and AIC_c for model selection (Burnham and Anderson 1998). As with equation 2, the $\log_e$-linear model assumes exponential growth, but is advantageous because the linear regression allows residual analysis and uses the $\log_e$ of the population count as the response variable rather than a ratio of counts. I evaluated three models: 1) a one-intercept, one-growth rate model (all 1902-1954); 2) a two-intercept, one-growth rate model (1902-1928 and 1936 to 1954); and 3) a two-intercept, two-growth rate model (1902-1928 and 1936-1954).

Population Models – 1970-2000

I ran preliminary analyses of all count data for the years before removals occurred (1970-1984 for the northern herd and 1970-1994 for the central herd) using $\log_e$-linear regression. This model regressed the $\log_e$ of count data against time, allowed inspection of residuals, and was used to detect abrupt changes in population growth rates (Piepho and Ogutu 2003). The time series of counts for the central herd during 1970-1994 revealed a significant breakpoint at 1982, with the piecewise regression model being more supported than a continuous model (Appendix B). Based on this finding, I developed a suite of density-dependent and density-independent models for the entire time series (1970-2000) and for two-period models allowing different density-dependent or density-independent dynamics during 1970-1981 and 1982-2000.

I considered two density-dependent model formations to evaluate the relative annual change in total size for each herd over 1970-2000. I calculated r_t using equation 2, which accounted for time periods with removals and reduced to equation 1 for periods without removals. The Ricker model assumed linear density dependence,

$$r_t = a + b(n_{t-1}) + \varepsilon \tag{4}$$

while the Gompertz model assumed a decrease in growth rates with $\log_e$ counts.

$$r_t = a + b(\log_e(n_{t-1})) + \varepsilon \tag{5}$$

In both these models, *b* represents the strength of density dependence and a population is said to be density-dependent if *b* differs significantly from zero (Zeng et al. 1998, Jacobson et al. 2004). I also considered two density-independent models, including the stochastic growth equation describing perturbed exponential growth (Eq. 3) and a random-walk model where population growth rate is uncorrelated with population size (Zeng et al. 1998, Jacobson et al. 2004):

$$r_t = \varepsilon \tag{6}$$

I explored the possibility population changes depended on time-delayed dynamics using partial rate correlation functions (PRCF) for all periods without removals (Berryman and Turchin 2001). The results suggested I did not need to consider time lags (i.e., delayed density dependence) >1 yr in the analysis. Therefore, the final a priori model suite included Gompertz, Ricker, and exponential growth models calculated with and without the estimation of the first-order (AR1) autocorrelation parameter (Table 1).

Table 1. Density-dependent (Gompertz and Ricker) and density-independent (exponential and random walk) equations for one period (1970-2000) and two period (1970-1981 and 1982-2000) models. The intercept term, *a*, represents population growth rate without influence of density, while *b* represents the strength of density dependence. Counts are represented by *n*, and *P* is an indicator variable for period of interest. Counts from *t-1* are taken after the removals, if any. Autocorrelation structure of lag 1 was added to all except the random walk models, resulting in 13 candidate models.

Model Name	**Model Form**	**Equation**
Gompertz	One Period	$r_t = a + b(\log_e(n_{t-1})) + \varepsilon$
	Two Periods	$r_t = a_1 + b_1(\log_e(n_{t-1})) + a_2(P) + b_2(P \times \log_e(n_{t-1})) + \varepsilon$
Ricker	One Period	$r_t = a + b(n_{t-1}) + \varepsilon$
	Two Periods	$r_t = a_1 + b_1(n_{t-1}) + a_2(P) + b_a(P \times n_{t-1}) + \varepsilon$
Exponential	One Period	$r_t = a + \varepsilon$
	Two Periods	$r_t = a_1 + a_2(P) + \varepsilon$
Random Walk	One Period	$r_t = \varepsilon$

I used program R 2.0.0 (R Development Core Team 2004) to fit models and estimate parameter coefficients for each modeling exercise. I calculated a corrected Akaike's Information Criterion ($\mathrm{AIC_c}$) value for each model and then ranked and selected the best approximating models using $\Delta\mathrm{AIC_c}$ values (Burnham and Anderson 1998). Finally, I calculated Akaike weights (w_i) to obtain a measure of model selection uncertainty (Burnham and Anderson 1998). In an analysis such as this, measurement error inflates the variance around the estimated population growth parameter because counts are estimates and may not accurately reflect the true population size. In the case of density-dependent models, this type of variance may result in over-estimation of the strength of density dependence (Shenk et al. 1998, Viljugrein et al. 2005). I did not expect this would be problematic because bison in Yellowstone are large, gregarious, and inhabit open landscapes, making count accuracy high relative to other herbivores (Hess

2002). I evaluated the potential influence of this additional source of variation by applying the restricted maximum likelihood (REML)-based method for partitioning process variation and sampling error in exponential models (Staples et al. 2004). Results indicated that growth rate estimates and variances were only slightly inflated by sampling error (0-0.02), suggesting the influence of sampling variance on the interpretation of results was slight. Recently developed state-space models (Viljugrein et al. 2005) could possibly be applied to this problem. However, I did not have estimates of measurement error and state-space methods have not yet been evaluated in cases where measurement error is unknown.

To explore the potential influence of annual climate variation on bison population dynamics, I evaluated one warm-season and one cold-season climate covariate. I used the Palmer Drought Severity Index (PDSI; Palmer 1968) from the National Climatic Data Center as the warm-season climate covariate because it incorporates multiple environmental factors and is used to gauge growing conditions across the USA (Alley 1985). I averaged PDSI over the growing season (May 1 through July 31) across region 1 of Wyoming. I predicted a positive correlation between PDSI and relative population change because dry years (i.e., low PDSI) would decrease plant production, thereby decreasing fat reserves for bison entering winter and resulting in lower calf survival. I lagged PDSI one year such that the drought index in $t-1$ affected the annual growth rate for year t (Appendix C). I used the accumulated daily value of snow water equivalent (SWE_{acc}) during October 1 to April 30 as the cold-season climate covariate because it integrates the depth, density, and duration of the snow pack (Garrott et al. 2003). SWE_{acc}

data were available from 1949-2000 for the northern range from the Tower Falls CLIM site, and from 1981-2000 for the central range from the Canyon SNOTEL site (Farnes et al. 1999; Appendix C). I re-scaled the PDSI covariate by adding 7 to each value to remove negative figures and allow a square-root transform. I re-scaled SWE_{acc} by dividing it by 1000 to enhance interpretability of coefficients and allow a quadratic transform. I added combinations of the warm- and cold-season covariates to the top ranked models based on the AIC_c model selection results from the density-dependent and density-independent model suite (Table 1). I considered non-linear transforms of the climate covariates in addition to linear models. I used AIC_c to rank a priori models (Table 2) and followed a stepwise model selection procedure to determine if nonlinear forms of the covariates were supported by the data (Borkowski et al., *in press*).

Table 2. A list of *a priori* models for annual growth rates of the central and northern bison herds in Yellowstone National Park during 1970-2000. The drought index (PDSI) was lagged one year, while snow water equivalent (SWE) was measured in the same year as r_t. Ellipses indicate the insertion of the density-dependent or density-independent model form selected from Table 1. Coefficients *c*, *d*, and *e* are the regression coefficients on each parameter or interaction term.

Hypothesis	**Model**
r_t is negatively correlated with PDSI	$r_t = a + ... + c(PDSI)\varepsilon$
r_t is negatively correlated with snowpack	$r_t = a + ... + c(SWE_{acc}) + \varepsilon$
The negative effects of PDSI and snowpack both describe r_t	$r_t = a + ... + c(PDSI) + d(SWE_{acc}) + \varepsilon$
The negative effects of snowpack and drought interact describe r_t	$r_t = a + ... + c(PDSI) + d(SWE_{acc}) + e(SWE_{acc} xPDSI) + \varepsilon$

Results

Population Models – 1902-1954

The piecewise $\log_e$-linear regression model allowing two intercepts and the estimation of two growth rates (1902-1928 and 1936-1950) was the most supported model for the central herd (1902-1954), receiving 98% of the Akaike model weight (Figure 3, Table 3). This model estimated the growth rate of the central herd at $\hat{r}$ = 0.06 (95% C.I. = 0.05, 0.07) during 1902-1928, and $\hat{r}$ = 0.10 (95% C.I. = 0.08, 0.13) after the herd was augmented with 71 bison in 1936.

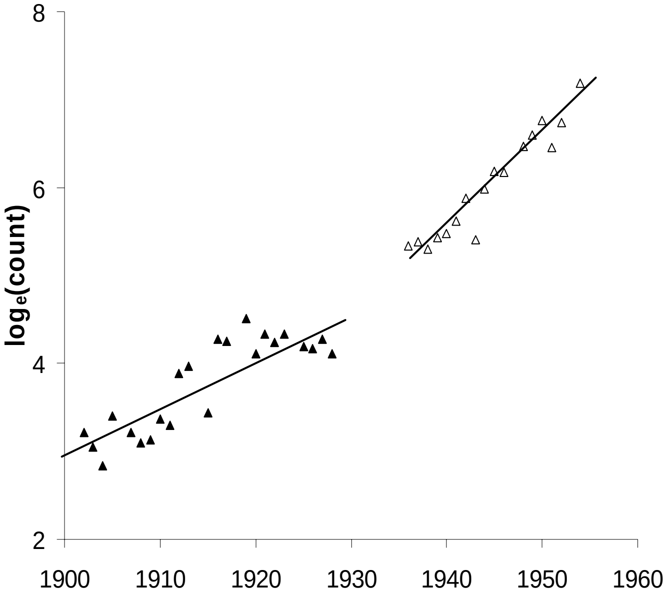

Figure 3. Piecewise $\log_e$-linear regression of count data for the central bison herd in Yellowstone National Park, Montana and Wyoming, during 1902-1954.

Table 3. Model selection results for regression of the factors influencing the $\log_e$ count of the central herd bison in Yellowstone National Park, Montana and Wyoming, during 1902-1954. The lowest AIC_c is the most parsimonious model. For all models, $n = 44$. Year is represented by Y, period is represented by indicator variable P (P = 0 for 1902-1931 and P = 1 for 1936-1954). The ß values represent coefficients estimated by least-squares regression, and r^2 is the percent of variation in the data described by the regression model.

MODEL	**AIC_c**	**Δ AIC_c**	**w_i**	**R^2**
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \beta_3(P \times Y) + \varepsilon$	7.44	0.00	0.98	0.97
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \varepsilon$	16.60	9.16	0.01	0.95
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \varepsilon$	17.78	10.34	0.01	0.95

The northern herd 1-period (1902-1950) and 2-period (1902-1925, 1926-1950) models received similar support from the data (1-period: $\Delta AIC_c = 0.0$, $w_i = 0.55$; 2-period: $\Delta AIC_c = 0.39$, $w_i = 0.45$). The population growth rate estimate for the 1-period model (1902-1950) was $\hat{r} = 0.16$ (95% C.I. = 0.13, 0.20). The population growth rate estimates for the 2-period model were $\hat{r} = 0.19$ (95% C.I. = 0.14, 0.23) for 1902-1925 and $\hat{r} = 0.14$ (95% C.I. = 0.08, 0.21) for 1926-1954.

Population Models – 1970-2000

The central herd showed evidence of a density-dependent response, with the 1-period Gompertz and 1-period Ricker receiving high model weight ($w_i = 0.40$ and 0.30, respectively). No other model was within 2 AIC_c units (Table 4). The addition of autocorrelation parameters did not improve the fit of any of the top models. I also found evidence of density dependence in the northern herd during 1970-2000, with the 2-period Ricker and 2-period Gompertz models receiving nearly equal model weight (Table 5, w_i = 0.43 and 0.35). During residual analysis, I censored one influential point from the northern herd (r_{1997}) when growth rate was estimated at 2.44, substantially higher than biologically feasible given reproduction and survival alone. This point was more than 3 standard deviations from the mean and was highly influential in the models, especially the Gompertz model.

Parameter estimates for the two-period Ricker equation (Table 1) were $\hat{a}_1$ = 1.16 (95% C.I. = 0.63, 1.68), $\hat{a}_2$= -0.48 (95% C.I. = -0.20, -0.19), $\hat{b}_1$ = -0.004 (95% C.I. = -0.006, -0.002), and $\hat{b}_2$ = 0.003 (95% C.I. = 0.001, 0.005). The first period was

Table 4. Density-dependent and density-independent model selection results for the central bison herd in Yellowstone National Park, Wyoming and Montana, during 1970-2000 (n =30). One-period models estimate one *r* for all data during 1970-2000, while two-period models estimate a separate *r* for 1970-1981 and 1982-2000 periods. AR1 models include a parameter estimating the autocorrelation coefficient for a lag of 1 year.

	MODEL	**AIC_c**	**Δ AIC_c**	**K**	**w_i**
CENTRAL HERD	Gompertz 1 Period	-18.93	0.00	3	0.40
	Ricker 1 Period	-18.32	0.61	3	0.30
	Ricker 1 Period AR1	-15.65	3.29	4	0.08
	Exponential 2 Period	-15.62	3.32	3	0.08
	Exponential 2 Period AR1	-14.62	4.31	4	0.05
	Exponential 1 Period	-13.59	5.34	2	0.03
	Ricker 2 Period	-13.41	5.52	5	0.03
	Gompertz 2 Period	-13.37	5.57	5	0.02
	Exponential 1 Period AR1	-11.38	7.55	3	0.01
	Ricker 2 Period AR1	-10.26	8.67	6	0.01
	Random	-9.91	9.02	1	0.00
	Gompertz 1 Period AR1	-5.24	13.69	4	0.00
	Gompertz 2 Period AR1	-1.21	17.72	6	0.00

Table 5. Density-dependent and density-independent model selection results for the northern bison herd in Yellowstone National Park, Wyoming and Montana, during 1970-2000, censoring 1997 (n =29). One-period models estimate one *r* for all data during 1970-2000, while two-period models estimate a separate *r* for 1970-1981 and 1982-2000 periods. AR1 models include a parameter estimating the autocorrelation coefficient for a lag of 1 year.

	MODEL	AIC_c	Δ AIC_c	K	w_i
NORTHERN HERD	Ricker 2 Period	13.25	0.00	5	0.45
	Gompertz 2 Period	13.69	0.44	5	0.37
	Ricker 2 Period AR1	16.33	3.07	6	0.10
	Exponential 2 Period AR1	16.92	3.67	4	0.07
	Exponential 1 Period AR1	21.41	8.15	3	0.01
	Gompertz 1 Period	26.38	13.12	3	0.00
	Exponential 1 Period	26.70	13.44	2	0.00
	Ricker 1 Period	26.82	13.57	3	0.00
	Exponential 2 Period	27.11	13.85	3	0.00
	Random	29.33	16.08	1	0.00
	Ricker 1 Period AR1	29.49	16.24	4	0.00
	Gompertz 2 Period AR1	35.49	22.24	6	0.00
	Gompertz 1 Period AR1	35.89	22.64	4	0.00

associated with rapid decline in growth rates with increasing density, as indicated by the negative value of $\hat{b}_1$ and 95% CI that did not encompass zero. There was a lessening of density dependence in the second period, as indicated by the positive value of $\hat{b}_2$ and 95% C.I. that encompassed zero. Thus, density had a stronger effect on northern herd growth during 1970-1981, when population counts were lower (182-457) compared to 1982-2000 when population counts were higher (405-756), with average growth rate higher in the later period (Figure 4).

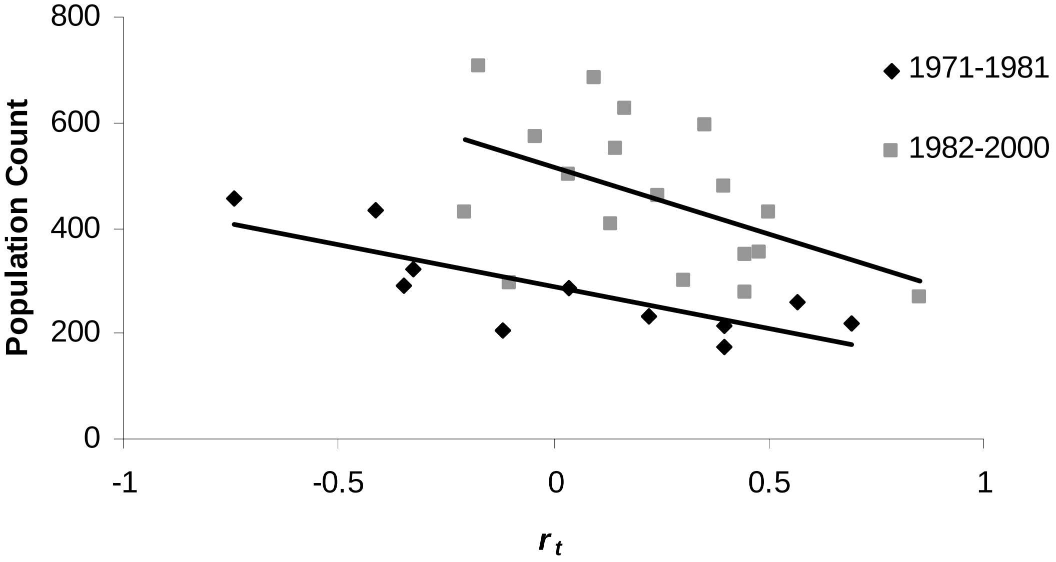

Figure 4. Graphical representation of the relative strengths of density-dependence in the 2-period Ricker model for the northern bison herd in Yellowstone National Park, Wyoming and Montana, during 1970-2000. The first period (1970-1981) is represented by black diamonds triangles, while the second period (1982-2000) is represented by gray squares. The slope of the lines indicate the strength of density dependence, where r_t declines more rapidly with population counts.

From the a priori list of density-dependent and density-independent population models, (Table 1) the 1-period Gompertz model was the most-supported population model for the central herd, and the 2-period Ricker model was the most-supported population model for the northern herd. I added climate covariates to these models, according to the a priori list of potential climate effects and interactions (Table 2), and according to availability of climate data (Appendix C). In both herds, transforming SWE_{acc} to SWE_{acc}^2 resulted in a decrease in 1-2 AIC points per model. No transformations were supported for PDSI. Although the Gompertz 1-period model received most of the model weight (79%), the coefficient on SWE_{acc}^2 supported its negative correlation with growth rate (ß = -0.007; 95% C.I. = -0.013, -0.002; Table 6). For the northern herd, the 2-period Ricker model without climate covariates was the top model, receiving 68% of the model weight. No other model was within 2 AIC_c (Table 7), and all climate covariates had coefficients overlapping zero, thus providing minimal support for effect of climate on population growth rates in the northern herd.

Table 6. Warm- and cold-season covariate models for the central bison herd in Yellowstone National Park, Wyoming and Montana during 1981-2000. The base model is the exponential model, and all covariates were added to this model.

MODEL	**AIC_c**	**Δ AIC_c**	**K**	**w_i**	**R^2**
1-Period Gompertz, No Covariates	-18.93	0.00	3	0.79	0.23
SWE_{acc}^2	-15.89	3.04	4	0.17	0.34
SWE_{acc}^2 + PDSI	-12.28	6.66	5	0.03	0.34
PDSI	-8.88	10.05	4	0.01	0.07
SWE_{acc}^2 + PDSI + SWE_{acc}^2 x PDSI	-8.59	10.34	6	0.00	0.36

Table 7. Warm- and cold-season covariate models for the northern bison herd in Yellowstone National Park, Wyoming and Montana during 1970-2000. The base model is the 2-period Ricker model and all covariates were added to this model.

MODEL	**AIC_c**	**Δ AIC_c**	**K**	**w_i**	**R^2**
2-Period Ricker, No Covariates	13.25	0.00	5	5	0.53
SWE_{acc}^2	16.34	3.08	6	6	0.53
PDSI	16.45	3.19	6	6	0.53
PDSI + SWE_{acc}^2	19.85	6.60	7	7	0.53
PDSI + SWE_{acc}^2 + PDSI x SWE_{acc}^2	22.77	9.52	8	8	0.54

Discussion

Growth rates of the central and northern bison herds varied substantially over time in response to different management, climate, and competitive stressors. Active management intervention was effective at recovering Yellowstone bison from a remnant population of 46 animals in 1902 to >1500 animals by 1954. During the early conservation efforts that included supplemental feeding (1902-1950), the northern herd reached a growth rate ($r = 0.16$) similar to the eruptive phases of bison population growth the Wainright Buffalo Park herd in Alberta and in the National Bison Range in Moise, Montana ($r = 0.17$; Roe 1951, Eberhardt 2002). The augmentation of the central herd with 71 bison in 1936 led to an increased growth rate ($r = 0.10$) compared to 1902-1928 ($r = 0.06$). The depressed growth rate prior to augmentation could have been the result of an Allee effect (Allee et al. 1949). Such an effect could have occurred if intense poaching before the conservation period resulted in an unfavorable age or sex structure or numbers that were too low for remaining central bison to establish social bonds necessary to facilitate population growth. However, undocumented survey methodology during 1902-1928 makes interpretation difficult because I do not know whether locations of surveys or survey effort changed among years.

Manipulative management of bison within the park was curtailed after 1968 and herds were regulated only by natural processes (Meagher 1973). In the absence of intensive husbandry and culling, bison numbers increased rapidly and I detected strong evidence of density-dependent feedbacks on the dynamics of both herds during 1970-

2000. Interestingly, the structure of density dependence was very different for the two herds over 1970-1981 and 1982-2000. Growth rates for the northern herd were strongly depressed by density-dependent processes during 1970-1981, but the influence of density dependence was substantially weaker during 1982-2000 when the number of animals in this herd exceeded that realized during the 1970-1981 period. Conversely, growth rates for the central herd were relatively high during 1970-1981, but decreased during 1982-2000. These divergent patterns between herds were unexpected because the herds were only separated by approximately 30 km, and both bison herds were free-ranging and at similar densities (0.2 bison/km^2) at the start of this period in 1970.

There are two plausible explanations for the divergent density-dependent dynamics I observed. Demographically, decreased survival and/or reproduction in the central herd, concurrent with increased survival and reproduction in the northern herd, would explain these patterns. However, such rapid and opposite changes in these vital rates for the two herds would seem unlikely. While there are no comparable estimates of vital rates for the two herds until 1995, herd-specific survival and reproductive rates estimated for radio-marked cows over 1995-2001 did not significantly differ (Fuller et al., unpublished data). Further, recruitment as indexed by calf-adult ratios during 1970-1997 did not significantly differ between herds or pre- and post-1981 periods (Fuller et al., unpublished data). A more probable explanation for the divergent dynamics of the two herds is that movement patterns changed, with bison from the central herd emigrating to the northern range. This emigration would have inflated population counts and growth rates of the northern herd, while resulting in opposite effects for the central herd. Winter conditions are known to cause large ungulates to disperse or migrate to find more accessible forage (Aanes et al. 2000, Larter et al. 2000). Winters are more severe in the central regions of Yellowstone and the drier northern range would be a logical option for dispersing central herd bison. Range expansion in the central herd was documented in the 1980’s as the central herd expanded westward into areas that were previously used rarely if at all (Taper et al. 2000 *in* Gates et al. 2005). Movement of central herd bison onto the northern range was also reasonable because there were no ecological barriers in this direction. An influx of central herd bison onto the northern range would not have been easily detected because no individual bison in Yellowstone were marked until recently.

Data collected after 1995 on marked bison demonstrate that movements occur from the central herd to the northern herd (Gates et al. 2005). If my hypothesis of a spatial response to density dependence is correct, then growth rates of the central and northern herds should be negatively correlated during 1982-2000 because emigration would decrease central herd growth rate and increase northern herd growth rate. Conversely, I would only expect weak correlation in population growth rates of the two herds during 1970-1981 due to limited or no movements between the herds. These predictions were strongly supported when I examined the correlation using a linear regression model. There was no significant correlation between northern and central herd growth rates during 1970-1981 ($P = 0.17$, $R^2 = 0.20$, slope = -1.09, 95% C.I. = -2.50, 0.32; Appendix D), but there was a strong negative correlation during 1982-2000 ($P < 0.01$, $R^2 = 0.40$, slope = -1.13, 95% C.I. = -1.81, -0.45; Appendix D). The latter regression does not include the population growth rate for 1997, which was 2.44 for the northern herd and -0.31 for the central herd. This influential point could be indicative of a large body of central herd bison moving to the northern herd in winter 1996-1997, and including this point in the regression increases the strength of the negative slope and the R^2 value. The hypothesized emigration of central herd animals to the northern herd after 1981 may have been triggered by the combination of relatively high bison densities during the winter of 1981-82, combined with the most severe snow pack of the decade resulting in strong resource limitation and starvation. Other studies have documented strong interactive effects of environmental variation and density on dispersal, migration, vital rates, and population dynamics of ungulates (Sæther 1997, Gaillard et al. 1998, 2000, Aanes et al. 2000, Larter et al. 2000). The negative correlation of population growth rates and the divergent trends in density-dependent responses of the herds provide convincing indirect evidence of increasing emigration from the central herd to the northern range.

This interpretation is also supported by count and removal data, which indicate the northern herd sustained the removal of >2000 bison during 1982-2000 even though counts never exceeded 900 bison. In contrast, the central herd sustained only half as many removals (1111 bison) even though it was 3 times larger (>3000 bison). I contend the northern herd could not have sustained this high removal rate without immigrants from the central herd. For example, 877 bison were counted on the northern range during 1996 and 725 bison were subsequently removed that winter. The count of northern bison the following year was 354, an increase of 230%. This increase could not have been realized solely from intrinsic productivity. Hence, substantial immigration must have occurred. Differential removals by sex could influence population growth rates, but the composition of approximately 1809 bison removed at the Park boundaries during the winters of 1988-1989 and 1996-1997 indicated approximately equal proportions of males and females. If Yellowstone bison herds have approximately equal sex ratios, as suggested in Shaw and Meagher (2000), then there was no overt bias in removals that would influence population growth rates

Ungulate populations generally become more sensitive to density-independent factors that affect resource availability as they approach high densities (Sæther et al. 1997, Gaillard et al. 1998, 2000). Therefore, I expected exogenous, density-independent processes such as drought and snow pack to have a major influence on the dynamics of both bison herds during 1970-2002. As predicted, the population growth rate of the central herd was negatively correlated with snow pack (SWE_{acc}), similar to the findings of numerous studies of large ungulates in relation to winter severity (Gaillard et al. 2000, Clutton-Brock and Coulson 2002, Garrott et al. 2003, Jacobson et al. 2004, Wang et al.2006). I did not observe a negative effect of snow pack on the northern herd, possibly due to influx from central herd bison during or immediately after severe winters. Spring precipitation has been shown to positively affect elk calf recruitment in Yellowstone and surrounding areas (Merrill and Boyce 1991, Coughenour and Singer 1996, Taper and Gogan 2002, Lubow and Smith 2004), as well as ungulate population growth in other biomes (Sinclair 1975, Van Vuren and Bray 1986, Mduma et al. 1999, Gaillard et al. 2000). However, I found no strong evidence of warm-season drought effect on population growth rates of either the central or northern bison herds. It is possible that the effect of spring and summer precipitation on bison calf survival exists, but the overall population effect was too small to be detected. Further research into these effects would be useful.

Many studies have documented the effects of density dependence on survival and reproduction (Sæther 1997, Gaillard et al. 2000, Eberhardt 2002, Festa-Bianchet et al. 2003), but few studies have documented the effects of density dependence on emigration and immigration (Sæther 1999, Amarasekare 2004). To some extent, the evolutionary legacies of large ungulate species may dictate whether density dependence will be manifest primarily through movement or changes in vital rates. Ungulate populations restricted to discrete habitat patches, such as mountain goats (*Oreamnos americanus*; Gross et al. 2002) and Dall's sheep (*Ovis dallii*; Nichols and Bunnell 1999), may have limited options for range expansion. Other ungulate species are adapted to large expanses of homogeneous terrain, where movement is an adaptive strategy in response to resource limitation. Caribou (*Rangifer tarandus*) herds travel over vast areas of tundra and boreal forest and commonly shift their seasonal ranges and movement patterns in response to density-related forage depletion (Messier et al. 1988, Ferguson et al. 2001). Like caribou, bison historically occupied the extensive interior grasslands of temperate North America, foraging in one area until the range was depleted and then moving to another area (Roe 1951). Similarly, bison reached relatively high densities in central Yellowstone during the 1980s, decreasing per capita resources and apparently leading to a density-dependent spatial response.

The restoration of bison in Yellowstone National Park represents a major achievement for wildlife conservation. At the start of the twentieth century, bison in Yellowstone occupied a relatively small proportion of the potential landscape in two sedentary, isolated herds numbering <50 animals. Aggressive management intervention during the first half of the century, and conservation policy in the second half of the century, resulted in an approximately 100-fold increase in Yellowstone's bison population to approximately 5000 animals in 2005. As numbers increased, an interaction between density and snow pack eventually led to resource limitation that fueled natural range expansion and the establishment of migratory patterns across much of the park. These same mechanisms also resulted in the apparent development of pulses of climate-induced dispersal from the central herd to the northern range, creating a source-sink dynamic that is contributing to the current controversy about management of bison when they leave the protection of the park and are culled to reduce the potential of brucellosis transmission to cattle (Cheville et al. 1998, National Park Service 2000).

The effective management of Yellowstone bison into the future will require a thorough understanding of the density-dependent and density-independent structure of the entire population. Thus, it is essential that telemetry studies continue to document the broad and fine-scale spatial dynamics of bison from the northern and central herds, which may elucidate the extent of interchange between the herds. Understanding how changing elk densities on the northern range interact with bison population demographics may also be important to future management. The decreasing density of elk on the northern range may temporarily increase forage availability to bison (White and Garrott 2005), possibly allowing the northern range to support a larger number of bison before forage limitation causes mass movements toward the low-elevation boundary area. Therefore, continued monitoring of vital rates and population trends is essential for evaluating further density-dependent responses as well as the formulation of a sound management policy.

CHAPTER 2

REPRODUCTION AND SURVIVAL OF YELLOWSTONE'S BISON HERDS: AN INTEGRATED ANALYSIS

Abstract

Rigorously estimated vital rates are helpful in parameterization of population models necessary to gain ecological and management insights. Bison in Yellowstone National Park (YNP) have increased from the brink of extinction to >4,000 in less than 100 years, but this conservation success is overshadowed by controversy. YNP bison are infected with brucellosis, a disease that causes abortion of calves. Concurrent with their increasing population numbers, bison increasingly attempt to use private lands in the State of Montana, raising concerns about transmission of brucellosis to domestic livestock and the resulting economic consequences. Here, I present the first rigorously estimated survival and reproduction estimates from Yellowstone bison; key information to understand the ecology of this keystone species and to interpret effects of management actions. The survival and reproduction data were gathered from 7 years of telemetry of bison individuals (1995-2001). These data were complemented with 28 years of early-season calf-adult ratios (1970-1997). I assessed density-dependent and density-independent sources of variation in each rate. Adult female survival was high (0.92) and constant throughout the study. Birth rates differed by brucellosis status and age structure, with primiparous individuals having lower birth rates than older individuals. I found no evidence for reproductive senescence. Although birth rates did not vary with density-dependent or density-independent factors, spring calf-adult ratios were negatively correlated with snow pack ($ß = -0.01-0.04$, $r^2 = 0.26-0.60$, $P < 0.05$). To understand population drivers and address the proposed management actions of culling and/or vaccination programs in disease control, I evaluated a Leslie matrix model parameterized with the survival and reproduction estimates. Integrating these vital rates into a matrix model resulted in a population growth rate estimate of $\lambda = 1.07$, which approximated the estimate of $\lambda = 1.05$ from count and removal data. As expected, λ was highly elastic to adult survival (0.51), but juvenile survival (0.36) was more elastic than expected, three times more so than fecundity (0.12). Simulating the effects of brucellosis eradication through vaccination programs resulted in $\lambda = 1.09$, a 29% increase. I concluded brucellosis eradication could further increase bison population growth rates and potentially exacerbate conflicts outside YNP.

Introduction

Large ungulates can be keystone species in many ecosystems because they exert strong direct and indirect effects on grassland communities (Frank 1998, Frank et al. 2002, Augustine et al. 2003, Bardgett and Wardle 2003). According to their ecological importance, and relative tractability, large ungulates have been the subject of much research. In general, ungulates have consistently high adult survival rates with high elasticity, moderately variable reproductive rates with intermediate elasticity, and variable juvenile survival rates with low elasticity (Gaillard et al. 2000, Eberhardt 2002). However, even closely-related species may experience variation in elasticity patterns due to differences in habitat or disturbance regimes (Heppell et al. 2000). Therefore, understanding basic population dynamics, and rigorously estimating vital rates from populations of interest, provides a foundation for parameterizing population models helpful in gaining ecological and management insights.

Emergent diseases are burgeoning issues for the management of many wildlife species (Altizer et al. 2003). Disease may limit or regulate some ungulate populations, but studies documenting population-level effects of disease are rare (Gulland 1995). Naturally-occurring parasites can influence ungulate populations (Albon et al. 2002), but the effects of introduced diseases may be more pronounced. Bovine tuberculosis in African water buffalo (*Syncerus caffer*) may be reducing population growth rates (Jolles et al. 2005), while a combination of tuberculosis (*Mycobacterium bovis*), brucellosis (*Brucella abortus*), and anthrax (*Bacillus anthracis*) may have caused the drastic declines seen in bison (*Bison bison*) of Wood Buffalo National Park in Canada (Mitchell and Gates 2002). Parameterization of mathematical models can aid in evaluating the impact of wildlife diseases at the population level. These can help determine whether intervention is warranted, and how disease control efforts (i.e. vaccination or selective culling) could affect population demography (Gulland 1995, Jolles et al. 2005). Thus, an integrated analysis of vital rates (and their variability) with disease ecology provides key insights to successful population management for species of concern.

In Yellowstone National Park (YNP), bison are keystone herbivores that have recovered from near extinction to >4,000 animals. As their abundance increased, bison began to move outside YNP and onto the Gallatin National Forest and private lands in the State of Montana. Bison then became a center of controversy because they are carriers of brucellosis (*Brucella abortus*); a disease that causes abortion in ungulates. The presence of bison outside YNP raised concerns about the potential economic consequences if bison transmitted brucellosis to cattle (Keiter 1997, Cheville et al. 1998). As a result, state agencies and park staff began to cull bison leaving YNP, and a Bison Management Plan for the State of Montana and Yellowstone National Park was published in December 2000 (NPS 2000). However, culling programs are costly and contentious, and future management plans for YNP bison are the subject of much debate. Several management alternatives have been proposed, ranging from minimal to aggressive brucellosis control (NPS 2000).

Bison demography in YNP is relatively unexplored, and little to no information is published on the key demographic rates needed to evaluate or predict the effects of these proposed management actions (Berger and Cain 1999). I present an analysis of 7 years of survival and reproduction of radio-collared adult female bison, complemented with calf-adult ratios from aerial and ground surveys. I evaluated adult survival rates, age-specific birth rates, neonatal survival, and sources of variation in each. I then integrated these rates to evaluate the effects of brucellosis eradication. The intensive monitoring efforts included repeated testing of individuals for brucellosis, allowing me to determine how the disease affects birth rates. Although brucellosis prevalence information is well-documented (Barmore 1968, Pac and Frey 1991, Meyer and Meagher 1995, Cheville et al. 1998), this is the first rigorous assessment of brucellosis influence on vital rates and overall population growth for YNP bison.

Study Area

Yellowstone National Park encompassed 9,018 km^2 in the western United States, including portions of Wyoming, Montana, and Idaho. The bison population existed almost entirely within the boundaries of the Park and consisted of the central and northern herds. Present-day ranges of the central and northern herds were comparable in size (1200 km^2; Hess 2002); but the herds existed with different plant communities, precipitation patterns, and competition potential with other large ungulates. The range of the northern herd encompassed a decreasing elevation gradient extending approximately 90 km between Cooke City and Gardiner, Montana (Houston 1982, Barmore 2003). The northern range was drier and warmer than the rest of the park, with mean annual precipitation decreasing from 35-25 cm along the elevation gradient (Houston 1982, Farnes et al. 1999, Barmore 2003). Average snow-water equivalents ranged from 29.5 cm to 2.0 cm in the higher- and lower-elevation portions of the range, respectively (Farnes et al. 1999). Upland grasses comprised the majority of forage in the northern range, followed by sedges (*Carex spp.*) and rushes (*Juncus spp*.; Barmore 2003). Bison shared this range with a large elk herd, which increased from approximately 3200 to >19000 counted individuals during 1968-1994, and then decreased to approximately 12000 counted individuals by 2002 (White and Garrott 2005).

The range of the central herd extended from the Hayden and Pelican Valleys in the east to the lower-elevation Madison-Firehole Valley in the west (Hess 2002). Winter conditions were severe, with snow-water equivalents averaging 35.1 cm and temperatures reaching -42 C (Meagher 1973, Farnes et al. 1999). Windswept areas in the upper portions of the Hayden Valley and snow-free geothermal areas throughout the range provided some relief from deep snows and facilitated access to forage (Kittams 1949, Craighead et al. 1973, Gates et al. 2005). The central range included a higher proportion of mesic meadows than the northern range, which contained grasses, sedges (*Carex* spp.), and willows (*Salix* spp.), with upland grasses in the drier areas (Craighead et al. 1973). The central herd coexisted with 400-600 elk during winter (Garrott et al. 2003).

Methods

Vital Rates

From 1995 through 2001, a field study of adult female bison in YNP was conducted to estimate adult survival, pregnancy, and birth rates. Twenty-six adult female bison from the northern herd and 27 from the central herd were captured according to methods described in Aune et al. (1998), and collared with either a VHF or GPS radio collar. The northern herd had 7 new captures in October 1995, 1 in May 1996, 9 in October 1996, 1 in May 1997, 4 in October 1997, 2 in May 1998, and 2 in May 1999. There was 1 new central herd capture in October 1995, 1 in May 1996, 2 in October 1996, 20 in October 1997, 2 in May 1998, and 1 in May 1999. No new adults were added to the marked population after 1999. Ages were determined by examination of incisor eruption patterns for bison up to 4 years old (Fuller 1959, Dimmick and Pelton 1996), with a jaw board demonstrating incisor wear patterns from known-aged bison used to estimate ages of older animals. Collared bison were monitored for survival monthly during November through January, 2-5 times monthly during February and October, and almost daily during the calving season, mid-March through June. Bison were monitored continuously for almost 7 years: from fall 1995 to spring 2001. Mortalities were quickly investigated to determine cause of death, and incisors were collected when possible to verify age through cementum annuli analysis (Moffitt 1998).

Insights into reproduction were obtained by collecting data for two response variables, pregnancy (PREG) and birth (BIRTH), through multiple recaptures of each instrumented animal during gestation, and intensive field observations during the calving season. Attempts were made to recapture each bison during early-term pregnancy (October), late-term pregnancy (February), and shortly after calving (April-May). Early-term pregnancy was determined using a portable ultrasonagraph (Aloca 5000) and/or pregnancy-specific protein B (PSPB) assays of serum collected from blood samples drawn at the time of capture (Haigh et al. 1991). Late-term pregnancy was determined using rectal palpation and PSPB assays. Final pregnancy determination (PREG) was derived from the results of the February tests, but if an individual was not re-captured in February, then October test results were used. Blood samples drawn at each capture were assayed to determine brucellosis exposure status (Roffe et al. 1999, Rhyan et al. 2001), which was evaluated as a potential covariate in statistical models of pregnancy and birth. Samples were classified into one of 3 serological categories: brucellosis negative (N), brucellosis positive (P), and sero-converter (C). The sero-converter classification was assigned to a previously brucellosis-negative bison the first calving year after it tested brucellosis-positive.

All pregnant females captured in February also received vaginal transmitters to facilitate intensive monitoring of the animals during and immediately following parturition to determine whether each pregnancy was successful. These data were used to develop the birth rate response variable (BIRTH). Sighting of a live calf in close association with the instrumented cow was required for the pregnancy to classify as a successful birth. Detection of an aborted fetus, a calf brought to term but found dead, or repeated failure to detect a calf associated with the instrumented cow was considered an unsuccessful pregnancy. Collared females were located and observed almost daily during the calving period (mid-March through the end of June) to assure a high degree of certainly in assigning birth status.

The telemetry-based study was conducted over a relatively short time interval that limited my ability to evaluate the potential influence of climate variation on bison reproduction. Thus, I complemented the field studies with a time series of calf-adult ratios collected during May and/or June aerial surveys that counted bison numbers on both the northern and central herd ranges during 1970 to 1997 (Dobson and Meagher 1996). The ratio of calves to adults (C-A) can be considered an index of bison reproduction that incorporates pregnancy, fetal loss, and neonatal mortality during the first 1-2 months of life. If two or more surveys occurred during May and June in one year, I used the sum of calves and sum of adults from the surveys to calculate separate calf-adult ratios for the northern ($C\text{-}A_N$) and central ($C\text{-}A_C$) herds.

Model Development and Evaluation

I created a mark-recapture history for each instrumented bison over age 1, censoring capture-related mortalities and management removals along the Park's boundary from survival analysis. Survival of long-lived large-bodied mammals is generally high in the absence of human-caused mortality (Eberhardt 2002). Thus, I anticipated that mortalities would be relatively rare and restricted the candidate a priori models to consider combinations of only 3 covariates: the year in the study (YEAR), the season over which survival was estimated (SEAS), and the herd membership of the individual bison (HERD). I predicted that survival during the relatively harsh winter season (October through March) would be lower than survival during summer (April through September), a pattern commonly documented in many large mammal populations occupying high latitude environments (Clutton-Brock et al. 1985, Clutton-Brock and Coulson 2002, Lubow and Smith 2004). I considered HERD as a covariate because the northern and central bison herds had different management histories, levels of potential interspecific competition, vegetation mosaics on their ranges, and weather conditions. I predicted there would be no differences in survival due to herd membership during the summer season, but because winter conditions on the central herd's range were more severe, I expected winter survival of central herd animals to be lower than northern herd animals. Finally, I considered YEAR as a categorical covariate to evaluate whether survival varied from year to year.

The a priori candidate list of 7 models included several combinations of these 3 covariates, as well as a null model representing a constant survival rate. I evaluated the survival model suite using the known-fate module in program MARK (Cooch and White 2005). I used Akaike's Information Criterion, adjusted for small sample size (AIC_c) to rank hypothesized models (Burnham and Anderson 1998), and I used 95% confidence intervals to assess the precision, magnitude, and direction of the estimated model parameters. Repeated measurements on the same individuals may result in lack of independence in the data, and potential underestimation of variance. I used the most complex model in the model suite, and calculated the overdispersion parameter, $\hat{c}$, from its deviance divided by deviance degrees of freedom (Burnham and Anderson 1998, Cooch and White 2005). If $\hat{c} > 1.0$, I adjusted AIC_c values to $QAIC_c$ and inflated the variance (Burnham and Anderson 1998). This method tends to be conservative, favoring more simple models (Burnham and Anderson 1998, Cooch and White 2005).

I developed a suite of a priori models for the pregnancy and birth response variables that included the HERD and YEAR covariates as described for the survival models, but also incorporated covariates that considered an individual's age, brucellosis sero-status, and two weather covariates representing warm season growing conditions and winter severity (Table 8). I considered two formulations of a categorical age covariate to represent alternative hypotheses on the influence of primiparity and senescence on PREG and BIRTH. Covariate AGE_3 had three categories: primiparous bison (age 3; PRIM), prime-age adults (age 4-8; ADULT), and senescent bison (age 9+; SEN) (Aune et al. 1998). My expectation was that primiparous and senescent bison would have a lower probability of pregnancy and birth than prime-age bison. An alternative two-category age covariate, AGE_2, assumed bison do not experience reproductive senescence, and was coded as 1 for bison 4+ years old at calving time, and 0 if the bison was 3 years old at the calving season, with an expectation that 3-year-old bison had a lower probability of pregnancy and birth than adult bison.

I formulated the brucellosis covariate (SERO) as a categorical variable corresponding to serological status negative (N), positive (P), or sero-converter (C). The effects of brucellosis are thought to be most pronounced immediately after it is contracted, and then wane over time (Davis et al. 1990, Cheville et al. 1998). I hypothesized sero-negative animals would have the highest probability of pregnancy and birth, with sero-converters having the lowest probability, and sero-positive animals having intermediate pregnancy and birth probabilities.

Table 8. A priori model suite for main effects pregnancy and birth rate models for 1995-2001 Yellowstone National Park bison data.

MODEL	Hypothesis
$R=ß_0$	One birth/pregnancy rate
$R=ß_0+ß_1(\mathrm{AGE}_2)$	2 age categories (primiparous and adult) describe bison reproduction
$R=ß_0+ß_1(\mathrm{AGE}_3)$	2 age categories (primiparous, adult, and senescent) describe bison reproduction
$R=ß_0+ß_1(\mathrm{HERD})$	Birth/pregnancy is different in the northern and central herds.
$R=ß_0+ß_1(\mathrm{PDSI})$	Birth/pregnancy is affected by drought the year of conception
$R=ß_0+ß_1(\mathrm{SERO})$	Birth/pregnancy is affected by the brucellosis serology of the dam
$R=ß_0+ß_1(\mathrm{SWE}_{acc})$	Birth rate is affected by snow pack during gestation
$R=ß_0+ß_1(\mathrm{YEAR})$	Birth/pregnancy varies by year in the study
$R=ß_0+ß_1(\mathrm{AGE}_3)+ß_2(\mathrm{HERD})$	Birth/pregnancy varies by 3 age categories and by herd membership
$R=ß_0+ß_1(\mathrm{AGE}_2)+ß_2(\mathrm{HERD})$	Birth/pregnancy varies by 2 age categories and by herd membership
$R=ß_0+ß_1(\mathrm{SERO})+ß_2(\mathrm{AGE}_2)$	Birth/pregnancy varies by brucellosis serology and by 2 age categories
$R=ß_0+ ß_1(\mathrm{SERO})+ß_2(\mathrm{AGE}_3)$	Birth/pregnancy varies by brucellosis serology and by 3 age categories
$R=ß_0+ß_1(\mathrm{SERO})+ß_2(\mathrm{AGE}_2)+ß_3(\mathrm{HERD})$	Birth/pregnancy varies by brucellosis serology, by 2 age categories, and by herd membership
$R=ß_0+ß_1(\mathrm{SERO})+ß_2(\mathrm{AGE}_3)+ß_3(\mathrm{HERD})$	Birth/pregnancy varies by brucellosis serology, by 3 age categories, and by herd membership
$R=ß_0+ß_1(\mathrm{SERO})+ß_2(\mathrm{HERD})$	Birth/pregnancy varies by brucellosis serology and by herd membership
$R=ß_0+ß_1(\mathrm{SWE}_{acc})+ß_2(\mathrm{AGE}_2)$	Birth/pregnancy varies by snow pack and 2 age categories
$R=ß_0+ß_1(\mathrm{SWE}_{acc})+ß_2(\mathrm{AGE}_3)$	Birth/pregnancy varies by snow pack and 3 age categories
$R=ß_0+ß_1(\mathrm{SWE}_{acc})+ß_2(\mathrm{AGE}_2) +ß_3(\mathrm{HERD})$	Birth/pregnancy varies by snow pack, 2 age categories, and depends on herd membership
$R=ß_0+ß_1(\mathrm{SWE}_{acc})+ß_2(\mathrm{AGE}_3) +ß_3(\mathrm{HERD})$	Birth/pregnancy varies by snow pack, 3 age categories, and depends on herd membership
$R=ß_0+ß_1(\mathrm{SWE}_{acc})+ß_2(\mathrm{PDSI})$	Birth/pregnancy varies by snow pack and drought during gestation
$R=ß_0+ß_1(\mathrm{YEAR})+ß_2(\mathrm{HERD})$	Birth/pregnancy varies by year in the study and herd membership

I considered one warm and one cold season weather covariate in the a priori model suite for PREG and BIRTH. During the warm season, quantity and nutritive quality of plants are correlated with precipitation, temperature, and the rate of evapotranspiration (Palmer 1968, Sala et al. 1988) which can be indexed by the Palmer Drought Severity Index (PDSI). I used the region 1, Wyoming, Palmer Drought Severity Index (PDSI) averaged over the growing season, defined as 1 May through 31 July, as the warm season climate covariate. I predicted a positive effect of PDSI on PREG and BIRTH as moist years (high PDSI) would have a longer growing season, increasing the forage quantity and quality, and improving fat reserves of bison entering winter, resulting in a higher over-winter physical condition. I predicted that dry years (low PDSI) would have the opposite affects (Caughley 1970, Choquenot 1991, Frank 1998, Cook et al. 2004).

An annual cold season covariate was calculated by summing the daily snow water equivalent (SWE) measurements obtained at automated climate data collection sites for the winter period (SWE_{acc}), defined as 1 October through 31 April (Garrott et al. 2003). SWE measures the amount of water present in a column of snow and is more biologically meaningful than snow depth as it also incorporates snow density which also influences the energetic costs of foraging and locomotion during the winter (Farnes et al. 1999, Garrott et al. 2003). SWE_{acc} data were available from 1949 to present for the northern range from the Tower Falls CLIM site, and from 1981 to present for the central range from the Canyon SNOTEL site. The Canyon station directly measured SWE, but the Tower Falls station measured daily temperature and precipitation and SWE was derived from these values (Farnes et al. 1999). I predicted SWE_{acc} would have a negative effect on PREG and BIRTH, as severe snow pack would accelerate the rate of depletion of fat reserves, reducing physiological condition of females and, thus reducing fetal viability (Garrott et al. 2003, Cook et al. 2004, Jacobson et al. 2004).

The a priori candidate model suite for PREG and BIRTH consisted of 21 models, including a null model representing a constant pregnancy or birth rate, and multiple combinations of HERD, YEAR, AGE2, AGE3, SERO, PDSI, and SWE_{acc} (Table 8). Pregnancy and birth were binomial response variables, and I evaluated these using multiple logistic regression, employing the logit transform to derive parameter estimates using Program R (R Core Development Team 2004). These data were also derived from measurements taken on the same individuals, and I calculated the overdispersion parameter, $\hat{c}$, as described above, and adjusted AIC_c values to $QAIC_c$ if $\hat{c} > 1.0$.

Pregnancy and birth rates were collected over only 7 years, and so I have limited ability to assess the variance in reproductive rates due to climate fluctuation. I supplemented these data with calf-adult ratios taken in May or June from 1970-1997 for the northern ($C\text{-}A_N$) and central ($C\text{-}A_C$) herds. These ratios came from count data, so I could not incorporate individual covariates in modeling. Instead, I examined the ratios separately for the northern and central herd, and incorporated 4 group covariates pertaining to warm season climate, cold season climate, intra-specific competition, and inter-specific competition. I included SWE_{acc} and PDSI into the model suite for describing variation in calf-adult ratios. Poor maternal body condition, whether due to poor growing conditions and unsuitable forage, or due to severe winter snow pack causing difficulty in foraging, can result in reduced fetal viability and neonatal survival, depressing spring calf-adult ratios (Cameron et al. 1993, Garrott et al. 2003). Intra-specific competition may also affect per capita forage availability, thus influencing calf-adult ratios, so I included the covariate BISON, representing the number of bison counted on each range the previous winter. Inter-specific competition may also be a factor for northern range bison. Elk and bison share a dietary overlap of about 63% (Singer and Norland 1994), and the northern range bison co-existed with a large elk herd that increased from approximately 5,500 to 20,000 over 1970-1994 (White and Garrott 2005). Thus, I incorporated the number of elk counted on the northern winter range during January or February as the covariate ELK in northern range C-A_N models. I did not include ELK in central herd (C-A_C) models because low numbers of elk winter with central range bison, and the elk population was relatively constant at 400-600 (Garrott et al. 2003). I predicted that increasing numbers of elk and/or bison would result in lower forage availability because of increased competition. This would lead to decreased body fat and lower physiological condition, resulting in decreased fecundity and neonatal survival (Clutton-Brock et al. 1987, Choquenot 1991, Cook et al. 2004) and lower spring calf-adult ratios.

The candidate model suite for C-A_N consisted of 21 models, including a null model representing a constant calf-adult ratio, and all possible combinations of the 4 covariates (ELK, BISON, SWEacc and PDSI). The model suite for C-A_C consisted of 11 models, including a null model representing a constant calf-adult ratio, and all possible combinations of the 3 covariates (BISON, SWEacc and PDSI). I scaled the covariates to simplify coefficient interpretation by dividing ELK by 10,000, SWE_{acc} and BISON by 1000, and adding 7 to PDSI to remove negative values to support the square-root transform. In addition to linear models, I considered non-linear transforms of the explanatory variables: SWE_{acc}^2 and $\sqrt{PDSI}$. I followed a stepwise model selection procedure to determine whether transforms of the covariates were supported by the data (Borkowski et al., *in press*). Sources of variation in spring calf-adult ratios were evaluated using multiple linear regression in program R 2.0.0 (The R Core Development Team 2004), with the previously described information-theoretic approach used to rank models and estimate parameters (Burnham and Anderson 1998).

Structure and Parameterization of the Matrix Model

I constructed a post-breeding, age-structured, deterministic Leslie matrix model for female bison using the vital rates I estimated above (Caswell 2001). No bison in this study were older than 15; nor were any of the 131 bison aged by cementum annuli records taken from the 1988-89 winter harvests (Pac and Frey 1991) nor any bison aged during the 1991-92, 1994-95, or 1996-97 harvests (MTFWP, unpublished data). Therefore, I used a 16x16 matrix model allowing bison to reach age 15 but no older. I did not have sufficient data to detect survival senescence, and so I assumed a constant adult survival rate. Biological reality may be that survival senescence is a significant factor, in which case the model may overestimate population growth rates. Bison in other systems have been recorded at or near age 20 (Shaw and Carter 1989, Berger and Cunningham 1994), and truncating the model at age 15 may underestimate population growth rates. To some extent, these two factors may compensate for one another in the matrix output, and I ran several simulations allowing bison to reach age 20, and imposing survival senescence in animals 12 and older, to determine the impacts of these assumptions on λ.

The fecundity input rate was derived in accordance with the results of the BIRTH models incorporating AGE_2 or AGE_3, and from the model averaged birth rates of brucellosis negative, positive, and sero-converting bison, weighted according to their proportion in the population, as in Jolles et al. (2005). Fecundity rates were divided in half because I assumed equal sex ratios at birth, and only females were included in this model. This assumption could be challenged pending future research on bison in YNP, but I believed it was appropriate here because of disparities in the conclusions of other studies, demonstrating higher male fetal sex ratios (Rutberg 1986), higher female sex ratios (Pac and Frey 1991), or approximately equal sex ratios (Fuller 1960, Shaw and Carter 1989). Calf survival rates were not able to be calculated from calf-adult ratios because there were no post-winter ratios to compare to the early-season ratios. Further, the early-season counts were taken after substantial neonatal mortality had occurred, which could result in a biased survival rate estimate. Instead, I used a rate estimated by Kirkpatrick et al. (1996) who compared calf counts in year t to yearling counts in year $t+1$.

This matrix model was useful for several calculations. First, I estimated the population growth parameter λ, and the elasticity for survival and fecundity of each age (Caswell 2001). I also summed the elasticity values for juvenile survival (age 0 through

2), adult survival (age 3 through 15), and fecundity (ages 3 through 15) to interpret the effect a proportional change in each category would have on λ (Heppell et al. 2000). To understand the management implications of brucellosis elimination, I created another matrix exactly as above, but input only the fecundity parameters estimated from brucellosis-negative bison and again estimated λ.

Results

Response Variables and Effects of Covariates

Fifty-three bison aged 1 to 15 (median = 6) were monitored for a total of 190 animal-years during 1995-2001. Twenty-six individuals from the northern herd were monitored for 101 animal-years, and 27 individuals from the central herd were monitored for 89 animal-years. Excluding capture-related deaths and removals, there were 15 mortalities of marked bison during the study: 5 from unknown causes, 4 from vehicle collisions, 3 from predation, 2 from winterkill, and 1 from injury. I found no evidence that overdispersion existed in this data set (i.e. $\hat{c} < 1$), and ranked survival models using AIC_c. Constant adult female survival was the most supported model at 0.92 (95% C.I. = 0.87, 0.95; Akaike weight = 0.54). The model differentiating survival by HERD was less than 2 AIC_c units away from the top model, but received less than half the Akaike weight ($w_i = 0.22$, Table 9). This model provided an estimated survival rate of 0.91 (95% C.I. = 0.84, 0.95) for the northern herd and 0.93 (95% C.I. = 0.85, 0.97) for the central herd. The heavily overlapping confidence intervals around the survival estimate indicate little difference between the herds.

Pregnancy rates were evaluated by monitoring 46 individual females, aged 3 or older, through 139 reproductive seasons, with 123 pregnancies recorded. Of these 139 records, 60 were attributable to brucellosis positive bison, 69 to brucellosis negative bison, and 10 to bison that sero-converted that year. Females of age 3 represented 14 records, females aged 4-8 represented 81 records, and females aged 9 or older represented 44 records. I found no evidence of overdispersion in these data. There were 7 models within 2 AIC_c units of one another, and the 4th model included no covariates, estimating an overall pregnancy rate of 0.88 (95% C.I. 0.82, 0.93; Table 10). However, the effect of AGE_2 was positive in two models, with ($P < 0.05$) and a 95% confidence interval that did not overlap zero (Appendix E), indicating bison aged 4 or older had higher pregnancy rates than bison aged 3. There was no evidence of senescence in pregnancy rates, as the coefficient on senescent bison (SEN) in AGE_3 models overlapped zero. There was some evidence that brucellosis-positive bison may have a lower pregnancy rate than sero-negative bison, but the 95% confidence interval for the coefficient on sero-positive bison did overlap zero ($P<0.1$; Appendix E).

Table 9. Program MARK output analyzing adult female survival rates for Yellowstone National Park bison 1995-2001. HERD is an indicator variable for northern or central herd, by year in the study (YEAR), and by 6-month period corresponding to cold and warm season (SEAS). K refers to number of parameters and w_i refers to AIC model weight.

MODEL	**AIC_c**	**ΔAIC_c**	**K**	**w_i**
$S = ß_0$	126.89	0	1	0.54
$S = ß_0 + ß_1$(HERD)	128.71	1.82	2	0.22
$S = ß_0 + ß_1$(SEAS)	128.91	2.02	2	0.20
$S = ß_0 + ß_1$(HERD) + $ß_2$(SEAS)	132.08	5.19	4	0.04
$S = ß_0 + ß_1$(YEAR)	137.08	10.19	7	0.00
$S = ß_0 + ß_1$(HERD) + $ß_2$(YEAR)	145.69	18.80	14	0.00

Birth rates were evaluated by monitoring 48 individual females aged 3 or older, which produced 96 live calves over the 145 monitored reproductive seasons. Of these 145 reproductive seasons, 66 were attributable to brucellosis positive bison, 69 to brucellosis negative bison, and 10 to bison that sero-converted that year. Females of age

Table 10. The model selection results for logistic regression of pregnancy data for Yellowstone National Park bison 1995-2001. *Pr* is the binomial response variable, pregnancy. The SERO covariate has 3 categories, N for sero-negative bison is the intercept ($ß_0$) when SERO is in the model, P for sero-positive bison, and C for sero-converter. AGE_2 is an indicator variable for that equals 0 if bison were aged 3, and 1 for bison 4 or older. AGE_3 has 3 categories, ADULT (the intercept when AGE_3 is in the model), SEN for senescent bison (age 9 or older) and PRIM for primiparous bison (aged 3). HERD is an indicator variable that equals 1 for bison in the northern herd and 0 for bison in the central herd. K refers to number of parameters and w_i refers to AIC_c model weight.

MODEL	**AIC_c**	**ΔAIC_c**	**K**	**w_i**
$P_r = ß_0+ß_1(\text{AGE}_2)$	99.89	0.00	2	0.14
$P_r = ß_0+ß_1(\text{AGE}_2)+ß_2(\text{HERD})$	100.65	0.75	3	0.10
$P_r = ß_0+ß_1(\text{P})+ß_2(\text{C})+ß_3(\text{AGE}_2)$	101.17	1.28	4	0.08
$P_r = ß_0$	101.29	1.40	1	0.07
$P_r = ß_0+ß_1(\text{HERD})$	101.48	1.59	2	0.06
$P_r = ß_0++ß_1(\text{AGE}_2)+ß_2(\text{P})+ß_3(\text{C})+ß_4(\text{HERD})$	101.58	1.69	5	0.06
$P_r = ß_0+ß_1(\text{SEN})+ß_2(\text{PRIM})$	101.74	1.85	3	0.06
$P_r = ß_0+ß_1(\text{SWE}_{\text{acc}})+ß_2(\text{AGE}_2)$	101.98	2.08	3	0.05
$P_r = ß_0+ß_1(\text{YEAR})$	102.10	2.21	2	0.05
$P_r = ß_0+ß_1(\text{P})+ß_2(\text{C})+ß_3(\text{HERD})$	102.59	2.70	4	0.04
$P_r = ß_0+ß_1(\text{P})+ß_2(\text{C})$	102.62	2.73	3	0.04
$P_r = ß_0+ß_1(\text{SEN})+ß_2(\text{PRIM})+ß_3(\text{HERD})$	102.62	2.73	4	0.04
$P_r = ß_0+ß_1(\text{SWE}_{\text{acc}})+ß_2(\text{AGE}_2)+ß_3(\text{HERD})$	102.63	2.74	4	0.04
$P_r = ß_0+ß_1(\text{YEAR})+ß_2(\text{HERD})$	102.76	2.87	3	0.03
$P_r = ß_0+ß_1(\text{PDSI})$	103.08	3.19	2	0.03
$P_r = ß_0+ß_1(\text{P})+ß_2(\text{C})+ß_3(\text{SEN})+ß_4(\text{PRIM})$	103.22	3.33	5	0.03
$P_r = ß_0+ß_1(\text{SWE}_{\text{acc}})$	103.28	3.39	2	0.03
$P_r = ß_0+ß_1(\text{P})+ß_2(\text{C})+ß_3(\text{SEN})+ß_4(\text{PRIM})+ß_5(\text{HERD})$	103.75	3.86	6	0.02
$P_r = ß_0+ß_1(\text{SWE}_{\text{acc}})+ß_2(\text{SEN})+ß_3(\text{PRIM})$	103.86	3.97	4	0.02
$P_r = ß_0+ß_1(\text{SWE}_{\text{acc}})+ß_2(\text{PDSI})$	104.61	4.72	3	0.01
$P_r = ß_0+ß_1(\text{SWE}_{\text{acc}})+ß_2(\text{SEN})+ß_3(\text{PRIM})+ß_4(\text{HERD})$	104.63	4.74	5	0.01

3 represented 15 seasons, females aged 4-8 represented 82 seasons, and females aged 9 or older represented 44 reproductive seasons. I did find evidence for overdispersion in these data, with $\hat{c} = 1.16$, thus I calculated $QAIC_c$ for model selection (Burnham and Anderson 1998). Six models had $QAIC_c$ values within 2 units of one another, each with similar Akaike model weights (Table 11). The model that estimated birth rates for bison by

Table 11. Model selection results for logistic regression of birth rate data for Yellowstone National Park bison 1995-2001. Overdispersion was estimated, and AIC values were adjusted to QAIC. *B* represents birth of a live calf, the response variable. . The SERO covariate has 3 categories, N for sero-negative bison is the intercept (β_0) when SERO is in the model, P for sero-positive bison, and C for sero-converter. AGE_2 is an indicator variable for that equals 0 if bison were aged 3, and 1 for bison 4 or older. AGE_3 has 3 categories, ADULT (the intercept when AGE_3 is in the model), SEN for senescent bison (age 9 or older) and PRIM for primiparous bison (aged 3). HERD is an indicator variable that equals 1 for bison in the northern herd and 0 for bison in the central herd. K refers to number of parameters and w_i refers to $QAIC_c$ model weight.

MODEL	**$QAIC_c$**	**$\Delta QAIC_c$**	**K**	**w_i**
$B = \beta_0+\beta_1(\mathrm{P})+\beta_2(\mathrm{C})+\beta_3(\mathrm{AGE}_2)$	150.09	0.00	4	0.23
$B = \beta_0+\beta_1(\mathrm{P})+\beta_2(\mathrm{C})$	150.30	0.21	3	0.21
$B = \beta_0+\beta_1(\mathrm{P})+\beta_2(\mathrm{C})+\beta_3(\mathrm{HERD})$	150.87	0.77	4	0.16
$B = \beta_0+\beta_1(\mathrm{AGE}_2)+\beta_2(\mathrm{P})+\beta_3(\mathrm{C})+\beta_4(\mathrm{HERD})$	150.88	0.79	5	0.16
$B = \beta_0+\beta_1(\mathrm{P})+\beta_2(\mathrm{C})+\beta_3(\mathrm{SEN})+\beta_4(\mathrm{PRIM})$	151.26	1.17	5	0.13
$B = \beta_0+\beta_1(\mathrm{P})+\beta_2(\mathrm{C})+\beta_3(\mathrm{SEN})+\beta_4(\mathrm{PRIM})+\beta_5(\mathrm{HERD})$	151.72	1.63	6	0.10
$B = \beta_0+\beta_1(\mathrm{AGE}_2)$	158.87	8.78	2	0.00
$B = \beta_0$	159.52	9.42	1	0.00
$B = \beta_0+\beta_1(\mathrm{SWE}_{\mathrm{acc}})+\beta_2(\mathrm{AGE}_2)$	159.96	9.87	3	0.00
$B = \beta_0+\beta_1(\mathrm{AGE}_2)+\beta_2(\mathrm{HERD})$	160.23	10.14	3	0.00
$B = \beta_0+\beta_1(\mathrm{HERD})$	160.64	10.55	2	0.00
$B = \beta_0+\beta_1(\mathrm{YEAR})$	160.65	10.56	2	0.00
$B = \beta_0+\beta_1(\mathrm{SEN})+\beta_2(\mathrm{PRIM})$	160.69	10.60	3	0.00
$B = \beta_0+\beta_1(\mathrm{SWE}_{\mathrm{acc}})$	160.71	10.61	2	0.00
$B = \beta_0+\beta_1(\mathrm{SWE}_{\mathrm{acc}})+\beta_2(\mathrm{AGE}_2)+\beta_3(\mathrm{HERD})$	161.15	11.05	4	0.00
$B = \beta_0+\beta_1(\mathrm{PDSI})$	161.29	11.20	2	0.00
$B = \beta_0+\beta_1(\mathrm{SWE}_{\mathrm{acc}})+\beta_2(\mathrm{SEN})+\beta_3(\mathrm{PRIM})$	161.87	11.78	4	0.00
$B = \beta_0+\beta_1(\mathrm{SEN})+\beta_2(\mathrm{PRIM})+\beta_3(\mathrm{HERD})$	161.98	11.89	4	0.00
$B = \beta_0+\beta_1(\mathrm{YEAR})+\beta_2(\mathrm{HERD})$	162.09	12.00	3	0.00
$B = \beta_0+\beta_1(\mathrm{SWE}_{\mathrm{acc}})+\beta_2(\mathrm{PDSI})$	162.35	12.26	3	0.00
$B = \beta_0+\beta_1(\mathrm{SWE}_{\mathrm{acc}})+\beta_2(\mathrm{SEN})+\beta_3(\mathrm{PRIM})+\beta_4(\mathrm{HERD})$	162.99	12.90	5	0.00

serology (SERO) and 2 age categories (AGE_2) was considered the best approximating model, with an Akaike model weight of 0.23. Sero-converters (C) had the lowest birth rates, brucellosis positive (P) bison had intermediate birth rates, and brucellosis negative (N) bison had the highest birth rates. Bison age 4 or older may have a slightly higher birth rate than bison age 3, although the 95% confidence interval on the AGE_2 coefficient did overlap zero ($P < 0.1$; Appendix E). The results suggested brucellosis exposure affected birth rates, and that 3 year old bison may have lower birth rates than bison aged 4 or older (Table 12). No reproductive senescence was detected because the senescent category (SEN) of the AGE_3 covariate was not significant ($P>0.1$) and its confidence interval encompassed zero. The covariate HERD also appeared in two of the top models, but the 95% C.I. encompassed zero, its coefficient was not significant ($P > 0.1$), and I concluded herd membership had a negligible effect on birth rates.

Twenty-eight spring calf-adult ratios were recorded in May and/or June from 1970-1997. Due to limitations with the availability of covariates (Appendix F), I analyzed a total of 20 spring calf-adult ratios for the northern herd and 17 spring calf-adult ratios for the central herd. The northern herd and central herd spring calf-adult ratios both showed a strong, negative correlation with SWE_{acc} (Figure 5). The best approximating model for central herd spring calf-adult ratios was the SWE_{acc} only model, and no other model was within 2 AIC units (Table 13). For the northern herd, $\sqrt{PDSI}$ was positively associated with calf-adult ratios, although it was only marginally significant at $P = 0.11$ (Table 14; Appendix E). The severe $\sqrt{PDSI}$ value of the 1978 drought was an influential point in the regression (Figure 2), illustrating the importance of extreme climatic events in ungulate limitation.

Table 12. Birth rates for Yellowstone National Park bison in two age categories and 3 brucellosis exposure categories over 1995-2001. Estimated reproductive rates are presented with standard errors and 95% lower and upper confidence intervals. Estimates are model averaged results from the top 2 models containing the age and serology covariates from logistic regression analysis of birth rate data.

BIRTH RATES	ESTIMATE	SE	LCI	UCI
Positive 3-year-old	**0.40**	0.13	0.15	0.65
Sero-converting 3-year-old	**0.10**	0.07	0.00	0.24
Negative 3-year-old	**0.63**	0.12	0.39	0.87
Positive 4+-year-old	**0.64**	0.06	0.52	0.76
Sero-converting 4+-year-old	**0.22**	0.12	0.00	0.46
Negative 4+-year-old	**0.81**	0.04	0.73	0.89

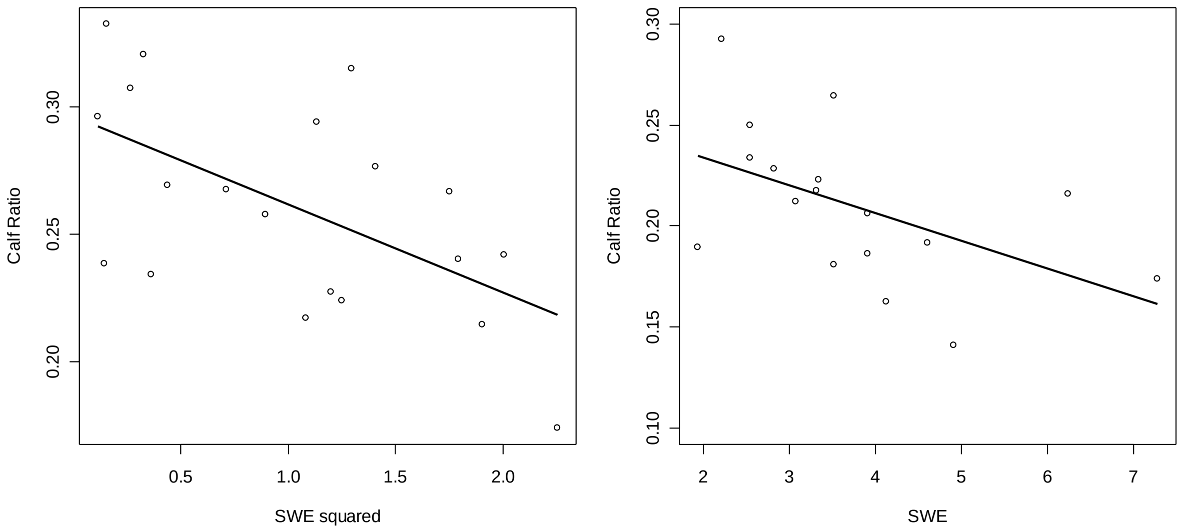

Figure 5. Regression of calf-adult ratios for the northern (left) and central (right) bison herds in Yellowstone National Park with snow pack (SWE_{acc}) over 1970-1997.

Table 13. The model selection results for the factors influencing spring calf-adult ratios ($C\text{-}A_c$) of the central herd bison in Yellowstone National Park 1981-1997. The lowest AIC_c is the most parsimonious model. SWE_{acc} refers to snow pack depth, density, and duration, PDSI refers to drought, and BISON refers to bison counts of the previous year. For all models, n =17, K refers to the number of parameters and w_i = AIC model weight.

MODEL	**AIC_c**	**Δ AIC_c**	**K**	**w_i**
$C\text{-}A_c = ß_0 + ß_1(SWE_{acc})$	-61.17	0.00	3	0.43
$C\text{-}A_c = ß_0 + ß_1(SWE_{acc}) + ß_2(PDSI)$	-59.15	2.02	4	0.16
$C\text{-}A_c = ß_0$	-59.12	2.05	2	0.15
$C\text{-}A_c = ß_0 + ß_1(SWE_{acc}) + ß_2(BISON)$	-58.15	3.02	4	0.10
$C\text{-}A_c = ß_0 + ß_3(BISON)$	-56.70	4.46	3	0.05
$C\text{-}A_c = ß_0 + ß_2(PDSI)$	-56.52	4.65	3	0.04
$C\text{-}A_c = ß_0 + ß_1(SWE_{acc}) + ß_2(PDSI) + ß_3(BISON)$	-55.76	5.41	5	0.03
$C\text{-}A_c = ß_0 + ß_1(SWE_{acc}) + ß_2(PDSI) + ß_4(SWE_{acc} \times PDSI)$	-55.04	6.13	5	0.02
$C\text{-}A_c = ß_0 + ß_1(SWE_{acc}) + ß_3(BISON) + ß_5(SWE_{acc} \times BISON)$	-54.04	7.13	5	0.01
$C\text{-}A_c = ß_0 + ß_2(PDSI) + ß_3(BISON)$	-53.75	7.41	4	0.01
$C\text{-}A_c = ß_0 + ß_2(PDSI) + ß_3(BISON) + ß_6(PDSI \times BISON)$	-50.99	10.18	5	0.00

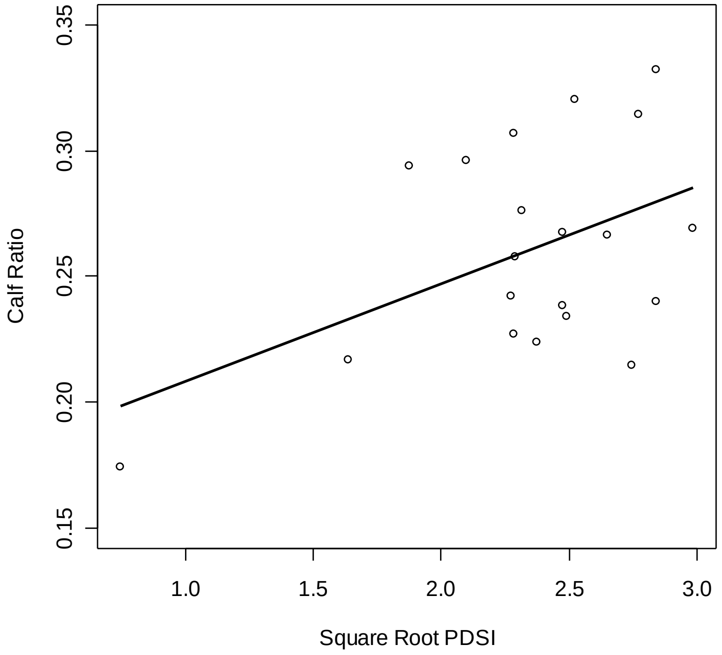

Figure 6. The relationship between √PDSI (drought) and the spring calf-adult ratios on northern herd bison in Yellowstone National Park 1970-1997.

Table 14. Model selection results for the factors influencing spring calf-adult ratios (C-A_n) of the northern herd bison in Yellowstone National Park 1970-1997. The lowest AIC_c is the most parsimonious model. SWE_{acc} refers to snowpack depth, density, and duration, PDSI refers to drought, BISON refers to bison counts and ELK refers to elk counts of the previous year. For all models, n = 20, K refers to the number of parameters and w_i = AIC model weight.

MODEL	**AIC_c**	**Δ AIC_c**	**K**	**w_i**
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(√PDSI)	-72.22	0.00	4	0.27
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$)	-72.21	0.01	3	0.27
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(BISON)	-70.23	1.98	4	0.10
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(ELK)	-69.78	2.44	4	0.08
C-A_n = ß$_0$ + ß$_1$(√PDSI)	-69.25	2.97	3	0.06
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(√PDSI) + ß$_3$(BISON)	-68.78	3.44	5	0.05
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(√PDSI) + ß$_3$($\text{SWE}_{\text{acc}}^2$ x √PDSI)	-68.68	3.53	5	0.05
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(BISON) + ß$_3$($\text{SWE}_{\text{acc}}^2$ x BISON)	-67.07	5.14	5	0.02
C-A_n = ß$_0$	-67.02	5.19	2	0.02
C-A_n = ß$_0$+ ß$_1$(√PDSI) + ß$_2$ (ELK)	-66.78	5.43	4	0.02
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(BISON) + ß$_3$(ELK)	-66.61	5.60	5	0.02
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$ (ELK) + ß$_3$($\text{SWE}_{\text{acc}}^2$ x ELK)	-66.21	6.01	5	0.01
C-A_n = ß$_0$+ ß$_1$(√PDSI) + ß$_2$(BISON)	-66.12	6.09	4	0.01
C-A_n = ß$_0$+ ß$_1$($\text{SWE}_{\text{acc}}^2$) + ß$_2$(√PDSI) + ß$_3$(BISON) + ß$_4$(ELK)	-64.61	7.61	6	0.01
C-A_n = ß$_0$+ ß$_1$ (BISON)	-64.60	7.62	3	0.01
C-A_n = ß$_0$+ ß$_1$(ELK)	-64.32	7.89	3	0.01
C-A_n = ß$_0$+ ß$_1$(√PDSI) + ß$_2$(BISON) + ß$_3$(ELK)	-63.58	8.64	5	0.00
C-A_n = ß$_0$+ ß$_1$(√PDSI) + ß$_2$ (ELK) + ß$_3$(√PDSI x ELK)	-63.19	9.03	5	0.00
C-A_n = ß$_0$ + ß$_1$(BISON) + ß$_2$(ELK)	-62.84	9.37	4	0.00
C-A_n = ß$_0$+ ß$_1$(√PDSI) + ß$_2$ (BISON) + ß$_3$(√PDSI x BISON)	-62.55	9.67	5	0.00
C-A_n = ß$_0$ + ß$_1$(BISON) + ß$_2$(ELK) + ß$_3$ (BISON x ELK)	-60.26	11.96	5	0.00

Integrating Vital Rates

The vital rates input in the matrix model included one adult survival rate incorporating all ages from 1 to 15 (0.92). I input two fecundity rates, one for 3 year old bison of 0.23, and one for bison aged 4 to 15 (0.35) because I found no evidence of reproductive senescence in these data. Overall fecundity rates were model averaged birth rates by age group (3 and 4+) and serological categories (N, P, and C) according to their abundance in the population, as in Jolles et al. (2005). The input fecundity rates represent females only, and were one half the model averaged birth rate estimates (assuming equal sex ratios). I input a calf survival rate of 0.76, following the findings of Kirkpatrick et al. (1996). The resulting λ = 1.07. Simulations enforcing survival senescence and allowing older age classes resulted in λ =1.07-1.08. Changes in survival rates of older animals did not have significant impact on λ because these rates had low elasticity. Age-specific elasticity values were highest for calf, 1, and 2 year old survival, where elasticity = 0.12 (Figure 7). λ was more elastic to age-specific survival than age-specific reproduction for all but the oldest age classes (i.e. ≥14 years). The sum of elasticity values by category demonstrated that adult survival had the highest elasticity (0.51), followed by juvenile survival (0.36), and fecundity (0.12). The highest reproductive value was for 4-year old bison (Figure 8), and the generation time was estimated at 8.6 years. The Leslie matrix model simulating brucellosis eradication was structured the same as above, but fecundity estimates came from the birth rates of brucellosis negative bison only. For 3 year old bison, the input fecundity was 0.32, and for 4 year old bison, the fecundity input was 0.41. This resulted in λ = 1.09: an increase of 29% in population growth rate if brucellosis were eliminated from the system.

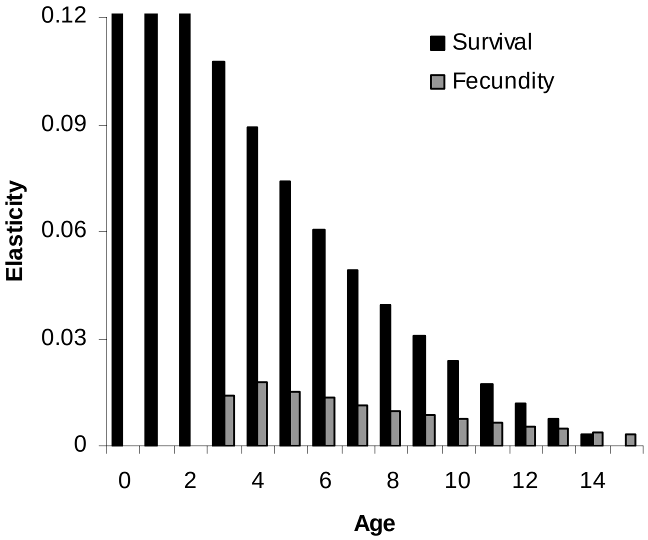

Figure 7. Age-specific elasticity for survival and fecundity rates in Yellowstone National Park bison using a Leslie matrix model based on data collected 1995-2001.

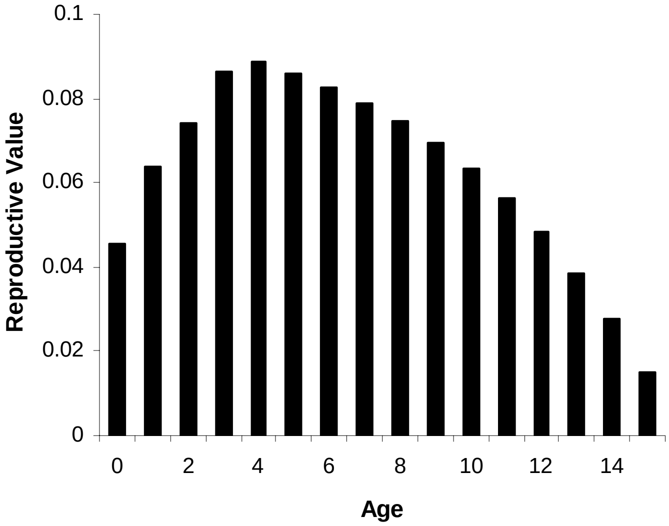

Figure 8. The relationship between age and reproductive value in Yellowstone National Park bison using a Leslie matrix model based on data collected 1995-2001.

Discussion

The history of the YNP bison herds chronicle a conservation success, as just 46 bison in 1902 recovered to nearly 5,000 today. The future management of YNP bison is highly-debated and contingent upon management of brucellosis. The bison management plan for the state of Montana and Yellowstone National Park proposes several alternative management strategies with the dual purpose of protecting domestic cattle outside YNP from brucellosis while ensuring the “wild and free-ranging nature of the bison herd” (NPS 2000). These alternatives range from minimal management to aggressive brucellosis control within YNP (NPS 2000), and include the development of an effective vaccine against brucellosis, an area of intense research effort (Cheville et al. 1998). Prediction of the effects of culling and vaccination, as espoused in the various management alternatives, is predicated on objective knowledge of population parameters. This manuscript presents the first set of rigorously-estimated population vital rates, the effects of brucellosis on reproduction, and an integrated analysis of how these factors ultimately affect population growth rates: information vital to the interpretation of alternative management strategies and the future of YNP bison.

Several studies suggest that climatic variability is most pronounced in neonatal survival, because conception and gestation require less energy than lactation to feed an offspring until weaning, and females may produce offspring they cannot actually wean (Clutton-Brock et al. 1989, Gaillard et al. 2000). In accordance with these studies, I found that pregnancy and birth rates were not variable with climate, but that spring calf-adult ratios significantly varied with both winter severity (SWE_{acc}) and warm-season growing conditions (PDSI). A function of calf production and calf survival, I suggest that the variability in spring calf-adult ratios is largely due to fluctuations in neonatal survival rather than fluctuations in birth rates. The adult survival rate (0.92) was comparable to, if slightly lower than, many unharvested large mammals (Gaillard et al. 1998, Eberhardt 2002). Vehicle mortality resulted in 4 out of 15 deaths, and the estimate of adult survival rate would certainly increase in the absence of this non-natural source of mortality. Due to small sample size, I was unable to detect any sources of variation in this rate, but adult survival is thought to be highly static for most large ungulate populations (Gaillard et al. 2000).

Brucellosis was epizootic in the YNP bison, with 52% of bison in both herds indicating exposure to brucellosis over the 145 monitored birth seasons. This is similar to other recent estimates of 54% over 1988-1989 and 50% over 1991-1992 (Pac and Frey 1991, Meyer and Meagher 1995). However, earlier estimates did indicate a lower brucellosis exposure in the central herd. Barmore (1968) found 54% prevalence in the northern herd, compared to lower prevalence rates in the Pelican (42%) and Hayden (26%) valleys of the central herd, but I found no difference in brucellosis prevalence between the herds. In 1968, bison were at low densities compared to present counts (Dobson and Meagher 1996), and as density increased, disease transmission rates also may have increased.

Birth rates varied significantly with brucellosis infection. Brucellosis is known to infect the reproductive tract, causing abortion of the first calf, although effects are thought to wane through time (Davis et al. 1990, Davis et al. 1991, Cheville et al. 1998). The data corroborate these findings, and indicate that sero-converters had the lowest birth rates, brucellosis positive bison had an intermediate birth rate, and the highest birth rates belonged to brucellosis negative bison. Possible recovery from brucellosis occurred in four bison that reliably tested brucellosis negative in years after having positive brucellosis tests, perhaps demonstrating a reduction in brucellosis antibodies to a level below detectability. I recognize the possibility some brucellosis positive bison actually sero-converted the year of their first capture, in which case they were simply assigned to the positive category because there were no prior tests on that individual. This would result in an underestimation of reproductive rates for the brucellosis positive bison, but I do not believe this would significantly impact results, as sero-converters were a low proportion of the sampled population in any one year (7%).

In large ungulates, the most variable vital rates tend to be the least elastic (Gaillard et al. 2000), but this was not strictly the case in YNP bison. Adult survival was the most elastic trait (0.51), followed by juvenile survival (0.36) and then fecundity (0.12), suggesting that small changes in adult survival could have large impacts to the population growth rate. Compared to other ungulates, the elasticity of fecundity was relatively low, while the elasticity and variability in juvenile survival was relatively high. However, compared to smaller ungulates, bison are relatively long lived, have a long generation time (>8 years), and a longer delay before primiparity (3-4 years rather than 1-2), which may result in different trends. Similar elasticities are recorded for other large-bodied grazers with similar life histories, such as elephants, primates, and marine mammals (Heppell et al. 2000). Elasticities estimated for African buffalo (*Syncerus caffer*) were nearly identical to those estimated here (Jolles et al. 2005).

I calculated a population growth rate based on Leslie matrix model results (λ = 1.07), which approximates an estimate of population growth rate of YNP bison based on aerial count data over 1990-2000 (λ = 1.05; 95% C.I. = 1.00, 1.10; Appendix G). Using counts and vital rate information to independently estimate λ is in accordance with a paradigm proposed by Eberhardt (2002). The agreement in λ between these two methods supports the validity of the overall population growth rate (5-7% per year) and the validity of the vital rate estimates. The λ values I calculated above represent the growth potential of YNP bison. However, the realized growth rate of YNP bison is much lower, due to large periodic removals that began in 1984. Over 1990-2000, the actual λ = 0.96 (95% C.I. = 0.92, 1.00; Appendix G).

I detected no evidence of density-dependent decreases in birth rates or spring calf-adult ratios, even though bison counts were at high levels (3,000-4,000 bison). However, there is increasing evidence that bison may be responding to density through spatial responses, including range expansion (Gates et al. 2005, Fuller et al. unpublished data). Yellowstone bison have a high potential growth rate (5-7% a year) and may continue to expand their range, creating further conflicts as they move out of Yellowstone Park and onto surrounding lands. However, I recognize that the data presented here were collected 4-8 years ago, and changes in the dynamic Yellowstone system could be occurring.

These results provided insights into several management scenarios. As the Yellowstone bison population expands, conflicts with private landowners outside the park may increase as well. To address these conflicts, it is essential for managers to continue reliably counting bison, and continue individual monitoring to detect any changes in fecundity and survival rates that may occur as densities increase. If vaccination plans are implemented, the eradication of brucellosis could result in higher population growth rates (29%), which may result in more bison leaving Yellowstone and entering the private lands outside the park. New bison hunting seasons imposed by the state of Montana may afford opportunities to slow population growth through selective harvest of adult females. Further, I suggest that cooperation between hunters, state, and federal agencies, could provide a wealth of data on population age structure, brucellosis prevalence, and fetal sex ratios through collection of incisors and tissue samples from harvested bison.

Continued monitoring of individually marked bison in Yellowstone is essential to detecting the relationships between variability in vital rates and density-dependent and density-independent factors. Although logistically challenging to obtain, I suggest that future research into quantifying the survival of calves and juveniles (0-2 years old) would be especially informative. Juvenile survival may be one of the first rates affected by density dependence (Sæther 1997), and so it is especially important to monitor this as populations continue to increase. Calf and juvenile survival have high elasticity, and so are very important to estimating λ, but I currently have little rigorous information about this population parameter. Yellowstone is a dynamic system, and continued monitoring of vital rates and population trends is essential for the formulation of a sound management policy.

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APPENDICES

APPENDIX A

BISON COUNTS AND REMOVALS BY HERD 1902-2000

Table 15. Counts of bison in the central and northern herds of Yellowstone National Park, Montana and Wyoming, during 1902-2000. Counts reported for 1970-2000 represent the summer counts (June-August) for each herd during each year. Counts were taken before removals.

YEAR	NORTH	CENTRAL	YEAR	NORTH	CENTRAL	YEAR	NORTH	CENTRAL	YEAR	NORTH	CENTRAL
1901	-	-	**1926**	889	65	**1951**	-	640	**1976**	259	901
1902	21	25	**1927**	977	72	**1952**	386	840	**1977**	457	893
1903	29	21	**1928**	1050	61	**1953**	-	-	**1978**	217	1362
1904	41	17	**1929**	1198	21[1]	**1954**	235	1319	**1979**	433	1307
1905	44	30	**1930**	1229	27[1]	**1955**	-	-	**1980**	287	1801
1906	57	-	**1931**	1302	10[1]	**1956**	231	1400	**1981**	298	1739
1907	61	25	**1932**	1238	-	**1957**	205	610	**1982**	405	1346
1908	74	22	**1933**	1192	-	**1958**	-	-	**1983**	462	1447
1909	100	23	**1934**	1127	-	**1959**	-	-	**1984**	588	1671
1910	123	29	**1935**	1094	-	**1960**	-	-	**1985**	517	1834
1911	147	27	**1936**	749	207	**1961**	212	657	**1986**	708	2068
1912	171	49	**1937**	473	218	**1962**	-	-	**1987**	595	2381
1913	170	53	**1938**	579	201	**1963**	-	656	**1988**	844	2303
1914	198	-	**1939**	649	229	**1964**	-	-	**1989**	430	2077
1915	243	31	**1940**	633	238	**1965**	172	608	**1990**	349	2672
1916	294	72	**1941**	748	274	**1966**	68[3]	228	**1991**	544	2568
1917	338	70	**1942**	713	358	**1967**	81[3]	319	**1992**	267	3090
1918	390	-	**1943**	751	224	**1968**	71[3]	351	**1993**	626	2703
1919	417	91	**1944**	757	397	**1969**	85[3]	474	**1994**	738	3376
1920	457	61	**1945**	445	487	**1970**	216	262	**1995**	712	3216
1921	533	76	**1946**	548	481	**1971**	322	394	**1996**	756	2828
1922	582	69	**1947**	449	101[2]	**1972**	232	379	**1997**	354	1816
1923	686	76	**1948**	550	647	**1973**	290	494	**1998**	572	1618
1924	766	-	**1949**	396	730	**1974**	205	716	**1999**	548	1688
1925	873	66	**1950**	458	864	**1975**	182	785	**2000**	634	2144

[1] 1929-1931 were considered incomplete counts for the central herd and were censored in the analysis.

[2] 1947 was an incomplete count for the central herd (Barmore 1968) and was censored from analysis.

[3] 1966-1969 were before the new survey scheme, considered undercounts, and were censored from analysis.

Table 16. Removals of bison from the central and northern herds of Yellowstone National Park, Montana and Wyoming, during 1902-2000.

YEAR	NORTH	CENTRAL	YEAR	NORTH	CENTRAL	YEAR	NORTH	CENTRAL	YEAR	NORTH	CENTRAL
1901	**-**	-	**1926**	23	-	**1951**	-	-	**1976**	-	-
1902	-	**-**	**1927**	41	-	**1952**	243	7	**1977**	-	-
1903	1	2	**1928**	54	4	**1953**	-	-	**1978**	-	-
1904	2	5	**1929**	106	-	**1954**	77	-	**1979**	-	-
1905	-	-	**1930**	132	-	**1955**	-	288	**1980**	-	-
1906	-	-	**1931**	120	-	**1956**	24	349	**1981**	-	-
1907	2	-	**1932**	222	-	**1957**	60	212	**1982**	-	-
1908	-	-	**1933**	207	-	**1958**	-	12	**1983**	-	-
1909	5	-	**1934**	177	-	**1959**	18	26	**1984**	88	-
1910	3	-	**1935**	264	-	**1960**	-	-	**1985**	41	16
1911	2	-	**1936**	109	-	**1961**	-	-	**1986**	-	7
1912	6	-	**1937**	17	-	**1962**	148	-	**1987**	2	37
1913	8	-	**1938**	25	-	**1963**	8	362	**1988**	569	2
1914	5	-	**1939**	67	-	**1964**	6	-	**1989**	1	3
1915	4	-	**1940**	3	-	**1965**	87	305	**1990**	-	14
1916	18	-	**1941**	212	1	**1966**	2	52	**1991**	249	22
1917	8	3	**1942**	200	2	**1967**	1	2	**1992**	-	79
1918	5	-	**1943**	9	2	**1968**	1	3	**1993**	-	5
1919	9	1	**1944**	405	2	**1969**	-	-	**1994**	307	119
1920	17	-	**1945**	-	-	**1970**	-	-	**1995**	26	344
1921	7	-	**1946**	200	38	**1971**	-	-	**1996**	725	358
1922	4	-	**1947**	7	-	**1972**	-	-	**1997**	-	11
1923	14	-	**1948**	237	-	**1973**	-	-	**1998**	-	94
1924	13	-	**1949**	-	-	**1974**	-	-	**1999**	-	-
1925	109	-	**1950**	228	-	**1975**	8	-	**2000**	-	-

APPENDIX B

LOGe – LINEAR REGRESSION OF COUNT DATA FOR CENTRAL HERD BISON 1970-1994

Figure 9. Graphical depiction of $\log_e$-transformed population counts for the central bison herd in Yellowstone National Park, Montana and Wyoming, during 1970-1994. Counts during the 1970-1981 period are represented by black diamonds, while counts during the 1982-1994 period are represented by gray squares.

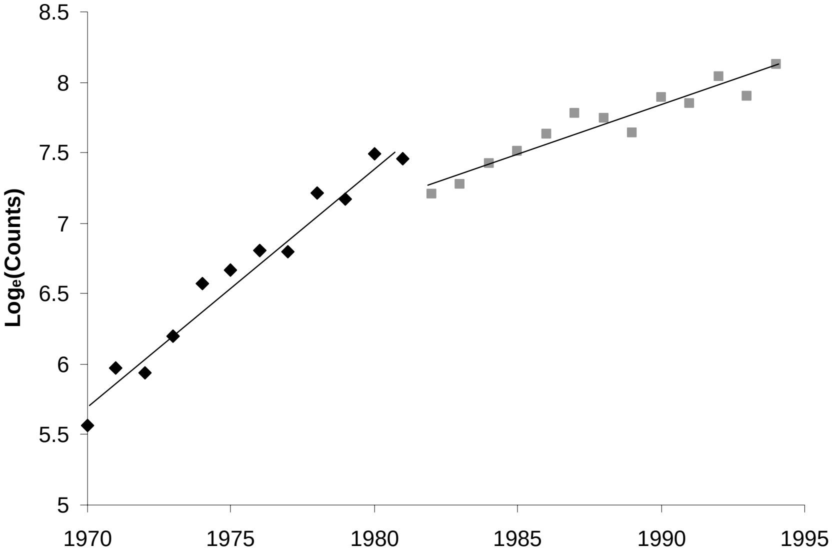


Table 17. Model selection results for regression of the factors influencing the $\log_e$ count of the central herd bison in Yellowstone National Park, Montana and Wyoming, during 1970-1994. The lowest AIC_c is the most parsimonious model. For all models, n = 25. Year is represented by Y, period is represented by indicator variable P (P = 0 for 1970-1981 and P = 1 for 1982-1994). The ß values represent coefficients estimated by least-squares regression, and R^2 is the percent of variation in the data described by the regression model.

MODEL	AIC_c	Δ AIC_c	W_i	R^2
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \beta_3(P \times Y) + \varepsilon$	-32.41	0.00	1.00	0.98
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \beta_2(P) + \varepsilon$	2.48	34.89	0.00	0.91
$\log_e(n_t) = \beta_0 + \beta_1(Y) + \varepsilon$	4.48	36.89	0.00	0.89

APPENDIX C

COVARIATES USED IN MULTIPLE REGRESSION MODELS

Table 18. Covariates used in multiple regression and model selection for the central and northern bison herds in Yellowstone National Park, Montana and Wyoming, during 1970-2000.

	NORTHERN HERD		**CENTRAL HERD**	
YEAR	**SWE$_{acc}$**	**PDSI**	**SWE$_{acc}$**	**PDSI**
1970[1]	891	2.88	-	2.88
1971	1381	0.55	-	0.55
1972	843	-0.88	-	-0.88
1973	1138	0.70	-	0.70
1974	376	-0.87	-	-0.87
1975	1095	-1.79	-	-1.79
1976	1339	1.08	-	1.08
1977	568	-0.64	-	-0.64
1978	1501	-6.44	-	-6.44
1979	1324	0.04	-	0.04
1980	1271	-1.77	-	-1.77
1981	503	-2.86	1933	-2.86
1982	389	1.07	4906	1.07
1983	617	2.36	3072	2.36
1984	709	-1.04	2543	-1.04
1985	1201	-1.25	3509	-1.25
1986	1117	-1.37	3908	-1.37
1987	601	-0.79	2214	-0.79
1988	335	-2.59	2816	-2.59
1989	1039	-4.32	4128	-4.32
1990	946	-1.76	3317	-1.76
1991	513	-1.79	3332	-1.79
1992	1416	-1.83	3511	-1.83
1993	1063	-3.48	3907	-3.48
1994	659	1.90	2533	1.90
1995	1187	-1.64	4611	-1.64
1996	646	0.87	6237	0.87
1997	1845	-0.13	7279	-0.13
1998	721	1.40	3511	1.40
1999	1066	-2.11	5008	-2.13
2000	1109	-3.84	3355	-3.62

[1] No SWE$_{acc}$ data were available for the central herd until 1981.

APPENDIX D

REGRESSION OF NORTHERN AND CENTRAL BISON HERD POPULATION GROWTH RATES 1970-1981 AND 1982-2000

Figure 10. Correlations between estimated annual population growth rates of the Yellowstone National Park northern and central bison herds during 1970-1981.

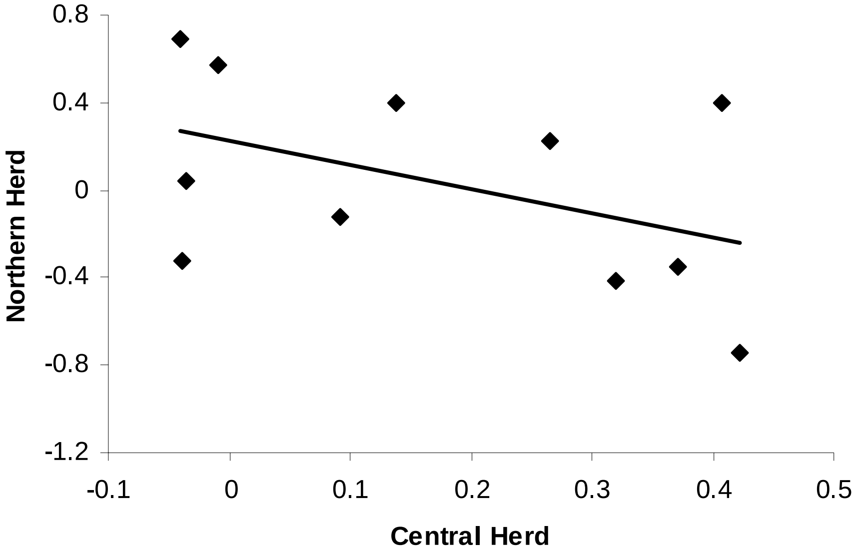


Figure 11. Correlations between estimated annual population growth rates of the Yellowstone National Park northern and central bison herds during 1982-2000, excluding the 1997 growth rate.

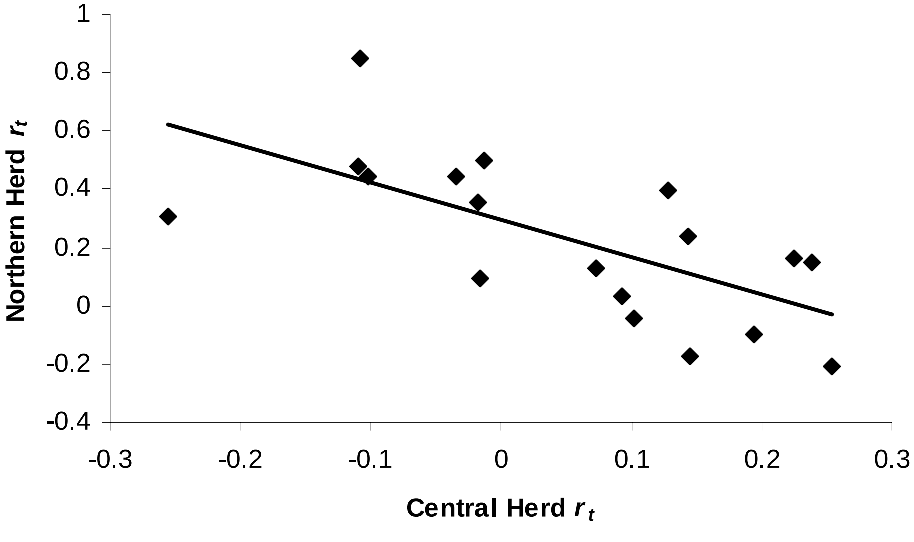
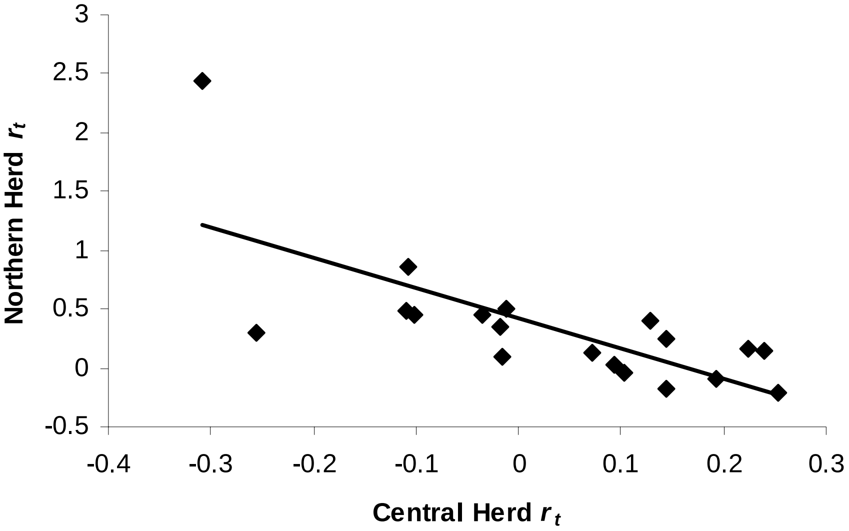


Figure 12. Correlations between estimated annual population growth rates of the Yellowstone National Park northern and central bison herds during 1982-2000, including the 1997 growth rate.



APPENDIX E

COEFFICIENT ESTIMATES FROM PREGNANCY AND BIRTH RATE MULTIPLE LOGISTIC CALF-ADULT RATIO LINEAR REGRESSION MODELS

Table 19. Untransformed coefficient values ($ß_i$) and 95% confidence limits on the three best approximating multiple logistic regression models identified through AIC model comparison techniques examining variability in pregnancy rates. Boldface entries were significant at $\alpha = 0.05$. The “Predictor Weight” column refers to the sum of model weights (w_i) that include that covariate.

		MODEL		
Covariate	Predictor Weight	$ß_{\text{(PREG, Model 1)}}$	$ß_{\text{(PREG, Model 2)}}$	$ß_{\text{(PREG, Model 3)}}$
AGE2	0.47	**1.33 (0.02, 2.63)**	1.23 (-0.10, 2.55)[1]	**1.37 (0.04, 2.71)**
HERD (N)	0.40		0.63 (-0.44, 1.70)	
C	0.26			-0.37 (-2.66 1.93)
P	0.26			-0.98 (-2.13 0.18)[1]

[1] Marginally significant at $P < 0.1$

Table 20. Untransformed coefficient values ($ß_i$) and 95% confidence limits on the four best approximating multiple logistic regression models identified through AIC model comparison techniques examining variability in birth rates. Boldface entries were significant at $\alpha = 0.05$. The “Predictor Weight” column refers to the sum of model weights (w_i) that include that covariate.

		MODEL			
Cov.	Predictor Weight	$ß_{\text{(BIRTH, Model 1)}}$	$ß_{\text{(BIRTH, Model 2)}}$	$ß_{\text{(BIRTH, Model 3)}}$	$ß_{\text{(BIRTH, Model 4)}}$
C	0.98	**-2.73 (-4.40, -1.06)**	**-2.84 (-4.53, -1.14)**	**-2.75 (-4.41, -1.10)**	**-2.86 (-4.53, -1.18)**
P	0.98	**-0.90 (-1.68, -0.12)**	**-0.92 (-1.70, -0.13)**	**-0.87 (-1.64, -0.10)**	**-0.88 (-1.66, -0.11)**
AGE2	0.39	0.98 (-0.18, 2.14)[1]	0.94 (-0.22, 2.10)		
HERD	0.42		0.48 (-0.27, 1.24)		0.51 (-0.24, 1.26)

[1] Marginally significant at $P < 0.1$

Table 21. Coefficient values ($ß_i$) and 95% confidence limits on the three best approximating linear regression models identified through AIC model comparison techniques examining variability in spring calf-adult ratios for the northern YNP bison herd (1970-1997). Boldface entries were significant at $\alpha = 0.05$. The “Predictor Weight” column refers to the sum of model weights (w_i) that include that covariate.

		MODEL		
Covariate	Predictor Weight	$ß_i$	$ß_i$	$ß_i$
SWE_{acc}^2	0.88	**-0.03 (-0.05, -0.01)**	**-0.03 (-0.06, -0.01)**	**-0.04 (-0.06, -0.01)**
$\sqrt{\text{PDSI}}$	0.48	0.03 (0.00, 0.06)		
BISON	0.22			0.00 (-0.01, 0.00)

Table 22. Coefficient values ($ß_i$) and 95% confidence limits on the two best approximating linear regression models identified through AIC model comparison techniques examining variability in spring calf-adult ratios for the central YNP bison herd (1970-1997). Boldface entries were significant at $\alpha = 0.05$. The "Predictor Weight" column refers to the sum of model weights (w_i) that include that covariate.

		MODEL	
Covariate	Predictor Weight	$ß_i$	$ß_i$
SWE_{acc}	0.88	**-0.01 (-0.03, 0.00)**	**-0.02 (-0.03, -0.01)**
PDSI	0.31		0.01 (0.00, 0.01)

APPENDIX F

CALF-ADULT RATIOS AND COVARIATES BY HERD 1970-2005

Table 23. Covariates by herd and year for spring calf-adult ratios for the northern and central bison herds in Yellowstone National Park 1970-2005.

YEAR	**Northern Herd Spring Calf Ratio**	**Central Herd Spring Calf Ratio**	**PDSI (Both Herds)**	**SWEacc Northern Herd**	**SWEacc Central Herd**	**BISON Northern Herd**	**BISON Central Herd**	**ELK Northern Herd**
1970	0.32	0.18	2.88	891	-	-	512	5543
1971	0.21	0.24	0.55	1381	-	216	511	7282
1972	0.27	0.30	-0.88	843	-	322	612	8215
1973	0.31	0.29	0.70	1138	-	232	728	9981
1974	0.24	0.28	-0.87	376	-	290	873	10529
1975	0.23	0.26	-1.79	1095	-	285	936	12607
1976	0.24	0.14	1.08	1339	-	224	951	10825
1977	0.32	0.26	-0.64	568	-	259	1119	10741
1978	0.17	0.22	-6.44	1501	-	457	1378	11878
1979	0.27	0.20	0.04	1324	-	262	1588	10807
1980	0.28	0.20	-1.77	1271	-	433	1801	-
1981	0.19	0.19	-2.86	503	1933	349	2067	-
1982	0.33	0.14	1.07	389	4906	330	1703	15114
1983	0.24	0.21	2.36	617	3072	542	1674	-
1984	0.31	0.23	-1.04	709	2543	483	1671	-
1985	0.31	0.26	-1.25	1201	3509	619	1919	-
1986	0.22	0.19	-1.37	1117	3908	647	2068	15387
1987	0.23	0.29	-0.79	601	2214	708	2381	16162
1988	0.30	0.23	-2.59	335	2816	712	2387	18737
1989	0.22	0.16	-4.32	1039	4128	868	2188	18945
1990	0.26	0.22	-1.76	946	3317	461	2672	14506
1991	0.31	0.22	-1.79	513	3332	541	2685	11330
1992	0.24	0.18	-1.83	1416	3511	741	3090	11072
1993	0.29	0.21	-3.48	1063	3907	570	2945	16011
1994	0.27	0.25	1.90	659	2533	673	3376	18832
1995	0.28	0.19	-1.64	1187	4611	770	3216	14752
1996	0.30	0.22	0.87	646	6237	771	2928	-
1997	0.14	0.17	-0.13	1845	7279	877	1620	-
1998	-	-	1.40	-	3511	-	-	-
1999	-	-	-2.11	-	5008	-	-	-
2000	-	-	-3.84	-	3355	-	-	-
2001	-	-	-4.17	-	2527	-	-	-
2002	-	-	-7.29	-	3817	-	-	-
2003	-	-	-7.63	-	3524	-	-	-
2004	-	-	-6.51	-	3273	-	-	-
2005	-	-	-8.46	-	2614	-	-	-

APPENDIX G

COUNT DATA FOR YNP BISON POPULATION AND LOG$_e$-LINEAR REGRESSION OF COUNT DATA WITH TIME (1970-2000)

Table 24. Count data for the entire YNP bison population derived from the single highest aerial survey conducted from 1990-2000.

YEAR	COUNT	REMOVAL
1990	3109	14
1991	3426	271
1992	3357	79
1993	3535	5
1994	4114	426
1995	3928	433
1996	3584	1084
1997	2170	11
1998	2138	94
1999	2231	0
2000	2930	5

I used the a simple exponential model to estimate the population growth rate (λ) from count data:

$$\log_e(\lambda_t) = a + \varepsilon \qquad (1)$$

where a represents population growth rate in the absence of density dependence and ε represents the stochastic contribution from noise and unmodeled processes (Zeng et al. 1998, Jacobson et al. 2004). I accounted for removals with the following modification:

$$\lambda_t = (n_t)/(n_{t-1} - R_{t-1}) \qquad (2)$$

where R_{t-1} represents removals taken after the count at n_{t-1} (Eberhardt 1987). I used the 1990-2000 time series and accounted for removals using eq. 2 to estimate the potential growth rate (λ) of the YNP bison herds, resulting in λ = 1.05 (95% C.I. = 1.00, 1.10). To determine the effect of removals, and estimate the actual population growth rate (λ), I did not adjust for removals using only eq. 1, resulting in λ =0.96 (95% C.I. = 0.92, 1.00).