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Population Ecology

Pregnancy Rates in Central Yellowstone Bison

PETER J. P. GOGAN,[1] *U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, USA*
ROBIN E. RUSSELL, *U.S. Geological Survey, National Wildlife Health Center, 6006 Schroeder Road, Madison, WI 53711, USA*
EDWARD M. OLEXA, *U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, USA*
KEVIN M. PODRUZNY, *Montana Fish, Wildlife and Parks, 1420 E. 6th Avenue, Helena, MT 59601, USA*

ABSTRACT Plains bison (*Bison b. bison*) centered on Yellowstone National Park are chronically infected with brucellosis (*Brucella abortus*) and culled along the park boundaries to reduce the probability of disease transmission to domestic livestock. We evaluated the relationship between pregnancy rates and age, dressed carcass weight, and serological status for brucellosis among bison culled from the central Yellowstone subpopulation during the winters of 1996–1997, 2001–2002, and 2002–2003. A model with only dressed carcass weight was the best predictor of pregnancy status for all ages with the odds of pregnancy increasing by 1.03 (95% CI = 1.02–1.04) for every 1-kg increase in weight. We found no effect of age or the serological status for brucellosis on pregnancy rates across age classes; however, we did find a positive association between age and pregnancy rates for bison ≥2 years old. Bison ≥2 years old had an overall pregnancy rate of 65% with markedly different rates in alternate ages for animals between 3 and 7 years old. Pregnancy rates were 0.50 (95% CI = 0.31–0.69) for brucellosis positive and 0.57 (95% CI = 0.34–0.78) for brucellosis negative 2- and 3-year-olds and 0.74 (95% CI = 0.60–0.85) in brucellosis positive and 0.69 (95% CI = 0.49–0.85) in brucellosis negative bison ≥4 years old. Only 1 of 21 bison <2 years old was pregnant. Our findings are important to accurately predict the effects of brucellosis on Yellowstone bison population dynamics. We review our results relative to other studies of Yellowstone bison that concluded serological status for brucellosis influences pregnancy rates.

KEY WORDS Bison, *Bison bison*, *Brucella abortus*, brucellosis, Greater Yellowstone Area, reproduction.

The plains bison (*Bison b. bison*) centered on Yellowstone National Park represent a key component in American bison conservation. In addition to meeting most of the criteria for a conservation herd, i.e., "a large population occupying extensive native landscapes where human influence is minimal and a full suite of natural limiting factors is present" (Gates and Gogan 2010), the Yellowstone population is one of the few plains bison populations with no evidence of cattle introgression (Polziehn et al. 1995, Halbert and Derr 2007). However, Yellowstone bison are chronically infected with brucellosis, an exotic disease caused by the bacterium *Brucella abortus* (Mohler 1917, Rush 1932), with ≥50% of the population seropositive for the disease (Cheville et al. 1998, Treanor et al. 2011). The disease is known to affect reproductive success among ungulates, typically by causing abortion among primiparous females (Cheville et al. 1998). The presence of this disease necessitates a complex management strategy to balance preventing potential brucellosis transmission from bison to livestock on lands adjacent to the park while maintaining Yellowstone bison as a conservation herd (Plumb et al. 2009, White et al. 2011).

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[1]*E-mail: peter_gogan@usgs.gov*

Seasonal shifts in bison distribution beyond the park boundaries in late winter and early spring lead to the possibility of disease transmission because of potentially close spatial and temporal associations between bison and livestock (Kilpatrick et al. 2009). Bison moving to the park boundaries have been subjected to intense management, including hazing and lethal removals (U.S. Department of Interior and U.S. Department of Agriculture, 2000) intermittently since the mid-1980s (Dobson and Meagher 1996, Cheville et al. 1998, Plumb et al. 2009). Management agencies continue to evaluate the effect of culling on reducing the likelihood of brucellosis transmission from bison to domestic stock, as well as the impacts on bison conservation (U.S. Department of Interior and U.S. Department of Agriculture, 2000, Plumb et al. 2009, White et al. 2011). Evaluating these trade-offs necessitates understanding the basic demographic factors that drive the population's trajectory. Accurate estimation of demographic parameters such as age of first reproduction, interbirth interval and prime-aged female reproductive rate are critical to assessing the population growth potential and predicting population changes (Eberhardt 1977, 2002; McCullough 1979; Bonenfant et al. 2009).

Females of large mammalian species typically exhibit age-specific differences in reproductive rates (Caughley 1977), with the age of first reproduction driven by a body mass threshold (Houston and Stevens 1988, Sand 1996).

Reproductive rates for all age classes are influenced by nutritional condition, which is linked to population density and weather effects (Gaillard et al. 2000, Bonenfant et al. 2009, Simard et al. 2010), and the reproductive rates of younger females are more sensitive to these factors than are those of prime-aged females (Eberhardt 1977, 2002; Bonenfant et al. 2009). Recent studies of reproduction in Yellowstone bison have suggested a negative relationship between serological status for brucellosis and pregnancy (Fuller et al. 2007, Geremia et al. 2009). In contrast, Joly and Messier (2005) did not detect an effect of the serological status for brucellosis on pregnancy rates in wood bison (*B. b. athabascae*). We necropsied central Yellowstone bison culled nonselectively during the winters of 1996–1997, 2001–2002, and 2002–2003 to determine pregnancy rates relative to age, dressed carcass weight, and serological status for brucellosis.

STUDY AREA

During this study, Yellowstone bison occurred as 2 subpopulations that were geographically separated much of the year. Subpopulations exhibited low levels of interchange (Olexa and Gogan 2007) and were genetically distinct (Halbert and Derr 2007, Halbert et al. 2012). The subpopulations exhibited differences in tooth wear (Christianson et al. 2005), reproductive rates (Kirkpatrick et al. 1996), and timing of parturition (Gogan et al. 2005). Our study focused on the central Yellowstone subpopulation that concentrated in the Hayden and Pelican Valleys during summer and wintered westward to the Firehole and Madison River drainages (Olexa and Gogan 2007) and northward to Yellowstone's northern range (Halbert and Derr 2007, Halbert et al. 2012; Fig. 1).

Elevations ranged from about 2,450 m in the Pelican Valley to 2,200 m in the Madison River drainage and 1,610 m on the lower northern range. Winters in this area are generally long and harsh with temperatures dropping to $\leq -40^\circ$ C (Meagher 1973) and snow accumulating from October through late March or early April (Despain 1991). Winter severity in the region is often indexed by snow water equivalents (SWE), a measure of the amount of water present in a column of snow and snow depth (Farnes et al. 1999). Our study included an especially severe winter (1996–1997) and 2 relatively mild winters (2001–2002 and 2002–2003). Cumulative SWE measured from 1 October to 31 April at the Canyon Climate Impact Meteorological station ranged from 7,279 cm during the winter of 1996–1997 to 2,527 and 3,817 during the winters of 2001–2002 and 2002–2003, respectively (Fuller et al. 2007). Yellowstone bison experience nutritional stress during winter (DelGiudice et al. 1994, DelGiudice et al. 2001) associated with greater over-winter mortality in severe winters (Green et al. 1997).

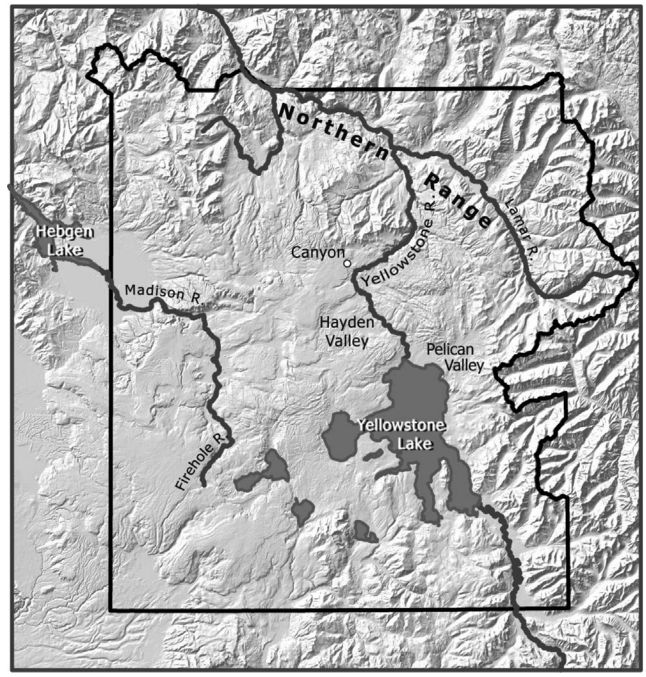

Figure 1. Map of Yellowstone National Park and vicinity Wyoming, Montana, and Idaho (R = river).

METHODS

We opportunistically necropsied female bison culled nonselectively at the boundaries of Yellowstone National Park under the interagency bison management plan (U.S. Department of Interior and U.S. Department of Agriculture, 2000) during January to April 1997, April 2002, and March 2003. Removals were accomplished via either test-and-slaughter or nonselective protocols (U.S. Department of Interior and U.S. Department of Agriculture, 2000). Nonselective removals were based solely on bison distribution relative to park boundaries rather than population or individual characteristics; bison were shot by agency personnel in areas beyond the park boundaries in 1997 or hazed to traps without regard to sex or age in all years prior to shipment to abattoirs. A female and newborn calf were released from a trap rather than culled in 2002. We recorded dressed carcass weight (weight hereafter) at time of death for bison culled at abattoirs. We removed the ovaries and uteri in toto and maintained them at temperatures $\leq 4^\circ$ C. Within 24–48 hours of death, we examined ovaries for signs of recent ovulation (corpora lutea of pregnancy) and uteri for the presence of a conceptus, and we determined uteri turgidity when a conceptus was not present. We classified as pregnant all bison with fetuses and those with signs of recent pregnancy including ovulation or distended uteri. We estimated maternal ages based on the pattern of eruption of incisors and incisiform canines for animals ≤ 4 years old (Fuller 1959, Winchell 1963) or dental annuli of first incisors for animals >4 years old (Moffitt 1998). We restricted our analyses to bison identified genetically as members of the central subpopulation (Halbert et al. 2012).

We screened blood samples for *B. abortus* antibodies with 7 standard *Brucella* tests: standard card, buffered acidified plate antigen (BAPA), standard plate test (SPT), rivanol (Riv), complement fixation (CF), standard tube test (STT), and fluorescence polarization assay (FPA). The latter is considered the gold standard (Schumaker et al. 2010), showing a positive relationship with active infection (Treanor et al. 2011). We classified test results as positive, suspect, or negative following the criteria of the brucellosis program Uniform Methods and Rules (U.S. Department of Agriculture 1998). We treated all bison classified as suspect as positive in our analyses.

We used logistic regression to determine the associations between age-specific pregnancy rates for non-selectively culled females ($n = 174$), and serological status for brucellosis, weight, and age. Age and weight were highly correlated (Pearson correlation coefficient = 0.78) for bison with recorded weights ($n = 124$). Therefore, we estimated weights for 50 additional bison based on their age, as the mean of the known weights of bison within each age class (Fig. 2). Because of the confounding of these 2 variables (age and weight), we did not include them in the same models for pregnancy rates. We also tested for associations among serological status, age, and weight. Lastly, because of the increased pregnancy rates in bison >1 year old we looked for associations between pregnancy rates and serological status, age, and weight separately for bison aged $\geq$2 years. We conducted all analyses using the glm function (family = binomial) in R (R Development Core Team 2012) and compared models using Akaike's Information Criterion (AIC). We estimated exact binomial confidence limits for observed positive seroprevalence and pregnancy rates using the function binom.confint in the R package binom (Sundar 2009).

RESULTS

The age structure of our samples ranged from <1 to 16 years old with most animals aged between 1 and 11 years (Fig. 2). We treated age as a continuous variable in all analyses and we assigned the age of 8 to all animals $\geq$8 years because of the relatively small sample size for any given age >7 years.

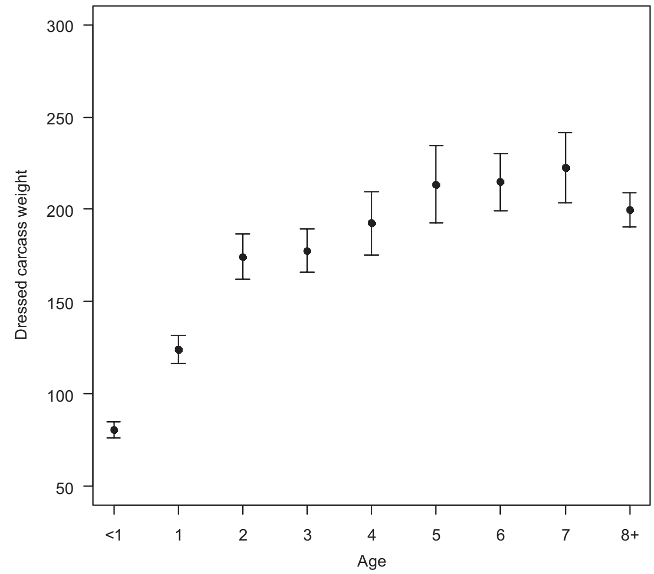

Figure 3. Dressed carcass weights (kg) by age for Central Yellowstone female bison sampled ($n = 124$) during the winters of 1996–1997, 2001–2002, and 2002–2003. Error bars represent 95% confidence limits.

Weights increased continuously with age, with the exception of a slight decline in the oldest age class (Fig. 3).

No bison <1 year old were pregnant (Fig. 4), and 1 of 21 (5%) 1-year-olds was pregnant. The overall pregnancy rate among $\geq$2-year-olds was 65%. Mean pregnancy rates increased markedly in alternate ages (2, 4, and 6 years) from 59% (95% CI = 39–76%) in 2-year-olds to 90% (95% CI = 59–99%) in 6-year-olds. Mean pregnancy rates were lesser in each subsequent age (3, 5, and 7 years) from 45% (95% CI = 28–68%) in 3-year-olds to 73% (95% CI = 43–95%) in 7-year-olds, although confidence intervals for all

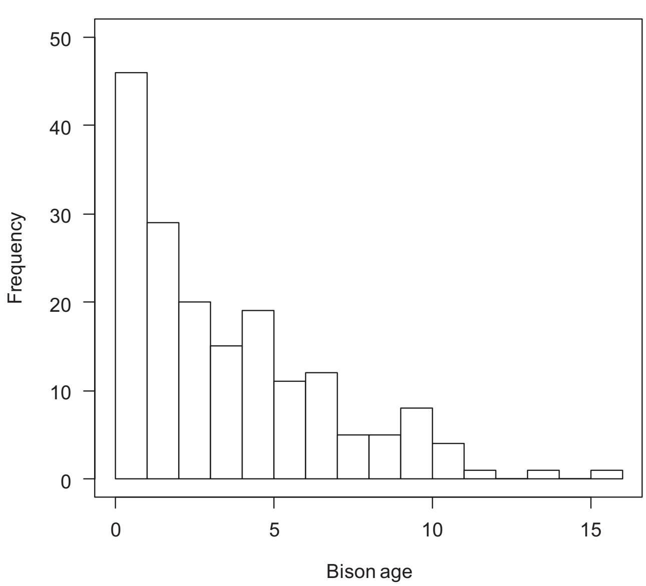

Figure 2. Age structure of Central Yellowstone female bison ($n = 174$) sampled during the winters of 1996–1997, 2001–2002, and 2002–2003.

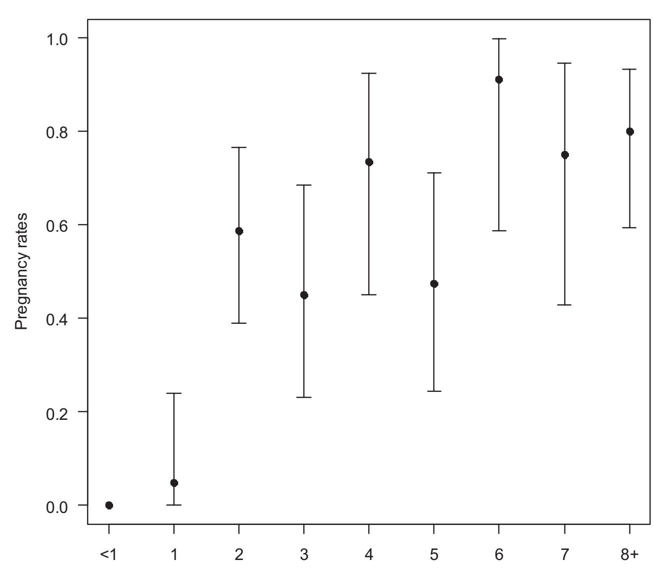

Figure 4. Pregnancy rates as a function of age for Central Yellowstone bison ($n = 174$) sampled during the winters of 1996–1997, 2001–2002, and 2002–2003. Error bars represent 95% confidence limits.

Table 1. Model selection results for models of pregnancy rates for Central Yellowstone bison (n = 174) sampled during the winters of 1996–1997, 2001–2002, and 2002–2003. AIC = Akaike Information Criterion, K = the number of parameters in the model, w_i = Akaike weight.

Model	AIC	K	ΔAIC	w_i
Weight	189.00	2	0.00	0.735
Weight + serology	191.11	3	2.11	0.256
Age	198.90	2	9.90	0.005
Age + serology	199.30	3	10.30	0.004
Year	239.00	2	50.00	0.000
Serology	244.30	2	55.30	0.000
Intercept only	247.23	1	58.23	0.000

Table 2. Parameter estimates from models of pregnancy rates of Central Yellowstone bison (n = 174) sampled during the winters of 1996–1997, 2001–2002, and 2002–2003. LCI = lower 95% confidence interval, UCI = upper 95% confidence interval.

Model	Statistic	Mean	LCI	UCI
Weight	intercept	−5.51	−7.55	−3.79
	weight	0.03	0.02	0.04
Weight + serology	intercept	−5.51	−7.56	−3.80
	weight	0.03	0.02	0.04
	serology	−0.09	−0.84	0.64
Age	intercept	−1.94	−2.66	−1.29
	age	0.46	0.32	0.62
Age + serology	intercept	−2.15	−2.97	−1.41
	age	0.45	0.31	0.60
	serology	0.44	−0.26	1.15
Serology	intercept	−0.43	−0.88	0.01
	serology	0.68	0.08	1.28
Intercept model	intercept	−0.06	−0.35	0.24

years overlapped (Fig. 4). We found no evidence of senescence in pregnancy rates.

We estimated pregnancy rates of 0.50 (95% CI = 0.31–0.69) and 0.57 (95% CI = 0.34–0.78) in 2- and 3-year-old brucellosis-positive (n = 28) and brucellosis-negative (n = 21) bison, respectively. Among ≥4-year-old bison, we estimated pregnancy rates of 0.74 (95% CI = 0.60–0.85) in those brucellosis-positive (n = 53), and 0.69 (95% CI = 0.49–0.85) for those brucellosis-negative (n = 29). Model selection using AIC indicated that the best model of pregnancy rates across all ages used weight as the only predictor (Table 1). Odds of pregnancy increased by 1.03 (95% CI = 1.02–1.04) for every 1-kg increase in weight. Observed and predicted values indicated a positive association between weight and pregnancy rates (Table 2, Fig. 5). This relationship held true for an aggregate sample of 124 bison with empirical weights and an additional 50 bison with imputed weights (Fig. 5).

Pregnancy rates also increased as a function of age (Table 2, note positive parameter estimates). The second best model (ΔAIC = 2.11, Table 1) included effects of serology and weight. However, given that the top 2 models only differed by 1 parameter, we found little evidence to support an effect of serology. Additionally, confidence interval for the odds ratio from this model for serology included 1 (0.91 [95% CI = 0.43–1.89]), indicating no detectable statistically significant effect of this variable after accounting for the effect of weight. Parameter estimates for the effects of age and weight were relatively similar among models (Table 2) in contrast to the parameter estimates for serology, which ranged from 0.68 for the single variable model to −0.09 for the model containing both weight and serology. As expected, seroprevalence increased as a function of age and weight, although the oldest bison displayed a decrease in seroprevalence (Fig. 6).

Results of our analysis restricted to bison ≥2 years old (n = 131) were similar to results for all bison. For these models, we treated age in 2 different ways: 1) in the same

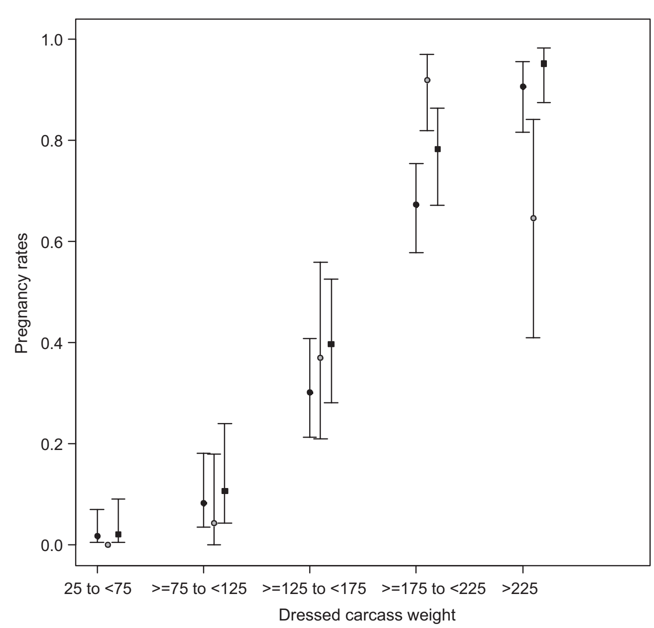

Figure 5. Observed (grey dots) and predicted pregnancy rates for Central Yellowstone bison sampled in the winters of 1996–1997, 2001–2002, and 2002–2003 as a function of dressed carcass weight (kg). Error bars represent 95% confidence limits. We estimated predicted pregnancy rates at the midpoint weight for all categories (i.e., 50, 100, 150, 200, and 250 kg) from a model developed using 174 bison including 50 with imputed weights (black dots) and for a model developed using a subset of 124 bison with empirical weights (black squares).

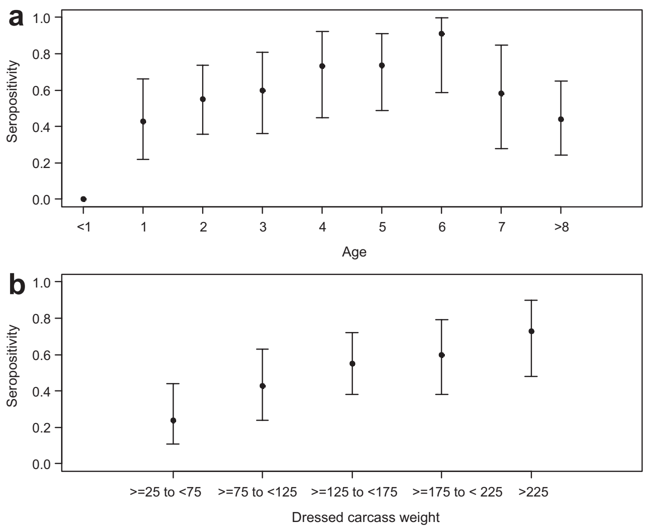

Figure 6. Observed positive seroprevalence rates for female central Yellowstone bison ($n = 174$) sampled in the winters of 1996–1997, 2001–2002, and 2002–2003 as a function of a) age and b) dressed carcass weight (kg). Error bars represent exact 95% binomial confidence limits.

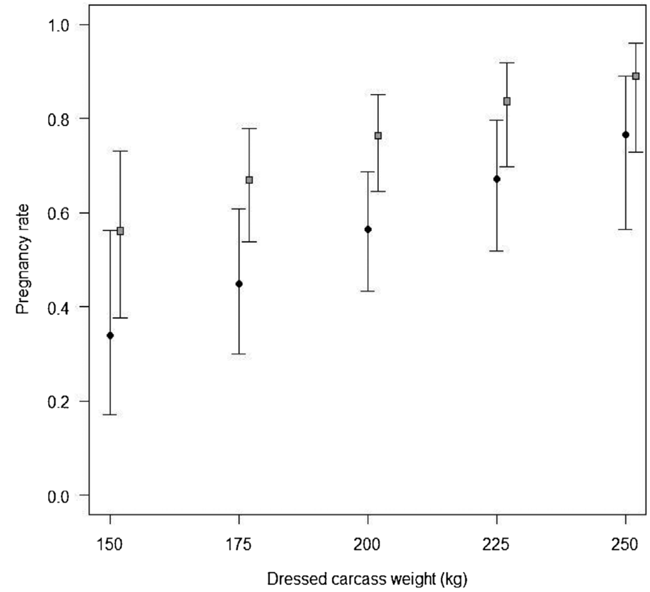

Figure 7. Pregnancy rates for central Yellowstone bison by dressed carcass weight for even-aged (2, 4, 6, 8, 10, 12, 14, and 16 years old; grey boxes) and odd-aged bison (3, 5, 7 9, 11, 13, and 15 years old; black circles) sampled in the winters of 1996–1997, 2001–2002, and 2002–2003. Error bars represent 95% confidence limits.

manner as the previous models, and 2) as a categorical variable. We hypothesized that if bison bred alternate years from the age of 2 years, then pregnancy rates in 2-, 4-, 6-, 8-, 10-, 12-, 14-, and 16-year-olds would differ from pregnancy rates in bison 3, 5, 7, 9, 11, 13, and 15 years old. Therefore, we pooled even-aged bison into 1 category and odd-aged bison into another for the categorical age models. The best model of pregnancy rates included age as a categorical variable and weight (Table 3, Fig. 7), with the odds of pregnancy increasing by 2.48 (95% CI = 1.16–5.47) for even- versus odd-aged bison. Two other models were within 2 AIC values of the best model, a model including categorical age, weight, and serology and a model including age only. For the second best model, the parameter estimates for age and weight were very similar to the estimates from the first model (Table 4). Confidence limits of the parameter estimate for serological status from all models included zero, indicating no substantive effect of serology (Table 4). The third best model included an effect of age as a continuous variable and indicated that for every year a bison aged, the odds of pregnancy increased by 1.23 (95% CI = 1.04–1.48).

DISCUSSION

The age of primiparity among ungulate populations is highly variable and strongly influenced by population density, forage availability, and weather conditions (Eberhardt 1977, Eberhardt 2002; Gaillard et al. 1992, Gaillard et al. 2000). Our detection of a single pregnant 1-year-old bison is consistent with reported low levels of breeding by yearling plains bison (Meagher 1973, Green 1990, Berger and Cunningham 1994) and wood bison (Fuller 1962); however, breeding by yearling female plains bison has not been detected in other populations (Haugen 1974, Pyne et al. 2010). Female American bison of both subspecies more commonly breed for the first time between 2 and 4 years (Fuller 1962, Haugen 1974, Wolfe et al. 1999). We detected a pregnancy rate among 2-year-old central Yellowstone bison (59%) much greater than that detected in 2-year-old wood bison (38%; Fuller 1962). No breeding was observed among 2-year-old females of 1 plains bison population (Van Vuren and Bray 1986).

Table 3. Model selection results for models of serology rates for female Central Yellowstone bison $\geq$2 years old ($n = 174$) sampled during the winters of 1996–1997, 2001–2002, and 2002–2003. AIC = Akaike Information Criterion, K = the number of parameters in the model, w_i = Akaike weight. Alternate year is an indicator variable where 1 = 2-, 4-, 6-, 8-, 10-, 12-, 14-, and 16-year-old and 0 = 3-, 5-, 7-, 9-, 11-, 13-, and 15-year-old bison.

Model	AIC	K	ΔAIC	w_i
Alternate year + weight	166.30	3.00	0.00	0.39
Alternate year + weight + serology	167.85	4.00	1.55	0.18
Age	167.90	2.00	1.60	0.17
Weight	169.80	2.00	3.50	0.07
Age + serology	169.90	3.00	3.60	0.06
Alternate year	170.53	2.00	4.23	0.05
Weight + serology	171.70	3.00	5.40	0.03
Intercept only	171.82	1.00	5.52	0.02
Alternate year + serology	172.53	3.00	6.23	0.02
Serology	173.80	2.00	7.50	0.01

Table 4. Parameter estimates from models of pregnancy rates of Central Yellowstone bison aged ≥2 ($n = 131$) sampled during the winters of 1996–1997, 2001–2002, and 2002–2003. LCI = lower 95% confidence interval, UCI = upper 95% confidence interval. Alternate year is a categorical variable indicating even- or odd-aged bison.

Model	Statistic	Mean	LCI	UCI
Alternate year + weight	intercept	−3.44	−6.6	−0.47
	even vs. odd	0.91	0.15	1.70
	weight	0.02	0.00	0.03
Alternate year + weight + serology	intercept	−3.56	−6.78	−0.57
	even vs. odd	0.95	0.17	1.76
	weight	0.02	0.00	0.04
	serology	−0.27	−1.08	0.52
Age	intercept	−0.45	−1.39	0.48
	age	0.21	0.04	0.39
Weight	intercept	−2.14	−5.00	0.57
	weight	0.01	0.00	0.03
Age + serology	intercept	−0.51	−0.04	0.24
	serology	0.10	−0.67	0.85
	age	0.21	0.04	0.39
Alternate year	intercept	−3.42	−0.24	0.79
	even vs. odd	0.91	−0.05	1.40
Weight + serology	intercept	−2.18	−5.03	0.54
	serology	−0.13	−0.92	0.63
	weight	0.01	0.00	0.03
Intercept model	intercept	0.61	0.25	0.98
Serology	intercept	0.57	0.00	1.17
	serology	0.06	−0.68	0.80
Alternate year + serology	intercept	0.26	−0.41	0.94
	even vs. odd	0.66	−0.06	1.40
	serology	0.02	−0.74	0.76

Our estimated overall pregnancy rate of 65% for central Yellowstone bison ≥2 years old (95% CI = 0.56–0.72) was greater than the range of annual pregnancy rates of 37–45% for ≥2-year-olds reported previously for this subpopulation (Kirkpatrick et al. 1996) and approximates the lowest annual pregnancy rates of 67–87% among ≥2–year-old plains bison elsewhere (McHugh 1958, Wolfe and Kimball 1989), and 72–85% for ≥2-year-old wood bison (Fuller 1962, Joly and Messier 2005). This pattern provides further evidence of temporal and spatial variation in bison pregnancy rates that likely reflect differences in population densities and environmental conditions (Coulson et al. 2000, Bonenfant et al. 2009, Gaillard et al. 2009).

Our detection of peaks and troughs in pregnancy rates among bison ≥2 years old indicates that a high proportion do not breed successfully in sequential years (Fig. 4), and is consistent with reports of 70–85% of pregnancies occurring in ≥3-year-old non-lactating central Yellowstone bison (Kirkpatrick et al. 1996). Alternate year reproduction was detected via observations of sequential calving success in brucellosis-free plains bison with calving peaks at 3, 5, and 7 years and troughs at 4, 6, and 8 years old (Halloran 1968). However, no evidence of alternate year calving was evident in the same population at lesser densities (Shaw and Carter 1989) and Pyne et al. (2010) found approximately 47% of >2.5-year-old female plains bison of another population bred each year in contrast to 26% prior to population reductions (Berger and Cunningham 1994). Similarly, Fuller (1962) suggested that an average pregnancy rate of 67% in lactating wood bison aged between 3 and 7–8 years was attributable to females breeding for 2 consecutive years (with a later born calf the second year) but not breeding the third year. Such annual variation in pregnancy rates is possibly attributable to the need for females to achieve a critical body weight by the breeding season. Lactating females loose more weight post-calving than do barren females (Green and Rothstein 1991, Wolff 1998) and may not be able to achieve a threshold body mass prior to the next breeding season. Reproductive pauses provide an explanation of the current low reproductive rate in central Yellowstone bison relative to other bison populations.

Body condition during the reproductive season is a key factor in determining the probability of pregnancy in a number of ungulate species (Parker et al. 2009, Tollefson et al. 2010). Age and weight were highly correlated in our study, and for bison ≥2 years old, age was a better predictor of pregnancy rates than was weight. Our parameter estimates for the effects of age on pregnancy rates for bison ≥2 years old (0.21) are similar to 3 of the 4 estimates reported previously (Geremia et al. 2009: Table 14.6). However, we found weight to be an influential factor in determining pregnancy rates of central Yellowstone bison <2 years old. Elsewhere, plains bison calving successfully as 2-year-olds weighed more as yearlings than did females that calved for the first time at age 3 or 4 years (Green and Rothstein 1991).

We found that older, heavier central Yellowstone bison were both more likely to be pregnant and more likely to be seropositive for brucellosis, but we found no relationship between pregnancy rates and serological status for brucellosis across a range of ages. Our findings are consistent with a review that determined that pregnancy rates and seroprevalence for brucellosis vary by age (Cheville et al. 1998) but contrast with previous studies that reported lesser pregnancy rates in Yellowstone bison seropositive for brucellosis (Fuller et al. 2007, Geremia et al. 2009). Also, our findings are consistent with a report of no effect of brucellosis serological status on pregnancy rates in wood bison (Joly and Messier 2005). *Brucella abortus* characteristically establishes in the bovine female's lymphatic system and uterus and proliferates during the latter stages of pregnancy to cause abortion or premature birth of weak calves (Rhyan et al. 2001, Carvalho Neta et al. 2010). Hence an explanation of how brucellosis infection affects pregnancy rates is unclear.

Considerable advances have been made in understanding the relationship between positive serological test results for brucellosis and levels of active infection (Roffe et al. 1999, Treanor et al. 2011). Brucellosis prevalence rates in Yellowstone bison based on tissue cultures peak in 2.75-year-olds (Treanor et al. 2011), whereas seroprevalence rates peak at >80% in 6-years-old female central Yellowstone bison (Fig. 6). These patterns make assessing the influence of serological status on pregnancy status difficult. Methodological differences could explain the difference between our study and previous studies of Yellowstone bison (Fuller et al. 2007, Geremia et al. 2009); we sampled nonselectively culled bison, whereas all bison in the Fuller et al. (2007) study and about 33% of the bison in the Geremia et al. (2009) study of reproduction in radio-marked Yellowstone bison were incorporated into their studies conditional on positive pregnancy status and good body condition (Rhyan et al. 2009). Thus, these studies may have incorporated an unintended bias as calving success has been shown to be significantly correlated with prior reproductive success in brucellosis-free plains bison (Pyne et al. 2010) and wood bison (Wilson et al. 2002). Additionally, since some 20% of Yellowstone bison convert from seronegative to seropositive for brucellosis between 1 and 3 years old (Treanor et al. 2011), associated with their first pregnancy (Cheville et al. 1998), any failure to conceive the following year may erroneously be attributed to positive serological status for brucellosis when other factors affecting pregnancy, such as body condition, are ignored. Additionally, classification of brucellosis status on the basis of seroprevalence may contribute to errors in estimates of active infection. Roffe et al. (1999) found a poor relationship between bison serological status for brucellosis and tissue culture results. However, if the misclassifications are random with respect to the covariates of interest (i.e., age, weight, pregnancy rates), then the estimated relationships between the variables (positive or negative) will be unaffected.

MANAGEMENT IMPLICATIONS

Estimation of demographic rates is necessary to predict the effects of alternative management actions, including population reductions to limit Yellowstone bison winter distribution and brucellosis seroprevalence rates (Ebinger et al. 2011, Udevitz and Gogan 2012). We found that weight was associated with pregnancy status across all age classes, regardless of serological status for brucellosis, supporting the influence of female nutritional condition on pregnancy rates. Thus, efforts to limit bison winter distribution via culling along the park boundaries may reduce population size and thereby enhance the nutritional condition of the remaining bison. A consequence may be an increase in pregnancy rates via a reduction in the frequency of reproductive pauses we documented in central Yellowstone bison and increased population growth rates. Our results suggest caution in identifying brucellosis infection as influencing pregnancy rates in central Yellowstone bison because we found no evidence to support this conclusion.

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