



Research Article

Pedigree-Based Genetic Management Improves Bison Conservation

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ABSTRACT Overhunting and widespread land use change nearly caused the extinction of North American bison (*Bison bison*) by the late 1800s. Recovery efforts focused on preserving the remaining individuals and establishing federally managed conservation herds to build more sustainable populations. Today, bison in conservation herds are maintained in small, isolated herds that are managed through an annual or biannual cull of individuals to maintain target population sizes. We assessed alternative culling strategies for maintaining genetic variation over the long term in managed wild bison herds. Our objective was to compare a strategy modeled after a United States Fish and Wildlife Service strategy (all-allele conservation culling strategy [AAC]) to a pedigree-based mean kinship strategy (MK) and to a Random strategy that does not incorporate genetic data and is used to manage some conservation herds. We built an individual-based model, parameterized in accordance with bison biology, to compare these culling strategies in 2 federally managed conservation herds at the Fort Niobrara National Wildlife Refuge (FTN herd) and the National Bison Range (NBR herd). Our MK strategy retained more genetic variation and slowed the accumulation of inbreeding relative to the AAC or Random strategies, and these findings were consistent across wild bison herds with different founding sizes and current genetic diversity. These findings extend previous work demonstrating the utility of pedigree-based management strategies in captive and wild population management, and show that such strategies maximize the retention of genome-wide variation in contemporary bison herds. The modeling approach used in this study was useful for assessing outcomes prior to implementation, and the specific models developed for this study can be easily adapted to other managed wildlife species. © 2018 The Wildlife Society.

KEY WORDS culling, Fort Niobrara National Wildlife Refuge, genetic variation, inbreeding, individual-based model, mean kinship, National Bison Range, pedigree-based management.

Bison (*Bison bison*) once roamed the North American plains by the millions (Shaw 1995). By the late 1800s, massive overhunting and land use change reduced the plains bison (*B. b. bison*) to roughly 1,000 individuals, <1% of the historical population size. Bison recovery efforts began with strict harvest regulations and the establishment of federally managed conservation herds at the turn of the twentieth century. Six conservation herds were established using <100 bison from 5 private herds and a single wild population in Yellowstone National Park (Coder 1975). As bison recovery continued, additional conservation herds were established; today, only about 4% of bison are managed for conservation in 54 herds totaling about 20,500 animals (Gates and Ellison 2010). Twelve conservation herds in the United States are

managed federally, by the Department of Interior (United States Fish and Wildlife Service [USFWS], National Park Service [NPS], and Bureau of Land Management [BLM]) to maintain the long-term viability of the species (Gates and Aune 2008). Each herd is managed independently with few bison transferred among herds because of the presence of cattle gene introgression and, in some cases, disease (Hedrick 2009, Dratch and Gogan 2010).

Each conservation herd is typically maintained at a target population size by removing animals at regular intervals. Population size targets are set to avoid permanent habitat damage and accommodate multiple management objectives on small, isolated reserves (Boyd 2003, Boyd et al. 2010). In these small herds, demographic stochasticity is amplified compared to larger populations and, as a result, small populations are more vulnerable to extinction (Lande 1988, Legendre et al. 1999, Melbourne and Hastings 2008). Bison managers minimize demographic stochasticity by minimizing year-to-year variation in population size and maintaining

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an even sex ratio in the herd. Both strategies reduce fluctuations in demographic parameters, thereby mitigating risks of extinction (Lande 1988, Ballou et al. 2010).

In addition to increased extinction risk through demographic stochasticity, small populations are also vulnerable to extinction through inbreeding depression and erosion of genetic variation (Allendorf and Leary 1986, Ralls et al. 1988, Lacy 1997). Management actions that preserve genetic variation and limit the accumulation of inbreeding are important to the long-term persistence of populations. For example, the same strategies that minimize demographic stochasticity, such as avoiding fluctuations in population size or sex ratios, mitigate extinction risk and benefit maintenance of genetic variation (Caballero and Toro 2000, Komers and Curman 2000). Retention of genetic variation can also be improved by extending mean generation length (Foose and Ballou 1988). Some bison managers target animals from the yearling population for removal, which results in more offspring born to older females, a longer generation time, and a lower rate of genetic variation loss (Foose and Ballou 1988, Gross 2000, Gross and Wang 2005).

Population management strategies can also be improved by managing genetic variation directly. The most effective genetic management strategies are those that consider genome-wide variation, rather than variation at a restricted suite of genetic loci. In particular, pedigree-based management strategies, designed to minimize kinship across a population, maximize the retention of genome-wide variation. In captive populations, pedigree-based breeding strategies have been shown by computer simulations (Ballou and Lacy 1995, Fernández and Toro 1999, Ivy and Lacy 2012) and empirical data (Montgomery et al. 1997) to be the best strategies for retaining genetic variation while limiting the accumulation of inbreeding. Pedigree-based management strategies are also useful for selecting individuals to cull, by preferentially removing individuals whose genomes are over-represented in the population (Eggert et al. 2010, Giglio et al. 2016).

Previously, we used simulations to investigate the performance of several generalized management strategies for maintaining genetic variation in bison herds (Giglio et al. 2016). We reported that strategies that based culling decisions on genetic information performed better at maintaining genetic variation than strategies based on demographic information alone. In particular, a pedigree-based culling strategy using mean kinship (MK; the average kinship between an individual and all living individuals, including itself) performed the best at maximizing the retention of genome-wide variation and minimizing the accumulation of inbreeding. In this study, we developed a model that approximates a USFWS management strategy, and compared it to an MK-based culling strategy and a Random strategy that does not consider genetic variation in culling decisions. The overall aim of the modeled USFWS strategy is to maintain as many alleles in the population as possible by ensuring the retention of rare alleles. Although an allele retention strategy can be effective at preserving rare variation at a

managed suite of loci (Wayne et al. 1986, Hedrick and Miller 1994), it also can lead to a loss of genome-wide variation by preferentially retaining in the population many relatives with shared rare variants (Haig et al. 1990, Vrijenhoek and Leberg 1991, Miller 1995). To mitigate this potential negative inbreeding effect, the modeled USFWS strategy also imposes a maximum number of copies of each rare allele present in the population. We evaluated these 3 culling strategies (USFWS-modeled all-allele conservation culling strategy [AAC], MK, and Random) across different USFWS-managed bison conservation herds with different founder sizes and different levels of genetic diversity. Our goal was to evaluate the utility of the AAC management strategy relative to other strategies for long-term genetic management of wild bison herds, and to evaluate long-term outcomes relative to differences in founding histories and current levels of genetic variation.

STUDY AREA

We conducted our study with the bison herds at the Fort Niobrara National Wildlife Refuge (FTN) in Valentine, Nebraska, USA, and the National Bison Range (NBR) in Moiese, Montana, USA. Both herds are federal conservation herds managed by the USFWS. The herds differ in the size of the founding population, and in the current level of genetic variation. As a result of the smaller founding population size, the FTN herd has lower contemporary genetic variation than the NBR herd (Halbert and Derr 2008, Giglio et al. 2016). As of 2018, each herd is managed for a target population size of about 350 bison through annual culling during a fall roundup.

The FTN herd was established in 1913 with only 8 bison (Gilbert herd from Friend, NE, $n = 6$; Yellowstone National Park, $n = 2$), with later supplementations made from Custer State Park (1935 and 1937) and the NBR (1952; Dratch and Gogan 2010). The FTN refuge is located where 6 different plant communities converge along the Niobrara River, providing habitat for a rich and unusual diversity of wildlife. Elevations on the refuge range from 610 m above sea level to 853 m. Native grasslands dominate the refuge and a variety of wooded land cover types associated with the Niobrara River deep canyons in the limestone rocks underlie the Sandhills. The climate of the region is highly variable and characterized by cold winters and hot summers. Total annual precipitation averages 46 cm with approximately 65% occurring during the May-to-September growing season. Winter precipitation is usually in the form of snow with the annual accumulation averaging 94 cm. Temperatures range from -39°C to 46°C with July and August being the warmest months (average high temperature $29\text{--}31^{\circ}\text{C}$) and January and February the coldest months (average low temperature -13 to -11°C). Winds ranging from 8–24 km/hour are common throughout the year.

The NBR was established in 1908 with 40 bison from 3 private sources (Conrad herd, Kalispell, MT, USA, $n = 36$; Corbin herd, NH, USA, $n = 3$; and Goodnight herd, TX, USA, $n = 1$), with only 12 new bison being added since 1910

(7-UP Ranch, Cameron, MT, USA, in 1939, $n = 2$; FTN in 1952, $n = 4$; Yellowstone National Park in 1953, $n = 2$; and Maxwell State Game Refuge, KS, USA in 1984, $n = 4$; Reffalt et al. 2008, Dratch and Gogan 2010). The NBR is located on a small, low-rolling mountain that connects to the Mission Mountain Range in northwest Montana. Range elevation varies from 788 m to 1,489 m above sea level. Topsoil on the range is generally shallow and mostly underlain with rock, which is exposed in many areas, forming ledges and talus slopes. Soils over the major portion of the range were developed from materials weathered from strongly folded pre-Cambrian quartzite and argillite bedrock. The National Bison Range is a diverse ecosystem of intermountain grasslands, Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forests, riparian areas, and ponds. In addition to herds of bison, it supports populations of Rocky Mountain elk (*Cervus canadensis nelsoni*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bears (*Ursus* spp.), bobcat (*Lynx rufus*), and over 200 species of birds. Average high temperatures in the Mission Valley range from approximately -1°C in December and January to 32°C in July; average low temperatures range from -8°C to 10°C . Most of the precipitation in the valley occurs during the spring and early summer, averaging more than 5 cm per month in May and June. Precipitation during the rest of the year averages between approximately 2.5 cm and 3.8 cm per month.

METHODS

We constructed an individual-based simulation in C++ using the Microsoft Visual Studio (2010) development environment to test the genetic effects of 3 culling strategies for management of bison herds. All culling strategies maintained balanced sex ratios and preferentially culled yearlings to maintain a target population size of 350 individuals.

Culling Strategies

The AAC was based on the general principles of the management strategy used by the USFWS, and was intended to maximize the retention of genetic variation by using a target set of microsatellite loci to guide culling decisions. In each model year, we calculated the frequency of each microsatellite allele in the total population and defined rare alleles as those falling below a threshold frequency; we tested values of 0.05 and 0.02. We initially marked all yearlings without rare alleles for cull. If this marked pool contained more individuals than were needed for cull, we randomly returned individuals to the pool of yearlings to keep. If additional culling was required to meet the target population size, we randomly chose yearlings for cull from the pool of individuals containing rare alleles. Once we reached the target population size, we optimized the yearlings in the keep and cull groups in an effort to reduce the contribution of rare alleles by individual successful breeding males. The optimization algorithm ensured that no more than 2 copies of any rare allele were present in the total population for the model year. The model

checked every allele at each locus; if a rare allele with >2 copies was encountered, yearlings were swapped between the keep and cull groups. The optimization was improved if the number of rare alleles with >2 retained copies was decreased by the swap. Yearlings with the only copy of a rare allele were not eligible for cull and were not included in optimization swaps. The group of yearlings to cull was finalized when swapping could not further improve the optimization.

We developed the MK strategy to minimize kinship across the herd, thereby maximizing the retention of genome-wide variation. We prioritized yearlings that had a high representation of their genome in the population (i.e., those with many relatives) for cull. We used mean kinship (Ballou and Lacy 1995), a measure of the representation of an individual's genome in the population, as the metric to rank individuals for cull. We iteratively selected yearling bison with the highest MK for cull until we reached the cull quota, and recalculated MK values after each individual cull.

The Random strategy randomly removed yearlings from the population until we reached the target size, with an even sex ratio. The MK and Random strategies were identical to those evaluated in Giglio et al. (2016).

Model Parameters and Flow

We used demographic and pedigree data from the FTN National Wildlife Refuge bison herd (2004–2010) to generate input parameters for our simulations (Table 1; Giglio et al. 2016), with input parameters being further augmented with existing data on bison reproduction (Borggreen 2010) and mortality (Meagher 1986) as needed. The target population size for each herd was 350 individual bison. We used the 2004 FTN herd and the 2013 NBR herd as the foundations for the populations used to start our simulations. Nearly complete data at 55 microsatellite loci were available for these starting populations, but we used a custom R script (R Foundation for Statistical Computing, Vienna, Austria) to generate missing genotypes by randomly drawing alleles from the frequency distributions observed at each locus across the genotyped portion of the relevant (FTN or NBR) starting population. We used this complete panel of 55 microsatellite loci to guide management decisions in the AAC strategy (the Random strategy required no genetic information and the MK used pedigree data rather than genotypes) and referred to it as the target suite of loci. Although it is not known how culling individuals based on rare alleles affects variation across the rest of the genome, previous research on captive populations reported that breeding individuals based on rare alleles at a limited number of loci can lead to a reduction in genome-wide genetic variation (Haig et al. 1990, Vrijenhoek and Leberg 1991, Miller 1995). Because reduction in genomic variation can have fitness-related consequences (Charlesworth and Charlesworth 1999), it is important to understand how variation is maintained at non-target loci, loci across the rest of the genome that are not used to make culling decisions. To determine the effects of genetic-based culling strategies on non-target microsatellite loci (representing the portion of the genome not actively used for culling), we simulated an

Table 1. Parameters used to simulate genetic variation and inbreeding in bison herds under 3 different culling strategies (all-allele conservation [AAC], mean kinship [MK], and Random) at the Fort Niobrara Wildlife Refuge (FTN), Nebraska, USA, and the National Bison Range (NBR), Montana, USA. We chose parameter values based on empirical data from the FTN bison herd (2004–2010). Microsatellite loci used to characterize the genetic variation of the initial population of the FTN (2004) and NBR (2013) bison herds included target loci, used to prioritize yearlings for cull, and non-target loci, used to represent genetic variation at loci not used to prioritize yearlings for cull. Rare alleles are those occurring in the population at a frequency lower than the rare allele threshold. Mortality and breeding parameters summarized from Giglio et al. (2016).

Parameters	Values
Input file parameters	
Founder total	FTN: 259, NBR: 344
Number of target loci	55
Number of non-target loci	55
Rare allele threshold (AAC only)	0.05, 0.02
Loop parameters	
Target population size	350
Number of years to run	100, 200, and 500
Number of iterations	1,000
Breeding parameters	
Age range females will breed	2–21
Age range males will breed	4–16
Offspring produced per breeding female	1
Proportion of males that will breed	0.46
Proportion of females that will breed	0.82
Dominant male breeding parameters	
Proportion of breeders that are dominant	0.21
Age range dominant males breed	8–12
Proportion of offspring produced by dominant males	0.4
Number of years males are dominant	1
Mortality parameters	
Female mortality	$0.03 \times 1.15^{\text{age}}$
Male mortality	$0.05 \times 1.16^{\text{age}}$
Max. age	24

additional panel of 55 microsatellite loci that we tracked and evaluated but did not use to guide culling prioritization. We generated these simulated, non-target loci using the same starting allele frequency distributions as the 55 target loci. For the AAC culling strategy, we tested rare allele frequency threshold values of 0.05 and 0.02.

The individual-based model followed the same general simulation steps described in Giglio et al (2016). These steps included 1) loading an initial starting population into the simulation (in this study, either the 2004 FTN herd or the 2013 NBR herd); 2) identifying breeding individuals based on user-defined breeding parameters (Table 1); 3) producing offspring by randomly assigning 1 allele from each parent across all loci; 4) calculating the number of individuals to be culled by subtracting half the target population size from the number of each sex in the population; 5) culling yearlings based on selection criteria outlined in the 3 culling strategies; 6) incurring mortality and aging according to user-defined rates (Table 1) and; 7) repeating steps 2–6 for 100, 200, and 500 years. We ran the simulation for 1,000 iterations under each culling strategy for each bison herd.

Evaluation of Culling Strategies

We evaluated culling strategies (AAC, MK, and Random) based on several measures of genetic variation and

inbreeding. We calculated allelic richness (A), measured as the mean number of alleles per locus, and observed heterozygosity (H_o), calculated directly for each locus across individuals and then averaged across loci (Hartl and Clark 1997), separately for target and non-target loci. We calculated proportional gene diversity (GD ; expected heterozygosity) as $1 - MK$, where MK is the average mean kinship in the population (Ballou and Lacy 1995). Average inbreeding in the population (\bar{F}) was equal to the kinship between an individual's sire and dam averaged across all individuals (Falconer 1981). We averaged these measures across 1,000 iterations of each culling strategy simulation for 3 time steps at 100, 200, and 500 years. We ran the AAC culling strategy using 2 different rare allele threshold values (0.02 and 0.05). Based on the pedigree from the FTN herd, males were most likely to breed as dominant males for 1 (mode) or 2 (mean, median) years (Fig. S1, available online in Supporting Information). In addition to simulations with dominant males selected every year, we also ran simulations in which males were assigned as dominant breeders for 2 consecutive years.

RESULTS

The founding FTN population had a mean allelic richness of 4.418 at target loci and 4.348 at non-target loci. Average observed heterozygosity was 0.585 for target loci and 0.591 for non-target loci. The founding NBR population had a mean allelic richness of 4.982 at target loci and 4.991 for non-target loci. The observed heterozygosity in our simulated starting dataset was 0.437 for target loci and 0.458 for non-target loci; this value is lower than previously reported for this herd (0.648; Halbert and Derr 2008). This is due to the number of missing genotypes for the 55 target loci that were simulated (33.4% for FTN and 35.5% for NBR). The observed heterozygosity was 0.656 for target loci prior to filling in missing genotypes. Because all founding individuals were assumed to be unrelated, pedigree-based calculations of gene diversity started at 0.998 and the average inbreeding coefficient at 0.000 for both of the founding populations (Tables S1 and S2, available online in Supporting Information).

Genetic variation (A , H_o , and GD) was reduced and inbreeding (\bar{F}) increased in all populations over time, as predicted for any population of finite size. All simulations succeeded in maintaining the target population size and balanced sex ratio. Differences among herds and among culling strategies in the amount of genetic variation retained and extent of inbreeding became more pronounced over time and were most evident at the 500-year mark. Simulations with a tenure system of male dominance (i.e., males were assigned as dominant breeders for 2 consecutive years rather than 1) resulted in a greater loss of genetic variation and higher level of population inbreeding compared to when dominant males were reselected each year. This pattern was observed for all strategies (Figs. S2 and S3, available online in Supporting Information).

For the FTN herd, the AAC culling strategy retained the highest allelic richness relative to the starting population but only for target loci. We observed this effect at both rare allele

frequency thresholds, with a decrease in allelic richness of 33% for the 0.05 threshold and 34% for the 0.02 threshold, relative to the initial population (Table S1, Fig. 1). The AAC strategy exhibited good retention of heterozygosity for target loci (24% and 28% decreases for 0.05 and 0.02 rare allele frequency thresholds) but large declines in heterozygosity for non-target loci (35% and 37% declines; Table S1, Fig. 1). The FTN population experienced the greatest decline in gene diversity (37% decline) and the greatest increase in inbreeding (0.363) under the AAC strategy (for the 0.02 threshold; Table S1).

The MK culling strategy retained the most variation at non-target loci with a decrease of 37% in allelic richness and 26% in heterozygosity in the FTN herd (Fig. 1). The MK strategy also retained the highest genome-wide variation with a decrease of 27% in gene diversity and yielded the smallest increase in inbreeding (to 0.262; Table S1, Fig. 1). The Random culling strategy yielded the greatest reduction in allelic richness and heterozygosity at target loci (decrease of 44% and 35%, respectively) and allelic richness at non-target loci (decrease of 45%; Fig. 1). Gene diversity was reduced by 36% and inbreeding increased to 0.360 under the Random strategy (Table S1, Fig. 1).

Variation among model iterations (measured by the coefficient of variation [CV]) was greatest for the Random strategy in terms of heterozygosity at target loci (0.076), allelic richness (0.059) and heterozygosity at non-target loci (0.087), gene diversity (0.041), and inbreeding (0.071; Table S1). Variation among model iterations was greatest for the AAC strategy (both 2% and 5% rare allele thresholds) for allelic richness at target loci (0.057 and 0.066, respectively). Variation among runs was lowest for the MK strategy for all measures of genetic variation (Table S1).

For the NBR herd, performance of culling strategies was similar to the FTN herd. The AAC culling strategy retained more variation at target loci (46% and 44% declines in allelic richness, and 17% and 16% declines in observed heterozygosity for the 0.05 and 0.02 rare allele frequency thresholds, respectively) but experienced very large declines in variation at non-target loci (58% and 52% allelic richness and 35% heterozygosity declines for both thresholds; Table S2, Fig. 2). Under the AAC strategy, considerable genome-wide variation was lost (36% decline in gene diversity for both rare allele frequency thresholds) and inbreeding was extensive (0.351 and 0.357 for 0.05 and 0.02 allele frequency thresholds, respectively; Table S2, Fig. 2). Genome-wide

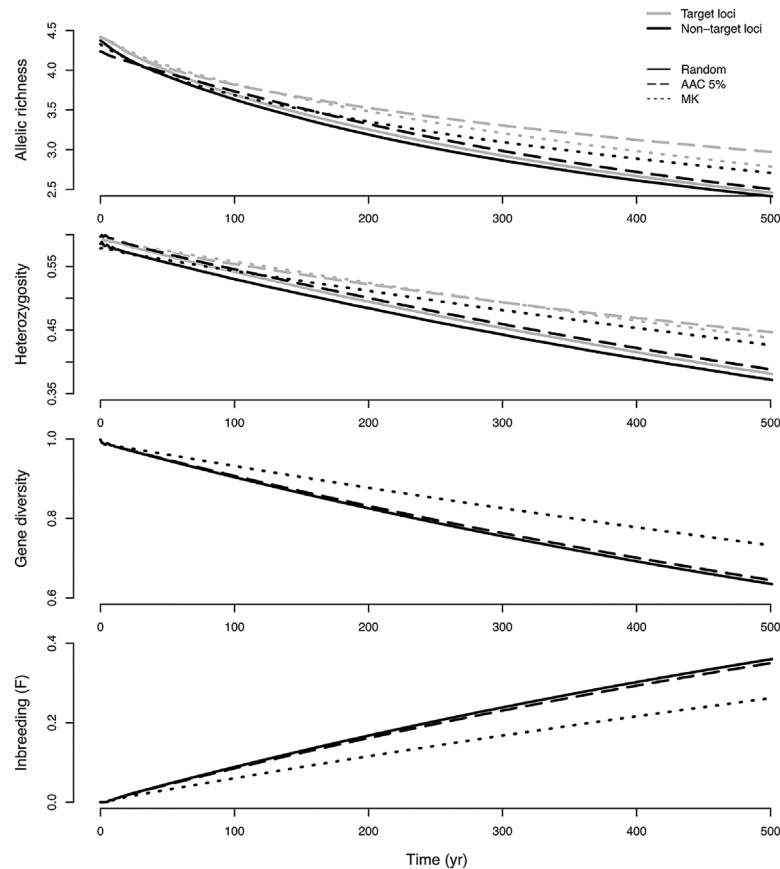


Figure 1. Simulated loss of genetic diversity and accumulation of inbreeding over time in the Fort Niobrara Wildlife Refuge (FTN), Nebraska, USA, bison herd under 3 different culling strategies: Random, all-allele conservation (AAC; with rare alleles defined as those falling below a frequency of 5% in the herd), and mean kinship (MK). We initialized simulations with microsatellite loci (55 target loci, used to prioritize yearlings for cull, and 55 non-target loci, used to monitor genetic variation at loci not considered when choosing yearlings for cull) from the FTN bison herd (2004) and run for 500 years. Allelic richness and heterozygosity are plotted for target and non-target loci under each culling strategy. The MK strategy retains the most genetic variation overall; although the AAC strategy retains diversity at target loci, it performs poorly for non-target loci. The MK strategy retains the highest gene diversity and best limits the accumulation of inbreeding.

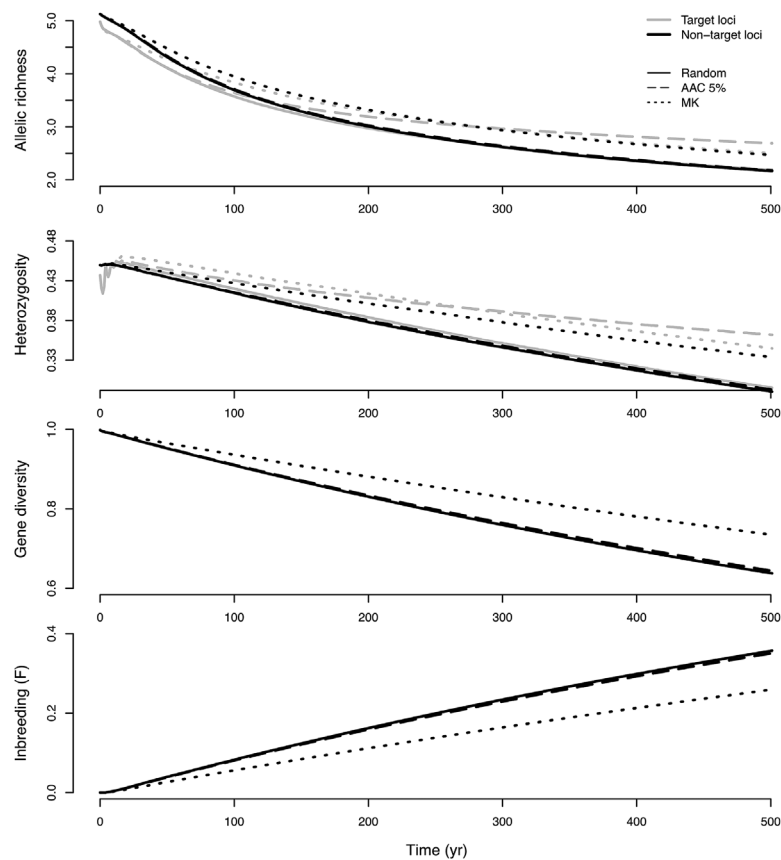


Figure 2. Simulated loss of genetic diversity and accumulation of inbreeding over time in the National Bison Range (NBR), Montana, USA, bison herd (initialized with microsatellite data from 2013 and run for 500 years). Allelic richness and heterozygosity are plotted for target loci, used to prioritize yearlings for cull, and non-target loci, not considered when making culling decisions, under 3 culling strategies: Random, all-allele conservation (AAC; with rare alleles defined as those that occur below a frequency of 5%), and mean kinship (MK). The MK strategy retains the most genetic variation overall; although the AAC strategy retains diversity at target loci, it performs poorly for non-target loci. The MK strategy retains the highest gene diversity and best limits the accumulation of inbreeding.

diversity retention was lowest for the AAC strategy (Table S2). The MK strategy yielded the highest retention of heterozygosity and allelic richness at non-target loci (Fig. 2), and retained the highest genome-wide variation with a 26% decrease in gene diversity and an increase in inbreeding to 0.262 (Table S2, Fig. 2). The Random strategy resulted in the lowest retention of allelic richness and heterozygosity at the target (decrease of 56% and 32%, respectively) and non-target loci (decrease of 58% and 35%, respectively; Fig. 2).

The Random strategy had the greatest variation among model iterations (CV) for all genetic diversity measures except allelic richness at target loci (Table S2). The AAC strategy had the greatest variation among model iterations for allelic richness at target loci, with a CV of 0.065 (2% threshold) and 0.067 (5% threshold). Variation among runs was lowest for the MK strategy for all measures of genetic variation (Table S2).

DISCUSSION

Management strategies that use pedigree information improve retention of genetic variation compared to strategies that rely solely on demographic information or strategies based on managing allelic diversity at a suite of loci.

Specifically, management of genetic variation in bison conservation herds can be improved using an MK strategy, which focuses on the retention of genome-wide variation. The improvements in genetic diversity retention and inbreeding accumulation translated to herds with different founding population sizes and genetic variation, suggesting that an MK strategy could be effective for managing bison conservation herds nationwide.

The MK strategy outperformed the AAC and Random strategies. Under the MK strategy, more genetic variation was preserved and inbreeding accumulated more slowly than under the Random strategy. This pattern was consistent across all genetic diversity metrics for target and non-target loci. The MK strategy also outperformed the AAC strategy in terms of genome-wide variation, as measured by gene diversity and inbreeding. Although the AAC strategy effectively maintained genetic variation at a suite of target loci, it was ineffective in maintaining genetic variation at non-target loci and thus genome-wide variation. In contrast, the MK strategy maximized the retention of genome-wide variation, making it the most effective method for culling individual bison. By choosing individuals for cull based on their overall relationships to the rest of the population, population-level inbreeding and genetic erosion can be

mitigated by equalizing the representation of individual genomes within a population. Our MK strategy is similar to pedigree-based strategies used by captive breeding programs that use mean kinships to select breeding pairs (Ivy and Lacy 2012). Breeding individuals with low MKs is effective for maintaining genetic variation while limiting inbreeding (Ballou and Lacy 1995, Montgomery et al. 1997, Fernandez and Torro 1999, Sonesson and Meuwissen 2001, Wisely et al. 2003). In wild populations, it is typically not feasible to select individual breeding pairs. However, adapting a pedigree-based breeding strategy to prioritize individuals with high MKs for removal is predicted to be a useful population management tool (Grueber and Jamieson 2008, Eggert et al. 2010, Giglio et al. 2016). For example, in New Zealand, the endangered takahe (*Porphyrio hochstetteri*) is managed to maintain genomic variation and reduce inbreeding by removing individuals with high MK values from the wild population and replacing them with unrelated individuals from captivity (Grueber and Jamieson 2008). Further, an MK-based strategy has been proposed for controlling the population size while maintaining genetic variation in the horses of Assateague Island National Seashore, Maryland, USA (Eggert et al. 2010). We showed that a kinship-based culling strategy improves the retention of genetic variation in managed bison herds relative to other strategies that have been employed.

The AAC strategy retained more genetic variation than the Random strategy but less than the MK strategy. Rare allele thresholds of 0.02 and 0.05 did not significantly affect retention of genetic variation or the accumulation of inbreeding in the FTN or NBR herds. The AAC strategy was designed to reflect the complex culling decisions conducted by the USFWS; however, our model differs from the manually implemented USFWS strategy in 2 ways. First, the AAC strategy uses an optimization algorithm to ensure that no more than 2 copies of any rare allele are present in the total population, whereas the USFWS strategy limited the number of copies of rare alleles in yearlings only. Retaining 2 copies of a rare allele in the yearling population would result in a higher chance that a particular allele persists in the total population but could reduce the number of rare alleles that could be retained. The effect of the optimization on inbreeding would likely depend on the specific situation. For example, 2 yearlings that share a rare allele could be siblings, but an adult and a yearling that share a rare allele could be a parent-offspring pair. The second difference between the AAC model and the USFWS strategy is that our model maintains an equal adult sex ratio, whereas the USFWS strategy maintained an even yearling sex ratio. In instances where there is a large skew in the population sex ratio, for example during establishment of a new herd, the 2 approaches would differ in how they restored a balanced sex ratio. For example, many conservation herds were historically managed for a female-biased population, including the FTN herd as modeled here. To get to a balanced sex ratio, the USFWS would have adjusted those sex ratios over perhaps a decade, with annual efforts to maintain an even yearling sex ratio. In contrast, the AAC model would adjust the

population sex ratio very quickly by culling female yearlings until the adult sex ratio was even. In our simulations, we did not specifically model herd establishment or environmentally based stochasticity in adult sex ratios, so we did not encounter this situation.

Our results using empirical data from 2 different bison herds demonstrated consistently improved retention of genetic variation under the MK strategy. The MK strategy proved optimal for preserving genetic variation and minimizing inbreeding for the FTN and NBR herds, which differed in the number of individuals and the genetic diversity in the founding population. Further, the MK strategy was robust to the incorporation of a tenure-based mating system where the same few males produced proportionally more offspring in consecutive years compared to the majority of the breeding males (Figs. S2 and S3). The NBR herd lost more genetic variation under all culling strategies compared to the FTN herd. This pattern was likely influenced by the presence of more alleles, and consequently more rare alleles, in the founding NBR herd compared to the FTN herd. Rare alleles are lost quickly through genetic drift, resulting in a stronger reduction in allelic richness and heterozygosity over time than in a population with fewer, more common alleles. Thus, bison herds with more rare alleles will experience an increased rate of loss in genetic variation due to the effects of genetic drift. Of the strategies we tested, the MK strategy does the best job of slowing the loss of genetic variation and limits the accumulation of inbreeding, and thus is predicted to increase long-term population persistence by reducing extinction risk. The MK strategy may also be implemented in metapopulation-based management. Currently, bison are not moved among herds because of concerns about cattle gene introgression and disease (Hedrick 2009). However, if future translocations occur, an MK strategy may be implemented to prioritize individuals for translocation (i.e., prioritize the translocation of individuals with the lowest MK when compared to the individuals in the target herd). We further recommend that the MK strategy be evaluated in other intensively managed wildlife populations. Our results suggest that a kinship-based management strategy may prove useful for bison and a wide range of other wildlife species that have regular genetic monitoring and require regular population size management (Rourke et al. 2008). An MK strategy can also be implemented to maintain captive populations that are maintained for genetic rescue or translocation to wild populations (Hedrick and Fredrickson 2008).

Of our modeled culling strategies, those using genetic data (AAC and MK) are the most expensive to implement in terms of money, time, and effort; however, using genetic data provides significant improvement at maintaining genomic variation and mitigating population inbreeding, particularly under the MK culling strategy. If the MK strategy is to be used, molecular data can successfully be used to determine parentage of calves prior to cull as yearlings. The microsatellite panel currently used by USFWS has high discriminatory power for parentage assignment, but other molecular markers could also be used. Regardless of the marker used, accurate parentage assignment is critical for

kinship-based strategies to be effective (Putnam and Ivy 2014).

MANAGEMENT IMPLICATIONS

Incorporating genetic data into management actions for size-limited and isolated populations improves the long-term persistence of bison. Our simulation results indicate that bison management can be improved by implementing a kinship-based strategy to prioritize individuals for cull from herds regardless of founding population size and genetic variation, indicating that the MK strategy would likely benefit most bison conservation herds. Further, consistency among model iterations was high under the MK strategy, which might be especially important in the face of stochastic environmental fluctuations. Genetic management to maintain diversity will help mitigate the risks of population extinction, assisted by continued management to minimize demographic stochasticity through population size and sex ratio manipulation. The forward-in-time simulations we employed, parameterized with data from existing bison conservation herds, were useful for assessing outcomes prior to implementation.

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