

Reproduction and Survival of Yellowstone Bison

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ABSTRACT The conservation of bison (*Bison bison*) from near extinction to >4,000 animals in Yellowstone National Park has led to conflict regarding overabundance and potential transmission of brucellosis (*Brucella abortus*) to cattle. We estimated survival and birth rates from 53 radiocollared adult female bison during 1995–2001, and we used calf:adult (C:A) ratios to estimate reproduction with the combined effects of pregnancy, fetal loss, and neonatal mortality during 1970–1997. Annual survival of adult females was high (0.92; 95% CI = 0.87–0.95) and constant. Birth rates differed by brucellosis status and age. Birth rates were 0.40 calves per female (95% CI = 0.15–0.65) for brucellosis-positive 3 year olds, 0.63 (95% CI = 0.39–0.87) for individuals testing negative, and 0.10 (95% CI = 0.00–0.24) for individuals contracting brucellosis that birth year (sero-converters). Birth rates were 0.64 (95% CI = 0.52–0.76) for brucellosis-positive individuals ≥ 4 years old, 0.81 (95% CI = 0.73–0.89) for brucellosis-negative individuals, and 0.22 (95% CI = 0.00–0.46) for sero-converters. Spring C:A ratios were negatively correlated with snow pack ($\beta = -0.01$ to -0.03 , $R^2 = 0.26$ – 0.60 , $P < 0.05$). Growth rate was highly elastic to adult survival (0.51), and juvenile survival (0.36) was 3 times more elastic than fecundity (0.12). Simulations suggested brucellosis eradication via vaccination would result in increased birth rates and a 29% increase in population growth ($\lambda = 1.09$), possibly leading to more bison movements outside the park. Our results will help park managers evaluate bison population dynamics and explore consequences of management actions and disease control programs. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2365–2372; 2007)

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The development of rigorously estimated vital rates is essential for understanding factors influencing population dynamics and for formulating appropriate management strategies. The demography of some North American ungulates with broad geographic distributions such as white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*) is well known. However, knowledge regarding the demography of bison is sparse due to the near eradication of free-ranging herds and limited restoration after the era of market hunting (Meagher 1973). Over a century of concerted conservation has recovered the bison population in Yellowstone National Park (YNP) from near extinction to >4,000 animals (Meagher 1973, Dobson and Meagher 1996, Gates et al. 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 about potential transmission of the *Brucella* pathogen to domestic livestock (Cheville et al. 1998). Since the 1980s, increasing numbers of bison have moved outside YNP, located in the western United States, including portions of Wyoming, Montana, and Idaho, USA, where >1,000 bison have been culled by various state and federal agencies in some winters, resulting in high costs and controversy (Baskin 1998, National Park Service 2000). Management of Yellowstone's bison will benefit from increased understanding of processes that influence bison spatial and population dynamics.

Our objectives were to 1) estimate pregnancy rates, birth

rates, adult survival, and population growth rates in each bison herd; 2) evaluate what factors influenced these rates; and 3) estimate a population growth rate (λ) from these vital rates. We expected survival of adult female bison would be high, with only modest annual variation associated with human-caused mortality (Van Vuren and Bray 1986, Gaillard et al. 1998, Larter et al. 2000), fluctuations in climate (Sæther 1997), and senescence in older aged animals (Eberhardt 1985). We expected bison age would influence pregnancy and birth rates because bison have delayed sexual maturity (Aune et al. 1998). We expected exposure to *Brucella* would reduce birth rates because bison that contract brucellosis (i.e., sero-converters) generally abort their next calf (Davis et al. 1990, 1991). In addition, we hypothesized recruitment would vary considerably among years due to interactive effects between density and stochastic climate covariates on juvenile survival (Sæther 1997, Gaillard et al. 2000, Eberhardt 2002). We expected pregnancy, birth, and survival rates to be lower in the central herd, which was at higher density and exposed to severe winter conditions.

STUDY AREA

Yellowstone National Park encompassed 9,018 km². The bison population existed almost entirely within the boundaries of the park and consisted of central and northern herds. The most recent ranges of these herds were comparable in size (1,200 km²; Hess 2002), but they existed with different plant communities, precipitation patterns, and densities of other large ungulates. The range of the northern herd encompassed a decreasing elevation gradient extending approximately 90 km between Cooke City and Gardiner,

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Montana, (Meagher 1973). The northern range was drier and warmer than the rest of the park, with mean annual precipitation decreasing from 35 cm to 25 cm along the elevation gradient (Farnes et al. 1999). 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, sedges (*Carex* spp.), and rushes (*Juncus* spp.) made up the majority of forage on the northern range. Bison shared this range with a large elk herd, which increased from approximately 3,200 to >19,000 counted individuals during 1968–1994 and then decreased to approximately 12,000 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 in the central herd's range were severe, with snow-water equivalents averaging 35.1 cm and temperatures reaching -42°C (Farnes et al. 1999), although 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 (Craighead et al. 1973). The central range included a higher proportion of mesic meadows than the northern range, and dominant forage included grasses, sedges, and willows (*Salix* spp.). The central herd coexisted with 400–600 elk during winter (Garrott et al. 2003).

METHODS

We captured adult female bison during October, February, and May 1995–1999 using immobilization with carfentanyl and xylazine (Aune et al. 1998). We fit bison with radiocollars equipped with motion-sensitive mortality sensors (Lotek Wireless, Newmarket, ON, Canada; Telonics, Mesa, AZ), and we aged them by tooth irruption and wear patterns (Fuller 1959, Dimmick and Pelton 1996). We used telemetry homing techniques to monitor the survival of radiocollared bison monthly during autumn 1995 through spring 2001. When we detected a mortality signal, we located the animal and we evaluated cause of death. We collected incisors to verify age using cementum annuli analysis (Moffitt 1998).

We attempted to recapture each radiocollared bison during early-term pregnancy (Oct), late-term pregnancy (Feb), and shortly after calving (Apr–May) during 1995–2001. We determined early-term pregnancy (Oct) using a portable ultrasonograph (model SSD-500V; Aloca, Tokyo, Japan) or pregnancy-specific protein B assays of serum (Haigh et al. 1991). We determined late-term pregnancy (Feb) using rectal palpation and pregnancy-specific protein B assays. We based pregnancy determinations on results of the February tests, when available, but we used October test results if we did not recapture an individual in February. We inserted vaginal transmitters (Advanced Telemetry Systems, Isanti, MN) in pregnant females captured in February to estimate birth rates (Cartensen et al. 2003, Johnstone-Yellin et al. 2006). We determined brucellosis status from blood

drawn at each capture using the card, buffered antigen plate agglutination, particle concentration fluorescence immunoassay, rivanol, complement fixation, standard plate tests, and standard tube tests (Roffe et al. 1999, Rhyan et al. 2001). Our repeated sampling also allowed detection of seroconversion, when an animal previously testing negative for brucellosis was exposed to the disease and subsequently tested positive.

We monitored bison daily during the calving season from mid-March through June. We considered birth successful when we observed a live calf in close association with the female. We considered birth unsuccessful if we observed an aborted fetus, stillborn calf, or if we repeatedly failed to detect a calf associated with the female. Field personnel generally confirmed births within 24 hours. We conducted our telemetry studies over a relatively short time, which limited our ability to evaluate the potential influence of climate variation on bison reproduction. Thus, we complemented these studies with a time series of C:A ratios collected during aerial surveys of bison on the central and northern ranges during May–June 1970–1997 (Dobson and Meagher 1996). The C:A ratio is an index of bison reproduction that incorporates pregnancy, fetal loss, and neonatal mortality during the first 1–2 months of life. If ≥ 2 surveys occurred during May and June in 1 year, we used the sum of calves and sum of adults from the surveys to calculate separate C:A ratios for the central ($C:A_C$) and northern ($C:A_N$) herds.

Vital Rate Analyses

We created a mark–recapture history for each instrumented bison over age 1 year, censoring capture-related mortalities and management removals. We considered combinations of 3 covariates in our a priori model list: 1) year of study, 2) season over which we estimated survival (Oct–Mar and Apr–Sep), and 3) membership in the central or northern herd. We used program MARK (White and Burnham 1999, Cooch and White 2005) and the known fate model to obtain 6-month survival estimates of radiocollared bison over 13 monitoring intervals between October 1995 and October 2001. We estimated an annual survival rate as the product of each 2 6-month intervals. We used Akaike's Information Criterion with small sample size adjustment (AIC_c) as model selection criterion (Burnham and Anderson 1998). We calculated the overdispersion parameter (\hat{c}) for our most complex model because repeated measurements of the same individuals may result in lack of independence in the data and potential underestimation of variance (Burnham and Anderson 1998, Cooch and White 2005). If $\hat{c} > 1.0$, we adjusted AIC_c values to quasi- AIC_c ($QAIC_c$), which inflated the variance and favored simpler models (Burnham and Anderson 1998, Cooch and White 2005).

We evaluated the binomial response variables pregnancy status and birth success using multiple logistic regression and using the logit transform to derive parameter estimates with Program R (R Core Development Team 2004). We calculated the overdispersion parameter and adjusted AIC_c values to $QAIC_c$ if $\hat{c} > 1.0$. The a priori models for

Table 1. Annual estimates of spring calf:adult ratios, Palmer Drought Severity Index (PDSI), accumulated snow water equivalent (SWE_{acc}), bison counts, and elk counts on the northern winter range of Yellowstone National Park, USA, during 1970–2005.

Yr	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		216	512	5,543
1971	0.21	0.24	0.55	1,381		322	511	7,282
1972	0.27	0.30	−0.88	843		232	612	8,215
1973	0.31	0.29	0.70	1,138		290	728	9,981
1974	0.24	0.28	−0.87	376		285	873	10,529
1975	0.23	0.26	−1.79	1,095		224	936	12,607
1976	0.24	0.14	1.08	1,339		259	951	10,825
1977	0.32	0.26	−0.64	568		457	1,119	10,741
1978	0.17	0.22	−6.44	1,501		262	1,378	11,878
1979	0.27	0.20	0.04	1,324		433	1,588	10,807
1980	0.28	0.20	−1.77	1,271		349	1,801	
1981	0.19	0.19	−2.86	503	1,933	330	2,067	
1982	0.33	0.14	1.07	389	4,906	542	1,703	15,114
1983	0.24	0.21	2.36	617	3,072	483	1,674	
1984	0.31	0.23	−1.04	709	2,543	619	1,671	
1985	0.31	0.26	−1.25	1,201	3,509	647	1,919	
1986	0.22	0.19	−1.37	1,117	3,908	708	2,068	15,387
1987	0.23	0.29	−0.79	601	2,214	712	2,381	16,162
1988	0.30	0.23	−2.59	335	2,816	868	2,387	18,737
1989	0.22	0.16	−4.32	1,039	4,128	461	2,188	18,945
1990	0.26	0.22	−1.76	946	3,317	541	2,672	14,506
1991	0.31	0.22	−1.79	513	3,332	741	2,685	11,330
1992	0.24	0.18	−1.83	1,416	3,511	570	3,090	11,072
1993	0.29	0.21	−3.48	1063	3,907	673	2,945	16,011
1994	0.27	0.25	1.90	659	2,533	770	3,376	18,832
1995	0.28	0.19	−1.64	1,187	4,611	771	3,216	14,752
1996	0.30	0.22	0.87	646	6,237	877	2,928	
1997	0.14	0.17	−0.13	1,845	7,279	354	1,816	
1998			1.40		3,511			
1999			−2.11		5,008			
2000			−3.84		3,355			
2001			−4.17		2,527			
2002			−7.29		3,817			
2003			−7.63		3,524			
2004			−6.51		3,273			
2005			−8.46		2,614			

pregnancy and birth response variables included combinations of 1) year, 2) herd membership, 3) bison age, 4) brucellosis sero-status, 5) a warm-season climate covariate, and 6) a cold-season climate covariate. We initially categorized bison age into 3 categories following Aune et al. (1998): 1) young (age 3 yr), 2) prime aged (4–8 yr), and 3) senescent (≥ 9 yr). Alternatively, we assumed bison did not experience reproductive senescence and aged bison into 2 categories: 1) 3 year olds and 2) ≥ 4 years old. We used the Palmer drought severity index (PDSI; Palmer 1968) as our warm-season climate covariate because it incorporates precipitation, temperature, and evapotranspiration, which are correlated with the quantity and nutritive quality of plants (Sala et al. 1988). We averaged the index for region 1 of Wyoming over the growing season (1 May–31 Jul). We used accumulated snow water equivalent (SWE_{acc}) during 1 October to 31 April as our cold-season climate covariate because this index incorporates snow depth and density (i.e., amt of water present in a column of snow) and the duration of snowpack, which influence the energetic costs of foraging and locomotion (Farnes et al. 1999, Garrott et al. 2003). The Canyon Snow Telemetry Station directly measured

snow water equivalent data, and we used an algorithm described by Farnes et al. (1999) to estimate snow water equivalent from precipitation and temperature data at the Tower Falls Climate Impact Meteorological station.

We evaluated spring C:A ratios for the northern and central herds by including all possible combinations of 1) SWE_{acc}, 2) PDSI, 3) the number of bison counted on each range the previous winter, and 4) the number of elk counted on the northern range (Table 1). We included the elk covariate for northern herd models due to the large numbers of elk on this range during winter (5,500–20,000; White and Garrott 2005). We did not include a similar covariate in the central herd models because elk numbers on this range were low and relatively constant (400–600; Garrott et al. 2003). We scaled covariates to simplify coefficient interpretation by dividing elk counts by 10,000, dividing bison counts and SWE_{acc} by 1,000, and adding 7 to the PDSI to remove negative values and support a square-root transform. We also considered nonlinear transforms of the climate explanatory variables (i.e., SWE_{acc}² and $\sqrt{\text{PDSI}}$). We followed a stepwise model selection procedure to determine whether the data supported transforms of the covariates

(Borkowski et al. 2006). We evaluated sources of variation in spring C:A ratios using multiple linear regression in Program R (R Core Development Team 2004) and an information-theoretic model selection approach (Burnham and Anderson 1998).

Matrix Model

We constructed a postbreeding, age-structured, deterministic Leslie matrix model for female bison using our vital rate estimates (Caswell 2001). No bison sampled during this study ($n = 53$ ad), harvested during 1988–1989 ($n = 513$; Pac and Frey 1991), or lethally removed from YNP during 1985–1998 ($n = 593$; R. Wallen; National Park Service, unpublished data), were >15 years old, and we could not detect senescence in survival from these data. Thus, we constructed a 16×16 matrix model with a constant adult survival rate and maximum age of 15 years. Because bison in other systems have lived 20 years (Shaw and Carter 1989, Berger and Cunningham 1994), however, we ran several simulations to determine the effects of these assumptions by allowing bison to reach age 20 years and imposing survival senescence in animals ≥ 12 years old.

We derived the fecundity rate input for the matrix model from model-averaged birth rates of brucellosis-negative, brucellosis-positive, and sero-converting bison weighted according to their proportion in the population (Jolles et al. 2005). We halved fecundity rates because we only included females in the model, and available evidence either suggested equal sex ratios at birth (Fuller 1960, Shaw and Carter 1989) or was inconclusive (Rutberg 1986, Pac and Frey 1991). We could not calculate calf survival rates from summer C:A ratios because surveys occurred after substantial neonatal mortality and there were no postwinter surveys. Thus, we used an estimate (0.76) derived by Kirkpatrick et al. (1996) from calf counts in year t and yearling counts in year $t + 1$.

We estimated the growth rate of the population (λ) and the elasticity for survival and fecundity of each age from the matrix model (Caswell 2001). We also summed elasticity values for juvenile survival (age 0–2 yr), adult survival (3–15 yr), and fecundity (3–15 yr) to evaluate how a proportional change in each category would affect λ (Heppell et al. 2000). To explore the management implications of brucellosis elimination, we constructed a separate matrix model that only input fecundity parameters estimated from brucellosis-negative bison.

RESULTS

We captured 26 bison from the northern herd and 27 bison from the central herd, which we monitored for 101 and 89 animal-years, respectively. There were 15 deaths of marked bison during 1995–2001, excluding capture-related deaths ($n = 7$) and removals ($n = 2$). Five bison died from unknown causes, 4 from vehicle collisions, 3 from predation, 2 from winterkill, and 1 from injury. We found no evidence of overdispersion in the data (i.e., $\hat{c} < 1$) and ranked survival models using AIC_c . There was considerable support for the model assuming constant survival ($AIC_c = 126.89$, Akaike

wt [$w_i = 0.54$, $K = 1$), with a maximum likelihood annual survival estimate of 0.92 (95% CI = 0.87–0.95). Model output supported separate estimation of central and northern herd survival rates ($\Delta AIC_c = 1.82$, $w_i = 0.22$, $K = 2$), with maximum likelihood estimates of 0.93 (95% CI = 0.85–0.97) for the central herd and 0.91 (95% CI = 0.84–0.95) for the northern herd, but substantial overlap in confidence intervals for these estimates suggested little difference between the herds. We found less support for survival variation by season ($\Delta AIC_c = 2.02$, $w_i = 0.20$, $K = 2$). Models assuming survival variation by herd and season ($\Delta AIC_c = 5.19$, $w_i = 0.04$, $K = 4$), year ($\Delta AIC_c = 10.19$, $w_i = 0.00$, $K = 7$), and herd and year ($\Delta AIC_c = 18.8$, $w_i = 0.00$, $K = 14$) had virtually no support.

We monitored pregnancy rates of 46 females aged ≥ 3 years through 139 reproductive seasons. Of these 139 records, 60 came from bison testing positive for brucellosis, whereas 69 records were from brucellosis-negative bison, and 10 records were from bison sero-converting that year. Few records came from 3-year-old females ($n = 14$), whereas 81 records were from 4–8-year-olds, and 44 records were from females ≥ 9 years. We found no evidence of overdispersion in these data. Model results supported the model assuming bison aged ≥ 4 years had higher pregnancy rates than did 3-year-olds ($\beta_1 = 1.3$ [95% CI = 0.02–2.63], $AIC_c = 99.89$, $w_i = 0.14$; Table 2). However, 6 other models were within 2 AIC_c units of this model, including a model assuming constant pregnancy ($\Delta AIC_c = 1.40$, $w_i = 0.07$) with a maximum likelihood estimate of 0.88 (95% CI = 0.82–0.93). There was no evidence of senescence in pregnancy rates because the coefficient for bison aged >9 years overlapped zero (-0.30 , 95% CI = -1.52 to 0.91). There was some evidence brucellosis-positive and sero-converting bison had lower pregnancy rates than sero-negative bison ($\Delta AIC_c = 1.28$, $w_i = 0.08$), but the 95% confidence intervals for the coefficient on sero-positive and sero-converting bison overlapped zero (positive: -0.98 [95% CI = -2.13 to 0.18]; converting: -0.37 [95% CI = -2.66 to 1.93]).

We monitored birth rates of 48 females aged ≥ 3 years, which produced 96 live calves in 145 reproductive seasons. Of these 145 records, 66 were from bison testing positive for brucellosis, whereas 69 records were from brucellosis-negative bison, and 10 records were from bison sero-converting that year. These records included 15 from 3-year-old females, 82 records from 4–8 year olds, and 44 records from females ≥ 9 years. There was evidence for overdispersion in these data, with $\hat{c} = 1.16$. Thus, we calculated $QAIC_c$ for model selection (Burnham and Anderson 1998). There was considerable support for variation in birth rates between age classes and brucellosis status ($QAIC_c = 150.09$, $w_i = 0.23$), though 6 other models were within 2 $QAIC_c$ units of this model (Table 2) and the 95% confidence interval on the age coefficient overlapped zero (0.98 [95% CI = -0.18 to 2.14]). Birth rates for 3-year-old bison were 0.40 (95% CI = 0.15–0.65) for animals testing positive for brucellosis, 0.63 (95% CI = 0.39–0.87)

Table 2. Top approximating models for logistic regression of pregnancy and birth rate data for bison in Yellowstone National Park, USA, during 1995–2001. The intercept (β_0) represented sero-negative bison when serological status was in the model. The intercept represented bison aged 4–8 years when AGE₃ was in the model.

Model ^a	AIC _c ^b	Δ AIC _c ^c	K ^d	w_i ^e
Pregnancy (P_r) models				
$P_r = \beta_0 + \beta_1(\text{AGE}_2)$	99.89	0.00	2	0.14
$P_r = \beta_0 + \beta_1(\text{AGE}_2) + \beta_2(\text{HERD})$	100.65	0.75	3	0.10
$P_r = \beta_0 + \beta_1(P) + \beta_2(C) + \beta_3(\text{AGE}_2)$	101.17	1.28	4	0.08
$P_r = \beta_0$	101.29	1.40	1	0.07
$P_r = \beta_0 + \beta_1(\text{HERD})$	101.48	1.59	2	0.06
$P_r = \beta_0 + \beta_1(\text{AGE}_2) + \beta_2(P) + \beta_3(C) + \beta_4(\text{HERD})$	101.58	1.69	5	0.06
$P_r = \beta_0 + \beta_1(\text{SEN}) + \beta_2(\text{PRIM})$	101.74	1.85	3	0.06
Birth rate (B) models ^f				
$B = \beta_0 + \beta_1(P) + \beta_2(C) + \beta_3(\text{AGE}_2)$	150.09	0.00	4	0.23
$B = \beta_0 + \beta_1(P) + \beta_2(C)$	150.30	0.21	3	0.21
$B = \beta_0 + \beta_1(P) + \beta_2(C) + \beta_3(\text{HERD})$	150.87	0.77	4	0.16
$B = \beta_0 + \beta_1(\text{AGE}_2) + \beta_2(P) + \beta_3(C) + \beta_4(\text{HERD})$	150.88	0.79	5	0.16
$B = \beta_0 + \beta_1(P) + \beta_2(C) + \beta_3(\text{SEN}) + \beta_4(\text{PRIM})$	151.26	1.17	5	0.13
$B = \beta_0 + \beta_1(P) + \beta_2(C) + \beta_3(\text{SEN}) + \beta_4(\text{PRIM}) + \beta_5(\text{HERD})$	151.72	1.63	6	0.10

^a AGE₂ (indicator variable for 3-yr-old or ≥ 4 -yr-old bison); AGE₃ (indicator variable for 3-yr-old, 4–8-yr-old, or ≥ 9 -yr-old bison); C (sero-converting bison); P (sero-positive bison); HERD (indicator variable for northern or central herd); PDSI (Palmer Drought Severity Index); PRIM (3-yr-old bison); SEN (bison ≥ 9 yr old); SWE_{acc} (accumulated snow water equivalent); and YEAR (yr of study).

^b Akaike's Information Criterion corrected for small sample size.

^c Difference in AIC value from top approximating model.

^d No. parameters.

^e Model wt.

^f For birth rate models, AIC values are corrected for small sample size when there is evidence for overdispersion in the data.

for brucellosis-negative animals, and 0.10 (95% CI = 0.00–0.24) for sero-converters. Birth rates for bison aged ≥ 4 years were 0.64 (95% CI = 0.52–0.76) for animals testing positive for brucellosis, 0.81 (95% CI = 0.73–0.89) for brucellosis-negative animals, and 0.22 (95% CI = 0.00–0.46) for sero-converters. There was no evidence of senescence in birth rates because 95% confidence intervals around the coefficient for bison aged > 9 years overlapped zero (0.22 [95% CI = –0.57 to 1.01]). The covariate for herd membership showed up in 2 of the top models, but the 95% confidence interval encompassed zero (0.48 [95% CI = –0.27 to 1.24]), suggesting herd membership had a negligible effect on birth rates.

We analyzed 20 spring C:A ratios for the northern herd and 17 spring C:A ratios for the central herd. Calf:adult ratios for both herds were negatively correlated with SWE_{acc} for the winter preceding the spring count (central: $\beta_1 = -0.01$ [95% CI = –0.03 to 0.00]; northern: $\beta_1 = -0.03$

[95% CI = –0.05 to –0.01]; Fig. 1). The best approximating model for central herd spring C:A ratios included only SWE_{acc} (AIC_c = –61.17, $w_i = 0.43$), and no other model was within 2 AIC units (Table 3). Calf:adult ratios for the northern herd were marginally correlated with $\sqrt{\text{PDSI}}$ ($\beta_1 = 0.03$ [95% CI = 0.00 to 0.06]; Table 3), likely because the severe $\sqrt{\text{PDSI}}$ value during the 1978 drought was an influential point in the regression (Fig. 2).

The initial matrix model incorporating one adult survival rate (0.92) and separate fecundity rates for 3-year-old (0.23) and 4–15-year-old (0.35) bison estimated $\lambda = 1.07$. Likewise, simulations enforcing survival senescence and allowing older age classes resulted in $\lambda = 1.07$ –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-year-old, and 2-year-old survival (Fig. 3). Lambda was more elastic to age-specific survival than age-specific reproduction for all

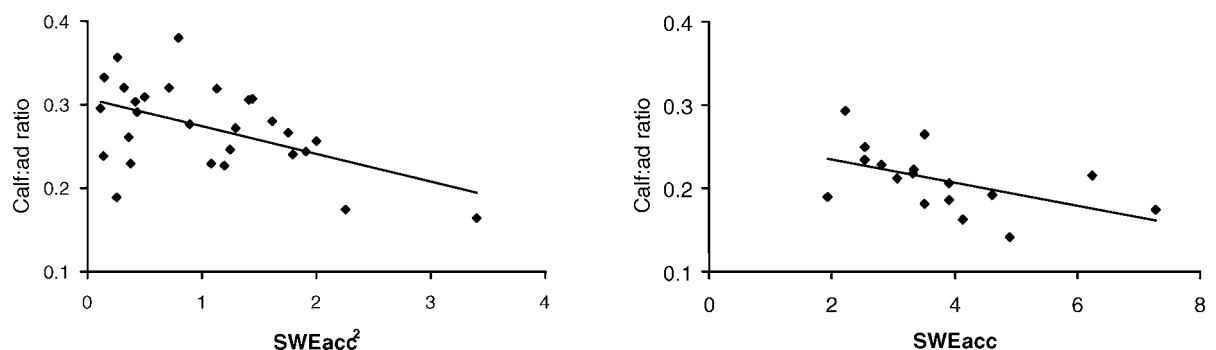


Figure 1. Relationship between snow pack (SWE_{acc}) and calf:adult ratios for the northern (left) and central (right) bison herds in Yellowstone National Park, USA, during 1970–1997.

Table 3. Top approximating models for factors influencing spring calf:adult ratios (C:A) of the central and northern bison herds in Yellowstone National Park, USA, 1981–1997.

Model ^a	AIC _c ^b	ΔAIC _c ^c	K ^d	w _i ^e
Central herd models (n = 17)				
C:A _C = β ₀ + β ₁ (SWE _{acc})	-61.17	0.00	3	0.43
C:A _C = β ₀ + β ₁ (SWE _{acc}) + β ₂ (PDSI)	-59.15	2.02	4	0.16
C:A _C = β ₀	-59.12	2.05	2	0.15
Northern herd models (n = 20)^a				
C:A _N = β ₀ + β ₁ (SWE _{acc} ²)	-72.22	0.00	4	0.27
C:A _N = β ₀ + β ₁ (SWE _{acc} ²) + β ₂ (√PDSI)	-72.21	0.01	3	0.27
C:A _N = β ₀ + β ₁ (SWE _{acc} ²) + β ₂ (BISON)	-70.23	1.98	4	0.10

^a BISON (bison count the previous yr); PDSI (Palmer Drought Severity Index); SWE_{acc} (accumulated snow water equivalent).
^b Akaike's Information Criterion corrected for small sample size.
^c Difference in AIC value from top approximating model.
^d No. of parameters.
^e Model wt.

but the oldest age classes (i.e., >14 yr). The sum of elasticity values by age category indicated 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 (Fig. 4) and generation time was estimated at 8.6 years. Given fecundity rates for brucellosis-negative 3-year old (0.32) and 4-year old (0.41) bison, the Leslie matrix model estimated λ = 1.09 for Yellowstone bison in the absence of brucellosis. These results suggested the growth rate of the population could increase approximately 29% if brucellosis were eliminated.

DISCUSSION

The estimated growth rate (λ = 1.07) for Yellowstone bison from the deterministic matrix model was similar to an estimate from an exponential model based on aerial count data during 1990–2000 (λ = 1.05; Fuller et al. 2007). The similarity between the estimates we derived from 2 independent methods lends credence to our estimates of growth rate and suggest our vital rate estimates are rigorous.

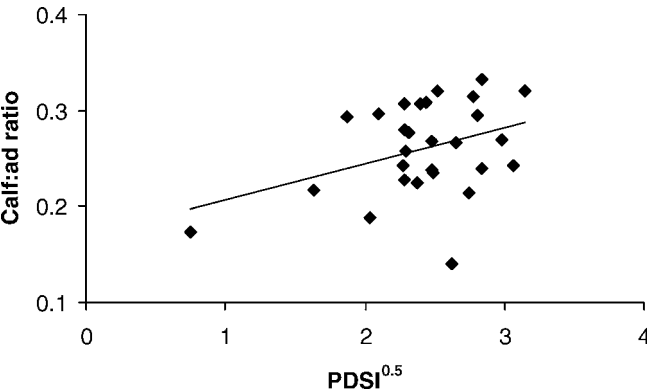


Figure 2. Relationship between the Palmer Drought Severity Index (PDSI^{0.5}) for Region 1 of Wyoming and spring calf:adult ratios for bison from the northern herd in Yellowstone National Park, USA, during 1970–1997.

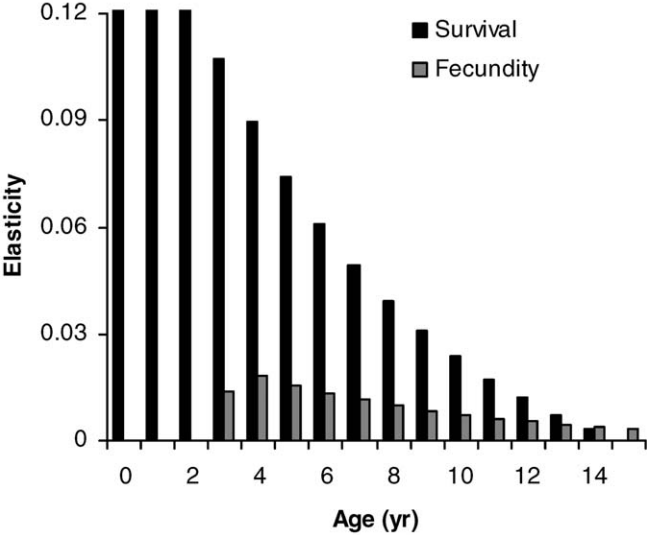


Figure 3. Age-specific (yr) elasticity for survival and fecundity rates of bison in Yellowstone National Park, USA, using a Leslie matrix model and data collected during 1995–2001.

Furthermore, our estimates are comparable with rates observed in other established bison populations (Fredin 1984, Gates and Larter 1990, Larter et al. 2000, Eberhardt 2002). For example, Larter et al. (2000) reported lower population growth rates of bison in Wood Buffalo National Park, Fort Smith, Northwest Territories, Canada (λ = 1.03), and Van Vuren and Bray (1986) reported higher population growth rates for bison in the Henry Mountains, Utah, USA (λ = 1.10).

Pregnancy and birth rates of Yellowstone bison did not vary with climate, but spring C:A ratios varied with both winter severity (SWE_{acc}) and warm-season growing conditions (PDSI). These results suggest the variability in spring C:A ratios was largely due to fluctuations in neonatal survival rather than fluctuations in birth rates, as reported in

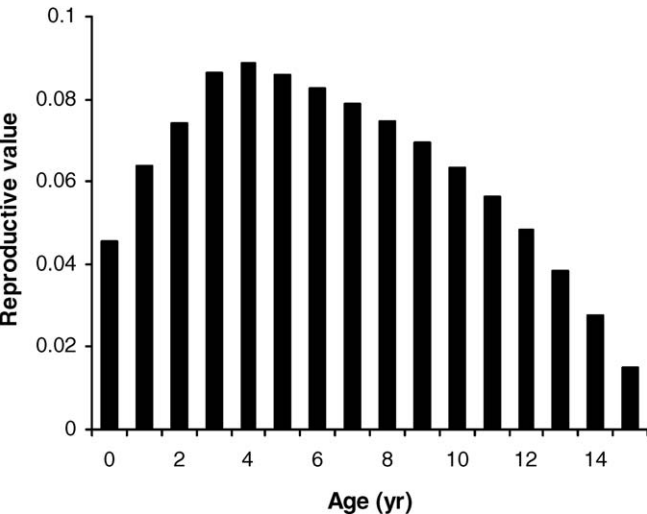


Figure 4. Relationship between age (yr) and reproductive value for bison in Yellowstone National Park, USA, using a Leslie matrix model and data collected during 1995–2001.

Wood Buffalo National Park (Larter et al. 2000). The effects of climatic variability on large ungulates are most pronounced on neonatal survival because conception and gestation require less energy than lactation, and nutritionally stressed females may produce offspring that will not survive the first 2 weeks of life, thus avoiding costs of lactation (Clutton-Brock et al. 1989, Gaillard et al. 2000). Adult female survival was high (0.92–0.96) and constant in bison from YNP, Wood Buffalo National Park (Larter et al. 2000), and the Henry Mountains (Van Vuren and Bray 1986). Thus, the differences in growth rates among these populations likely reflect differences in calf survival, which was highest in the Henry Mountains (0.94), lower in Yellowstone (0.76; Kirkpatrick et al. 1996), and lowest in Wood Buffalo National Park (0.49–0.63).

As expected, 3 year olds had lower pregnancy and birth rates than did older individuals. However, we did not detect reduced survival in older animals (>9 yr) due to senescence. Brucellosis is enzootic in Yellowstone bison, with 50–55% of bison in both herds having apparently been exposed to brucellosis (Pac and Frey 1991, Meyer and Meagher 1995). Brucellosis infections reduced birth rates in both age categories, although these effects were most prevalent in bison that were exposed to brucellosis that year (i.e., seroconverters) and effects seemed to wane thereafter. Interestingly, 4 radiocollared bison began to test negative for brucellosis in years after having previously tested positive. Brucellosis antibody levels in these animals may have decreased to a level below detectability.

The most variable vital rates in large ungulates tend to be the least elastic (Gaillard et al. 2000), but this was not strictly the case in Yellowstone bison. As expected, the relatively constant adult survival was the most elastic trait (0.51), with small changes having large effects on the population growth rate. However, juvenile survival was apparently highly variable year to year, as determined by C:A ratios and as seen in other studies (Larter et al. 2000); yet, this rate had relatively high elasticity (0.36). The elasticity of fecundity was also relatively low (0.12) compared with other ungulates (Heppell et al. 2000). These differences may reflect bison being relatively long lived, with a longer generation time (>8 yr) and delay before first reproduction (3–4 yr) compared with smaller ungulates (1–2 yr). Similar elasticities occur in 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*; Jolles et al. 2005) were nearly identical to those we estimated for Yellowstone bison.

MANAGEMENT IMPLICATIONS

The future management of Yellowstone bison is highly debated and contingent upon the management of brucellosis. Our findings suggest that if vaccination plans are implemented and successful at substantially reducing or eradicating brucellosis, then population growth rates could increase approximately 29%. Increased growth rates could

contribute to more movement outside the park because bison respond to increased density through spatial responses (Gates et al. 2005, Fuller et al. 2007). Even without the threat of brucellosis transmission, such movements would exacerbate societal conflicts regarding overabundance and property damage. Future research should focus on estimating juvenile survival because this rate is currently largely unknown, but it seems to have a relatively high effect on population growth rates (elasticity = 0.36).

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