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Management and Conservation Article

Survival and Breeding Transitions for a Reintroduced Bison Population: a Multistate Approach

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ABSTRACT The iconic plains bison (*Bison bison*) have been reintroduced to many places in their former range, but there are few scientific data evaluating the success of these reintroductions or guiding the continued management of these populations. Relying on mark–recapture data, we used a multistate model to estimate bison survival and breeding transition probabilities while controlling for the recapture process. We tested hypotheses in these demographic parameters associated with age, sex, reproductive state, and environmental variables. We also estimated biological process variation in survival and breeding transition probabilities by factoring out sampling variation. The recapture rate of females and calves was high (0.78 ± 0.15 [SE]) and much lower for males (0.41 ± 0.23), especially older males (0.17 ± 0.15). We found that overall bison survival was high ($>$0.8) and that males (0.80 ± 0.13) survived at lower rates than females (0.94 ± 0.04), but as females aged survival declined (0.89 ± 0.05 for F $\geq$15 yr old). Lactating and non-lactating females survived at similar rates. We found that females can conceive early (approx. 1.5 yr of age) and had a high probability (approx. 0.8) of breeding in consecutive years, until age 13.5 years, when females that were non-lactating tended to stay in that state. Our results suggest senescence in reproduction and survival for females. We found little support for the effect of climatic covariates on demographic rates, perhaps because the park's current population management goals were predicated from drought-year conditions. This reintroduction has been successful, but continued culling actions will need to be employed and an adaptive management approach is warranted. Our demographic approach can be applied to other heavily managed large-ungulate systems with few or no natural predators.

KEY WORDS Badlands National Park, *Bison bison*, breeding state transition, culling, demography, mark–recapture, reintroduction.

Human encroachment into ecosystems often results in local extinctions of large ungulate populations and elimination of their natural predators. This lack of natural predation can cause reintroduced ungulates to experience overpopulation and severe depletion of resources (Baker et al. 1997, Howell et al. 2002, Kaye et al. 2005, Hansen et al. 2007). These reintroduced populations require intensive management, often culling, to maintain ecosystem diversity and sufficient forage. Thus, assessing the status of reintroduced species, as well as the efficacy of management actions, is vital (Morell 2008). Population models can characterize dynamics of reintroduced populations, but these models require parameterization with estimates of key demographic rates (e.g., survival and reproduction probabilities). Modern analytical methods can provide these estimates from mark–recapture data.

One iconic species that has been the subject of numerous reintroductions, and is still a focus of concern, is the plains bison (*Bison bison*; Sanderson et al. 2008). Considered a keystone species by many, bison were abundant in the central grassland region of North America from the end of the Wisconsin glaciations until the twentieth century (Mack and Thompson 1982, Knapp et al. 1999). Records show that 30–60 million bison existed at the time of European settlement (McHugh 1972, Flores 1991). By 1903 the species was hunted into functional extirpation, with only a reported 1,644 surviving in zoos, private herds, and Yellowstone National Park (Meagher 1986). Since this near-extinction, conservation efforts, mainly by the American Bison Society, have resulted in reintroductions and recoveries in United States national and state parks and bison management remains a major concern for North American land and wildlife management agencies (Berger and Cunningham 1994).

The United States National Park Service reintroduced bison to Badlands National Park (BNP), South Dakota, in 1963 to help "preserve the flora, fauna, and natural processes of the mixed grass prairie ecosystem" (E. Childers, National Park Service, unpublished report). Wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), the most significant natural predators of bison, do not currently inhabit BNP, and the park is not large enough to support an unmanaged herd of bison. The bison herd persists as a healthy, viable population only through management practices designed to maintain

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adequate forage and limit negative bison–park-visitor interactions. Using an annual cull in October, the park sustains herd numbers near 700 individuals, a strategy based on estimated vegetation productivity values for drought years (E. Childers, unpublished report). A formal population modeling framework and the associated demographic parameters would inform an adaptive management plan focused on optimal culling strategies and guide intended reintroductions to other parts of the park (Williams et al. 2002).

Multiple studies have estimated demographic parameters for survival, birth rates, or both for bison populations in Yellowstone National Park (Kirkpatrick et al. 1996, Aune et al. 1998, Fuller et al. 2007), Wind Cave National Park (Millspaugh et al. 2008), the Henry Mountains (Van Vuren and Bray 1986), Witchita Mountains National Wildlife Refuge (Shaw and Carter 1989), and in BNP (Berger and Cunningham 1994). In general bison have high survival and calving rates (Berger and Cunningham 1994). Female bison begin reproducing between the ages of 2 years and 4 years and are thought to be at peak fertility between the ages of 4 years and 14 years (Meagher 1986, Shaw and Carter 1989, Berger and Cunningham 1994). In nearly all cases, each reproducing female has only one calf, but skipped breeding is common (Meagher 1986). Most births occur from April to mid-May (Meagher 1986, Berger and Cunningham 1994). Calves generally nurse for $\geq$7–8 months (Meagher 1986). Male bison may copulate with females as early as 3 years but tend not to breed until age 6 years when they have attained their full size (Meagher 1986). Bison in the wild may live to 20 years, although there are records of bison that have lived $\geq$30 years (Meagher 1986).

In the above studies, parameter estimation methods varied, with some studies relying on raw counts, uncorrected for recapture rates, to estimate survival (e.g., Millspaugh et al. 2008). Others used methods that resulted in complete knowledge (i.e., radiotelemetry; Fuller et al. 2007), but may have had limited sample sizes due to cost. Multistate mark–recapture models have the ability to estimate biologically meaningful transition rates, such as the transition from breeding to nonbreeding states, while correcting for recapture rates (Lebreton et al. 2009). A few studies employed such modern mark–recapture models to estimate demographic rates for other large mammals (e.g., Weladji et al. 2008), but to our knowledge, no studies have employed such models to estimate bison demographic rates from mark–recapture–resight data.

Previous research has shown male competition for mates reduces their survival, that they roam in smaller, more difficult-to-recapture groups, and that female fertility varies by age (Berger and Cunningham 1994, Aune et al. 1998, Fuller et al. 2007). Not taking such age- and sex-specific recapture probabilities into account when estimating demographic parameters will lead to biased results (Williams et al. 2002). Estimating the transition between nonbreeding and breeding status not only quantifies an aspect of the fecundity of the population, but breeding status may also be important if survival, or recapture, varies with breeding status and age. Because forage quality, mainly determined by growing season precipitation and temperature, may affect survival of bison (especially young animals), understanding effects of annual differences in climate is also of interest. We used our knowledge of these and other aspects of bison biology to construct a set of testable hypotheses we could model. True temporal (or process) variation in the underlying parameters of interest is often required for population modeling activities, but all too often sampling variation (associated with the estimation process and that the probability of recapture is <1) is included with process variation, a practice that can lead to erroneous results (Gould and Nichols 1998).

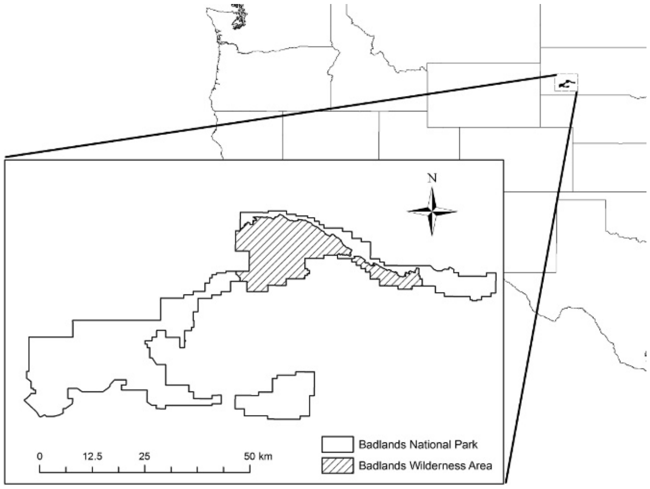

Figure 1. Location of Badlands National Park in southwest South Dakota, USA. Bison were collected in roundups from the Badlands Wilderness Area from 2002 to 2007.

We developed a demographic parameter estimation framework and tested hypotheses associated with age, sex, and environmental variation in demographic parameters. Thus, our objectives, using a 5-year mark–recapture data set from the BNP bison herd, were 1) to perform a demographic analysis of bison mark–recapture data controlling for the detection process, 2) to test hypotheses that survival varies by sex, age, breeding state, time, and climatic covariates, 3) to test the hypothesis that breeding transition probabilities vary by age, current breeding state, time, and climatic variables, 4) to estimate process variation in these parameters, and 5) to provide recommendations to improve bison data collection at BNP.

STUDY AREA

Fences and steep cliffs restricted bison at BNP to the 26,000-ha Badlands Wilderness Area, the north unit of the park (Fig. 1; 43.749°N latitude, 101.941°W longitude [Berger and Cunningham 1994; E. Childers, unpublished report]). The Wilderness Area consisted mainly of uplands dominated by typical northern mixed grass prairie vegetation, riparian corridors dominated by cottonwoods (*Populus deltoides*), and prevalent badland formations (Berger and Cunningham 1994). In addition to 2 permanent springs and several ephemeral streams, bison had access to 10 manmade water impoundments (Berger and Cunningham 1994). Mean annual precipitation was 300 mm, falling mainly in the form of summer thunderstorms (Berger and Cunningham 1994). Mean annual temperature at the nearby Rapid City airport, 50 km from the park, during the study period was 8.27° C. Temperatures during the study ranged from 43° C to −29.4° C.

METHODS

Data Collection

We used data collected during yearly roundups between 2002 and 2007. In mid-October, National Park Service employees and volunteers herded a large proportion of the park's bison into holding pens. Employees and volunteers used all-terrain vehicles, pick-up trucks, and horses to collect bison over a 3–7-day period. Most animals were rounded up during the first days of concentrated effort and additional stragglers were brought in as they were found. Park personnel located animals from the Sage Creek road using pick-up trucks and by horseback in the Sage Creek Wilderness Unit. Bison were held in holding pens the entire weekend (about 3 days) before processing began. Unmarked individuals received unique identification tags and were aged and sexed. Park personnel placed preloaded American Veterinary Identification Devices microchips under the skin in the back of the ear, enabling personnel to scan the animal as it came through the chute. Park personnel also placed a metal ear tag as a backup and a temporary hip tag on each animal for sorting and shipping purposes. A United States Department of Agriculture Animal and Plant Health Inspection Service (APHIS) veterinarian and a local large animal vet aged all animals by tooth wear, number, and replacement using eruption-wear methodology. The APHIS vet had worked the roundup at BNP since 2002 and the local large animal vet had worked the roundup at BNP for >20 years, thereby reducing the chance of inter-observer ageing bias and ensuring consistent ageing of animals.

In addition, the large animal vets determined breeding status (lactating or non-lactating) of females by palpating the udder on all of the females ≥2.5 years that were processed. Lactating females were defined as females with a full udder at the time of roundup or females that were nursing a calf. Once the animals were processed, some individuals were removed from the population and sold to local Native American communities (hereafter, culling). The general culling strategy included a random selection of 85–95% of the caught 1.5-year-olds. Although such a high culling rate of young bison may appear detrimental to the population size and growth rate, not all bison were captured during roundup activities each year. Population growth was still positive, even with seemingly high culling. We censored culled individuals from the data set at the time of culling after we recorded their breeding state, because we were focused on estimating natural survival. Old male bison (>14.5 yr) were dangerous in pens, less likely to be rounded up, and few in numbers. Thus, BNP did not target them for management efforts.

Modeling Survival, Recapture, and Transition Probabilities

We estimated annual survival (φ) and recapture (p) probabilities for all ages and both sexes and annual breeding-state transition probabilities for females (i.e., from lactating to non-lactating and vice versa; ψ). We employed a multistate model to analyze our mark–recapture data, as available in Program MARK (White and Burnham 1999, Lebreton et al. 2009). We constructed a model set to describe a priori hypotheses that explain variation in parameter estimates (see Model Set below) using the following assumptions: 1) every animal alive in the population at a given sampling occasion, in a given stratum, had an equal chance of being captured; 2) every marked animal alive in the population at a given sampling occasion, in a given stratum, had an equal chance of survival until the next sampling occasion; 3) there were equal transition probabilities between strata for all animals in a stratum at a particular occasion; 4) transition and recapture probabilities did not depend on past history of the animal; 5) identifying tags were not lost; 6) sampling periods were short and recaptured animals were released immediately; 7) because BNP was fenced, no emigration occurred (i.e., this bison population was closed); 8) all data were recorded without error.

We performed a goodness-of-fit (GOF) test on a general model. Because data included loss-on-capture events (i.e., culling at the roundup), and no software can account for this issue in multistate models with GOF tests, we disregarded the loss-on-capture information and performed a median $\hat{c}$ test as available in Program MARK (White and Burnham 1999). We used Akaike's Information Criterion (with small sample size correction; AIC$_c$) for model selection and averaged parameter estimates over our entire model set to account for model selection uncertainty (Burnham and Anderson 2002). We also calculated cumulative AIC$_c$ weights for each variable to aid in interpreting its importance (Burnham and Anderson 2002). Temporal variances of the point estimates included both sampling variance and biological process variance. To estimate true temporal process variation (τ^2), we used methods as formulated by Link and Nichols (1994) and Gould and Nichols (1998):

$$\tau^2 = S^2 - \frac{1}{n}\sum_{1}^{n} \hat{E}[\mathrm{Var}(\hat{\varphi}|F)] + \frac{2}{n(n-1)}\sum_{i<j} \hat{E}\left[\mathrm{Cov}\left(\hat{\varphi}_i,\hat{\varphi}_j\right)|F\right]$$

where the first term (S^2) is estimated total temporal variance of the point estimates, the second term is the average of time-specific sampling variance estimates, and the third term is the average of time-specific sampling covariance estimates (Gould and Nichols 1998, eq 2). Using this approach, it is possible to obtain negative process variance estimates, which have no biological meaning. We adjusted such results to zero.

Model Set

We constructed 4 models of recapture probability (p). Because recapture is conditional on animals being captured initially, the earliest age for which we could estimate such probabilities was 1.5 years. We modeled recapture as either constant or a function of sex. We thought that males might be harder to catch than females because males tend to form smaller, inconspicuous groups (Berger and Cunningham 1994). We did not use an age structure to estimate female recapture probabilities because females tend to form large, multiage groups (Berger and Cunningham 1994), but we did incorporate 2 age structures into parameter estimates for males. We used ages 1.5–9.5 years and >10.5 years, based on the assumption that older males were less likely to be caught. We also used 3 age classes, 1.5–2.5 years, 3.5–9.5 years, and >10.5 years, to test whether younger males, those that might be closely associated with mothers, would be more easily caught than older males. We also incorporated sampling year into our model of recapture probabilities.

We modeled survival (φ) according to sex, breeding state, and 1 of 3 age structures. We thought that females might survive better than males because males engage in rut behavior (Berger and Cunningham 1994). Age structures we considered were 1) 0.5 years and >1.5 years to indicate that calves would survive differently than older individuals, 2) 0.5 years, 1.5 years, 2.5–9.5 years, and >10.5 years to indicate that calves and 1.5-year-olds might survive differently than mature animals, but that older animals might not survive as well, and 3) a different age structure for males and females (M: 0.5 yr, 1.5 yr, 2.5–9.5 yr, >10.5 yr; F: 0.5 yr, 1.5 yr, 2.5–14.5 yr, >15.5 yr). For this third age structure, we felt that because females congregate in larger herds, older females may not have distinct differences in survival from their younger counterparts. Males, however, begin to show differences in wandering and rutting behavior as they age, which may result in distinct survival rates (Berger and Cunningham 1994). In addition, we modeled survival as being variable across sampling years (t) or as a function of a series of climatic covariates (no. of days >32° C, growing season precipitation [May–Sep] of the current yr, and growing season precipitation of the previous yr). Our choice of 32° C was somewhat arbitrary, but we felt that the annual number of days above this temperature adequately captured the thermal intensity of summer growing seasons. We thought the current year's precipitation might directly affect forage quality. We thought that the previous year's precipitation might affect the animal's body condition at the start of the current year. We obtained climatic variables from the Mesowest database (Horel et al. 2002) for Rapid City Regional Airport, the closest weather station to the park (50 km) with data from 2002 to 2007.

For female breeding-state transitions (ψ), we modeled the transition from lactating to non-lactating and from non-lactating to lactating separately (the complement being remaining in a particular state). We considered these transitions as constant or as a function of 2 possible age structures: 1) 1.5 years, 2.5–12.5 years, and >13.5 years, to indicate that very young females, females at their peak, and old females might have different probabilities, and 2) 1.5 years, 2.5–3.5 years, 4.5–12.5 years, and >13.5 years, to include an additional differentiation among very young females, young females, and females at their peak. We expected very young females to have much lower transition probabilities from non-lactating to lactating, the highest probability in the middle age class and old females to have the lowest probability. In the model with 4 age classes, we expected young females (2.5–3.5 yr) to have a lower transition probability than the middle age class (4.5–12.5 yr) and the other trends to be the same. We note that females may begin conceiving at 1.5 years and give birth the following spring; thus, females can only transition from non-lactating to lactating (or to stay in the non-lactating state) during this transition period. Additionally, we modeled these transitions as being variable by year, as a function of growing season precipitation of the current year or previous year or the number of days >32° C. We created a balanced model set by constructing every combination of recapture, survival, and breeding transition model substructure (e.g., Table 1), which allowed us to confidently calculate and interpret cumulative AIC weights for each substructure.

RESULTS

Because individuals were uniquely marked, a record existed for each individual captured at each roundup. We had 3,281 observations of 1,718 bison marked between the years 2002 and 2007 (Table 2). In most years, approximately the same number of newborn males and newborn females were captured at each roundup. As bison aged, fewer males than females were captured. The number of older (>14.5 yr) bison captured was small; an average of 17 each year. An average of 67% of adult (>2 yr) females in a roundup were recorded as lactating, although we note that this is probably an underestimate of fecundity. The roundup occurred approximately 5 months after the average birth date of calves in this population (Berger and Cunningham 1994). Calves suckled for an average of 7–8 months, so underestimation of fecundity due to calves becoming weaned before roundup may be substantial (Meagher 1986).

We interpreted our median $\hat{c} < 1.15$ to indicate that our global model had adequate fit. Thus we chose not to use an inflation variation factor adjustment. Fourteen models had an AIC_c weight of ≥ 0.01 (Table 3). Models with the smallest AIC_c values included one recapture model substructure, 2 survival model substructures, and several transition probability model substructures (Tables 1, 3).

For recapture probability, p, the only model substructure with substantial AIC_c weight had separate parameters for different sexes, divided males into 3 age classes (1.5–2.5 yr, 3.5–9.5 yr, >10.5 yr) and included year. Female recapture probability was high for both lactating and non-lactating individuals (0.78 ± 0.15 [SE]). Males had lower probabilities of recapture than did females, and recapture probability declined with age (0.73 ± 0.17 for young M, 0.41 ± 0.23 for middle-aged M, and 0.17 ± 0.15 for older M). Although there is a large difference between point estimates of male and female recapture rates, 95% confidence intervals for females and young males (<10.5 yr) overlapped.

Table 1. Model structures we used in multistate models to estimate survival, recapture, and female breeding-state transition probabilities for bison in Badlands National Park, South Dakota, USA, from 2002 to 2007. The first column contains a model substructure identifier. For each identifier, the associated sex and state coding, age structure, and temporal or environmental covariates (growing season precipitation [Precip]) are listed. "Time" indicates that we modeled each year separately. Cumulative Akaike's Information Criterion (with small sample size correction) weight (AIC_c wt) across the entire model for each substructure set is in the last column. Only model structures with >0.01 cumulative AIC_c weight are shown.

Parameter	Sex and state	Age class set (yr)	Covariates	Cumulative AIC_c wt
Survival				
$\varphi29$	M	0.5, 1.5, 2.5–9.5, >10.5	Time	0.801
	F	0.5, 1.5, 2.5–14.5, >15.5		
$\varphi39$	M	0.5, 1.5, 2.5–9.5, >10.5	Time	0.194
	Non-lactating F	0.5, 1.5, 2.5–14.5, >15.5		
	Lactating F	0.5, 1.5, 2.5–14.5, >15.5		
Recapture				
$p6$	M	1.5–2.5, 3.5–9.5, >10.5	Time	1.000
	F			
Transition				
$\psi2$		1.5, 2.5–12.5, >13.5		0.272
$\psi3$		1.5, 2.5–3.5, 4.5–12.5, >13.5		0.361
$\psi4$		1.5, 2.5–12.5, >13.5	Days >32° C	0.052
$\psi5$		1.5, 2.5–12.5, >13.5	Precip—current yr	0.036
$\psi6$		1.5, 2.5–12.5, >13.5	Precip—previous yr	0.044
$\psi9$		1.5, 2.5–3.5, 4.5–12.5, >13.5	Days >32° C	0.059
$\psi10$		1.5, 2.5–3.5, 4.5–12.5, >13.5	Precip—current yr	0.051
$\psi11$		1.5, 2.5–3.5, 4.5–12.5, >13.5	Precip—previous yr	0.104
$\psi12$		1.5, 2.5–3.5, 4.5–12.5, >13.5	Precip—previous and current yr	0.014

For the survival parameter, φ, model $\varphi29$ had the highest AIC_c weight (cumulative AIC_c wt = 0.80; Table 1), followed by model $\varphi39$ (cumulative AIC_c wt = 0.19; Table 1). The first model, $\varphi29$, included 4 age classes for males (0.5 yr, 1.5 yr, 2.5–9.5 yr, >10.5 yr) and females (0.5 yr, 1.5 yr, 2.5–14.5 yr, >15.5 yr), as well as annual variation (t), whereas $\varphi39$ included these categories and also distinguished between lactating and non-lactating females. Model-averaged survival was high for all young animals (0.94 ± 0.04 for 0.5-yr-old M, 0.93 ± 0.03 for 1.5-yr-old M, 0.96 ± 0.02 for 0.5-yr-old F, and 0.94 ± 0.04 for 1.5-yr-old F) and for all females but the oldest (0.89 ± 0.05 for F ≥15 yr; Fig. 2). Males >1.5 years had survival rates considerably lower than females (0.80 ± 0.13 for middle-aged M and 0.80 ± 0.12 for older M). There was more temporal process variance among male survival rates than females rates (Fig. 2). Point estimates were similar for all sexes and ages, and confidence intervals among all sexes and ages overlapped considerably, indicating that there was not much evidence for age- or sex-specific differences in survival.

For the 2 transition parameters, $\psi_{\mathrm{N-L}}$ (from non-lactating to lactating) and $\psi_{\mathrm{L-N}}$ (from lactating to non-lactating), the models with the highest cumulative AIC_c weights were $\psi2$ (cumulative AIC_c wt = 0.27), $\psi3$ (cumulative AIC_c wt = 0.36), and $\psi11$ (cumulative AIC_c wt = 0.104; Table 1). The

Table 2. Number of bison caught and culled for calves (0.5 yr), yearlings (1.5 yr), adults by sex and breeding status (Lac F = F with full udder, Non F = F without full udder) from 2002 to 2007 in Badlands National Park, South Dakota, USA.

	No. of individuals						
Yr	Calves captured	Yearlings captured	Ad captured	Total captured	Yearlings culled	Ad culled	Total culled
2002	46 M 46 F	63 F 48 M	106 Non F 81 Lac F 104 M	494	33 F 22 M	46 F 36 M	137
2003	75 F 78 M	60 F 56 M	55 Non F 138 Lac F 89 M	551	28 F 28 M	37 F 37 M	130
2004	71 F 54 M	56 F 51 M	52 Non F 119 Lac F 76 M	479	55 F 51 M	48 F 25 M	179
2005	91 F 88 M	94 F 89 M	61 Non F 156 Lac F 80 M	659	89 F 71 M	57 F 49 M	266
2006	70 F 89 M	104 F 96 M	49 Non F 155 Lac F 94 M	657	61 F 87 M	29 F 47 M	224
2007	58 F 52 M	56 F 62 M	52 Non F 106 Lac F 55 M	441	37 F 62 M	23 F 30 M	152

Table 3. Model selection results describing survival, recapture probabilities, and breeding transition rates for bison in Badlands National Park, South Dakota, USA, from 2002 to 2007. Only models containing ≥0.01 Akaike's Information Criterion (with small sample size correction; AIC_c) weight are shown and specific model substructures are described in Table 1. Models are ranked by AIC_c. ΔAIC_c is the difference in AIC_c units from the highest ranking model. AIC_c weights (w_i), model likelihood, number of parameters (K), and deviance are also shown. AIC_c weights sum to 1 and models with higher likelihood have more weight. Model likelihood is the likelihood of a model relative to the other models. Deviance is the difference in (−2log × likelihood) of the current model and (−2log × likelihood) of the saturated model.

Model	AIC_c	ΔAIC_c	w_i	Model likelihood	K	Deviance
φ29, *p*6, ψ3	3,763.96	0.00	0.29	1.00	26	1,634.33
φ29, *p*6, ψ2	3,764.53	0.57	0.22	0.75	24	1,639.01
φ29, *p*6, ψ11	3,766.44	2.48	0.08	0.29	28	1,632.69
φ39, *p*6, ψ3	3,766.79	2.83	0.07	0.24	28	1,633.04
φ39, *p*6, ψ2	3,767.34	3.37	0.05	0.19	26	1,637.70
φ29, *p*6, ψ9	3,767.57	3.61	0.05	0.16	28	1,633.82
φ29, p6, ψ4	3,767.83	3.86	0.04	0.15	26	1,638.19
φ29, *p*6, ψ10	3,767.89	3.92	0.04	0.14	28	1,634.14
φ29, *p*6, ψ6	3,768.18	4.21	0.04	0.12	26	1,638.54
φ29, *p*6, ψ5	3,768.55	4.58	0.03	0.10	26	1,638.91
φ39, *p*6, ψ11	3,769.35	5.39	0.02	0.07	30	1,631.47
φ39, *p*6, ψ9	3,770.46	6.50	0.01	0.04	30	1,632.58
φ29, *p*6, ψ12	3,770.50	6.53	0.01	0.04	30	1,632.62
φ39, *p*6, ψ4	3,770.68	6.71	0.01	0.03	28	1,636.93

ψ2 model included 3 age classes (1.5 yr, 2.5–12.5 yr, >13.5 yr) and the ψ3 model included 4 age classes (1.5 yr, 2.5–3.5 yr, 4.5–12.5 yr, >13.5 yr); neither had covariates or year effects. The ψ11 model had the same 4 age classes and a covariate of growing season precipitation values from the previous year. We found a great deal of uncertainty in our estimation of female transition rates from lactating to non-lactating and vice versa (Tables 1, 3). Overall, probability of a female transitioning from non-lactating to lactating increased with age early and remained high until females

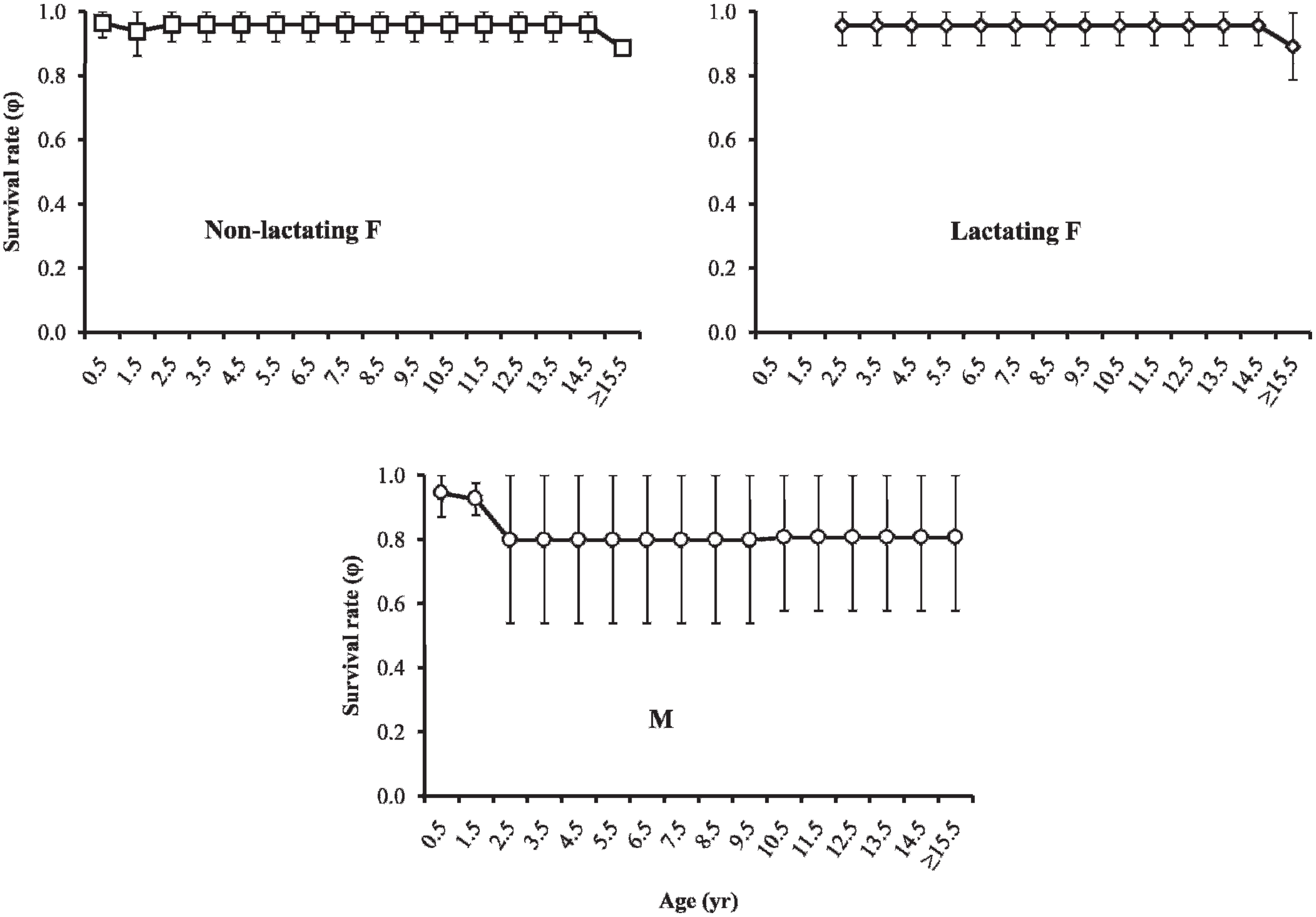

Figure 2. Survival probability estimates for male, non-lactating female, and lactating female bison aged 0.5 years to ≥15.5 years in Badlands National Park, South Dakota, USA, from 2002 to 2007. We model-averaged estimates across the entire model set and estimates include model-selection uncertainty. Error bars are 95% large sample approximation confidence intervals only of process variation.

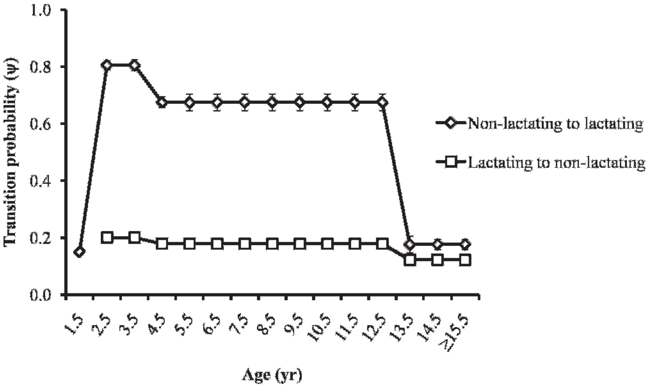

Figure 3. Breeding-state transition probability estimates from non-lactating to lactating and from lactating to non-lactating for female bison aged 1.5 years to ≥15.5 years in Badlands National Park, South Dakota, USA, from 2002 to 2007. We model-averaged estimates across the entire model set and estimates include model-selection uncertainty. Error bars are 95% large sample approximation confidence intervals only of process variation. The error associated with the lactating to non-lactating transition estimates is so small that error bars do not extend beyond the box representing the point estimate.

became old (>12.5 yr; Fig. 3). The transition rate from lactating to non-lactating was not as strongly age-dependent and was low (approx. 0.20; Fig. 3). We estimated all the variation of our estimates was due to sampling variation.

DISCUSSION

We estimated probability of recapture to be <1 and found that it varied across sex, age, and year. To date, bison analyses have assumed that recapture probability equals 1 and that all marked animals are always recaptured, which is a reasonable assumption in cases that rely on radiotelemetry data (e.g., Fuller et al. 2007) but may not be in other studies (e.g., Millspaugh et al. 2008). Assuming recapture probability is 1 when detection is imperfect can lead to biased estimates (Pollock et al. 1990, Lebreton et al. 1992). In the case of bison, assuming a probability of recapture equal to 1 would result in finding strong survival senescence when in fact older bison (especially males) are not recaptured at the same rate as younger bison. Indeed, older bison are preferentially not captured in BNP due to their disagreeable demeanor and ability to harm other bison and people during roundups. Using field data collection and analysis methods to account for these nuisance recapture rates is important when estimating demographic parameters, especially if these parameters are to have any use in predictive models or management plans. Although there is overlap of confidence intervals between females and young males, the large difference in estimates led us to believe that recapture probabilities of males and females are indeed different despite the overlapping confidence intervals.

Probability of Survival

All sex, breeding, and age classes of bison had survival rates ≥80% (Fig. 2), consistent with the hypothesis that even very young bison experience low predation. We detected senescence in female survival, contrary to other large mammal studies (e.g., Gaillard et al. 2000). We did not detect senescence in survival for males, which may be partly due to our adjusting for recapture rates. However, our sample size for bison ≥10 years old was small and our power to detect such differences may have been small as well.

We also did not detect differences in survival between the 2 female states, similar to a study by Weladjii et al. (2008) of reproduction costs in female reindeer, which could indicate reproductive costs associated with bearing and nursing young has no impact on bison survival. However, our data collection schedule (i.e., recording breeding state during autumn roundups) made interpretation of this state parameter difficult. Because we assigned the females' state (lactating or non-lactating) in October, we measured survival probability from this time until the following October. If suckling a calf through a harsh late autumn and winter is considered a survival cost to the mother, then the date of assigning the states was appropriate, because the cost was subsumed within the assigned year. However, if suckling the entire year is considered a survival cost for the mother, then our state assignment would be compromised because the cost would span the census date. Bison mothers suckle their calves for an average of 7–8 months, and orphaned calves as young as 2 months have survived (Meagher 1986), which suggests that our census date is, on average, consistent with bison biology, although calves have been known to suckle for up to 1 year. Likewise, if pregnancy is considered costly to the mother in terms of survival, then we did not have those data (because no palpation occurred during the roundup), which leads to reduced detection of differences in survival between the 2 states. With our data we could not distinguish between these 2 scenarios. Additional data collection to explore these survival probabilities is needed. Nevertheless, we estimated that female survival was high and we found little evidence of large survival differences between the states.

Female Breeding-State Transition Probabilities

There was much uncertainty and sampling variance in estimated female transition rates from lactating to non-lactating and from non-lactating to lactating. We found that females can conceive at an early age (<2.5 yr) as suggested by others in the literature (Meagher 1986, Berger and Cunningham 1994). We also found that once females reach breeding maturity, they often breed in consecutive years. However, once females reach about 13.5 years of age and transition to non-lactating, there is a high probability (approx. 0.8) that they will stay non-lactating the next year, which may be evidence of reproductive senescence. Berger and Cunningham (1994) found that 0.26 (6 of 23) of females produced calves in each year of a 4-year study (1986–1989), whereas our results suggest a higher rate, close to 0.47, which is just outside the upper bound of Berger and Cunningham's 95% CI (0.08, 0.44). The lower reproductive rates during Berger and Cunningham's study period may be due to the stresses of a density-dependent population, because no culling occurred during that time. Managers currently keep the BNP herd size low; probably well under carrying capacity. In contrast, bison populations kept closer to carrying capacity, such as the herd on Catalina Island, experience delayed breeding and skipped breeding, reducing the reproductive rate (Lott 2002).

We found the multistate model useful for tracking breeding transition rates and estimating survival, as well as for controlling by recapture rates. Except for the possible misalignment of state designation with when the states actually change in female bison, our data set met our assumptions well, especially because permanent emigration is not possible in this herd.

We also note that there are no data on age misclassification with bison using eruption-wear methodology. Previous research by Hamlin et al. (2000) found that eruption-wear methodology tended to underestimate older individuals and overestimate younger individuals in assessments of Rocky Mountain elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) ages. Hamlin et al. (2000) did find, however, that this method still accurately predicted ($>80\%$) within ± 1 year the actual age for mule deer and elk ≤ 5 years of age (approx. 82% of individuals in our data set were initially aged at ≤ 5 yr of age). To date, BNP personnel have not been able to address the issue directly using known-age animals. This problem potentially limits the reliability of the age-specific survival patterns we found, especially for old animals, but our use of general age classes instead of a full age-specific model helped mitigate the effect of age classification error.

We found little evidence that environmental covariates explain substantial variation in demographic rates, although temperature and precipitation varied noticeably during the study period. Others (Gaillard et al. 1998, 2000) have also found large adult herbivores robust to changes in environmental conditions, which may indicate that the park is keeping the bison herd at a low enough level that there is enough forage, even in drought years, so as not to negatively affect survival. In fact, the population goal of 700 animals is based on drought-year forage values (E. Childers, unpublished report). However, future climate variability may be more extreme due to global climate change (Intergovernmental Panel on Climate Change 2007). Recent work has shown that climate variability can affect weight gain in managed bison populations (Craine et al. 2009), which could potentially lead to differences in survival in bison and other large herbivores if future climate conditions exceed climate extremes experienced in the past. One interesting avenue for continued research would be to investigate the interactions among a variety of different culling strategies and climate covariates.

We also note that ours is the first analysis of bison demographic data to correct for the recapture rate, as well as to focus on estimating process variance. We believe that presenting process variance estimates (and factoring out the sampling variance; e.g., Gould and Nichols 1998) for biological parameters of interest is useful because the process variance is what biologists need to interpret and use in population models. The distinction between process and sampling variance is often not made. Our methods, parameter estimates, associated variances, and their overarching trends can be used in population models to predict growth rates, a need for many bison-related disease models (e.g., Kilpatrick et al. 2009), and to inform culling strategies for bison. Our methods and approach should also be useful to evaluate reintroduction programs for other large herbivores.

MANAGEMENT IMPLICATIONS

Our analysis suggests that bison in BNP have high survival rates and high probabilities of producing young (i.e., being in a lactating state). Thus, the reintroduction was successful and the current management plan is working well. Additional sampling work at other times of year could help produce better demographic estimates as well as help inform the survival cost of lactation. We could gain further insight into bison demography by focusing additional data collection on understanding the survival costs of different breeding states (e.g., nursing or pregnant) or the potential impact of global climate change on demographic parameters.

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