Bison Conservation in Northern Great Plains National Parks and the Need for Reliable Funding

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Introduction

Badlands, Theodore Roosevelt, and Wind Cave national parks, located in the Northern Great Plains region of the United States, have played a crucial role in restoring the American bison (*Bison bison*) from the brink of extinction. Thanks in part to these parks, the global bison population now numbers in the hundreds of thousands (Gates et al. 2010). Yet in spite of the significant numerical recovery of the species, bison remain a species of conservation concern in part because of genetic issues (Dratch and Gogan 2008). The National Park Service (NPS) has called for heightened bison management in its vision document *A Call to Action* (National Park Service 2011) and the Department of the Interior has an explicit goal of conserving bison herds of 1,000 or more animals (US Department of the Interior 2008).

Bison were restored to Wind Cave in 1913, Theodore Roosevelt in 1956, and Badlands in 1963. Bison thrived in all three units. Due to the absence of apex predators, the parks conducted recurrent culling operations to keep the herds at desired population levels. Culling generally consisted of rounding up bison and live-transferring surplus animals to other entities. Collectively, the three parks have provided approximately 10,000 live bison to at least 50 American Indian tribes, eight state parks and zoos, nonprofit organizations, and several federal entities. A goal of the transfers was that the recipients of the surplussed bison would use the animals to start new herds or augment existing ones. Assuming 16% annual population growth, the distributed bison could have grown to over 100,000 animals in just 16 years, i.e., the lifespan of a bison. However, such growth was not realized as recipients harvested many of the bison.

Prior to 2010 the three parks funded the culling operations using an arrangement known as *cost recovery*. Under cost recovery the recipients of surplus bison shared the costs of the culling operations. The use of cost recovery within the agency goes at least as far back as the

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1930s at Yellowstone National Park (Anonymous 1932). Culling expenses at Badlands, Theodore Roosevelt, and Wind Cave typically include helicopters to push bison into processing facilities, veterinary services and supplies, overtime for staff, and other roundup-associated costs. In 2009, the cost of the roundup and cull at Wind Cave was about $50,000 with 96 animals being surplussed (Roddy et al. 2009). The cost recovery model generally allowed the parks to conduct strategic, efficacious, and scientifically defensible bison culls.

However, in 2010 the parks were ordered by the NPS national office to cease using cost recovery. I could not find any written record justifying or explaining the change in policy. Parks were provided no explanation other than the claim that there had been a solicitor's opinion saying cost recovery was illegal; however, no official solicitor's opinion appears to exist and subsequent to the change in policy two former solicitors expressed surprise that the practice had been discontinued, and they reiterated that the practice was in fact legal (Brian Kenner, pers. comm., October 2013). A 2015 investigative article in the *Rapid City* (South Dakota) *Journal* indicates that lobbying of Washington, D.C., officials by a tribal organization was instrumental in the change in policy (Tupper 2015). The same article states that as of 2015 park staff were still unsure as to why the policy was changed, a consequence of the contradictory information and the lack of written documentation. More importantly from the perspective of bison management, no replacement funding or authority was provided.

Subsequently, the parks have tried a variety of low-cost methods to cull surplus bison. For example, in 2013 Wind Cave tried to lure bison into a corral using bait distributed from a pickup truck, a method that could lead to increased habituation and injuries to visitors (some animals were enticed into the corral, but the number was deemed insufficient to conduct a culling operation). At Badlands, park staff used vehicles to push bison into a corral where the animals were held for an extended period of time as the park waited for more bison to walk within herding distance of the corrals: the confined animals broke through a fence and onto private property. The few culls that have occurred since 2010 were funded using sources that cannot be relied on in the future. For example, Theodore Roosevelt conducted a bison cull using funds received for a feral horse (*Equus ferus*) study and Badlands used Recreational Fee Program funds—a funding source that might be inappropriate for routine bison management activities. The new policy has also affected population goals; Theodore Roosevelt attempted to cull the herd well below the long-term average size out of fear that funds would not be available in future years.

Fortunately, 2010–2014 was a period of above-average precipitation in the Northern Great Plains. That, along with the low stocking rates the parks had circa 2010 has precluded bison overabundance and range damage. However, the herds continue to grow and drought is an inevitable occurrence in the Great Plains. I modeled pre-2010 and likely post-2010 culling scenarios to identify potential impacts to bison genetics and herd and ecosystem health as a result of the changes in policy.

Methods

To better understand, document, and predict the possible impacts of unreliable funding on bison demographics and genetics, I modeled each of the park herds under several culling scenarios using the software program VORTEX, version 10.0.7.3 (Lacy 2000; Lacy and Pollak 2014). I parameterized the model to maintain herd sizes at the current park goals. Badlands strives to keep its herd around 700 animals (Pyne et al. 2010). Wind Cave manages for a herd of about 425 bison (National Park Service 2006). Theodore Roosevelt has North Unit and South Unit herds that it attempts to keep at around 200 and 350 bison, respectively (National Park Service 2015). I assumed the four herds could increase to up to three times the targeted size with no ill effect on bison or ecosystem health. At three times the targeted herd size the model started imposing density-dependent reductions in survival and recruitment under the assumption that range degradation was beginning.

Baseline reproduction rates were derived from the bison roundups at the parks (Millspaugh et al. 2005). I parameterized age-specific mortality rates with the mid-points of the values reported by Millspaugh et al. (2005) and Pyne et al. (2010); those values were also derived from the park's bison roundups.

For each of the four herds I seeded the model with the respective allele frequencies from Halbert (2003). To account for differential male breeding success by age, all males ages 9–11 were assumed to be in the breeding pool, with declining inclusion for younger and older males. To account for disproportionate breeding success associated with dominance, all males in the initial population and all males born during the simulation were randomly assigned a dominance score that they kept throughout their life. A male's reproductive success within a year was a probabilistic factor of their age and dominance score. The output reasonably approximated the reported male breeding success rates reported by Berger and Cunningham (1994) for the Badlands herd. I did not alter female reproductive success by dominance as there is no evidence for that based on the Badlands study (Berger and Cunningham 1994). I did not enable inbreeding depression in the model due to a lack of evidence that the herds were impaired (Licht, in prep.).

For each of the four herds I modeled five culling scenarios. Two scenarios consisted of annual culls and are comparable with pre-2010 practices. The three other scenarios assumed multiple years between culls and are comparable with what has transpired post-2010 and will likely continue into the future in the absence of adequate and reliable funding and/or culling authority. I excluded calves from all culls as the parks typically do not cull that cohort. The five modeled scenarios were:

1. *Cull Yearlings Annually.* In this scenario a cull occurred annually, comprised only of yearlings, split evenly between the sexes. The cull reduced the herd to the respective population target. This scenario mimics what Wind Cave routinely did prior to 2010 (National Park Service 2006).
2. *Cull Yearlings + Adults Annually.* In this scenario a cull occurred annually, comprised of 50% yearlings, 25% 2.5-year-olds, and 25% older adults, split evenly between the sexes. The cull reduced the herd to the respective population target. The multi-cohort cull is similar to what Badlands and Theodore Roosevelt historically conducted, although the frequency of culls varied from nearly annually at Badlands to every few years at Theodore Roosevelt.

3. *Cull Every Fourth Year.* In this scenario a cull occurred every fourth year. To keep the long-term average herd size near the target level, the cull reduced the herd to 74% of the target population. Under this scenario the cull was comprised of 25% yearlings, 25% 2.5-year-olds, and 50% adults, split evenly between the sexes. This cull approximates the frequency of culling that could happen post-2010, although rigorous adherence to quadrennial schedule is unlikely.
4. *Cull Every Fourth Year from an Accessible Subpopulation.* In this scenario a cull occurred every fourth year using the same basic assumptions as scenario #3. However, this scenario also assumed two subpopulations within the park, only one of which could be culled. This mimics a situation whereby there are insufficient funds to use helicopters to push distant herds into the corrals. The scenario assumed that 33% of animals aged 2–5 from the unharvested (and oversaturated) subpopulation dispersed into the harvested subpopulation and 2% dispersed the other direction.
5. *Cull at a 0.25 Probability.* In this scenario culls occurred probabilistically in 25% of the years. When culls occurred the herd was reduced to about 47% of the target level. The more severe cull was necessary to minimize the risk of exceeding the carrying capacity in subsequent years as an unknown number of years could go by before the next cull. However, a competing goal was to keep the minimum population as large as possible to better conserve genetic diversity.

The population goals established by the parks are generally viewed as conservative, i.e., well below the potential forage-based carrying capacity at the sites. For example, the Badlands goal of 700 bison is reportedly based on drought conditions (Pyne et al. 2010). The Theodore Roosevelt South Unit goal is based in large part on indicator plants sensitive to elk (*Cervus canadensis*) herbivory (Westfall et al. 1993) and is considered conservative for bison (National Park Service 2015). The Wind Cave bison management plan (National Park Service 2006) acknowledges that its population targets are conservative. The use of conservative targets is deliberate as smaller populations of bison are easier to manage, require less funding, and provide a buffer for herd growth should funding for culls not be available in future years. However, under such a strategy the herds are not realizing their full conservation potential. I determined the ecological carrying capacity for each site using standard range management methods. For each site I summed the annual plant productivity, i.e., forage production (Natural Resources Conservation Service 2014). I assumed that half of the annual plant growth was needed by the plants for growth and maintenance and should not be consumed. I assumed that 15% of the balance would be lost to insects, rodents, weather damage, or decay, or was unpalatable or otherwise unavailable to ungulates. Ungulate consumption rates are typically reported as oven-dried rates so I reduced the air-dried forage values by 10%. At Theodore Roosevelt South Unit I assumed the presence of 360 elk and 100 feral horses. At Wind Cave I assumed the presence of 300 elk. Depending on the site I also assumed lesser amounts of deer (*Odocoileus* spp.) and pronghorn antelope (*Antilocapra americana*) and bighorn sheep (*Ovis canadensis*). I allocated forage to these species using the weight and intake values in Westfall et al. (1993). After accounting for these species the remaining forage was considered available for bison. I assumed a typical bison weighed 1,000 pounds (Licht, in prep.) and consumed the equivalent of 22 pounds of oven-dried forage daily (Feist 2000) for 365 days. To get the bison carrying capacity, I divided the remaining plant mass by the bison forage needs. To illustrate the conservation benefits of maintaining larger bison herds, I ran the VORTEX model across a range of herd sizes, using the allele frequencies of the Theodore Roosevelt South Unit herd and an assumed cull of all cohorts every fourth year.

Results

The two annual culls showed the least variability in late-summer (post-calving) herd size over time, with the variability about 5% of the herd size (Table 1). In contrast, the random-year culling scenario had the greatest variability in post-calving herd size, with a standard deviation about equal to the population goal for the herd. The random-year culling scenario was the only scenario to exceed the density-dependent threshold (i.e., three times the target level); it exceeded the threshold in 10.8% of the years for the small Theodore Roosevelt North Unit herd and 4.9% of the years for the large Badlands herd (Figure 1).

The two annual culls removed the fewest number of animals per cull on average and with the least variability (Table 1). The three multi-year culls had the largest number of animals removed per cull. The random-year cull showed the most variability, with some of the culls removing more bison than the population goal for the site.

Gene diversity (heterozygosity) was best conserved by the two annual culls (Table 1). For example, the annual yearling-only cull lost only 3.32% of its gene diversity over 100 years

Figure 1. Three iterations of simulated bison herd size assuming a 0.25 probability of a cull in a given year. The desired population size is 500 bison; culls reduce the herd to 200 bison.

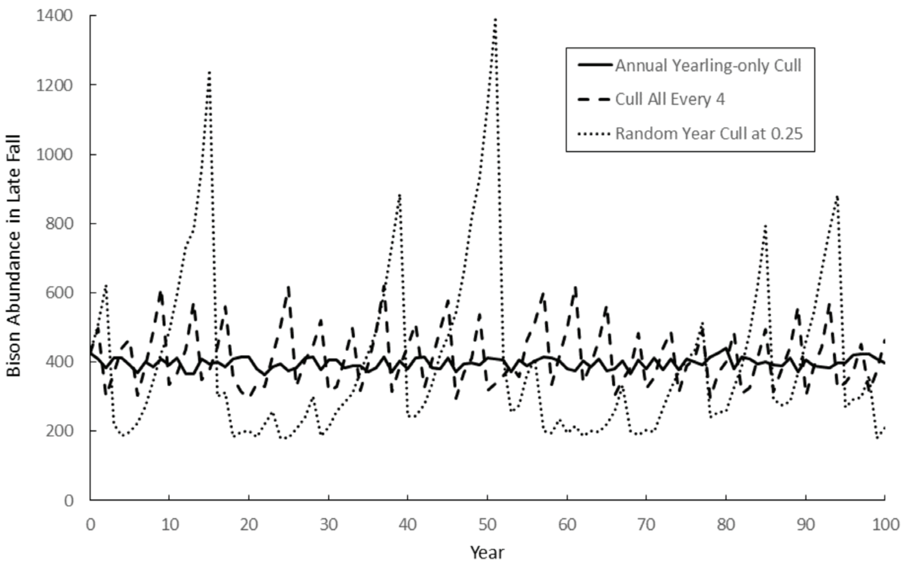


Table 1. 100-year simulations of the demographics and genetics of the four herds under the five culling scenarios.

Result by Scenario	Badlands NP	Theodore Roosevelt NP, North Unit	Theodore Roosevelt NP, South Unit	Wind Cave NP
Mean Post-cull Population	700	200	350	425
Post-calving Population and SD				
Annual Yearling Cull	810 ± 46	233 ± 14	411 ± 18	493 ± 25
Annual All Cohort Cull	830 ± 34	235 ± 12	415 ± 20	504 ± 26
Cull All Every Fourth Year	843 ± 193	235 ± 53	418 ± 95	506 ± 117
Cull Subpopulation Every Fourth Year	806 ± 181	238 ± 61	402 ± 84	470 ± 97
Cull Random Years P=0.25	780 ± 570	278 ± 210	398 ± 298	535 ± 430
Number Harvested Per Cull and SD				
Annual Yearling Cull	116 ± 40	34 ± 13	59 ± 23	67 ± 25
Annual All Cohort Cull	129 ± 40	34 ± 12	64 ± 19	77 ± 21
Cull All Every Fourth Year	550 ± 126	147 ± 38	267 ± 66	320 ± 88
Cull Subpopulation Every Fourth Year	412 ± 67	135 ± 38	230 ± 49	275 ± 48
Cull Random Years P=0.25	429 ± 501	157 ± 180	220 ± 277	272 ± 346
Heterozygosity Yr 100 and % Decline				
Annual Yearling Cull	0.547 (–2.34%)	0.464 (–7.07%)	0.536 (–4.15%)	0.615 (–3.32%)
Annual All Cohort Cull	0.545 (–2.71%)	0.448 (–10.27%)	0.525 (–6.17%)	0.606 (–4.69%)
Cull All Every Fourth Year	0.536 (–4.37%)	0.423 (–15.21%)	0.508 (–9.22%)	0.588 (–7.54%)
Cull Subpopulation Every Fourth Year	0.528 (–5.87%)	0.411 (–17.59%)	0.502 (–10.26%)	0.580 (–8.79%)
Cull Random Years P=0.25	0.528 (–5.73%)	0.401 (–19.77%)	0.500 (–10.57%)	0.575 (–9.60%)
Alleles / Loci Yr 100 and % Decline				
Annual Yearling Cull	4.20 (–6.25%)	3.04 (–12.14%)	3.84 (–8.35%)	4.42 (–7.53%)
Annual All Cohort Cull	4.09 (–8.71%)	2.93 (–15.32%)	3.73 (–10.98%)	4.34 (–9.01%)
Cull All Every Fourth Year	3.96 (–11.61%)	2.78 (–19.65%)	3.57 (–14.80%)	4.16 (–12.97%)
Cull Subpopulation Every Fourth Year	3.85 (–14.06%)	2.69 (–22.48%)	3.45 (–17.86%)	4.03 (–15.51%)
Cull Random Years P=0.25	3.90 (–12.95%)	2.66 (–23.12%)	3.48 (–17.14%)	4.02 (–15.90%)

at Wind Cave; in contrast, the quadrennial all-cohort cull reduced gene diversity 7.54%, the cull of a subpopulation quadrennially reduced it to 8.79%, and the random-year cull reduced it 9.60%. The simulations showed a similar change in allele richness over time, with the annual culls better conserving alleles than the culls separated by multiple years (Table 1).

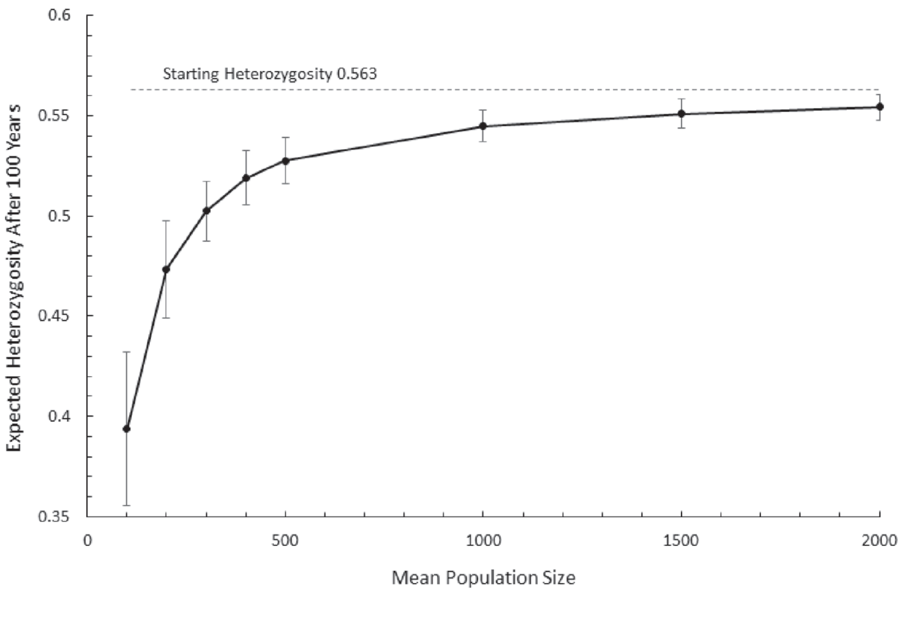
The conservation of heterozygosity and allele richness improves with increasing herd size, assuming other variables remain the same (Table 1; Figure 2). Assuming a starting gene diversity of 0.563 and a cull every fourth year, a herd of 2,000 animals would conserve about 98% of the original heterozygosity after 100 years, whereas a herd of 100 animals conserves only about 70% (Figure 2).

The analysis of a forage-based carrying capacity for the sites indicates that the parks could support substantially more bison than their current population goals (Table 2). If bison were allowed to consume about 25–30% of annual plant productivity, the parks would support about three times as many bison as they currently do.

Discussion

Bison conservation at NPS units in the Northern Great Plains has been a great success by many measures, including the conservation and recovery of an imperiled species (Coder 1975), conservation of the bison genome (Halbert 2003), restoration of an ecological process (Wallace and Dyer 1995), and enhanced visitor experiences (Vequist and Licht 2013).

Figure 2. Conservation of expected heterozygosity under varying herd sizes. Simulations start at 0.563 heterozygosity using allele frequencies from the Theodore Roosevelt South Unit herd. Assumes a cull every fourth year from all yearling and adult cohorts.



Scenario	Potential Ecological Carrying Capacity				
	Current Population Goal	Modeled Allocation to Bison in Normal Year	Unfavorable (i.e., Drought) Year	Normal Precipitation Year	Favorable (i.e., Wet) Year
Badlands NP	700	30%	1,188	2,162	2,776
Theodore Roosevelt NP, North Unit	200	28%	NA	994	NA
Theodore Roosevelt NP, South Unit	350	25%	NA	1,644	NA
Wind Cave NP	425	26%	821	1,332	1,831

Table 2. Current population goals and potential herd sizes (includes calves) based on forage productivity.

However, some of those successes are now jeopardized due to unreliable funding for bison roundups.

Under the current management paradigm it's likely that bison culls will occur less frequently, more haphazardly, and in a piecemeal fashion. As a result, bison population levels could deviate greatly from park-established targets. In the random-year cull simulations, the herds often exceeded the level at which the model assumed range degradation and density-dependent changes to vital rates. In the subpopulation scenario, the unharvested subpopulation would also have exceeded the carrying capacity in that portion of the park were it not for the high rate of dispersal assumed in the model.

In reality, range impairment levels may not be reached at the rates modeled here as there would be increased motivation within the agency to implement a cull once range degradation was imminent. Furthermore, the model assumed that carrying capacity was exceeded at three times the herd goals, yet the carrying capacity analysis conducted here—plant productivity data from the US Department of Agriculture's Natural Resources Conservation Service—suggests that the parks might be able to support at least that many animals or more with no impairment. Nevertheless, the simulations illustrate the risks that parks now confront in the absence of a dependable funding mechanism to cull bison.

An argument can be made that large swings in bison abundance—as simulated in the multi-year culling scenarios—better mimic natural patterns and processes. However, historical variability in bison abundance was likely a response to regional weather patterns and landscape-level disturbances (e.g., fire). Under the status quo, variability in bison abundance is primarily due to fiscal, logistical, and staffing factors, and not environmental conditions. Ideally, parks would have dependable funding, or a suitable culling authority, that would allow managers to cull herds in a way that best meets conservation goals and mimics natural processes. Ecologically, the ideal scenario for bison management would be one where the size of the herd would essentially "follow the rain," i.e., during periods of favorable precipitation the population would grow and during years of drought the herd would be reduced.

If the parks had reliable funding for culls they could manage for larger herds to the betterment of the bison genome. The model demonstrated that gene diversity is efficiently conserved once a herd reaches about 1,000 animals. Such results are consistent with the recommendations made by Gross and Wang (2005), Dratch and Gogan (2008), and Derr et al. (2011), and with Department of the Interior goals (US Department of the Interior 2008). Reliable funding would also allow parks to implement annual culls of yearlings, which are the most effective strategy for conserving genetic diversity. Yearling culls reduce the likelihood of removing a dam and her offspring and lengthen the intergenerational time of the herd. An annual cull of all cohorts is also effective, and has the additional benefit of a more natural sex-age structure. Conversely, the multi-year culling strategies lose genetic diversity at about twice the rate of annual culling. However, the greater loss of genetic diversity under the multi-year culls could be mitigated for by maintaining larger herd sizes. For example, the Theodore Roosevelt South Unit herd had a 100-year heterozygosity of 0.525 under an annual cull of all cohorts; the same amount of gene diversity could be retained under a quadrennial all-cohort cull if the long-term population goal were increased from 350 to 450.

The current conservative stocking rates at the parks are due in part to unreliable funding, yet they are sometimes justified as conserving biological diversity. However, unnaturally low grazing levels can retard the conservation of black-tailed prairie dogs (*Cynomys ludovicianus*), black-footed ferrets (*Mustela nigripes*), swift fox (*Vulpes velox*), and burrowing owl (*Athene cunicularia*), among other grazing-dependent species. Although present in some of the parks evaluated in this study, these species are not realizing their full potential in part because of the inability to effectively manage bison populations, demonstrating the cascading effect of unreliable funding for bison management.

This study focused on the risks to bison genetics and ecosystem health as a consequence of unreliable funding. However, the absence of reliable funding also raises animal welfare and human safety concerns. For example, in 2014 Badlands confined an excessively large number of bison to their holding pasture for an extended period of time in hope of collecting more animals. During confinement a calf was born and subsequently trampled and fatally injured. Wind Cave had five bison mortalities in 2014, well above the long-term average; the deaths might have been due to the excessively long period of bison confinement that year, as the park used horseback riders to push bison into corrals versus using the more expedient helicopters. As roundups are spread out over longer periods, and more bison are processed per roundup, there are more stresses on infrastructure, park funds, and worker safety.

Some risks of not having reliable funding for bison management include:

1. Loss of genetic diversity.
2. Potential to exceed the ecological carrying capacity.
3. Difficulty in finding recipients of surplus animals due to uncertainties in culls.
4. Diverting funds from other programs or using inappropriate funding sources for culls.
5. Use of capture methods that conflict with policy or have harmful consequences.
6. Increased risk to staff safety and infrastructure due to larger culls.
7. Increased cost per cull.

8. Loss of data collection opportunities, resulting in less refined management.

To better manage bison, the parks need a reliable and adequate funding mechanism and/or enhanced authorities to remove surplus bison. Bison are a valuable commodity, with a herd of 1,000 capable of generating upward of $250,000 annually on the open market (Licht 2014). Although NPS bison should not be managed as a commodity, the unique values of the animal makes them conducive for innovative funding mechanisms, such as is done for micro-organisms at Yellowstone National Park. Bison conservation has been successful for the past 100 years at NPS units in the Northern Great Plains. It seems reasonable to assume that the agency intends to manage bison for at least another 100 years, so a reliable culling program is warranted. If the three Northern Great Plains parks had reliable funding and culling authorities they could manage their herds in ways that better conserve the species and meets department and agency bison conservation goals. Each year that goes by puts the ecosystems at risk and decreases the genetic diversity of the herds. The clock is ticking.

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