

# CHAPTER 14

## Demography of Central Yellowstone Bison: Effects of Climate, Density, and Disease

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### Theme

Over a century of concerted conservation recovered the bison population in Yellowstone National Park from 23 animals in 1901 to 5000 by 2005. This conservation success led to societal conflicts and disagreements among various management entities regarding classic issues of overabundance (Garrott *et al.* 1993), combined with concerns over the risk of brucellosis transmission to domestic livestock when bison migrate out of the park (Cheville *et al.* 1998). As a result, more than 6700 bison have been culled since 1983 as they attempted to leave the park (Gates *et al.* 2005). These large-scale removals are aimed at brucellosis risk management, but likely influence bison demographics and vital rates. The development of rigorously estimated vital rates that incorporate the effects of brucellosis and associated management actions is essential for formulating appropriate management strategies (*e.g.*, vaccination, culling) for long-term bison conservation. These estimates will also contribute to the growing scientific understanding of how climate, disease, and density affect managed ungulate populations. Fuller *et al.* (2007b) found high and consistent adult female survival and lower birth rates in

brucellosis seropositive Yellowstone bison during 1995–2001. We focused on the central herd and incorporated additional information collected during 2002–2006 to extend those analyses by investigating density, climate, and brucellosis seroprevalence effects on age-specific survival and fecundity.

## I. INTRODUCTION

It is widely accepted that increasing density regulates ungulate populations by decreasing per capita resources and, in turn, negatively influencing nutrition, condition, reproduction, and survival (Sinclair 1975; Caughley 1976; Eberhardt 1977, 2002). Stochastic climatic conditions such as drought or snow pack can exacerbate these effects by further limiting the availability of forage and increasing energetic costs (Clutton-Brock *et al.* 1985, Sæther 1997, Gaillard *et al.* 2000). An increase in energy demands during periods of forage limitation likely influences susceptibility to infectious disease. However, the role infectious diseases play in limiting ungulate populations is not as well developed as other density-dependent mechanisms. Disease effects are typically understood in terms of virulence or the degree of harm induced by a parasite, and focus on affecting survival (Ewald 1994). The result is an incomplete understanding of the impacts of diseases that minimally influence mortality rates, but largely affect reproduction (Joly and Messier 2005). Consequently, the limiting role of chronic diseases is often underestimated when evaluating the drivers of vital rates (Jolles *et al.* 2005).

Diseases such as brucellosis that cross the wildlife-livestock and wildlife-human interfaces are of particular interest due to their potential effects on public health and economic well-being (Cheville *et al.* 1998, Godfroid 2002). Brucellosis has largely been eradicated in cattle herds across the United States, but bison and elk in the Greater Yellowstone Ecosystem persist as one of the last reservoirs of infection (Gates *et al.* 2005). Brucellosis is a bacterial disease caused by *Brucella abortus* that may induce abortions or birth of nonviable calves in livestock and wildlife (Davis *et al.* 1990, 1991; Rhyen *et al.* 2001). When livestock are infected, it also results in economic loss from slaughtering infected cattle herds and imposed trade restrictions (Godfroid 2002). Because of the difficulty and cost of controlling disease in wildlife, managers often employ strategies such as aggressive culling that may unintentionally threaten the viability of otherwise healthy populations and are unpalatable to some constituencies (Plumb *et al.* 2007).

After intensively managing bison numbers for 60 years through husbandry and culling, Yellowstone National Park instituted a moratorium on culling ungulates inside the park in 1969 and allowed numbers to fluctuate in response to weather, predators, and resource limitations (Cole 1971). Bison numbers increased rapidly under this policy and since the mid-1980s increasing numbers have moved outside the park during winter where more than 3100 animals were culled by state and federal agencies during 1984–1997 (National Park Service 2000, Gates *et al.* 2005, Fuller *et al.* 2007b). These movements and removals led to claims that bison were overabundant and had degraded their range (Kay 1998, Wagner 2006). In turn, critics called for intensive management to limit the number and distribution of bison in the park, including fencing, fertility control, hunting, and brucellosis test-and-slaughter programs (Hagenbarth 2007, Kay 2007, Schweitzer 2007). In 2000, the federal government and state of Montana agreed to an Interagency Bison Management Plan that established guidelines for managing the risk of brucellosis transmission from bison to cattle by implementing hazing, test-and-slaughter, hunting, and other actions near the park boundary (National Park Service 2000).

Yellowstone bison provide an excellent opportunity to investigate how the demography of an ungulate population is affected by density, climate, and chronic disease. There is little information regarding bison demography due to the near eradication of free-ranging herds during the era of market hunting (Meagher 1973). Also, little is known about the effects of chronic infection with brucellosis on a bovid population since cattle herds in North America are generally destroyed after testing positive for the disease. Elucidating the processes that drive bison demography will help managers formulate appropriate management strategies for Yellowstone bison, including planning brucellosis vaccination strategies, estimating population abundance, and setting culling guidelines (National Park Service 2000).

Our objectives were to: (1) estimate adult female survival, pregnancy, and birthing rates; (2) evaluate the effects of climate, density, and brucellosis exposure on these rates; (3) explore the effects of management removals near the park boundary on adult female survival; and (4) estimate the population growth rate ( $\lambda$ ) from these vital rates.

## II. METHODS

### A. Study Area and Population

After bison were nearly extirpated from the Greater Yellowstone Ecosystem in the early twentieth century, the population was restored through intensive husbandry, protection, and the reintroduction of bison into the Hayden and Firehole valleys (Meagher 1973). Today, Yellowstone bison function in two semi-distinct subpopulations that include the central and northern herds (Meagher 1993, Aune *et al.* 1998, Taper *et al.* 2000, Gates *et al.* 2005, Fuller *et al.* 2007a, Olexa and Gogan 2007). The central herd generally occupies the central plateau of Yellowstone, extending from the Pelican and Hayden valleys with a maximum elevation of 2400 m in the east to the lower-elevation and thermally-influenced Madison headwaters area in the west. Winters are often severe, with snow water equivalents (SWEs) (*i.e.*, mean water content of snow pack) averaging 35 cm and temperatures reaching  $-42^{\circ}\text{C}$  (Meagher 1973, Farnes *et al.* 1999). This area contains a high proportion of mesic meadows comprised of grasses, sedges, and willows, with upland grasses in drier areas (Craighead *et al.* 1973).

Central herd bison congregate in the Hayden valley for the breeding season (15 July–15 August). Most bison move between the Madison, Firehole, Hayden, and Pelican valleys during the remainder of the year. However, some animals travel to the northern portion of Yellowstone and commingle with the northern herd before returning to the Hayden Valley for the subsequent breeding season. Population counts of the central herd varied widely during 1995–2006 because bison that left the park in winter were subject to culling and up to 20% of the total population was removed annually. Counts decreased from 2593 to 1399 bison during 1996–1998 and varied between 2512 and 3531 animals during 2002–2006.

### B. Demographic Variables

The Montana Department of Fish, Wildlife, and Parks and the U.S. Geological Survey conducted a study of adult female bison in Yellowstone National Park during 1995–2001 to evaluate survival, pregnancy, and birth rates. The National Park Service completed a similar study during 2002–2006. We coalesced data from these studies and differentiated central herd animals based on their breeding season distribution during mid-July through mid-August. We included bison proximal to the Hayden and Pelican valleys as central herd animals. Our designation of herd based on breeding distribution was different from other recent studies of Yellowstone bison demography that used autumn (Fuller *et al.* 2007b) and winter (Gates *et al.* 2005) distributions. Eighty bison were radio collared and monitored during 1995–2006, with animals entering the study throughout the duration of the project (Figure 14.1). One animal entered the study during the winter of October 1995 through April 1996 (*i.e.*, 1995–1996), three during 1996–1997, 21 during 1997–1998, and one during 1999–2000. The radio collars were removed from all surviving bison in 2001, after which another study began with 14 animals entering during 2001–2002, 17 during 2003–2004, 15 during 2004–2005, and eight during 2005–2006. Bison were captured by immobilization with carfentanil and xylazine (Aune *et al.* 1998) or at handling facilities near the boundary of the park (Figure 14.2; National Park Service 2000). Bison were fitted with mortality-sensing telemetry collars (Lotek, Newmarket, Ontario, Canada; Telonics, Mesa, Arizona, USA) and aged into three classes (3, 4–8, and  $\geq 9$ -year-olds) by tooth eruption and wear patterns



**FIGURE 14.1** Immobilization of an adult female bison in early winter near Slough Creek in Yellowstone National Park (National Park Service photo by Jenny Jones).



**FIGURE 14.2** Bison held in a processing pen at the Stephen's Creek capture facility in Yellowstone National Park prior to brucellosis testing during February 2003. Additional bison are seen in the background moving towards the park boundary (National Park Service photo by Jim Peaco).

(Dimmick and Pelton 1996, Fuller 1959). The fourth incisor was collected from a sample of bison during capture to verify age through cementum annuli analysis (Moffitt 1998).

Bison were observed at least once per month to estimate survival, and mortalities were investigated to interpret the cause of death. We divided the year into summer (May–October) and winter (November–April) encounter periods. Bison <2 years old were excluded from analyses and animals

captured during 1995–2001 did not enter the risk set until the start of the encounter period following initial collaring. Bison entered the risk set immediately after capture during 2002–2006 because collaring efforts overlapped the beginning of each encounter period. We censored (*i.e.*, excluded) animals that died within 30 days after handling from these analyses as potential capture-related deaths. We assumed the survival status of each bison was known at the beginning and end of every encounter period. Therefore, we right-censored the survival records for collar malfunctions during the encounter period in which they occurred.

Collared bison were captured each year to evaluate pregnancy rates. During 1995–2001, bison were handled during February and pregnancy status was determined through pregnancy-specific protein B serum assays (Haigh *et al.* 1991) and rectal palpation. Vaginal implant telemetry devices were inserted in animals palpated as pregnant. During 2002–2006, bison were captured during November and December and pregnancy status was determined using pregnancy-specific protein B serum assays.

Bison provide an excellent opportunity to evaluate birth rates because they predominantly calve near large groups and in open areas. Also, neonate calves are highly visible since they remain in close association with females (Green *et al.* 1989, Lott 1991). Brucellosis is believed to affect birth rates by inducing an abortion during the first and, possibly, second pregnancy following infection (Cheville *et al.* 1998, Rhyan *et al.* 2001). Consequently, bison fitted with vaginal implants were monitored through the calving period during 1995–2001 to evaluate birth rates. Biologists attempted to locate expelled transmitters and the affiliated female within 24 hours of release. Each transmitter expulsion site was examined for indications of an abortion event and cows were observed to determine if calves were nursing. Radio-collared bison determined to be pregnant during 2002–2006 were located 1–3 times per week beginning in April. Once females were observed with distended udders, they were observed daily to determine if a newborn calf was present. We considered birth successful if biologists observed a birthing event or a live calf in close association with the female. We considered birth unsuccessful if we observed an aborted fetus, stillborn calf, or repeatedly failed to detect a calf associated with the female. Field personnel generally confirmed births within 12–72 h.

### C. Bison and Climate Covariates

We defined the annual covariate, BISON, to investigate the regulating effect of density as animals competed for diminishing per capita resources, such as forage. BISON was indexed as the maximum count of the central herd during aerial surveys of the Firehole, Madison, Hayden, and Pelican valleys between July and August (Hess 2002) each year.

We defined a continuous, individual covariate, AGE, using the incisor eruption patterns of bison <5 years old and cementum annuli analysis results for older animals. We also defined the categorical age class covariate, AGE<sub>Y/P</sub>, whereby we differentiated 3-year-old bison from older animals. Bison ≥4 years old were coded with the reference value of 0.

It is generally accepted that brucellosis negatively affects reproduction in bison (Davis *et al.* 1990, 1991). However, detection is complicated since the bacteria can persist within lymphoid tissue until late pregnancy when it may replicate and infect the reproductive tract (Enright 1990). Serologic tests are the most cost-effective and reliable diagnostic tool available for assessing infection status in live animals (Sutherland and Searson 1990, Gall *et al.* 2000). However, these tests may be misleading since they provide indirect evidence of infection by detecting antibodies, which are a response to infection (Treanor *et al.* 2007). Roffe *et al.* (1999) were able to culture *Brucella* bacteria from 46% of seropositive Yellowstone bison removed during management culls, suggesting roughly one-half of seropositive bison are actively infected. We collected serum and tested for brucellosis exposure status when bison were captured during February (1995–2001) and November–December (2002–2006; Roffe *et al.* 1999, Rhyan *et al.* 2001). Animals were categorized as seropositive or seronegative based on the results of



fluorescence polarization assay, card, buffered antigen plate agglutination, rivanol, complement fixation, standard plate, and standard tube tests performed by the Montana Department of Livestock Diagnostics Laboratory, Bozeman, Montana, USA (Gall *et al.* 2000). We created the categorical covariate, SERO, using these seroprevalence results. Bison testing seronegative were coded with the reference value of 0 and seropositive animals were coded as 1.

Snow is a fundamental limiting factor for ungulates occupying high-elevation, montane environments because it influences the energetic costs of foraging and locomotion. We used a validated snow pack simulation model (Watson *et al.* 2006; Chapter 6 by Watson *et al.*, this volume) to predict daily estimates of average SWE. We averaged SWE values across all  $57 \times 57$  m pixels within a 99% kernel of bison use generated from year-round aerial surveys during 1997–2006 (Hess 2002). We generated a cold season covariate of accumulated SWE ( $SWE_{acc}$ ) by adding daily SWE averages during 1 October through 31 April to index snow pack severity (Garrott *et al.* 2003).

We used the normalized differential vegetation index (NDVI) to generate a warm season covariate as a surrogate for primary productivity because it directly assesses the spatial and temporal variability in vegetation growth (Diallo *et al.* 1991, Rasmussen 1998; Chapter 7 by Thein *et al.*, this volume). This remote sensing value was derived from the ratio of red to near-infrared light reflected by the vegetation, and is highly correlated with green biomass (Goward and Prince 1995). Because bison are primarily grazers, we selected nine large meadows that were distributed across the elevation gradient of the central range. We integrated the 14-day composite NDVI values recorded by the AVHRR satellite at a spatial resolution of approximately  $1 \text{ km}^2$ . We chose to evaluate the absolute integral over each season ( $NDVI_{L-int}$ ), averaged across all meadows.

#### D. Model Development and Evaluation

We evaluated the strength of evidence in the data for competing *a priori* models describing the variability of response variables for adult female survival, pregnancy, and birth rates. Our general analytical approach was to use logistic multiple regression to fit the *a priori* models to the data using the logit link and derive estimates of covariate coefficients. We scaled the year covariates BISON,  $SWE_{acc}$ , and  $NDVI_{L-int}$  by dividing each by 1000. We calculated variance inflation factors (VIF), which measure multi-collinearity among variables, and retained those *a priori* models with annual covariate (e.g., BISON,  $SWE_{acc}$ , and  $NDVI_{L-int}$ ) combinations with  $VIF < 6$  (Kutner *et al.* 2005). We also assessed the correlations between all pairs of annual covariates in the models that met the VIF criterion and removed those that had correlation coefficients of  $R^2 > 0.50$ . Akaike's Information Criteria corrected for small sample size ( $AIC_c$ ) was used as our model selection criterion (Burnham and Anderson 2002). Since we repeatedly collected measurements from the same animals, we calculated the over-dispersion parameter,  $\hat{c}$ , as the model deviance divided by the degrees of freedom and adjusted  $AIC_c$  values to  $QAIC_c$  if  $\hat{c} \gg 1.0$ . Akaike model weights ( $w_i$ ) were used to address model selection uncertainty. We calculated the predictor weight for each covariate as the sum of all model weights including that covariate to gain insight into the relative importance of each predictor. Model-averaged coefficient estimates for each covariate were calculated across all models receiving sufficient weight when there was no clear support for a single model (Burnham and Anderson 2002). We tested the goodness of fit for the most parameterized model from each *a priori* candidate suite using the le Cessie-van Houwelingen test (le Cessie and van Houwelingen 1991, Hosmer *et al.* 1997). All statistical analyses were performed using the R statistical package (R Core Development Team 2006).

While prior analyses of bison demography did not detect seasonal differences in adult female survival (Fuller *et al.* 2007b), the majority of deaths for many large ungulates living in high-latitude environments occur during winter (Sæther 1997, Gaillard *et al.* 2000; Chapter 11 by Garrott *et al.*, this volume). We analyzed winter and summer survival rates independently to evaluate seasonal differences given more years of data. We defined the response variable SSURV to evaluate summer

survival during the 6-month period from April through September. We chose to evaluate two response variables for winter survival because analyses were complicated by brucellosis management actions whereby bison were frequently removed from the population after exiting the park. We defined WSURV to evaluate winter survival when records for culled bison were censored, and  $W_r$ SURV to evaluate winter survival when these records were treated as deaths.

We considered 22 *a priori* models for the WSURV and  $W_r$ SURV responses, including combinations of, and interactions between, the AGE,  $SWE_{acc}$ , BISON, and  $NDVI_{L-int}$  covariates. When management culls were censored from analyses, we anticipated adult female winter survival (WSURV) would be dependent on age, with bison exhibiting consistently high survival through the majority of their life followed by a period of senescence. Thus, we expected a negative AGE coefficient. We predicted that forage availability would influence survival, with snow pack ( $SWE_{acc}$ ) negatively affecting over-winter forage availability and forage productivity ( $NDVI_{L-int}$ ) positively affecting forage availability during the following winter. We predicted that animal density (BISON) would negatively affect survival due to decreased per capita forage. In addition to considering all combinations of the main effects, we predicted the effects of snow pack, forage productivity, and density would be more pronounced for older animals. Thus, we considered single interaction models with either an AGE by snow pack ( $SWE_{acc}$ ), density (BISON), or forage productivity ( $NDVI_{L-int}$ ) term. When management culls were treated as deaths, we anticipated predictors of migration would best explain the variability in adult female survival ( $W_r$ SURV). The number of bison culled annually is a function of migration to lower-elevation areas during winter and spring because removals only occur when bison repeatedly attempt to leave the park (Chapter 12 by Bruggeman *et al.*, this volume). Hence, we expected snow pack ( $SWE_{acc}$ ) and animal density (BISON) would negatively affect survival. We also considered a snow pack ( $SWE_{acc}$ ) by density (BISON) interaction, predicting that the impetus to move would be exacerbated by increasing snow pack at higher densities.

We considered 11 *a priori* models to evaluate SSURV including combinations of, and interactions between, the AGE, BISON, and  $NDVI_{L-int}$  covariates. These models were a subset of the models considered to evaluate WSURV and  $W_r$ SURV because all models with the  $SWE_{acc}$  covariate were not included. We predicted AGE, BISON, and  $NDVI_{L-int}$  would have similar effects on summer survival as during winter.

We increased the age of each female at the time pregnancy status was determined to the next year to reflect her age at calving. We expected to detect delayed sexual maturity with 3-year-old bison having lower pregnancy rates than prime-aged adults. The extent of reproductive senescence in large mammals is variable among species (Eberhardt 2002) and has not been detected in Yellowstone bison (Fuller *et al.* 2007b). To consider both lower pregnancy rates in young and older bison and meet the assumptions of logistic regression, we used a two step approach to evaluate the response variable PREG. First, we used the 2-category  $AGE_{Y/P}$  covariate to investigate pregnancy rates in 3-year-olds compared to adult ( $\geq 4$  years old) animals. We excluded all annual covariates due to our limited number of 3-year-olds. We evaluated five *a priori* models that included all combinations of, and interactions between,  $AGE_{Y/P}$  and SERO. Since the  $AGE_{Y/P}$  covariate was supported (see Section III), we censored the records for 3-year-old animals and developed a second set of models to evaluate PREG for bison  $\geq 4$  years old. We considered a restricted suite of 17 *a priori* models given the limitations of our data, including all combinations of AGE, SERO,  $NDVI_{L-int}$ , and BISON. Fuller *et al.* (2007b) found weak evidence during their analysis of the 1995–2001 data that brucellosis exposure may reduce pregnancy rates. Thus, we predicted a negative SERO coefficient. We also considered an age by serology interaction because the preliminary analysis using the 2-category age covariate suggested the negative effects of serology may be exacerbated in bison  $\geq 4$  years old (see Section III). We assumed bison may experience reproductive senescence and predicted that the AGE coefficient would be negative. We expected that  $NDVI_{L-int}$  and BISON would have similar effects on pregnancy as on survival.

We defined the response variable  $BIRTH_P$  to evaluate the probability of known pregnant bison being observed with a live calf during the calving period. Three-year-old bison were included in the analysis set

and we considered 32 *a priori* models, including all combinations of the AGE, SERO, BISON,  $SWE_{acc}$ , and  $NDVI_{int}$  covariates. Brucellosis negatively influences birth rates because infection of the reproductive tract may induce abortion or birth of a nonviable calf (Cheville *et al.* 1998, Rhyan *et al.* 2001). Thus, we anticipated a negative SERO coefficient. We expected AGE, BISON,  $SWE_{acc}$ , and  $NDVI_{L-int}$  would have similar effects on birth as on pregnancy and survival. We considered an AGE by SERO interaction because most bison are exposed to brucellosis at a young age and the effects may wane with time (Cheville *et al.* 1998). Also, the effects of increasing snow pack and density may be more pronounced on older animals. Therefore, we considered AGE by  $SWE_{acc}$  and AGE by BISON interactions. However, we decided not to include models incorporating an interaction term in our *a priori* suite because of the limited amount of available data. Instead, we considered these exploratory models *post priori*.

### E. Matrix Model

We constructed a prebreeding, age-structured, deterministic Leslie matrix model for female bison using our vital rate estimates. We encountered 18- and 19-year-old animals during boundary management reductions occurring within the timeframe of this study (National Park Service, unpublished data). Thus, we constructed a  $21 \times 21$  matrix model using age-specific survival estimates and a maximum age of 20 years. Survival estimates were generated using model-averaging techniques for the top models that evaluated adult female survival when management removals were censored. We used the predicted 2-year-old survival estimate for yearling survival. Calf survival was derived from ground-based composition surveys completed annually in July during 2003–2006 (National Park Service, unpublished data). We used the two-sample change-in-ratio methods of Hanson (1963) and Paulik and Robson (1969) to estimate survival as described by Skalski *et al.* (2005). However, the calf survival estimate (0.81) may be inflated because of some unknown mortality that occurs during the first few weeks of life.

Age-specific fecundity was derived as the product of pregnancy and birth estimates. These estimates were generated using model-averaging techniques for the top models evaluating pregnancy and birth for brucellosis seropositive and seronegative bison. Since age-specific pregnancy and birth was only estimated through 12 years, we assumed constant fecundity thereafter. We halved fecundity estimates because available evidence suggests equal sex ratios at birth (Pac and Frey 1991; National Park Service, unpublished data).

To explore the inherent population dynamics of the central herd and then consider the contribution of brucellosis we constructed two separate matrix models and estimates of the growth rate of the population ( $\lambda$ ). First, we input fecundity parameters where model averaged estimates were weighted according to the proportion of seropositive (0.48) and seronegative (0.52) adult, female bison in the population as determined from seroprevalence information collected during winter reductions in 2003–2006 (National Park Service, unpublished data). Then, we only input fecundity parameters estimated from seronegative animals.

## III. RESULTS

We collected 153 bison-years of age-specific survival observations during summer and 150 bison-years during winter. The average number of bison-years of data was 13.4 per age for bison  $\leq 11$  years old. For animals 12–15 years of age, we collected 19 bison-years of data during the summer and 16 during the winter. We documented 28 deaths of radio-collared bison during the study, including 19 (68%) during winter and 9 (32%) during summer. Management operations removed 3438 bison, including 370 during 1995–1996 when 26 were culled at the northern boundary and 344 were culled at the western



boundary (*i.e.*, north = 26, west = 344), 1083 during 1996–1997 (north = 725, west = 358), 94 during 1998–1999 (west = 94), 6 during 2000–2001 (west = 6), 202 during 2001–2002 (west = 202), 244 during 2002–2003 (north = 231, west = 13), 280 during 2003–2004 (north = 266, west = 14), 115 during 2004–2005 (north = 1, west = 114), and 1044 during 2005–2006 (north = 979, west = 65). Thirteen study animals were removed as part of these management operations, with one (8%) occurring at the western boundary and 12 (92%) occurring at the northern boundary. Four additional bison were culled (north = 3, west = 1) but not included in these totals because the animals were initially handled just prior to removal and, as a result, did not enter the study. We documented six other winter mortalities, including two deaths due to motor vehicle accidents, two drownings, and two deaths due to unknown natural causes. The causes of death for the nine summer mortalities were three due to motor vehicle accidents, two due to late-winter malnutrition, one suspected bear predation, and four deaths due to unknown natural causes.

We collected 101 bison-years of age-specific pregnancy data, including 17 years from 3-year-olds and 79 years from 4- to 11-year-olds. There were 48 seropositive and 53 seronegative animals. We monitored 73 known pregnant animals through the parturition season, including 30 seropositive and 43 seronegative bison. There were five records for seropositive bison 12–15 years old collected from three individuals. Each of these animals was pregnant and later observed with a calf. We censored these records from both analyses due to the limited number of observations per age.

Variations in  $SWE_{acc}$  and  $NDVI_{L-int}$  during the study period generally spanned the range of variability in the historic data.  $SWE_{acc}$  metrics generated using the snow pack simulation model (Chapter 6 by Watson *et al.*, this volume) ranged from 1181 (2000–2001) to 4774 (1996–1997), with a mean of 2448 cm ( $CV = 0.41$ ) during the study period. The range of these metrics generated annually during 1970–2006 was from 643 (1976–1977) to 4774 (1996–1997), with a mean of 2461 cm ( $CV = 0.37$ ). The minimum value observed during the study was the second smallest  $SWE_{acc}$  in the historic record. The maximum  $SWE_{acc}$  of 4774 was substantially greater than the second-highest value in the 37-year time series (*i.e.*, 3893 cm in 1976–1977). Therefore, we chose to use a  $SWE_{acc}$  value of 4000 cm to simulate severe snow pack severity in our model-averaged prediction exercises.  $NDVI_{L-int}$  metrics were available since 1989 and the range for the historic data and study period was from 2178 to 2716. The mean values for the historic data and the study period were 2475 ( $CV = 0.07$ ) and 2511 ( $CV = 0.07$ ), respectively. The central herd increased in size after the conclusion of within-park reductions during 1969 through 1986 when sporadic management culls reduced the population by up to 20% annually. Population counts ranged from 261 (1970) to a maximum of 3531 (2005). The minimum count during the study period was 1399 bison in 1997.

The correlation coefficient of  $SWE_{acc}$  and  $NDVI_{L-int}$  was  $R^2 = -0.68$ , even though each of the year covariates (BISON,  $SWE_{acc}$ , and  $NDVI_{L-int}$ ) satisfied the criterion of  $VIF \leq 6$ . This negative relationship was not entirely unexpected because higher  $NDVI_{L-int}$  values indicate prolonged visible green vegetation, perhaps suggesting delayed establishment of the snow pack and lower  $SWE_{acc}$ . We removed models including  $SWE_{acc}$  and  $NDVI_{L-int}$  as additive main effects from the *a priori* model set evaluating each response variable. Therefore, we considered 18 *a priori* models to evaluate winter survival and 24 models for birth rate. We used  $AIC_c$  to evaluate all model suites because we did not detect over-dispersion during any of the modeling exercises.

Evaluation of the *a priori* models for adult female survival when management removals were censored (WSURV) provided no single highly-supported model. There were four models within two  $AIC_c$  units and all models evaluated received some model weight (Table 14.1). The predictor weight of the AGE covariate was 0.88, suggesting it provided meaningful information in describing variability in the data. The AGE coefficient was negative, did not span zero ( $\hat{\beta}_{AGE} = -0.28$ , 95% CI =  $-0.55, -0.01$ ) in the model only considering AGE, and was stable in other main effects models including the  $SWE_{acc}$ ,  $NDVI_{L-int}$ , and BISON covariates. There was some evidence suggested by predictor weights that  $SWE_{acc}$  (0.52) and BISON (0.53) negatively affected survival, but coefficients estimates were unstable and confidence intervals spanned zero (Table 14.2). The most general model fit to the data based

on the goodness of fit test ( $P = 0.61$ ). To generate our best estimate of age-specific survival probabilities, we model averaged the eight models receiving  $\geq 0.05$  of  $w_i$ , fixing BISON,  $SWE_{acc}$ , and  $NDVI_{L-int}$  covariates at the median values observed during the study. These results indicated senescence in survival, with consistently high survival for 2–11-year-old bison and progressively lower survival for older animals (Figure 14.3).

**TABLE 14.1** Model selection results of *a priori* models for winter survival of adult female bison in the central herd when management culls were censored (WSURV)

Model	$K$	$\Delta AIC_c$	$w_i$
AGE + $SWE_{acc}$ + BISON + (AGE $\times$ $SWE_{acc}$ )	5	0.00	0.24
AGE	2	1.19	0.13
AGE + $SWE_{acc}$ + (AGE $\times$ $SWE_{acc}$ )	4	1.68	0.10
AGE + BISON + (AGE $\times$ BISON)	4	1.96	0.09
AGE + $SWE_{acc}$	3	2.14	0.08
AGE + $SWE_{acc}$ + BISON	4	2.49	0.07
AGE + BISON	3	2.73	0.06
AGE + $NDVI_{L-int}$	3	3.19	0.05
Constant	1	4.07	0.03
AGE + $NDVI_{L-int}$ + (AGE $\times$ $NDVI_{L-int}$ )	4	4.20	0.02
AGE + BISON + $NDVI_{L-int}$	4	4.60	0.02
BISON	2	5.43	0.02
$SWE_{acc}$	2	5.44	0.02
AGE + $NDVI_{L-int}$ + BISON + (AGE $\times$ $NDVI_{L-int}$ )	5	5.63	0.01
BISON + $SWE_{acc}$	3	5.85	0.01
$NDVI_{L-int}$	2	5.87	0.01
$NDVI_{L-int}$ + BISON	3	7.05	0.01

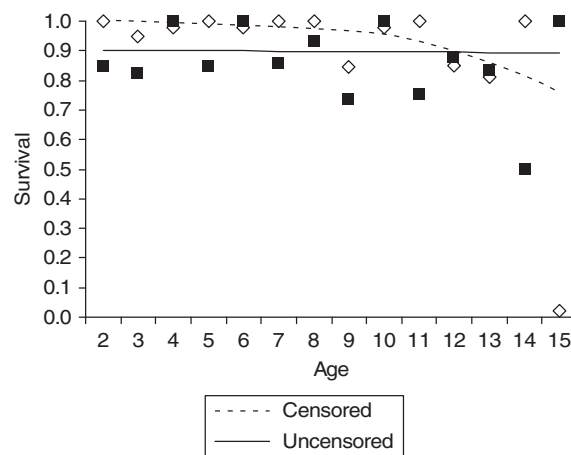
The  $AIC_c$  value for the top model was 47.23.  $K$ , the number of parameters;  $AIC_c$ , Akaike's Information Criteria corrected for small sample size;  $\Delta AIC_c$ , the change in  $AIC_c$  relative to the best model; and  $w_i$ , Akaike weight. Model covariates included the AGE, age of the animal in years; BISON, the maximum summer count of bison in the central herd;  $SWE_{acc}$ , an index of snow pack severity; and  $NDVI_{L-int}$ , an index of annual forage productivity.

**TABLE 14.2** Coefficient estimates of all models within two  $AIC_c$  units of the most-supported model evaluating the effects of age, snow pack, forage productivity, and bison density on adult female survival of central herd bison when management culls were censored (WSURV)

Model	AGE	BISON	$SWE_{acc}$	(AGE $\times$ $SWE_{acc}$ )	(AGE $\times$ BISON)
AGE + $SWE_{acc}$	<b>-1.58</b>	-1.52	<b>-6.50</b>	<b>0.50</b>	
+ BISON	<b>(-2.91,</b>	(-3.25, 0.20)	<b>(-12.16,</b>	<b>(0.00, 0.99)</b>	
+ (AGE $\times$ $SWE_{acc}$ )	<b>-0.24)</b>		<b>-0.85)</b>		
AGE	<b>-0.28</b>				
	<b>(-0.55,</b>				
	<b>-0.01)</b>				
AGE + $SWE_{acc}$	<b>-0.99</b>		-3.39	0.28 (-0.05,	
+ (AGE $\times$ $SWE_{acc}$ )	<b>(-1.93,</b>		(-6.92, 0.15)	0.61)	
	<b>-0.06)</b>				
AGE + BISON	0.49	2.45 (-1.25,			-0.31
+ (AGE $\times$ BISON)	(-0.42,	6.15)			(-0.68,
	1.39)				0.06)

Values in bold indicate coefficients with 95% confidence intervals that do not span zero. Abbreviations are as in Table 14.1.

Evaluation of the *a priori* models for adult female survival when management removals were included as deaths ( $W_rSURV$ ) indicated that the additive and interactive models including BISON and  $SWE_{acc}$  covariates were most supported and essentially equivalent with model weights of 0.31 and 0.32, respectively (Table 14.3). Predictor weights indicated that the BISON (0.97) and  $SWE_{acc}$  (0.79) covariates were the only predictors with reasonable support from the data, with ambiguous support for AGE (0.23) and  $NDVI_{L-int}$  (0.12). The BISON and  $SWE_{acc}$  coefficients were negative and estimates and confidence intervals were stable among additive models (Table 14.4). The most general model provided the best fit to the data based on the goodness of fit test ( $P = 0.50$ ). We model-averaged the eight models receiving  $>0.01$  of  $w_i$  to illustrate the estimated effects of BISON and  $SWE_{acc}$ . We considered BISON values from 500 to 4000 and  $SWE_{acc}$  as the minimum (1182 cm), median (2145 cm), and near maximum (4000 cm) values observed during the study. AGE and  $NDVI_{L-int}$  were held at the median of observed values during the study period. The resulting plots demonstrate the combined effects of



**FIGURE 14.3** Age-specific survival estimates for adult female bison in the central herd when management culls were censored and treated as deaths (*i.e.*, uncensored) in Yellowstone National Park during 1995–2006. Estimates were generated using model-averaging techniques for the eight models receiving  $\geq 0.05$  and  $>0.01$  of the Akaike model weight ( $w_i$ ) for the censored and uncensored data sets, respectively. Diamonds and squares represent the observed proportion of animals surviving each age class when culls were censored and treated as deaths, respectively.

**TABLE 14.3** Model selection results of *a priori* models for winter survival of adult female bison in the central herd when management culls were treated as deaths ( $W_rSURV$ )

Model	$K$	$\Delta AIC_c$	$w_i$
BISON + $SWE_{acc}$ + (BISON $\times$ $SWE_{acc}$ )	4	0.00	0.32
BISON + $SWE_{acc}$	3	0.05	0.31
AGE + $SWE_{acc}$ + BISON	4	1.94	0.12
$NDVI_{L-int}$ + BISON	3	2.74	0.08
AGE + $SWE_{acc}$ + BISON + (AGE $\times$ $SWE_{acc}$ )	5	4.03	0.04
BISON	2	4.04	0.04
AGE + BISON + $NDVI_{L-int}$	4	5.81	0.03
AGE + BISON	3	5.95	0.02
AGE + $NDVI_{L-int}$ + BISON + (AGE $\times$ $NDVI_{L-int}$ )	5	6.83	0.01
(AGE $\times$ BISON)	4	7.33	0.01

The  $AIC_c$  value for the top model was 107.21. Abbreviations are as in Table 14.1.

bison density and snow pack severity on survival when management culls were treated as deaths (Figure 14.4). Since management culls were the overwhelming source of mortality for this data set, these relationships can be interpreted as the influence of bison densities and snow pack severity on bison movements outside of the park boundaries.

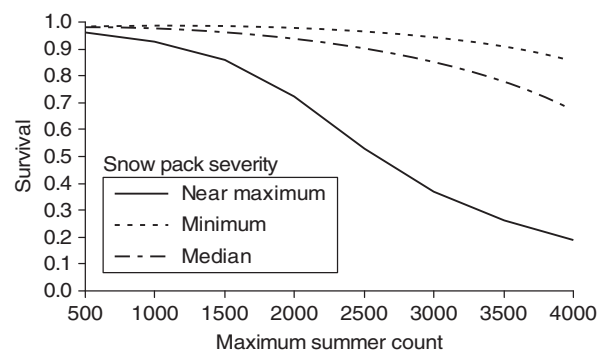
We did not detect a significant main effect when evaluating summer survival rates. Thus, we used the null model to predict a single rate of  $0.95 \pm 0.02$ . The predicted survival rate from the null model for adult females during winter when culls were censored was  $0.96 \pm 0.03$ , compared to a rate of  $0.87 \pm 0.05$  when culls were treated as deaths. We estimated the annual survival rate when removals were censored as  $0.91 \pm 0.05$ , compared to  $0.83 \pm 0.06$  when removals were treated as deaths.

Evaluation of the *a priori* models for pregnancy using the 2-category age covariate indicated that model weight was distributed between the AGE<sub>Y/P</sub> (0.33;  $\Delta AIC_c = 0.19$ ), additive (0.26;  $\Delta AIC_c = 0.68$ ), and interactive (0.36;  $AIC_c = 98.10$ ) models including the AGE<sub>Y/P</sub> and SERO covariates. There was considerable support that 3-year-old bison had lower pregnancy rates than bison  $\geq 4$  years old since the AGE<sub>Y/P</sub> covariate was negative with a confidence interval that did not span zero ( $\beta_0 + \beta_1(\text{AGE1})$ :  $\hat{\beta}_{\text{AGE}_{Y/P}} = -1.51$ , 95% CI =  $-2.63, -0.39$ ). The top supported model included an age by serology interaction, suggesting that the negative effect of serology on pregnancy was most apparent in bison  $\geq 4$  years old ( $\beta_0 + \beta_1(\text{AGE}_{Y/P}) + \beta_2(\text{SERO}) + \beta_3(\text{AGE}_{Y/P} \times \text{SERO})$ :  $\hat{\beta}_{\text{AGE}_{Y/P}} = -2.53$ , 95% CI =  $-4.20, -0.86$ ,  $\hat{\beta}_{\text{SEROLOGY}} = -1.24$ , 95% CI =  $-2.51, 0.03$ ,  $\hat{\beta}_{\text{AGE}_{Y/P} \times \text{SEROLOGY}} = -1.98$ , 95% CI =  $-0.36, 4.31$ ).

**TABLE 14.4** Coefficient estimates of all models within two  $AIC_c$  units of the most-supported model evaluating the effects of age, snow pack, forage productivity, and bison density on adult female survival of central herd bison when management culls were treated as deaths ( $W_1\text{SURV}$ )

Model	AGE	BISON	SWE <sub>acc</sub>	(BISON $\times$ SWE <sub>acc</sub> )
BISON + SWE <sub>acc</sub> + (BISON $\times$ SWE <sub>acc</sub> )		1.62 (−2.29, 5.53)	1.27 (−2.26, 4.80)	−1.14 (−2.74, 0.46)
BISON + SWE <sub>acc</sub>		<b>−1.20</b> (−2.00, −0.40)	<b>−1.22</b> (−2.24, −0.20)	
AGE + SWE <sub>acc</sub> + BISON	−0.04 (−0.19, 0.11)	<b>−1.20</b> (−2.01, −0.39)	<b>−1.23</b> (−2.26, −0.20)	

Values in bold indicate coefficients with 95% confidence intervals that do not span zero. Abbreviations are as in Table 14.1.



**FIGURE 14.4** Survival estimates for adult female bison in the central herd when management culls were treated as deaths in Yellowstone National Park during 1995–2006. Predicted relationships were generated using model-averaging techniques for the eight models receiving  $>0.01$  of the Akaike model weight ( $w_i$ ). The three lines represent predictions assuming the minimum, median, and near maximum snow pack severities (SWE<sub>acc</sub>) observed during the study.

For the data set that censored the 3-year-old animals, we found the additive and interactive models including the AGE and SERO covariates were most supported (Table 14.5). Predictor weights suggested that the SERO (0.81) and AGE (0.58) covariates provided useful information in describing the variability in the data, while the effects of BISON (0.35) and  $NDVI_{L-int}$  (0.32) were ambiguous. The coefficient estimates and confidence intervals for both the SERO and AGE covariates were stable among additive models (Table 14.6). As predicted, the SERO coefficient was negative with a confidence interval that did not span zero, indicating that bison exposed to brucellosis had lower probability of pregnancy. The AGE covariate was positive with a confidence interval that marginally spanned zero, indicating that probability of pregnancy likely increased with age. Therefore, we found no evidence for reproductive senescence. The most general model that excluded the categorical seroprevalence covariate fit to the data ( $P = 0.65$ ) based on the le Cessie-van Houweilingen test. We model-averaged the eight models within two  $AIC_c$  units of the most-supported model to illustrate the differences in age-specific pregnancy curves for seropositive and seronegative animals while holding  $NDVI_{L-int}$  and BISON at the median observed values during the study (Figure 14.5).

Results of our evaluation of the probability of a successful birth given the female was known to be pregnant were ambiguous with the null model receiving the most model weight (0.13) and six models ranked within two  $AIC_c$  units of the top-supported model (Appendix 14A.1). All models received some model weight and the confidence intervals of all main effect regression coefficients spanned zero. However, there was weak support in the data for AGE and SERO effects. The predictor weight of the AGE covariate was 0.44 with a coefficient estimate that was positive, stable, and did not change sign across the main effects models. The SERO predictor weight was 0.42 with a negative coefficient estimate that also did not change sign across the models including main effect terms, despite a confidence interval that spanned zero. The most general model that excluded the categorical seroprevalence covariate fit to the data ( $P = 0.92$ ). Our *post priori* analysis provided additional insight into the influence of AGE and SERO on birth rates because the interactive AGE  $\times$  SERO model was 0.65  $AIC_c$  units lower than the most-supported *a priori* model. The predictor weights of AGE and SERO

**TABLE 14.5** Model selection results of *a priori* models for pregnancy rates of central herd bison  $\geq 4$  years old

Model	$K$	$\Delta AIC_c$	$w_i$
AGE + SERO + (AGE $\times$ SERO)	4	0.00	0.17
AGE + SERO	3	0.61	0.13
SERO	2	0.87	0.11
SERO + BISON	3	1.70	0.07
AGE + SERO + BISON	4	1.83	0.07
SERO + BISON + $NDVI_{L-int}$	4	1.84	0.07
AGE + SERO + $NDVI_{L-int}$	4	1.84	0.07
SERO + $NDVI_{L-int}$	3	1.99	0.06
AGE + SERO + BISON + $NDVI_{L-int}$	5	2.21	0.06
Constant	1	2.70	0.05
BISON	2	3.36	0.03
AGE	2	3.55	0.03
$NDVI_{L-int}$	2	4.28	0.02
BISON + $NDVI_{L-int}$	3	4.28	0.02
AGE + BISON	3	4.48	0.02
AGE + $NDVI_{L-int}$	3	5.21	0.01
AGE + BISON + $NDVI_{L-int}$	4	5.57	0.01

The  $AIC_c$  value for the top model was 70.00. Model covariates included AGE, age of the animal in years; SERO, brucellosis serological status; BISON, the maximum summer count of bison in the central herd;  $SWE_{acc}$ , an index of snow pack severity; and  $NDVI_{L-int}$ , an index of annual forage productivity. Abbreviations are as in Table 14.1.



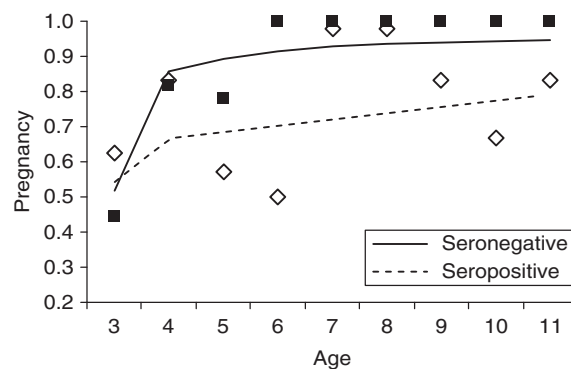
**TABLE 14.6** Untransformed coefficient estimates of all models within two  $AIC_c$  units of the top supported model evaluating the effects of age (AGE), seroprevalence (SERO), forage productivity ( $NDVI_{L-int}$ ), and density (BISON) on pregnancy rates of central herd bison  $\geq 4$  years in Yellowstone National Park during 1995–2006

Model	AGE	SERO	BISON	$NDVI_{L-int}$	AGE $\times$ SEROLOGY
AGE + SERO + (AGE $\times$ SERO)	0.95 (–0.29, 2.20)	2.96 (–3.24, 9.16)			–0.85 (–2.13, 0.43)
AGE + SERO	0.21 (–0.07, 0.50)	<b>–1.46</b> (–2.78, –0.13)			
SERO		–1.24 (–2.52, 0.04)			
SERO + BISON		–1.23 (–2.52, 0.05)	–0.45 (–1.21, 0.32)		
AGE + SERO + BISON	0.20 (–0.08, 0.48)	<b>–1.43</b> (–2.77, –0.10)	–0.39 (–1.17, 0.38)		
SERO + BISON + $NDVI_{L-int}$		<b>–1.41</b> (–2.75, –0.06)	–0.64 (–1.50, 0.21)	6.12 (–2.32, 14.55)	
AGE + SERO + $NDVI_{L-int}$	0.21 (–0.07, 0.49)	<b>–1.55</b> (–2.91, –0.20)		3.95 (–3.80, 11.70)	
SERO + + $NDVI_{L-int}$		<b>–1.35</b> (–2.66, –0.04)		3.90 (–3.55, 11.36)	

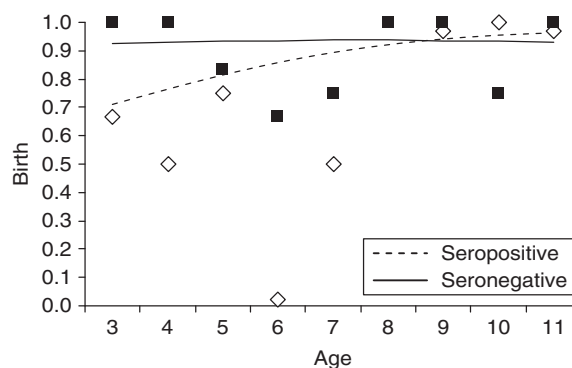
Values in bold indicate coefficients with 95% confidence intervals that do not span zero. Abbreviations are as in Table 14.1.

increased to 0.52 and 0.50, respectively. We created model-averaged estimates of age-specific birth rate for seropositive and seronegative animals using the *post priori* AGE  $\times$  SERO model and the top five *a priori* models receiving  $\geq 0.05$  of the model weight.  $SWE_{acc}$ , BISON, and  $NDVI_{L-int}$  covariates were held at the median observed value during the study. These results indicated that birth rates were high and consistent for seronegative animals, but lower for 3–8-year-old seropositive bison (Figure 14.6). The combined effect of seroprevalence on pregnancy and birth rates resulted in lower calf production of seropositive bison across all ages (Figure 14.7).

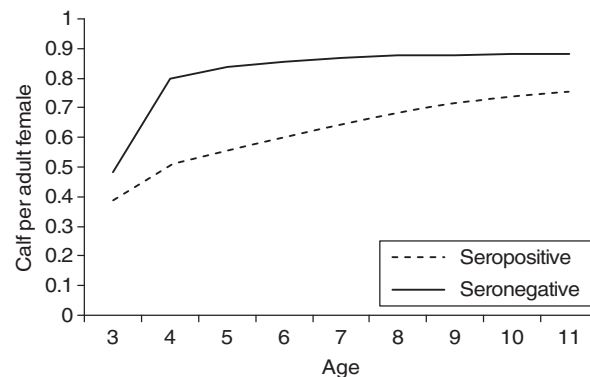
The initial matrix model incorporating age-specific survival (0.34–0.99; Figure 14.3) and fecundity (0.18–0.33, Figure 14.7) weighted for seropositive (0.48) and seronegative (0.52) bison estimated  $\lambda = 1.12$ . The model using fecundity estimates (0.19–0.36) for just seronegative bison estimated



**FIGURE 14.5** Age-specific pregnancy rate estimates for seronegative and seropositive bison in the central herd at Yellowstone National Park during 1995–2006. Estimates were generated using model-averaging techniques for three models receiving  $>0.03$  and eight models receiving  $\geq 0.06$  of the Akaike model weight ( $w_i$ ) for 3-year-old and  $\geq 4$ -year-old animals. Diamonds and squares represent the observed proportion of seropositive and seronegative pregnant animals in each age class, respectively.



**FIGURE 14.6** Age-specific birth rate estimates of known pregnant seronegative and seropositive bison in the central herd at Yellowstone National Park during 1995–2006. Estimates were generated using the AGE  $\times$  SEROLOGY model and top five *a priori* models receiving  $\geq 0.05$  of the Akaike model weight ( $w_i$ ). Diamonds and squares represent the observed proportion of seropositive and seronegative pregnant animals in each age class, respectively.



**FIGURE 14.7** Age-specific calf production estimates of seronegative and seropositive bison  $\geq 3$  years of age generated from the product of model-averaged predictions of pregnancy and birth rates of central herd bison in Yellowstone National Park during 1995–2006.

$\lambda = 1.14$ . Therefore, the growth rate of a brucellosis-free central herd could be  $>15\%$  higher than the current population where approximately one-half of reproductively mature females exhibit exposure.

#### IV. DISCUSSION

Our analyses strongly support that large-scale removals aimed at managing brucellosis risk to cattle and chronic infection with the *Brucella* pathogen affect the demography of central herd bison. Adult female survival is highly age-dependent and management culls provide the overwhelming source of mortality, but were not age-specific. Likewise, our fecundity analyses provide intriguing and novel insights into the limiting effects of chronic brucellosis infection on the demography of Yellowstone bison. We detected what appear to be pronounced effects of chronic brucellosis infection on pregnancy rates. We found lesser effects on birth rates, and *Brucella*-induced abortions were uncommon.

We detected senescence in survival beginning after 12 years of age. In contrast, younger animals had relatively high survival typical of long-lived mammals that are not hunted (Eberhardt 2002). The proximate cause of senescence in large herbivores is believed to be tooth wear that decreases the ability of animals to efficiently crop forage and reduce plant material into small enough particles to facilitate efficient digestion by rumen microbes (Laws 1981, Van Soest 1994). The nutritional value of winter diets cannot meet maintenance requirements since nearly all plants used as forage by large herbivores in temperate and high latitudes are dormant during the cold season (Hobbs *et al.* 1981). Hence, sub-maintenance forage quality, combined with reduced forage availability and increased energetic costs due to snow pack (Parker and Robbins 1984, Wickstrom *et al.* 1984), contribute to prolonged nutritional deprivation (DelGuidice *et al.* 1994; Chapter 9 by White *et al.*, this volume). The compromised dentition of senescent animals exacerbates the level of nutritional deprivation and results in their survival being more sensitive to decreased food availability during the winter than prime-aged animals with intact teeth (Chapter 11 by Garrott *et al.*, this volume).

The onset of senescence in survival at approximately 12 years of age (Figure 14.3) was corroborated by age at death information collected during historic within-park culling operations (Meagher 1973) and recent boundary removals (Pac and Frey 1991). Senescence began at a surprisingly young age

compared to the documented life span of >20 years for wild bison populations (McHugh 1958, Fuller 1966, Halloran 1968, Berger and Peacock 1988). The shortened longevity of central Yellowstone bison may result from the unique regional geology of Yellowstone's volcanic caldera, with its elementally-enriched geothermal waters and rhyolite soils. Similar to elk in this area, central Yellowstone bison likely ingest high levels of fluoride and highly-abrasive silica through consumption of water, plants, and soil particles (Garrott *et al.* 2002; Chapter 10 by Garrott *et al.*, this volume). Excessive dietary fluoride ingested while permanent teeth are developing in young animals interferes with matrix formation and mineralization of teeth, resulting in dental lesions and uneven and excessively rapid tooth wear (Shupe *et al.* 1984, Fejerskov *et al.* 1994, Kierdorf *et al.* 1996), which would undoubtedly be exacerbated by the abrasive action of silica. The pathological consequences of fluoride toxicosis were evident in many of the mandibles recovered from carcasses of adult bison in the Madison headwaters area (Chapter 16 by Becker *et al.*, this volume).

Brucellosis exposure indirectly lowered bison survival because more bison were culled due to concerns regarding transmission to cattle when bison attempted to migrate to lower-elevation areas outside the park. The magnitude and timing of migration by bison in the central herd from high-elevation summer range to lower-elevation wintering areas was driven by density and exacerbated by snow pack severity (Bruggeman 2006; Chapter 12 by Bruggeman *et al.*, this volume), similar to ungulates in many temperate areas (Maddock 1979, Bergerud 1988, Fryxell and Sinclair 1988). We detected a significant decrease in adult female survival when the number of bison in the central herd exceeded 2000–2500 animals and this decrease was exacerbated during winters with severe snow pack. Removals of Yellowstone bison were not age-specific because animals apparently migrated to the park boundary and were culled regardless of age. Thus, culls generally reflected the relative proportion of bison in each age class, similar to late-season elk hunts in the region (White and Garrott 2005).

Our finding that seropositive animals had significantly lower pregnancy rates across all age classes compared to seronegative bison was unexpected, but did not appear spurious because it was supported by two independent data sets (*i.e.*, animals radio-collared during 1995–2001 and 2002–2006;  $n = 101$  bison-years), as well as animals captured in the Stephen's Creek pen near Gardiner, Montana ( $n = 203$ ) during February–March 2004 (Appendix 14A.2). The majority of our understanding of brucellosis in bison is drawn from research on cattle with the assumption that the disease functions similarly in both species (Davis *et al.* 1990, Roffe *et al.* 1999, Rhyan *et al.* 2001). *B. abortus* is known to infect the reproductive tract, inducing abortion during the first and, sometimes, second pregnancies following infection (Enright 1990, Cheville *et al.* 1998). However, evidence supporting that *B. abortus* affects conception is lacking (Cheville *et al.* 1998). Thus, our findings do not directly implicate brucellosis infection as the causal mechanism for lower pregnancy rates in seropositive animals, but suggest this disease may play a role in reducing fecundity in chronically infected bison.

The potential mechanisms negatively affecting conception are difficult to ascertain since infectious birth tissues are believed to be the primary source of transmission. However, the effect of chronic diseases (Jolles *et al.* 2005, Joly and Messier 2005), parasite loading (Albon *et al.* 2002, Stien *et al.* 2002), and food availability (Caron *et al.* 2003) have been shown to decrease pregnancy rates in large ungulates. While *B. abortus* is less virulent than *Mycobacterium bovis* that causes bovine tuberculosis and decreases fecundity in wood buffalo (Joly and Messier 2005), morbidity from *Brucella* infection may be substantial enough to cause the diminished pregnancy rates we observed. Pregnancy rates for Yellowstone bison reaching reproductive maturity were similar for both seropositive and seronegative animals (Figure 14.5). The negative effect of seroprevalence was apparent starting at 4 years of age, suggesting that the effect of brucellosis infection became pronounced after the first and potentially failed pregnancy.

Uterine infections (*e.g.*, metritis—inflammation of the uterus) subsequent to a disruptive pregnancy or injury at the time of an abortion could reduce conception or induce early abortions (Neiland *et al.* 1968, Thorne *et al.* 1978). The postpartum reproductive tract is an ideal environment for bacterial growth and retained placental tissues may predispose the uterus to infection (Senger 1997).

Postpartum infection of the uterus by pathogenic bacteria can result in subfertility due to delayed ovulation and lower conception rates (Sheldon and Dobson 2004). Also, chronically infected individuals can develop carpal bursitis (*i.e.*, lameness) that may cause a substantial decrease in body condition (Neiland *et al.* 1968, Thorne *et al.* 1978, Cheville *et al.* 1998, Joly and Messier 2005), thereby further reducing fertility.

Our finding of lower birth rates in younger and seropositive bison was expected (Fuller *et al.* 2007b) and the difference in observed births between seropositive and seronegative bison provides insight into the effects of chronic brucellosis infection on this population (Figure 14.8). Abortions have rarely been observed in Yellowstone bison (Rhyan *et al.* 1994, Olsen *et al.* 1998) and, by definition, the term “chronic” implies a substantial degree of immunity for many individuals that retards the usual course of disease (Cheville *et al.* 1998). Age-specific seroprevalence rates of Yellowstone bison indicate that approximately 50% of bison are exposed prior to reproductive maturity (Treanor *et al.* 2007). This early exposure may allow immature bison to develop resistance to infection, thereby reducing the occurrence of *Brucella*-induced abortions (Meyer and Meagher 1997). Calves may acquire infections *in utero* or through ingesting contaminated milk (Nicoletti 1980). Vertical transmission of *B. abortus* from cow to calf through infected milk has been documented in cattle (Nicoletti and Gilsdorf 1997) and bison (Olsen *et al.* 2003). However, vertical transmission alone is unlikely to account for the differences in seroprevalence observed in adult male (75%) and female (49%) bison (National Park Service, unpublished data). Horizontal transmission through infected birth tissues likely plays an important role in transmission despite the lack of observed abortions. In fact, the degree of horizontal transmission occurring during live births may be substantial (National Park Service, unpublished data).

Exposure to *B. abortus* early in life may provide bison with some natural resistance to acute infection when reproductively mature. We observed 100% (2 of 2) of seropositive and pregnant 3-year-old bison producing viable calves and documented 80% (4 of 5) of similar births during a concurrent study of northern herd bison (Fuller *et al.* 2007b). However, Davis *et al.* (1990, 1991) reported that nearly all bison injected with a high dose of field strain *B. abortus* during mid-gestation aborted their first calf, suggesting that the timing and dose of exposure is important in determining the likelihood that an animal develops acute infection resulting in abortion. We found 63% (5 of 8) and 75% (3 of 4) of



**FIGURE 14.8** Radio collared bison from the central herd of Yellowstone National Park licking her stillborn calf along the Madison River during May 2007 (National Park Service photo by Jenny Jones).



reproductively mature animals that were initially seronegative were not observed with calves during their first and second pregnancies, respectively, after converting to seropositive (Fuller *et al.* 2007b). These observations support that exposure during pregnancy, when internal conditions and hormonal signals are favorable for *B. abortus* infection, can result in fetal loss (Cheville *et al.* 1998). Seroconversion occurred in reproductively mature bison of ages 3, 4, 7, and 10, suggesting that all seronegative adult bison may be susceptible to a *Brucella*-induced abortion if exposed during gestation.

The Interagency Bison Management Plan that was established in 2000 assumed that bison culled at the northern boundary near Gardiner, Montana, would come from the northern herd, while bison culled at the western boundary near West Yellowstone, Montana, would come from the central herd (National Park Service 2000). Our findings based on radio-collared bison suggest that the vast majority of bison culled at both the northern and western boundary areas during 1995–2006 came from the central herd. The exception was during 1996–1997 when snow pack conditions on the northern range were more severe than during any other winter in the past 50 years and the entire northern range herd moved to the Gardiner basin (Taper *et al.* 2000). The finding that most bison culled at the northern boundary during our study came from the central herd is supported by time series and modeling analyses that suggest pulses of movement during winter from the central interior to the northern range in response to resource limitation began in approximately 1982 (Coughenour 2005, Fuller *et al.* 2007a). These movements and subsequent removals differentially affected the central herd during 1982–2000 by decreasing its growth rate while the growth rate of the northern herd increased (Fuller *et al.* 2007a).

The future management of Yellowstone bison is highly debated and contingent upon the management of brucellosis. Our findings suggest that the combined effect of brucellosis on pregnancy and birth rates resulted in lower fecundity across all ages. Consequently, chronic brucellosis infection may lower growth rate by more than 15%. Additionally, brucellosis exposure indirectly lowered bison survival because more bison were culled due to concerns regarding transmission to cattle when bison attempted to migrate to lower-elevation areas outside the park. These effects of brucellosis on the demography of Yellowstone bison are evident in time series data that indicate the population grew at a much slower rate than their biological potential during 1970–2000, even though densities were relatively low and per capita food resources should have been relatively high (Gates *et al.* 2005, Fuller *et al.* 2007a).

Bison have evolved to sustain robust population growth and are readily adapted to move when stressed by resource limitation (Gates *et al.* 2005; Chapter 12 by Bruggeman *et al.*, this volume). Thus, the problems at the boundaries of Yellowstone are likely to continue, challenging society and policy makers with a bison population that exits the park in response to density and climate effects. If vaccination plans are implemented and successful at substantially reducing brucellosis, then population growth rates will likely increase and exacerbate bison dispersal attempts. Therefore, the future challenge of conserving Yellowstone bison involves developing a strategy that mitigates the societal conflict resulting from bison dispersing or migrating outside the park.

## V. SUMMARY

1. We monitored 80 adult female bison from the central herd in Yellowstone National Park during 1995–2006 to estimate vital rates that incorporated the effects of brucellosis and could be used to formulate appropriate management strategies (*e.g.*, vaccination, culling).
2. Animals testing positive for exposure to brucellosis had significantly lower pregnancy rates across all age classes compared to seronegative bison. We do not understand the causal mechanism for this finding, which is difficult to ascertain since shedding through reproductive events is believed to be the primary route of brucellosis transmission.

3. Birth rates were high and consistent for seronegative animals, but lower for younger, seropositive bison. Seronegative bison that converted to seropositive while pregnant were likely to abort their first and second pregnancies. Thus, naïve seronegative adult bison may be highly susceptible compared to animals exposed before they were reproductively mature.
4. We detected pronounced senescence in survival for animals >12 years old. Also, brucellosis exposure indirectly lowered bison survival because more bison were culled over concerns about transmission to cattle when bison attempted to move to lower-elevation areas outside the park.
5. We detected a significant decrease in adult female survival when the number of bison in the central herd exceeded 2000–2500 animals, which was exacerbated during winters with severe snow pack because more bison moved outside the park. Except during 1996–1997, the vast majority of radio-collared bison culled at the northern and western boundaries during 1995–2006 came from the central herd.
6. Our findings suggest the combined effect of brucellosis on survival, pregnancy, and birth rates lowered the growth rate in the central herd. Thus, population growth rates will likely increase by more than 15% if vaccination plans are implemented and successful. Wildlife managers would then be challenged with greater numbers of disease-free bison dispersing or migrating outside of the park in response to density and climate effects.

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## APPENDIX

### Appendix 14A.1

Model selection results of *a priori* models for birth rates of known pregnant central herd bison  $\geq 3$  years old in Yellowstone National Park during 1995–2006 (Appendix 14A.1). The  $AIC_c$  value for the top model was 62.25. Model covariates included two individual covariates, age of the animal in years (AGE) and brucellosis serological status (SERO), and three annual covariates, the maximum summer count of bison in the central herd (BISON), an index of snow pack severity ( $SWE_{acc}$ ), and an index of annual forage productivity ( $NDVI_{L-int}$ ). Model abbreviations are the number of parameters (K), Akaike's Information Criteria corrected for small sample size ( $AIC_c$ ), the change in  $AIC_c$  relative to the best model ( $\Delta AIC_c$ ), and Akaike model weight ( $w_i$ ). *Post priori* we considered AGE by SERO, AGE by  $SWE_{acc}$  and BISON by SERO interactions. The AGE  $\times$  SERO model lowered  $AIC_c$  by 0.65 units below the top model.



**APPENDIX 14A.1** Model selection results of *a priori* models for birth rates of known pregnant central herd bison  $\geq 3$  years old

Model	<i>K</i>	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	<i>w<sub>i</sub></i>
Constant	1	62.25	0.00	0.13
AGE	2	62.86	0.61	0.09
SERO	2	62.94	0.69	0.09
AGE + SERO	3	63.06	0.81	0.08
BISON	2	63.59	1.34	0.06
SERO + BISON	3	64.24	1.99	0.05
SWE <sub>acc</sub>	2	64.26	2.00	0.05
AGE + BISON	3	64.26	2.01	0.05
NDVI <sub>L-int</sub>	2	64.34	2.09	0.04
AGE + SERO + BISON	4	64.35	2.10	0.04
AGE + SWE <sub>acc</sub>	3	64.92	2.67	0.03
AGE + NDVI <sub>L-int</sub>	3	65.04	2.79	0.03
SERO + SWE <sub>acc</sub>	3	65.11	2.85	0.03
SERO + NDVI <sub>L-int</sub>	3	65.12	2.87	0.03
AGE + SERO + SWE <sub>acc</sub>	4	65.30	3.05	0.03
AGE + SERO + NDVI <sub>L-int</sub>	4	65.32	3.07	0.03
BISON + SWE <sub>acc</sub>	3	65.40	3.15	0.03
BISON + NDVI <sub>L-int</sub>	3	65.70	3.45	0.02
AGE + BISON + SWE <sub>acc</sub>	4	66.14	3.89	0.02
SERO + BISON + SWE <sub>acc</sub>	4	66.33	4.08	0.02
SERO + BISON + NDVI <sub>L-int</sub>	4	66.48	4.23	0.02
AGE + BISON + NDVI <sub>L-int</sub>	4	66.49	4.24	0.02
AGE + SERO + BISON + SWE <sub>acc</sub>	5	66.52	4.27	0.01
AGE + SERO + BISON + NDVI <sub>L-int</sub>	5	66.68	4.43	0.01
<i>Post priori:</i>				
AGE + SERO + (AGE $\times$ SERO)	4	61.60		
AGE + SWE <sub>acc</sub> + (AGE $\times$ SWE <sub>acc</sub> )	4	67.04		
BISON + SERO + (BISON $\times$ SERO)	4	66.01		

## Appendix 14A.2

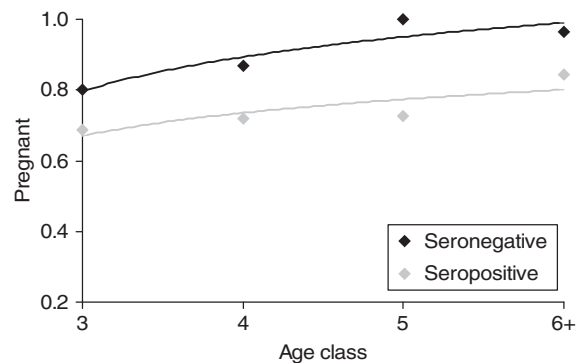
Age class-specific pregnancy rate estimates of seronegative (dark) and seropositive (gray) central herd bison handled at the Stephens Creek capture pen in Yellowstone National Park during February and early March 2004.

### Methods

We augmented the sample of radio-collared bison with pregnancy data collected from 176 adult female bison during a capture operation at the Stephens Creek pen near the northern boundary of Yellowstone National Park in February and early March 2004 (National Park Service 2000). Some of our study animals were in each of the captured groups, suggesting that many of the 176 bison were members of the central herd. Animals were aged into 3, 4, 5, 6, and older classes using incisor eruption patterns (Fuller 1959). We determined pregnancy status using pregnancy-specific protein B serum assays (Haigh *et al.* 1991). Bison were classified as seropositive or seronegative to brucellosis exposure status based on the results of the fluorescence polarization assay, card, buffered antigen plate agglutination, rivanol, complement fixation, standard plate, and standard tube tests performed by the Montana Department of Livestock Diagnostics Laboratory, Bozeman, Montana, USA (Roffe *et al.* 1999, Gall *et al.* 2000, Rhyen *et al.* 2001).

## Results

We estimated the probability of pregnancy for seronegative and seropositive bison for each age class as the observed proportion pregnant for each age class. There were 21 3-year-old bison (seronegative = 5, seropositive = 16), 40 4-year-old bison (seronegative = 15, seropositive = 25), 16 5-year-old bison (seronegative = 5, seropositive = 11), and 99  $\geq 6$ -year-old bison (seronegative = 28, seropositive = 71). The proportion of pregnant seropositive bison ranged from 11% to 27% lower than seronegative animals (Figure 14A.1).



**FIGURE 14A.1** Age class-specific pregnancy rate estimates of seronegative (dark) and seropositive (gray) central herd bison handled at the Stephens Creek capture pen during February and March 2004. Points represent the observed proportion of pregnant bison.