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Managing Genetic Diversity and Extinction Risk for a Rare Plains Bison (*Bison bison bison*) Population

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Abstract

Unfenced plains bison are rare and only occur in a small number of locations throughout Canada and the United States. We examined management guidelines for maintenance of genetic health and population persistence for a small and isolated population of plains bison that occupy the interface between a protected national park and private agricultural lands. To address genetic health concerns, we measured genetic diversity relative to other populations and assessed the potential effects of genetic augmentation. We then used individual-based population viability analyses (PVA) to determine the minimum abundance likely to prevent genetic diversity declines. We assessed this minimum relative to a proposed maximum social carrying capacity related to bison use of human agricultural lands. We also used the PVA to assess the probability of population persistence given the limiting factors of predation, hunting, and disease. Our results indicate that genetic augmentation will likely be required to achieve genetic diversity similar to that of other plains bison populations. We also found that a minimum population of 420 bison yields low probability of additional genetic loss while staying within society-based maxima. Population estimates based on aerial surveys indicated that the population has been below this minimum since 2007. Our PVA simulations indicate that current hunting practices will result in undesirable levels of population extinction risk and further declines in genetic variability. Our study demonstrates that PVA can be used to evaluate potential management scenarios as they relate to long-term genetic conservation and population persistence for rare species.

Keywords Genetic diversity · Conservation · Population thresholds · Social carrying capacity · Sustainable harvest

Introduction

Determining abundance thresholds for wildlife populations is a fundamental yet challenging aspect of environmental management, particularly when species of conservation concern are involved (Shaffer 1981; Thomas 1990; Chadès et al. 2012). For management purposes, abundance thresholds represent transitions between desired and undesired population states and may be established relative to ecologically and socially relevant values (Martin et al. 2009). For example, achieving spatial coexistence between humans and wildlife often involves trading off a maximum wildlife population size determined by social tolerance with a minimum population size required to meet conservation goals. Determining the adequacy of proposed thresholds, and assessing the feasibility of maintaining desired population targets, usually requires predictions regarding the future state of populations relative to natural history information and anticipated limiting factors.

A common tool for predicting the future condition of populations is a population viability analysis (PVA), which can be used to quantify both extinction risk and changes to genetic variation through time (Reed et al. 2002; Hoban et al. 2012). Well-informed PVAs are useful for those who

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seek to prevent unacceptable risk to population persistence or to limit abundance consistent with management goals. In addition, PVA can evaluate potential alterations to the maintenance of genetic diversity relative to various management scenarios and help prevent unwanted diversity losses. Thus, PVA can be a conservation planning tool for small and isolated populations with sizes that are limited due to conflict with humans, such as North American plains bison (*Bison bison bison*).

Large herbivores often come into conflict with humans because they forage in or near agricultural areas (Hofman-Kaminska and Kowalczyk 2012; Ranglack and Du Toit 2016; Valls-Fox et al. 2018). In North America, historical abundances of plains bison were in the tens of millions (Shaw 1995). After European settlement in the 1800s plains bison were nearly extirpated from their natural habitat (Hedrick 2009), which is now dominated by human agriculture. Plains bison have been designated as threatened by the Committee on the Status of Endangered Wildlife in Canada since 2004. Conservation planning for bison typically considers monitoring and management of genetic variability to be a priority because the majority of populations are small and have limited space to expand (Freese et al. 2007; Sanderson et al. 2008). Genetic diversity of plains bison in North America presumably declined after the 1800s; however, long-term consequences of this decline are unknown. Probable effects of inbreeding depression, such as decreased natality and low calf survival, have been documented in at least one herd, the Texas State Bison Herd, which was managed at a low population size (40 to 100 individuals) from the 1970s to the early 2000s (Halbert et al. 2005; Hedrick 2009). Therefore, assessing the relative current genetic variation that exists in isolated populations of plains bison and maintaining or increasing these levels when possible is a key component of ensuring long-term sustainability of the subspecies.

Our study population, the Sturgeon River plains bison (SRPB) population (SK, Canada), constitutes one of only a few unfenced plains bison populations in North America. The population is noteworthy relative to many other bison herds because it undergoes natural selection pressures from predators such as wolves. The SRPB population was established in 1969 from ~10 to 22 founders, which originated from a fenced conservation herd 400 km away in Elk Island National Park, AB, Canada. The SRPB inhabit the interface between a protected national park and private agricultural lands and their population has declined more than 50% since 2005 (Merkle et al. 2015). The population was estimated to be 222 individuals in 2013 (Merkle et al. 2015) and is thought to have declined further in more recent years. Potential factors contributing to the decline include unrestricted hunting (Sigaud et al. 2017), anthrax (Shury et al. 2009), and wolf predation (Fortin et al. 2015). The

small size and recent decline of the population has resulted in concern regarding the minimum number of bison required to preserve long-term genetic diversity and achieve a reasonable probability of population persistence. However, the target size for the population is constrained by a socially based maximum abundance threshold that we define as the regional social carrying capacity for plains bison. We consider social carrying capacity to be the stakeholder tolerance for real, perceived, and potential impacts that a species may have on humans. During regional management planning activities, stakeholders estimated the current social carrying capacity to be 430 bison given the number of conflicts and property damage that occurred when the population was above this size (SRPB Management Plan 2013).

The SRPB periodically come into conflict with humans when they leave the national park and occupy private lands because they damage crops, forage on hayfields, and pose a safety concern (Sigaud et al. 2017). No hunting is permitted within national park boundaries but hunting by Indigenous individuals is allowed at any time of the year outside the park on land owned by the provincial government or with private landowner permission. Bison are drawn to high-quality forage on pastures adjacent to the park where they predictably congregate in late summer, which has resulted in an ecological trap (Sigaud et al. 2017). Over numerous years bison have been observed returning, often on a daily basis, to the same agricultural patches despite repeated hunting at these locations (Sigaud et al. 2017). Hunting is therefore a considerable concern for those interested in the long-term preservation of this bison population.

The objective of this study was to evaluate the likelihood of sustaining long-term conservation goals for the SRPB given their population size and proposed social carrying capacity threshold. These goals include population persistence and conservation of adequate genetic diversity relative to other existing plains bison populations. We therefore evaluated the current level of genetic variation in our study population relative to similar plains bison populations (Wilson and Strobeck 1999). Next, we developed a PVA in the form of individual-based simulation models to predict future changes to genetic diversity at various potential long-term population sizes. We determined the minimum population abundance threshold required to maintain genetic diversity measured as expected heterozygosity. We considered adequate maintenance of long-term genetic diversity to be the conservation of 90% of the population's current genetic variability over 200 years (Soulé et al. 1986; Allendorf and Ryman 2002; and Frankham et al. 2002). Quantifying the current and potential future genetic diversity of the SRPB will provide insight into how population size restrictions and the number of founding individuals affect long-term genetic diversity of plains bison populations established from Elk

Island, which include all conservation populations in Canada. We also used the PVA to model the probability of population persistence given the population's size and demographic structure in 2013 when detailed demographic data were available. We applied social carrying capacity and other limiting factors, such as unrestricted hunting, predation, and anthrax outbreaks to determine long-term extinction risk. Finally, we updated population estimates for the SRPB with an additional 4 years of recent aerial survey data to assess differences between proposed population abundance targets and current population size.

Materials and Methods

Study Area

The SRPB inhabit an area of ~1000 km^2 in central SK, Canada. The majority of their range is within the southwest corner of Prince Albert National Park (53°44′ N, 106°39′ W) and consists of deciduous and coniferous forest mixed with shrublands, meadows, and water bodies. Approximately 11% of their range is on agricultural lands adjacent to the national park. Range expansion of plains bison outside of Prince Albert National Park is largely restricted by agricultural practices and other human developments.

Genetic Variability

To quantify genetic variability, we collected bison blood samples ($n = 25$; 24 females and 1 male) during capture and handling events in 2005, 2007, and 2010. During captures, animals were cared for in accordance with the policies and guidelines of the Canadian Council on Animal Care (http://www.ccac.ca). We determined genetic variability by following the methods of Wilson and Strobeck (1999), which allowed for a direct comparison with estimates of genetic variability of other populations of plains bison (including the founding population, Elk Island National Park). Genotyping was conducted by the Molecular Biology Facility in the Department of Biological Sciences at the University of Alberta. Our genotypes were generated with ten microsatellite loci (Table 1). A Qiagen DNeasy® Blood and Tissue extraction kit (Qiagen, Valencia, CA, USA) was used to isolate total genomic DNA. Five PCR reactions were completed per individual and pooled into a single capillary on a 3730 DNA analyzer (Applied Biosystems, Foster City, CA). Genotypes were generated using Gene-mapper (Applied Biosystems, Foster City, CA) and standardized to allele calls previously generated by Wilson and Strobeck (1999).

We calculated the number of alleles, allele frequencies, observed heterozygosities, expected heterozygosities, and

Table 1 Number of alleles (N_A), allelic richness (R_t), observed heterozygosities (H_O), expected heterozygosities (H_e), and probability of identities (pI) for each of ten microsatellite loci ($n = 25$; collected in 2005, 2007, and 2010) in the Sturgeon River plains bison population

Locus	N_A	R_t	H_O	H_e	pI
BM143	4	4.00	0.84	0.71	0.13
BM2830	3	2.95	0.28	0.34	0.44
BMC1222	2	2.00	0.48	0.50	0.37
BM1225	4	4.00	0.80	0.71	0.12
BOVFSH	4	3.76	0.64	0.69	0.15
Eth121	2	2.00	0.32	0.33	0.48
RT9	2	2.00	0.24	0.28	0.54
RT24	2	2.00	0.44	0.39	0.43
RT27	2	2.00	0.52	0.48	0.38
RT29	4	4.00	0.96	0.75	0.10
	2.9	2.87	0.55	0.52	–

Bottom summary row indicates mean values across loci for each diversity metric

probabilities of identity (pI) for each locus. We used these values to calculate three measures genetic variability: allelic richness, mean expected heterozygosity, and overall pI. We calculated allelic richness using rarefaction methods described by Petit et al. (1998), where the average estimated number of alleles per locus was standardized to the lowest sample size. We calculated expected heterozygosities with Nei's unbiased gene diversity equation (Nei 1987) and then averaged them over all loci to obtain mean heterozygosity. We determined unbiased pI values using the methods of Paetkau et al. (1998) and overall pI by multiplying pI values for all loci. We tested deviations from the Hardy–Weinberg equilibrium with the true probability-test or 'exact test' in GenePop 4.0 (Raymond and Rousset 1995). Because each locus had fewer than five alleles, we calculated exact p-values with the complete enumeration method described by Louis and Dempster (1987). We compared genetic variability in the SRPB population to variability in its founding population and the Pink Mountain plains bison population in northern British Columbia, Canada. The Pink Mountain population also originated from Elk Island but with a higher number of founders ($N = 48$, COSEWIC 2013). We calculated genetic variation parameters for Pink Mountain ($n = 19$) and Elk Island ($n = 31$) using data from Wilson and Strobeck (1999); however, we excluded locus BM4513 because it was fixed in the populations we assessed.

Population Viability Analysis

We used individual-based simulation models for PVA developed with the software program VORTEX 10.1 (Lacy and Pollak 2015), which simulates the effects of deterministic factors and demographic, environmental, and genetic

Table 2 Population-limiting scenarios that were considered in population viability models for the Sturgeon River plains bison population

Scenario	Scenario-specific population mortality[a]	Annual probability of occurrence (%)
Anthrax outbreak	10%	5, 10, 15, 20, and 25
Rare anthrax outbreak (high mortality)	50%	2
Harvest	8 females and 12 males	100
Harvest with anthrax outbreak	10%	5, 10, 15, 20, and 25
	8 females and 12 males	100
Harvest with rare anthrax outbreak (high mortality)	50%	2
	8 females and 12 males	100
Harvest moratorium	0% until N = social K	100 until N = social K

Simulations were run 1000 times over 200 years to determine the annual probability of population extinction. Model parameters and values are given in Appendix 1

[a]Scenario-specific mortality is in addition to mortality rates listed in Appendix 1. See Appendix 1 for age distribution of harvested males and females

stochasticity on populations. These simulations predict population dynamics and population genetic change on the basis of probabilities of annual events (e.g., birth, aging, death, and allele transmission) according to constants or random variables and user-specified distributions. Individual-based VORTEX models are widely used and have been validated as a reliable tool for conservation planning (Brook et al. 2000). VORTEX has been used to evaluate management strategies (e.g., Bach et al. 2010; Chilvers 2012; Carroll et al. 2013) and to predict future genetic diversity in small and isolated populations (e.g., Vonholdt et al. 2008; Zachos et al. 2009)

We designed our simulation models to predict the minimum population abundance threshold required to meet the long-term goal of maintaining 90% of the population's genetic variability over 200 years. We considered this goal to be obtained when 95% of the simulations resulted in maintenance of ≥90% genetic variability. Our models predicted the future probability of population persistence given the population's size and potential limiting scenarios (Table 2). We based model parameters on data specific to the SRPB population and published literature on other bison populations (Appendix 1). We used initial population size and age classes from Merkle et al. (2015) because these were the only available estimates that include specific age and sex classes. For all simulations, we ran 1000 iterations for 200 years or until all iterations resulted in extinction.

Minimum population abundance threshold for genetic maintenance goals

We used an incremental range of a priori minimum population thresholds to illustrate potential long-term population size scenarios and explore how these would affect genetic variability, measured as expected heterozygosity. We predicted genetic variability by running a series of models that used each of the potential thresholds as a carrying capacity (K). When population size (N) exceeded K at the end of a model time cycle, we imposed additional mortality across all age and sex classes to reduce the size of the simulated population to K. During this process, we set the probability of individual mortality to $(N − K)/N$ (Lacy et al. 2015). We assessed changes in genetic variability by assigning each individual in the original population two unique alleles at a hypothetical locus (the infinite alleles model; Kimura and Crow 1964) and then simulating the Mendelian transmission of alleles from parents to offspring. We used the infinite alleles model as opposed to genetic data from the SRPB population because genetic diversity at a small number of neutral microsatellite loci may not be appropriate for predictions regarding inbreeding and ability to adapt to environmental changes. The infinite alleles model may in fact be more applicable to the rest of the genome.

Probability of population persistence relative to limiting scenarios

Predation, anthrax, and hunting have been identified as potential limiting factors for bison populations. Predation was inherent in all of our models because the survival parameters were calculated with values derived from other bison populations subject to predation by wolves. However, we ran simulations to examine the potential effects of anthrax outbreaks and current levels of unrestricted hunting pressure (Table 2). We estimated a 10% population mortality during typical anthrax events. Approximately 7% of the population died during the only documented anthrax outbreak in the SRPB population, in 2008 (Shury et al. 2009); however, some carcasses undoubtedly were undetected. Our 10% estimate of mortality is within the range documented in other populations (Salb et al. 2014). Because the frequency of future anthrax outbreaks is uncertain, we examined the sensitivity of the PVA to a range of plausible annual probabilities of an outbreak (5, 10, 15, 20, and 25%). An outbreak every 4 years (25% annual probability) is approximately equivalent to the long-term average for the Slave River Lowlands and Wood Buffalo National Park region in the Northwest Territories, Canada,

where surveillance of anthrax in bison has occurred since 1962 (Salb et al. 2014). This was considered the upper range of outbreak frequency for the SRPB because to date only one outbreak is known to have occurred. We also modeled a rare anthrax scenario with a mortality rate of 50%. We chose this value because observations during a 2012 anthrax outbreak in the Mackenzie bison sanctuary, Northwest Territories, Canada indicated a minimum 30% mortality rate; however, subsequent population estimates suggested that mortality may have been higher (Government of Northwest Territories, unpublished data). We modeled this potential rare anthrax scenario at an annual probability of 2% (on average once every 50 years) because to our knowledge an outbreak of this magnitude has only been documented once in wild bison populations in ~50 years of observations.

To simulate the effects of current unrestricted hunting on the potential for population persistence, annual harvest rate was assumed to be constant across years and was set at the observed 2013 harvest rate for the SRPB population (see Appendix 1). We used harvest data from 2013 because it was considered to be a representative year in terms of the number of bison harvested (Saskatchewan Ministry of Environment, unpublished data). The year 2013 also was one of the few years we collected age and sex data from a substantial portion of the harvested bison. Harvest data were determined through direct observation of hunting, opportunistic observations of gut piles, voluntary reporting by hunters, and communications with owners of lands on which hunting occurred. Both sex and age of 13 of 20 bison were determined in the field (Sigaud et al. 2017). In addition, we had only age data for one bison and only sex data for six bison. For bison of unknown sex or age, we randomly assigned that unknown parameter on the basis of the distribution of known values. We estimated that 8 females and 12 males were harvested in 2013. Our modeled estimates of extinction risks due to hunting are conservative because our data may not account for all animals harvested.

In our anthrax and unrestricted harvest simulations, we used a K equal to the social carrying capacity ($K = 430$) and assumed that extinction occurred when only one sex remained. Therefore, this aspect of the simulations assumed that abundance was maintained at the maximum social carrying capacity threshold if that threshold was reached (i.e., by restricted and sustainable harvest or other culling techniques). We ran the unrestricted harvest simulation that used 2013 harvest levels both with and without the effects of anthrax. We used our PVA to approximate and test a long-term average sustainable harvest by simulating a moratorium on hunting until the social carrying capacity was reached and then estimating the mean number of individuals removed per year to maintain this target. Finally, we updated SRPB population estimates from

Merkle et al. (2015) with an additional 4 years of recent data. We used these estimates to compare proposed minimum population abundance thresholds to current population sizes. Briefly, we estimated population size with an N-mixture model, informed by a resource selection function, that was based on how habitat use of GPS-collared bison during the 5 weeks before and after annual aerial surveys influenced detection probability (see Merkle et al. 2015—Supporting Information).

Results

Genetic Variability

The order from greatest to least amount of genetic variability as determined by all three measures was Elk Island > Pink Mountain > SRPB (Fig. 1). The allelic richness in the SRPB population was 2.87 (SE = 0.31). The SRPB population had a mean expected heterozygosity of 0.52 (SE = 0.06) and $\log_{10}$ of 1/overall unbiased pI of 5.8. We did not estimate error for overall pI values because they were calculated as the product of the individual pI at each locus. We did not detect deviations from the Hardy–Weinberg equilibrium at any individual locus (all p-values for exact tests >0.22).

Population Viability Analysis

Minimum threshold for genetic maintenance goals

Our models predicted that a minimum of 420 bison will meet the goal of maintenance of ≥90% of genetic variability over 200 years. The range of potential abundances that we assessed resulted in predictions of genetic variability that were between 11% (95% CI: 0–46%) and 98% (95% CI: 97–98%) of current levels after 200 years (Fig. 2). Gains in genetic variability retained through increases in abundance plateaued as abundances increased.

Probability of population persistence relative to limiting scenarios

When we applied the 2013 harvest data for the SRPB annually to population simulations, the probability of population extinction was 14% by 2040, 37% by 2060, and levelled off near 45–50% by the year 2100 (Fig. 3). When we modeled anthrax with a 10% mortality with annual harvest rates equivalent to those observed in 2013, the probabilities of population extinctions after 200 years ranged between 72% (for a 5% annual probability of an outbreak) and 100% (for a 25% annual probability of an outbreak—Fig. 3). When we considered the effects of
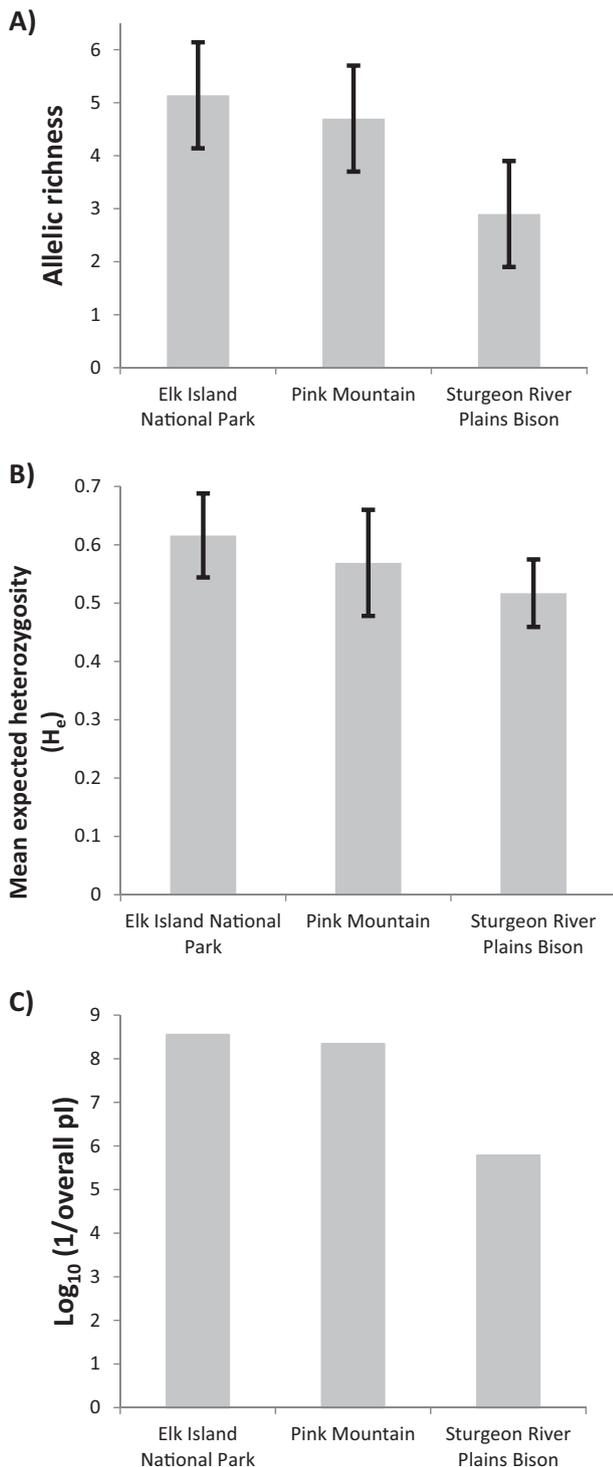
Fig. 1 **a** Allelic richness, **b** mean expected heterozygosity (H_e), and **c** $\log_{10}$ of 1/overall unbiased probability of identity (pI) for Elk Island National Park ($n = 31$), Pink Mountain ($n = 19$), and Sturgeon River ($n = 25$; collected in 2005, 2007, and 2010) plains bison populations. Data from Elk Island and Pink Mountain were calculated from Wilson and Strobeck (1999). Error bars for **a** and **b** represent ±SE

hunting in combination with the rare anthrax scenario (50% mortality and 2% frequency), assuming annual harvest rates

equal to those in 2013, the probability of extinction was >97% after 200 years (Fig. 3). In the absence of unrestricted harvest, none of the anthrax outbreak simulations resulted in probabilities of extinction above zero over a 200 year period. However, the 20 and 25% annual probabilities of an outbreak with a 10% population mortality and the rare anthrax scenario resulted in mean population sizes (range = 393 to 411) below the minimum abundance predicted to meet the long-term genetic maintenance goals ($N = 420$). The mean simulated population size reached social carrying capacity after 10 years in the absence of harvest and anthrax. Once social carrying capacity was reached, the average number of individuals randomly selected and removed per year to maintain social carrying capacity ranged from 25.6 to 31.1 (SD range: 28.7–32.9). Updated population estimates from aerial surveys indicated the population has been below our predicted minimums to maintain genetic diversity since 2007 (Fig. 4).

Discussion

Our results demonstrate how the number of founding individuals and long-term population size affect differences in genetic variability among plains bison populations founded from a single source population. Founding new populations with a limited number of individuals can result in a founder effect or genetic bottleneck. The consequences of a genetic bottleneck generally depend on the amount of genetic diversity prior to population declines, severity of population declines, and length of time that low population sizes persist (Nei et al. 1975; Lambrinos 2004; Chen et al. 2006). Both the SRPB and Pink Mountain populations were founded at approximately the same time. However, the SRPB population was founded from a smaller number of bison, which likely is why their genetic variability was lower than that of the other populations we assessed. The Pink Mountain population, which also originated with descendants from Elk Island, likely has more genetic variability than the SRPB population because it was founded with ~2–5 times more individuals and is maintained at a larger population size ($N \sim 1300$, COSEWIC 2013).

There is ample evidence to suggest that low levels of genetic variability and inbreeding depression in mammals affect birth weight, survival, reproduction, and susceptibility to disease (Keller and Waller 2002). Our results indicate the SRPB population has less genetic diversity than its founding population, which could reduce its relative resilience to inbreeding or environmental change. Future genetic augmentation may increase genetic variability to levels similar to that of its founding population or other populations that were founded with a higher number of individuals. This could be achieved by relocating breeding
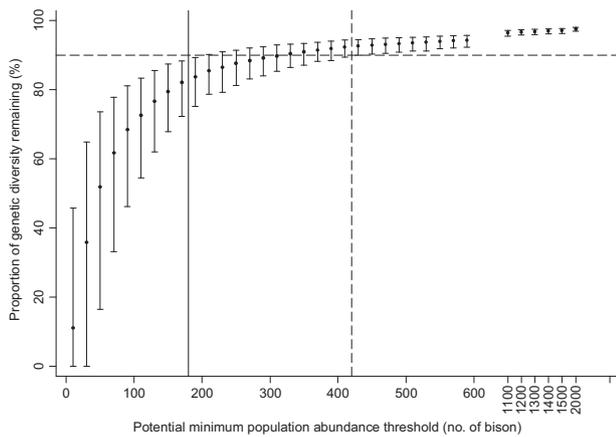
Fig. 2 The relative amount of genetic variability (%) remaining when the indicated minimum bison population abundance thresholds are sustained over 200 years. Results are the mean of extant populations for 1000 model iterations and error bars represent the 5th and 95th percentiles. The horizontal dashed line represents the goal of maintaining 90% of current levels of genetic variability for 200 years. The vertical dashed line represents the abundance required for a 95% probability of achieving the genetic maintenance goal. The vertical solid line represents the 2017 population estimate

Fig. 4 Population estimates and 95% confidence intervals from an N-mixture model for plains bison (*Bison bison*) in Prince Albert National Park, Canada, 1996–2017 that was informed by a resource selection function. Updated from Merkle et al. (2015)
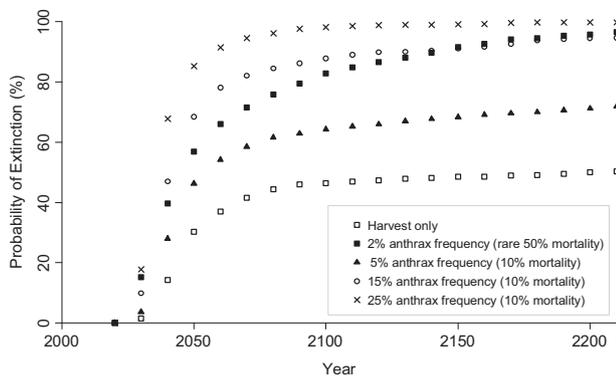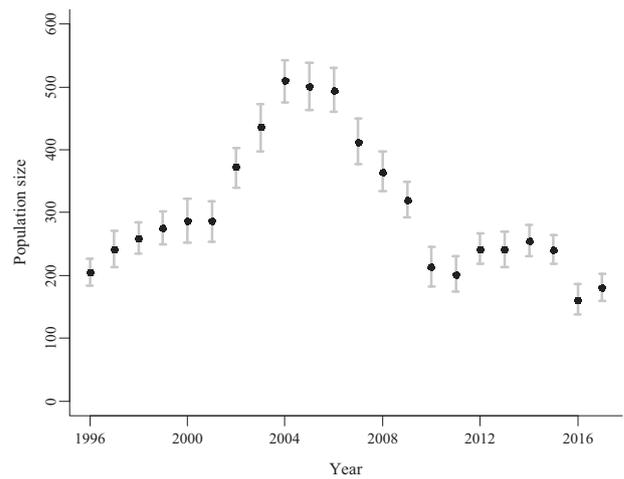

Fig. 3 Probability of extinction for the Sturgeon River plains bison population when the 2013 level of harvest is assumed to occur annually with a 5, 15, and 25% annual probability of an anthrax outbreak (assuming 10% mortality during an outbreak) and 2% annual probability of a rare anthrax outbreak (assuming 50% mortality). See Table 2 for details on scenarios. Probabilities of population extinction are illustrated at 10 year intervals as the percentage of 1000 model iterations that resulted in extinction. In the absence of unrestricted harvest, none of the anthrax outbreak simulations resulted in probabilities of extinction above zero over 200 years

bulls from other populations or artificial insemination (Lessard et al. 2009). If translocations are considered then appropriate mitigations should be implemented to prevent potential disease transmission. In addition, during long-term genetic management a more detailed analysis of introduced genetic variability may be required to fully understand the potential for outbreeding depression.

Future planning for genetic augmentation will likely be required for the SRPB; however, achieving and maintaining a population abundance target that prevents further declines in genetic variability and allows for a reasonable probability of population persistence will be of more immediate importance. Our results indicate a population abundance target ≥420 bison would be high enough to allow for long-term genetic conservation. This size is only marginally below the social carrying capacity, which makes it challenging to maintain the narrow target that meets both genetic conservation goals and social constraints. Working with local stakeholders and landowners to increase the social carrying capacity will be beneficial for the long-term conservation of the population. Factors that could increase social carrying capacity with local landowners include seasonal conservation easements that allow bison to forage outside the park for short periods of time, increased education about available crop insurance benefits, strategic exclusionary fencing in high conflict zones, and allowing local landowners to participate in a sustainable harvest when management targets are exceeded.

Keeping the population ≥420 bison would increase the likelihood that any augmented genetic material would be conserved, assuming the population persists. However, both our current population estimate and population viability simulations indicate that population targets deemed sufficient to attain genetic maintenance goals may not be achievable under current management conditions. The selection of a specific target is somewhat arbitrary and flexibility does exist in terms of the amount of genetic diversity that should be retained and the appropriate level of

prediction probability. However, our 2017 estimate of population size was 180 bison, indicating the population has been far below our estimated minimum abundance required to meet genetic conservation goals since 2007 (Fig. 4). Many of our simulated population-limiting scenarios resulted in high probabilities of extinction (>40%), which are much greater than the extinction-risk thresholds of 5% that are commonly used in wildlife recovery and conservation planning (Carroll et al. 2013). Small populations are more prone to extinction caused by predation (Festa-Bianchet et al. 2006), hunting (Frank and Woodroffe 2001), and catastrophic events (Hebblewhite et al. 2010) than large populations. Therefore, in addition to genetically viable population targets, the probability of overall population persistence must be considered in relation to foreseeable limiting factors.

Predation by wolves has been observed in certain areas of the SRPB range (Harvey and Fortin 2013, Fortin et al. 2015). However, detailed predation rates have not been documented and are presumed to be relatively low compared with predation on other ungulates (Fortin et al. 2003, Urton and Hobson 2005). Anthrax is the only disease of management concern presently known to affect the SRPB, and according to our disease simulations, anthrax alone is unlikely to increase the risk of population extinction. Including anthrax outbreaks in the PVA simulations did, however, exacerbate the effects of unrestricted harvest. Conceivably, the greatest threat to the SRPB population, and the main contributing factor to high probabilities of extinction in our simulations, is the current annual harvest rate. At present, only indigenous hunters are legally permitted to harvest bison in the area, and only when the bison are outside of Prince Albert National Park. The SRPB population is particularly vulnerable to harvest because the majority of the population predictably congregates during late summer and autumn on small, open sections of agricultural land where road access for hunters is reasonably easy. Repeated hunting in the same location does not appear to deter bison from congregating on agricultural lands with high-quality forage (Sigaud et al. 2017), which appears to be a different behavioral response to hunting than that of bison populations in other areas, such as the Henry Mountains, southern Utah, USA (Ranglack and Du Toit 2015). The unregulated nature of the harvest means that long-term and detailed information regarding potential fluctuations in annual bison harvest rates is lacking. Annual harvest pressure was assumed to remain constant in our PVA simulations due to the spatial and temporal predictability of bison presence outside protected areas where hunting occurs. We believe this assumption is valid due to repeated observations of hunting in these same locations

multiple years in a row, resulting in an ecological trap (Sigaud et al. 2017). However, if assumptions regarding consistent harvest pressure change in the future then predictions regarding population viability may require adjustments.

Numerous other studies have found that direct human-induced mortalities are major contributing factors to the extinction of wide-ranging species that move outside isolated wildlife reserves and into attractive, sink-like habitats (Woodroffe and Ginsberg 1998; Falcucci et al. 2009; Packer et al. 2013). It has been suggested that conservation efforts in these instances should prioritize mitigation of human-induced mortality and maximize the size of protected areas (Woodroffe and Ginsberg 1998). On the basis of our simulations, if a temporary moratorium on hunting occurred until social carrying capacity was achieved, the population could potentially sustain an annual average harvest of 26–31 randomly selected individuals while maintaining a population size above 420. However, variation in the annual number of individuals removed in simulations to maintain social carrying capacity was high even in the absence of hunting and anthrax. Therefore, ongoing population monitoring will be important to understand and account for stochastic events that may lead to real-time adjustments to sustainable harvest estimates, which are based on simulated long-term averages. Given the current size of the SRPB, unrestricted hunting in the short term will result in undesirable levels of population extinction risk and a lower probability of achieving and maintaining the population size required to prevent further declines in genetic diversity. Unfenced plains bison populations within their historic range that coexist with natural predators are exceedingly rare in North America (Freese et al. 2007; Sanderson et al. 2008). Given the distinctiveness of the SRPB population, we believe that it will be important to continue working towards maintenance of conservation thresholds and increasing social carrying capacity.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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Appendix 1. Individual-based population simulation model parameter values for Sturgeon River plains bison

- Initial population size: 205 (2013 estimate from Merkle et al. 2015—excluding calves).
  - 101 adult females (≥3 years old)
  - 59 adult males (≥3 years old)
  - 23 juvenile females (1–2 years old)[a]
  - 22 juvenile males (1–2 years old)[a]
- Stable age distributions were determined and used within each sex-age class
- Minimum age for producing offspring: three for females (Berger and Cunningham 1994, Wilson et al. 2002); six for males (Maher and Byers 1987, Wilson et al. 2002)
- Reproductive system: polygynous
- Maximum age for reproduction: 20 for females; 14 for males (Wilson et al. 2002)
- Annual male breeding success: 20%
- Maximum lifespan: 20 years (Meagher 1973)
- Maximum number of progeny/year: 1
- Sex ratio at birth: 50%

- Percent breeding-aged females reproducing per year: 69.6% (SD = 14.3%) based on the mean annual percentage of pregnant SRPB cows ($n = 59$) captured in 2005, 2007, 2012–2015 (mean of 9.3 per year)

- Adult and juvenile female mortality rate: 5.6% (SD = 1.3%) based on a mean ($n = 7$) of annual rates available from bison populations exposed to wolf predation (Bradley and Wilmshurst 2005[b])

- Adult and juvenile male mortality rate: 7.6% (SD = 1.3%) based on a mean ($n = 7$) of annual rates available from bison populations exposed to wolf predation (Bradley and Wilmshurst 2005[b])

- Calf mortality rate: 49.2% (SD = 21.4%) based on a mean ($n = 23$) of annual rates available from bison populations exposed to wolf predation (VanCamp and Calef 1987, Larter et al. 2000)

- Female harvest: one (age 1–2), two (age 2–3), and five (after age 3).

- Male harvest: one (age 1–2), two (age 2–3), three (age 3–4), three (age 4–5), two (age 5–6), one (after age 6)

All SD values were approximated with methods for small sample sizes described in Lacy et al. (2015). Observed ranges were divided by expected ranges for a sample of n values from a normal distribution

[a]Juvenile: cow values from Merkle et al. (2015) were used to estimate the number of juveniles in the population. A 50% sex ratio was assumed for juveniles because gender-specific data were not available for this age category

[b]Mortality rates from Bradley and Wilmshurst (2005) were adapted from Joly (2001) and Wilson et al. 1995 to include mortality due to wolf predation. Data from populations that had both tuberculosis and brucellosis were excluded

References

Allendorf FW, Ryman N (2002) The role of genetics in population viability analysis. In: Beissinger SR, McCullough DC (eds) Population Viability Analysis. University of Chicago Press, Chicago, IL, p 50–85

Bach LA, Pedersen RBF, Hayward M, Stagegaard J, Loeschcke V, Pertoldi C (2010) Assessing re-introductions of the African Wild dog (*Lycaon pictus*) in the Limpopo Valley Conservancy, South Africa, using the stochastic simulation program VORTEX. J Nat Conserv 18:237–246

Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akcakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387

Bradley M, Wilmshurst J (2005) The rise and fall of bison populations in Wood Buffalo National Park: 1971 to 2003. Can J Zool 83:1195–1205

Berger J, Cunningham C (1994) Bison: mating and conservation in small populations. Columbia University Press, New York, NY

Carroll C, Fredrickson RJ, Lacy RC (2013) Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. Conserv Biol 28:76–86

Chadès I, Curtis JMR, Martin TG (2012) Setting realistic recover targets for two interacting endangered species, sea otter and northern abalone. Conserv Biol 26:1016–1025

Chen YH, Opp SB, Berlocher SH, Roderick GK (2006) Are bottlenecks associated with colonization? Genetic diversity and diapauses variation of native and introduced *Rhagoletis complete* populations. Oecologia 149:656–667

Chilvers BL (2012) Population viability analysis of New Zealand sea lions, Auckland Islands, New Zealand's sub-antarctics: assessing relative impacts and uncertainty. Polar Biol 35:1607–1615

COSEWIC (2013) COSEWIC assessment and status report on the Plains Bison Bison bison bison and the Wood Bison Bison bison

athabascae in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, p xv+109

Falcucci A, Ciucci P, Maiorano L, Gentile L, Boitani L (2009) Assessing habitat quality for conservation using an integrated occurrence-mortality model. J Appl Ecol 46:600–609

Festa-Bianchet M, Coulson T, Gaillard JM, Hogg JT, Pelletier F (2006) Stochastic predation events and population persistence in bighorn sheep. Proc R Soc B 273:1537–1543

Fortin D, Fryxell JM, O'Brodovich L, Frandsen D (2003) Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134:219–227

Fortin D, Merkle JA, Sigaud M, Cherry SG, Plante S, Drolet A, Labrecque M (2015) Temporal dynamics in the foraging decisions of large herbivores. Anim Prod Sci 55:376–383

Frank LG, Woodroffe R (2001) Behaviour of carnivores in exploited and controlled populations. In: Gittleman J, Funk S, Macdonald DW, Wayne R (Eds.) Carnivore Conservation. Conservation Biology 5. Cambridge University Press, Cambridge, MA, p 419–442

Frankham R, Ballou JD, Broscoe DA (2002) Introduction to Conservation Genetics. Cambridge University Press, Cambridge, UK

Freese CH, Aune KE, Boyd DP, Derr JN, Forrest SC, Gates CC, Gogan PJP, Grassel SM, Halbert ND, Kunkel K et al. (2007) Second chance for the plains bison. Biol Cons 136:175–184

Halbert ND, Grant WE, Derr JN (2005) Genetic and demographic consequences of importing animals into a small population: a simulation model of the Texas State Bison Herd (USA). Ecol Model 181:263–276

Harvey L, Fortin D (2013) Spatial heterogeneity in the strength of plant-herbivore interactions under predation risk: the tale of bison foraging in wolf country. PLoS ONE 8:e73324

Hebblewhite M, White C, Musiani M (2010) Revisiting extinction in national parks: mountain caribou in Banff. Conserv Biol 24:341–3464

Hedrick PW (2009) Conservation genetics and North American bison (Bison bison). J Hered 100:411–420

Hoban S, Bertorelle G, Gaggiotti OE (2012) Computer simulations: tools for population and evolutionary genetics. Nat Rev Genet 13:110–122

Hofman-Kaminska E, Kowalczyk R (2012) Farm crops depredation by European Bison (Bison bonasus) in the vicinity of forest habitats in northeastern Poland. Environ Manag 50:530–541

Joly DO (2001) Brucellosis and tuberculosis as factors limiting population growth of northern bison. Ph.D. thesis. University of Saskatchewan, Saskatoon, SK

Kimura M, Crow JF (1964) The number of alleles that can be maintained in a finite population. Genetics 49:725–738

Keller LF, Waller DM (2002) Inbreeding effects in wild populations. Trends Ecol Evol 17:230–241

Lacy RC, Pollak JP (2015) Vortex: A Stochastic Simulation of the Extinction Process. Version 10.1. Chicago Zoological Society, Brookfield, Illinois, USA

Lacy RC, Miller PS, Traylor-Holzer K (2015) Vortex10 user's manual. 15 April 2015 update. IUCN SSC Conservation Breeding Specialist Group, and Chicago ZoologicalSociety, Apple Valley, Minnesota, USA

Lambrinos JG (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. Ecology 85:2061–2070

Larter NC, Sinclair ARE, Ellsworth T, Nishi J, Gates CC (2000) Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. Anim Conserv 4:299–309

Lessard C, Danielson J, Rajapaksha K, Adams GP, McCorkell R (2009) Banking North American buffalo semen. Theriogenology 71:1112–1119

Louis EJ, Dempster ER (1987) An exact test for Hardy–Weinberg and multiple alleles. Biometrics 43:805–811

Martin J, Runge MC, Nichols JD, Lubow BC, Kendall WL (2009) Structured decision making as a conceptual framework to identify thresholds for conservation and management. Ecol Appl 19:1079–1090

Merkle JA, Cherry SG, Fortin D (2015) Bison distribution under conflicting foraging strategies: site fidelity vs. energy maximization. Ecology 96:1793–1801

Maher CR, Byers JA (1987) Age-related changes in reproductive effort of male bison. Behav Ecol Sociobiol 21:91–96

Meagher M (1973) The bison of Yellowstone National Park. National Park Service Scientific Monograph Series 1, Washington, DC, USA

Nei M (1987) Molecular Evolutionary Genetics. Columbia University Press, New York, NY

Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. Evolution 29:1–10

Packer C, Loveridge A, Canney S, Caro T, Garnett ST, Pfeifer M, Zander KK, Swanson A, MacNulty D, Balme G et al. (2013) Large carnivore conservation: dollars and fence. Ecol Lett 16:635–641

Paetkau D, Waits LP, Clarkson PL, Craighead L, Vyse E, Ward R, Strobeck C (1998) Variation in genetic diversity across the range of North American brown bears. Conserv Biol 12:418–429

Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. Conserv Biol 12:844–855

Ranglack DH, Du Toit JT (2015) Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland. Ecol Indic 56:145–151

Ranglack DH, Du Toit JT (2016) Bison with benefits: towards integrating wildlife and ranching sectors on a public rangeland in the western USA. Oryx 50:549–554

Raymond M, Rousset F (1995) An exact test for population differentiation. Evolution 49:1280–1283

Reed JM, Mills LS, Dunning JB, Menges ES, McKelvey KS, Frye R, Beissinger SR, Anstett MC, Miller P (2002) Emerging issues in population viability analysis. Conserv Biol 16:7–19

Salb A, Stephen C, Ribble C, Elkin B (2014) Descriptive epidemiology of detected anthrax outbreaks in wild wood bison (bison bison athabascae) in northern Canada, 1962–2008. J Wildl Dis 50:459–468

Sanderson EW, Redford KH, Weber B, Aune K, Baldes D, Berger J, Carter D, Curtin C, Derr J, Dobrott S et al. (2008) The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. Conserv Biol 22:252–266

Shaffer ML (1981) Minimum population sizes for species conservation. BioScience 31:131–134

Shaw JH (1995) How many bison originally populated western rangelands? Rangelands 17:148–150

Shury TK, Frandsen D, O'Brodovich L (2009) Anthrax in free-ranging bison in the Prince Albert National Park area of Saskatchewan in 2008. Can Vet J 50:152–154

Sigaud M, Merkle JA, Cherry SG, Fryxell JM, Berdahl A, Fortin D (2017) Collective decision-making promotes fitness loss in a fusion-fission society. Ecol Lett 20:33–40

Soulé M, Gilpin M, Conway W, Foose T (1986) The millenium ark: how long a voyage, how many staterooms, how many passengers? Zoo Biol 5:101–113

Sturgeon River Plains Bison Management Plan. 2013. Produced by Sturgeon River Plains Bison Management Planning Coordinating Committee. http://www.bisonstewards.ca/

Thomas CD (1990) What do real population dynamics tell us about minimum viable population sizes? Conserv Biol 4:324–327

Urton EJM, Hobson KA (2005) Intrapopulation variation in gray wolf isotope (δ^{15}N and δ^{13}C) profiles: implications for the ecology of individuals. Oecologia 145:317–326

Valls-Fox H, Chamaille-Jammes S, de Garine-Wichatitsky M et al. (2018) Water and cattle shape habitat selection by wild herbivores at the edge of a protected area. Anim Conserv 21:365–375

VanCamp J, Calef GW (1987) Population dynamics of bison. In: Reynolds HW, Hawley AWL (eds.), Bison ecology in relation to agricultural development in the Slave River Lowlands, NWT. Canadian Wildlife Service Occasional, Paper No 63, Edmonton, Alberta, Canada, T6B 2X3 pp. 21–24

Vonholdt BM, Stahler DR, Smith DW, Earl DA, Pollinger JP, Wayne RK (2008) The genealogy and genetic variability of reintroduced Yellowstone grey wolves. Mol Ecol 17:252–274

Wilson GA, Strobeck C (1999) Genetic variation within and relatedness among wood and plains bison populations. Genome 42:483–496

Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128

Wilson E, Mercer G, Morgan J (1995) Bison movement and distribution study final report. Technical Report TR 93–06 WB

Wilson GA, Olson W, Strobeck C (2002) Reproductive success in wood bison (*Bison bison athabascae*) established using molecular techniques. Can J Zool 80:1537–1548

Zachos FE, Hajji GM, Hmwe SS, Hartl GB, Lorenzini R, Mattioli S (2009) Population viability analysis and genetic diversity of the endangered red deer *Cervus elaphus* population from Mesola, Italy. Wildl Biol 15:175–186