

Bison Conservation in Northern Great Plains National Parks

No Need to Panic

Daniel S. Licht

ABSTRACT—Bison (*Bison bison*) are a keystone species in the North American Great Plains. They are also a species of conservation concern in part because they suffered a severe population bottleneck at the end of the 19th century and now exist in mostly small and isolated populations. Wind Cave National Park introduced 20 bison in 1913–16; Theodore Roosevelt National Park introduced 29 animals to a South Unit in 1956 and subsequently transferred 20 bison from that herd to the park's North Unit in 1962; and Badlands National Park introduced 53 animals in 1963–64 and another 20 in 1984. The four herds are confined within fences, and no known introduction of new bison into the gene pools has occurred. The four herds are routinely culled down to approximately 425, 350, 200, and 700 animals, respectively. I found no evidence of inbreeding depression as measured by annual population growth and reproductive rates. A population viability analysis also failed to find persuasive evidence of inbreeding depression. Under current management scenarios, gene diversity in 100 years should remain above levels currently known to cause inbreeding depression in bison. I found no compelling reason to introduce new bison into the herds or transfer bison between herds in the foreseeable future.

Key Words: bison, genetics, inbreeding depression, minimum viable population, national parks, northern Great Plains, population viability analyses

Introduction

The American plains bison (*Bison bison bison*) is a key-stone and iconic wildlife species. It is also a species of conservation concern (Redford and Fearn 2007; Sanderson et al. 2008; Gates et al. 2010). From a population that might have numbered in the tens of millions (Shaw 1995), it was reduced to just a few hundred by 1900 (Department of the Interior 1902; American Bison Society 1908). Many of the surviving animals were in private herds, some of which were exposed to cross-breeding with domestic cattle (Coder 1975; Halbert 2003). As a result, in 1912 a portion of Wind Cave National Park was redesignated as a “game reserve” for purposes of conserving bison. Fourteen bison were reintroduced to the site in 1913 and another six in 1916. Twenty-nine bison were reintroduced to the South Unit of Theodore Roosevelt National Park in 1956; 20 bison from that unit

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were transferred to a North Unit in 1962. The Badlands National Park herd started with 53 bison in 1963–64; it was augmented with 20 animals in 1984. Post-cull herd sizes at the three parks have generally been in the 200–700 range. The four herds are confined within fences and no known introduction of new bison into the gene pools has occurred.

Small and isolated populations are prone to inbreeding, which can lead to reductions in fitness (the ability to survive and reproduce), a phenomenon known as inbreeding depression (Lacy 1997). Reed and Frankham (2003) reviewed 34 data sets, comprised of plants, invertebrates, and vertebrates, and found that population genetic diversity and population fitness were significantly correlated, that is, as genetic diversity declined so did fitness. Similarly, Crnokrak and Roff (1999) reviewed the data on a variety of wild plant and animal populations and found that 54% of the inbred populations also experienced significant levels of inbreeding depression. In the small and isolated Texas State Bison Herd, inbreeding probably triggered the low recruitment and high calf mortality rates observed in the herd, and could have

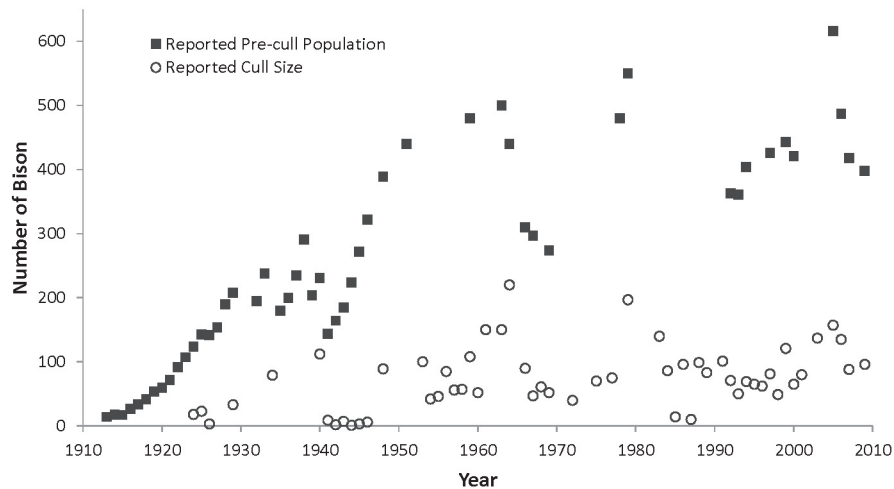


Figure 1. Number of bison culled at Wind Cave National Park by year and pre-cull population size, 1914–2013.

eventually led to extirpation of the population (Halbert et al. 2004). I evaluated the four National Park Service bison herds for evidence of inbreeding depression and risks to long-term viability. Specifically, I hypothesized that if there were no change over time in recorded measures of fitness, and simulation models mimicked herd trajectories without inclusion of inbreeding depression parameters, then there was no compelling evidence of inbreeding depression in the herds.

Background

In 1912 Congress established the 1,620 ha Wind Cave National Game Preserve for the purpose of being a “permanent national range for a herd of buffalo” (August 10, 1912, c. 284, 37 Stat. 293). In November 1913, six male and eight female bison from the New York Zoological Society were released at the site. (Some sources [e.g., Coder 1975] report that the founders consisted of seven male and seven female bison; however, internal park files and the preponderance of information [e.g., the census table in American Bison Society 1914] indicate that the herd started with six males and eight females.) It appears that the New York Zoological Society herd originated around 1899 with seven animals from the Texas-Oklahoma area and was supplemented four years later with 26 bison from a herd owned by William C. Whitney (Hornaday 1910), who had purchased the animals in 1897 from H. K. Glidden of Jackson, Wyoming (American Bison So-

ciety, cited in Coder 1975). In 1916 the Wind Cave herd was supplemented with two bulls and four cows from the Lamar Valley herd of Yellowstone National Park; however, the original source of those animals can be traced to 18 female bison from western Montana, three male bison from the Texas-Oklahoma area, and perhaps a small number of bison from the Yellowstone central herd (Coder 1975; Wallen et al. 2015). The Wind Cave herd grew to approximately 200 animals by 1930, and herd population levels have been maintained at 200–500 animals since that time (Fig. 1). The bison now have access to about 11,500 ha and the current management goal is 350–500 animals (National Park Service 2006). The bison stocking density equates to about a 10% utilization of plant productivity in normal-precipitation years (Licht 2016a). No other bison have been deliberately introduced to the herd; however, occasional incursions of bison from neighboring Custer State Park have been reported (Wind Cave National Park internal files, National Park Service 2006, Halbert and Derr 2007). Per agreement between the agencies the transgressor animals have been killed or pushed back into Custer State Park as soon as possible (National Park Service 2006). A reverse pedigree analysis of genetic samples collected 1999–2006 did not find evidence of breeding between the herds (Halbert and Derr 2007).

Twenty-nine bison were introduced to Theodore Roosevelt National Park in 1956. The bison came from Fort Niobrara National Wildlife Refuge. That herd was started in 1912 from seven bison owned by John Gilbert

of Friend, Nebraska, and two bulls from Yellowstone National Park (Coder 1975). The Fort Niobrara herd was subsequently augmented in the 1930s with eight animals from Custer State Park and in 1952 with five bison from the National Bison Range (Halbert 2003). In 1962, 20 bison from the South Unit of Theodore Roosevelt were transferred to the North Unit. The park now manages for a herd of about 150–250 bison on 9,600 ha in the North Unit and 200–500 bison on 18,400 ha in the South Unit. The stocking density equates to about a 7% forage utilization in both units in normal-precipitation years (Licht 2016a). The two herds are not adjacent to other bison herds and no known immigration of other bison has occurred.

In 1963, 28 bison were introduced to Badlands National Park. The following year another 25 bison were introduced. All but three of the animals came directly from Theodore Roosevelt National Park. The remaining three came from Fort Niobrara National Wildlife Refuge, which was also the source herd for the Theodore Roosevelt herd. In 1984 the park introduced an additional 20 bison from Colorado National Monument; those animals apparently descended from two females and a single male (Berger and Cunningham 1994). The males introduced from the Colorado National Monument herd apparently contributed little if any genetic diversity to the Badlands herd, and the offspring of the Colorado-lineage females showed evidence of outbreeding depression (Berger and Cunningham 1994, 1995). The park now manages for a herd of about 700 bison post-cull. The herd ranges over about 19,500 ha. Forage utilization by bison is about 12% of plant productivity in normal-precipitation years (Licht 2016a). Until recently, the herd was not adjacent to other bison herds. No known immigration of other bison has occurred.

All three parks regularly remove surplus bison, typically by roundups and disposal of live animals. During the 1940–70s Wind Cave culled bison by slaughter as part of a brucellosis control program. Many of the roundups in recent decades used helicopters. The helicopters captured a larger percentage of the herd and were also used for post-roundup aerial censuses of uncaptured bison. Captured bison were routinely marked with unique tags allowing park personnel to monitor individuals over time and to determine demographic rates (Millsbaugh et al. 2005; Millsbaugh et al. 2008; Pyne et al. 2010). Biological samples were taken for genetic analysis (Halbert 2003).

Methods

I reviewed internal park files, the bison roundup databases from each park, and published literature for historical information on the herds. I was generally able to find usable census information for the early years of the herds, but as herd and pasture sizes increased the information became less frequent and reliable. In recent decades herd counts and demographic information has greatly improved at all three parks. Park personnel have conducted regular bison roundups, during which they have tagged captured animals with unique identifying marks and used computer technology to process and store roundup data, and, in some cases, they have used helicopters to conduct post-roundup censuses. I evaluated the reported herd sizes for credibility and rejected records deemed unsuitable for analysis. For example, in a few cases it appears that the reported herd size was simply a projection based on previous counts and assumed rates of growth: I excluded those records. In a few other cases the reported herd sizes and proximate cull sizes were biologically infeasible, in which case I generally gave credence to the culls and rejected the reported herd sizes. As a result, I censored about 3% of the historical reported herd sizes.

I used the remaining reported herd sizes to calculate the rate of year-to-year population growth using the formula

$$\Lambda = N_{t+1} / N_t$$

where N is the reported herd size and t is the year. For years when no census was reported I interpolated the rate of annual growth from preceding and subsequent censuses, assuming no culls or augmentations occurred over the period of interest. My null hypothesis was that there was no change in lambda over time.

I analyzed the proportion of calves in the Wind Cave herd for evidence of changes over time. I used the proportion of calves in the herd versus conventional cow:calf ratios because counts of adult cows were unavailable in many early years. Fortunately, the park has consistently managed for natural sex ratios so the assumption of non-varying bull:cow ratios appears tenable. The data from Badlands and Theodore Roosevelt was insufficient for such an analysis. I did not evaluate density-dependent changes to herd growth or recruit-

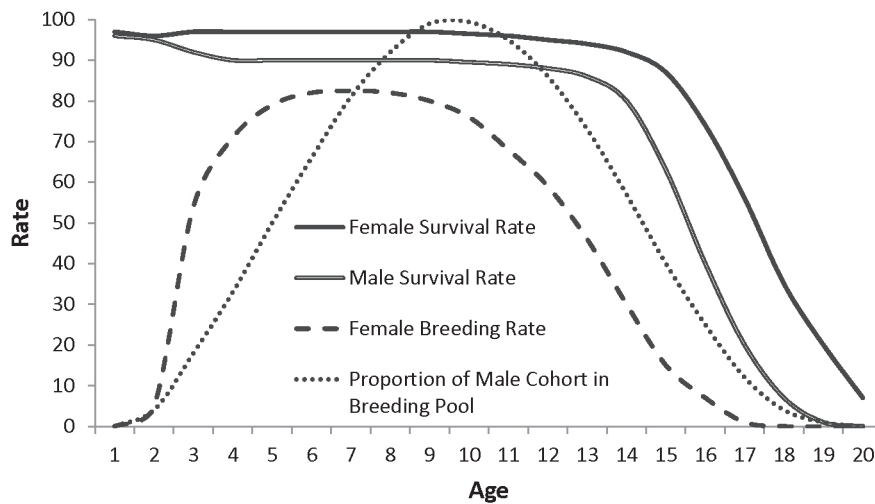


Figure 2. Demographic rates used in simulation model. Male breeding success was a probabilistic function of age and dominance score.

ment, as density-related effects were unlikely due to the low stocking rates (Licht 2016a). I reviewed the available information for other evidence of inbreeding, such as tallies of malformed bison, but was unable to find usable quantitative information.

I used the software program VORTEX (Lacy and Pollak 2014) to model historical and future herd demographics and genetics. VORTEX is designed for population viability analyses (PVA) but is flexible enough for a variety of uses. It is an individual-based model that simulates population dynamics as a series of discrete annual events such as breeding, natural mortality, and harvest. A simulation can be run many times to account for natural variability and uncertainty. I parameterized the model using reported survival and reproductive rates derived from the four herds (Fig. 2: based on Millspaugh et al. 2005; Millspaugh et al. 2008; Pyne et al. 2010). To account for differential male breeding success by age (Berger and Cunningham 1994), I included essentially all males ages 9–11 in the breeding pool, with declining inclusion for younger and older males (Fig. 2). To account for dominance (Berger and Cunningham 1994; Ungerer et al. 2013), all males were randomly assigned a dominance score at initialization of the model or at birth. A review of the simulation outputs verified that the distribution of male breeding success was similar to what was reported by Berger and Cunningham (1994). I did not vary female reproductive success by dominance nor did I alter the probability of female reproduction by prior-year parity. Evidence of such correlations is weak,

as demonstrated by studies of the Badlands herd (Berger and Cunningham 1994; Pyne et al. 2010).

VORTEX models the impact of inbreeding depression using lethal equivalents (LEs: O'Grady et al. 2006; Lacy et al. 2015). I tested a range of LEs against the known history of the 100-year-old Wind Cave herd for evidence of inbreeding depression. I first attempted to recreate the historic population trajectory of the herd using the reported culls to control growth, but found that the simulations often resulted in a runaway growth or extinction. This was likely due in part to model stochasticity and the long time span of the simulation, but could have also been due to spurious cull records. Therefore, I controlled herd growth by truncating the population at the reported herd size for the year. For years with no reported census I estimated the herd size for the year by interpolating growth from prior and subsequent reported censuses taking into account culls. I postulated that if the retrospective simulation with LEs = 0 reasonably tracked the historic herd trajectory, then inbreeding depression was not occurring; however, if simulations with LEs > 0 better tracked the known historic trajectory, then inbreeding depression might be occurring. Similarly, I compared the number of animals truncated (i.e., culled) under the simulations to the reported cull sizes to see which simulations best approximated historical cull rates. However, I could not rule out that historic reproductive and survival rates were greater than the rates in the baseline model, rates that were derived from data collected since 1966 (Millspaugh et al. 2005; Millspaugh

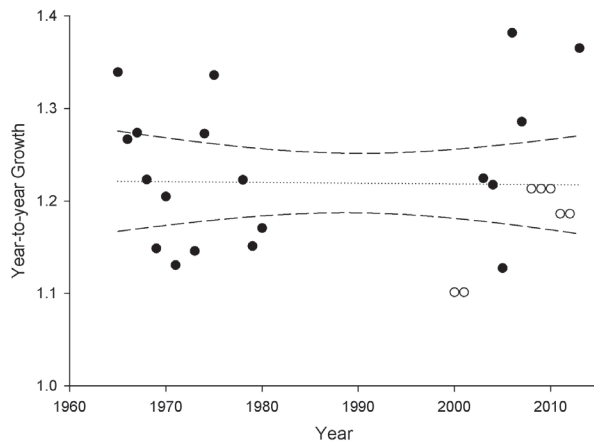


Figure 3. Long-term trend in the year-to-year population growth in Badlands bison herd, 1965–2013. Unfilled circles are interpolated from multi-year intervals. $Y = 1.380 \times -0.00008b$. $P = 0.93$. $R_2 = 0.00$.

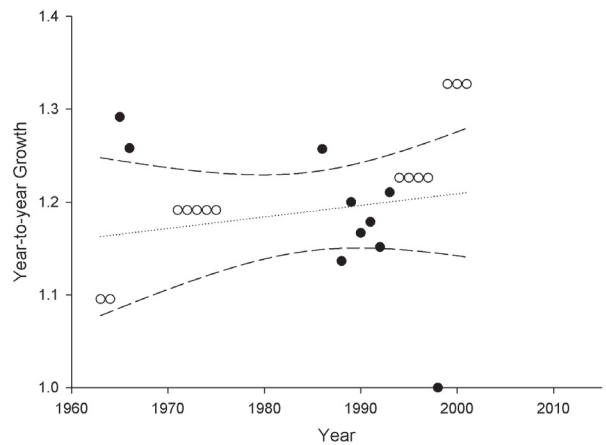


Figure 4. Long-term trend in the year-to-year population growth in Theodore Roosevelt North Unit bison herd, 1963–2013. Unfilled circles are interpolated from multi-year intervals. $Y = -2.232 \times 0.00174b$. $P = 0.61$. $R_2 = 0.16$.

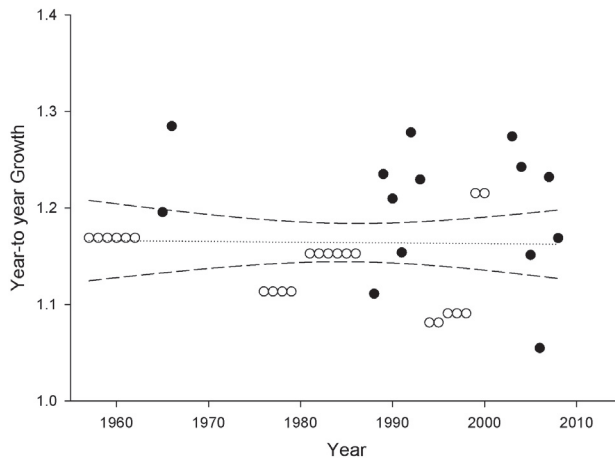


Figure 5. Long-term trend in the year-to-year population growth in Theodore Roosevelt South Unit bison herd, 1957–2013. Unfilled circles are interpolated from multi-year intervals. $Y = 1.315 \times -0.00008b$. $P = 0.91$. $R_2 = 0.00$.

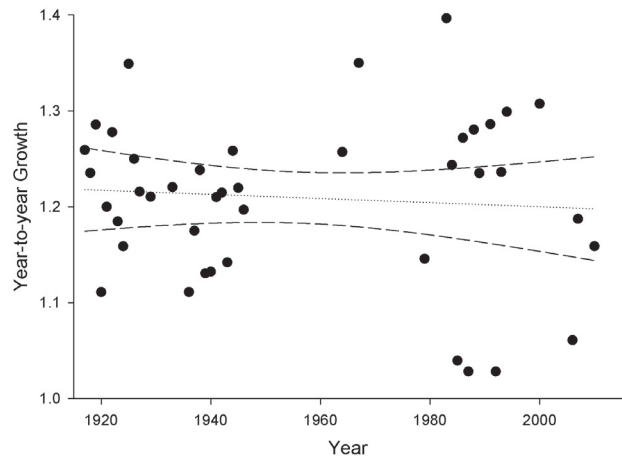


Figure 6. Long-term trend in the year-to-year population growth in Wind Cave bison herd, 1914–2009. $Y = 1.737 \times -0.00029b$. $P = 0.31$. $R_2 = 0.01$.

et al. 2008; Pyne et al. 2010). Therefore, to evaluate the scenario of historically higher reproductive and survival rates I also ran simulations parameterized with those rates 10% greater than currently estimated.

To better understand the likely rate of change in genetic diversity over time I used the model to estimate the past and future levels of genetic diversity in the herds. To estimate the historical founder herd expected heterozygosity (H_e), I ran simulations for a timespan equivalent to when the respective herds were established up to the year 2000, that is, the approximate year when Halbert (2003) collected her tissue samples from the herds. The

estimated founder H_e was the level that resulted in a year 2000 H_e equivalent to what Halbert (2003) found using genetic markers. To estimate genetic diversity of the herds 100 years into the future I seeded simulations with the 54 allele frequencies Halbert (2003) found for each herd. I then ran the simulations for 115 years to account for the 15 years between when Halbert (2003) collected her data (ca. 2000) and the time of my analysis. I ran simulations that assumed an annual cull of yearlings only and simulations that assumed a cull every third year from the yearling and adult age classes. The former

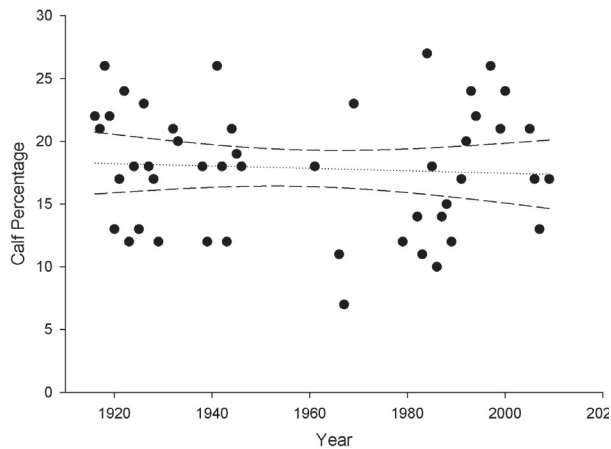


Figure 7. Percentage of calves in the Wind Cave bison herd, 1916–2009. $Y = 36.540x - 0.00954b$. $P = 0.68$. $R^2 = 0.00$.

best conserves genetic diversity (Licht 2016b) whereas the latter is more cost-efficient.

Results

The mean discrete annual growth of the Badlands herd was 1.22 over the life of the herd; for the Theodore Roosevelt North Unit herd it was 1.19, for the Theodore Roosevelt South Unit herd it was 1.16, and for the Wind Cave herd it was 1.16. Lambda did not significantly change over time for any of the four herds ($P > 0.05$; Figs. 3–6).

Calves comprised an average of 17.8% (SD = 4.95) of the Wind Cave herd each year from 1916 to 2009. The rate of calves in the herd did not change significantly over time ($P > 0.05$; Fig. 7).

When I simulated the historical Wind Cave herd with inbreeding depression disabled, the modeled annual population sizes averaged 0.93 of the historical herd sizes. Although slightly below the reported or interpolated historical herd estimates, this appeared a reasonable approximation as the model could only approach, but not exceed, the historical herd sizes due to the truncation. When I modeled the herds with 3.14 LEs, the annual population size was 0.83 of the historical herd sizes, and when I used 6.29 LEs, the modeled population was only an average of 0.43 of the historical herd sizes (Fig. 8). When I used 6.29 LEs the population went extinct in 8% of the iterations. Even when I increased initial survival and reproductive rates by 10% the simulation with 6.29 LEs had annual herd sizes far below the non-LE

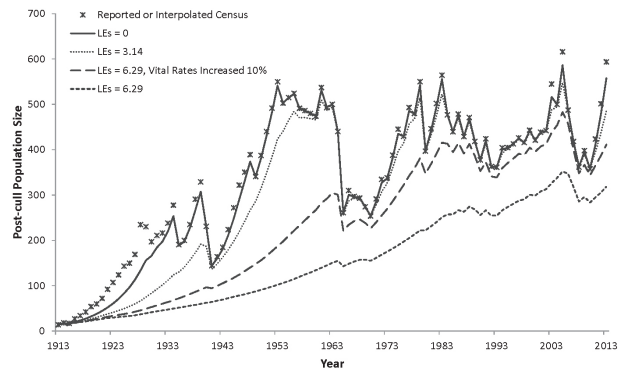


Figure 8. Simulated Wind Cave bison herd historical population trajectories. The no-lethal-equivalent simulation essentially mimics the reported trajectory. Simulations that model varying levels of lethal equivalents showed lower herd sizes. Even when reproduction and survival rates were increased by 10%, the herd size was below reported herd sizes due to modeled lethal equivalents. The model suggests inbreeding depression has not had a substantial impact on the herd.

model (Fig. 8). From 1914 to 2013 a reported 4,038 bison were culled at the park. The simulation with inbreeding depression disabled truncated bison at a rate of 1.30 of the reported historical culls. The simulations assuming 3.14 and 6.29 LEs truncated bison at a rate of only 0.68 and 0.09 of the reported historical culls, respectively. A simulation at 1.57 LEs truncated bison at a rate of 0.99 of the reported historical culls.

I modeled the future retention of genetic diversity in the four herds with LEs set to zero as the analysis of lambda and annual calf-recruitment showed no evidence of inbreeding depression and the PVA also suggested the rate was negligible. Assuming an annual cull of yearlings, H_e in the year 2115 will be 0.564, 0.455, 0.531, and 0.608 for the Badlands, Theodore Roosevelt North Unit and South Unit, and Wind Cave herds, respectively (Table 1). Assuming a cull every third year, comprised of yearlings and adults, the respective 100-year H_e was estimated as 0.523, 0.394, 0.490, and 0.568 for the herds, respectively. The estimated retrospective H_e for the herds at the time of establishment ranged from 0.558 to 0.697 (Table 1).

Discussion

Bison remain a species of conservation concern in part because many of the public herds—sometimes classified as conservation herds (Sanderson et al. 2008; Gates et al. 2010)—exist in small and long-isolated populations. Such conditions can lead to inbreeding depression and

Table 1. Modeled founder herd H_e , H_e reported by Halbert (2003) from 54 loci, and modeled future H_e assuming an annual cull of yearlings.

Herd	Historic conditions		He reported by Halbert [14] from samples ca. 2000	Modeled post-cull population goal	Modeled results in year 2115 and percentage change from 2015		
	Founder size and year(s) introduced	Modeled founder population H_e			Effective population size	Average alleles per loci (Percentage change)	He (Percentage change)
Badlands NP	53 in 1963–64 and 20 in 1984	0.592	0.574	700	332	4.13 (–7.8%)	0.564 (–1.7%)
Theodore Roosevelt NP North Unit	20 in 1962	0.558	0.513	200	92	2.96 (–14.5%)	0.455 (–11.3%)
Theodore Roosevelt NP South Unit	29 in 1956	0.601	0.574	350	160	3.77 (–10.0%)	0.531 (–7.5%)
Wind Cave NP	14 in 1913 and 6 in 1916	0.697	0.653	425	189	4.35 (–8.8%)	0.608 (–3.0%)

ultimately, risks to viability (Lacy 1997; Halbert et al. 2004). The Badlands, Theodore Roosevelt North and South Unit, and Wind Cave National Park bison herds have long been isolated. I evaluated the four herds in the three parks and found no evidence of inbreeding depression as measured by lambda and percentage of calves in the herd. The PVA simulations provided some evidence of a very low rate of inbreeding depression; however, the results were unconvincing and the modeled rate would have negligible impact on future herd demographics. The current rates of population growth for the four herds are all within the reported range for bison (see Reynolds et al. 2003) and should remain at those levels for the foreseeable future. The four herds will likely continue to be a source of surplus animals for bison herds throughout North America (National Park Service 2006; Licht 2016b).

The only bison herd that I am aware of that showed strong evidence of inbreeding depression is the Texas State Bison Herd at Caprock Canyons State Park (Halbert et al. 2004). That herd appears to have originated from five animals in the 1880s and was maintained at <250 animals for most of its history, including an average of about 40 animals from 1997 to 2003 (Coder 1975; Halbert et al. 2004). Halbert et al. (2004) concluded that the low recruitment and high mortality rates of the herd were due to low observed heterozygosity ($H_o = 0.387$). The Badlands, Theodore Roosevelt North Unit

and South Unit, and Wind Cave herds had average H_e of 0.574, 0.513, 0.574, and 0.653, respectively, from samples collected 1997–2002 (Halbert 2003). Assuming a yearling-only annual cull regime, the H_e for the herds will be 0.564, 0.455, 0.531, and 0.608 in 100 years and therefore above the level that caused inbreeding depression for the Texas State Bison Herd. However, other culling scenarios are less effective at conserving genetic diversity (Pérez-Figueroa et al. 2012; Licht 2016b). Within the three parks the herd with the highest risk of inbreeding depression is the North Unit herd at Theodore Roosevelt National Park; a cull every third year could result in H_e of 0.394 in the year 2115.

VORTEX version 10 uses a default value of 6.29 lethal equivalents (O’Grady et al. 2006; Lacy et al. 2015) to model inbreeding depression. That value resulted in modeled Wind Cave herd sizes well below the reported 1913–2013 herd sizes and even caused extinction in 8% of the iterations. Halbert et al. (2004) used VORTEX to model the viability of the Texas State Bison Herd. When they conducted their analysis, the VORTEX default lethal equivalent was 3.14; their model predicted a 99% chance of extinction in 41 years. The analysis conducted here suggests that 3.14 might be too high for bison. Daleszczyk and Bunevich (2009) estimated 2.46 lethal equivalents for European bison (*Bison bonasus*) fecundity, a rate not inconsistent with my simulations, which best tracked the historical reported herd sizes

and culls for Wind Cave. A fair criticism of the PVA analysis conducted here is that the demographic rates at the time of herd establishment might have been greater than they currently are and therefore, the current and ostensibly healthy rates are actually the diminished result of long-term inbreeding depression. However, the time series analysis of lambda showed no changes over time. Furthermore, the growth rates of the four herds all equaled or exceeded the 16% and 10% annual growth rates reported for the first half of the 20th century for the Yellowstone northern and central herds, respectively (Fuller et al. 2007).

Why is there no compelling evidence of inbreeding depression in the four bison herds in the National Park Service units in the northern Great Plains? One possible explanation is that the herds grew quickly and have generally been near or above the lower range recommended for the conservation of genetic diversity in wildlife populations (Franklin 1980). Furthermore, the herds are not exposed to stressors that can exacerbate inbreeding depression, such as predators and food shortages (O'Grady et al. 2006). As a result, the herd's demographic response to inbreeding is more comparable to a captive population than a wild population (Crnokrak and Roff 1999). Another possibility is that bison might be predisposed to avoid breeding with closely related animals, as is apparently the case in some species (Archie et al. 2007; Hoffman et al. 2007; Dunn et al. 2012). Yet another possibility is that heterozygous animals could be more successful breeders (Bensch et al. 2006). Although I found no persuasive evidence of inbreeding depression, inbreeding effects could be occurring that are not so severe as to manifest themselves in demographic analyses. For example, Wołk and Krasieńska (2004) suggested that patho-morphological changes in European bison over a 20-year period were due to a decline in immunity as a result of inbreeding. Berger and Cunningham (1994) noted hoof malformations in Badlands bison and such malformations were also observed by park staff at Wind Cave (internal park files). Regrettably, disfigurement data were not collected in a manner conducive to trend analyses.

Mixing bison among the federal herds using a meta-population approach has long been discussed (Dratch and Gogan 2008; Hedrick 2009), although the specific reasons for such action have not always been clearly articulated. The International Union for Conservation of Nature cautions against transferring bison between herds unless there is a "loss of genetic diversity or in-

breeding" (Gross et al. 2010, 90). I found no evidence of significant loss of genetic diversity or inbreeding depression in the four herds. Transferring bison into the herds would have to be justified for other reasons. However, we should be extremely cautious about moving bison between herds (Gross et al. 2010). We know that Badlands bison are significantly larger than Wind Cave bison (Licht 2016a) and we know that Wind Cave bison have at least 10 unique alleles (Halbert 2003). Were we to introduce Badlands bison into Wind Cave, it is possible that the larger Badlands bulls would be reproductively more successful. Over time the private alleles of the Wind Cave herd could be diluted or lost, to the detriment of global bison genetic diversity. Perhaps the smaller Wind Cave bison are better adapted to a warming world, or they have brucellosis-resistant traits, developed from when the herd was infected in the 1940–60s (Licht et al. unpubl. data). Wood et al. (2016) showed that even small populations have adaptive potential. Conversely, introduced bison might not randomly integrate with the resident herd, as was the case with the 20 bison introduced to Badlands National Park in 1984. In that instance the introduced males failed to mate. The introduced females did mate with resident males; however, their interbred offspring showed retarded growth and development (Berger and Cunningham 1994, 1995). Champagnon et al. (2012) listed a variety of potential negative effects from introducing conspecifics, including changes in behavior, morphology, and demography of the recipient populations, potential spread of pathogens, and loss of local adaptation to homogenization. Rather than mixing bison *in situ*, a wiser first step would be to experimentally mix bison of separate lineages on new sites, of which there appear to be several opportunities in the northern Great Plains (Licht 2014a, 2014b). Increasing herd sizes would also help to conserve genetic diversity (Licht 2016b).

Conclusion

The analysis conducted here underscores the importance of collecting accurate bison demographic data. Regrettably, there are large information gaps regarding the park bison herds. Even the most basic of data, such as how many bison are in the park, is not collected in a systematic manner. Informed management requires robust information. To better manage bison in National Park Service units more emphasis needs to be placed

on collecting usable and scientifically defensible demographic data.

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