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Long-term Viability of Department of the Interior Bison Under Current Management and Potential Metapopulation Management Strategies

Natural Resource Report NPS/NRSS/BRD—2020/2097

ON THE COVER
Bison at the National Bison Range, National Wildlife Refuge System
Photography by: DAVE FITZPATRICK

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Executive Summary

The North American plains bison (*Bison bison bison*) once numbered in the tens of millions, with a range that extended from northern Mexico to central Canada. Yet by the end of the 1800s, a combination of commercial hunting, novel diseases, and habitat destruction had driven plains bison to the brink of extinction. The establishment of a small number of protected, federally managed herds in the early 1900s saved the subspecies from extinction in the wild. As a result of those efforts, the Department of the Interior (DOI) is now the primary national conservation steward of North American plains bison supporting approximately 11,000 plains bison in 19 herds on 4.6 million acres of National Park Service (NPS), US Fish and Wildlife Service (FWS), and Bureau of Land Management (BLM) lands in 12 states.

While plains bison are no longer threatened by demographic extinction, most DOI bison continue to exist in relatively small, isolated, range-restricted herds, confined by fences and further bound by socio-political concerns that limit their ecological recovery. Small, isolated populations are vulnerable to extirpation due to random catastrophic events such as disease outbreaks or extreme weather events. Small, isolated populations also lose genetic diversity more quickly than large populations through the process of genetic drift, which in turn can decrease the viability of populations through an accumulation of inbreeding and loss of adaptive capacity.

To mitigate the loss of genetic diversity in these isolated populations, previous researchers have suggested restoring effective gene flow among herds and managing DOI bison herds as a metapopulation. Gene flow can be restored either through the restoration of natural movements between populations or through the translocation of animals (or gametes) among populations.

In this project, the NPS partnered with the Wildlife Conservation Society (WCS) and the FWS to evaluate the ability of metapopulation management strategies to ensure the long-term population viability of DOI bison. This study had three major components:

- In collaboration with other stakeholders including the BLM, state wildlife managers, non-government organizations, and Canadian bison managers, we collected standardized, up-to-date genetic, demographic, and management data on 16 DOI and two Parks Canada herds (collectively simplified and referred to as DOI bison herein), to assess current existing genetic variation within and between herds (Chapter 2);
- We used these genetic, demographic, and management data to develop and parameterize individual-based, genetically explicit simulation models to project the long-term viability of each bison herd under current management practices (Chapter 3);
- We used this model to evaluate the effects of alternate metapopulation management strategies with varying levels of genetic exchange (translocations) between herds to ensure the long-term viability of DOI bison (Chapter 4).

To evaluate and compare the performance of the alternate bison management strategies modeled in this study, project partners established the following quantitative criteria for successful management:

- All DOI bison herds must have a 99% probability of surviving and maintaining currently established abundance objectives for 200 years;
- The existing genetic diversity within each individual bison herd must be maintained or improved;
- Existing genetic diversity within the DOI metapopulation as a whole must be maintained; and
- Genetic redundancy should be retained within the DOI metapopulation, such that the loss of any one DOI bison herd does not substantially reduce the genetic diversity of DOI herds as a whole.

Results from our genetic analyses (Chapter 2) identify considerable variation in the level of genetic diversity within, and significant genetic differentiation between, existing bison herds. Current levels of genetic diversity within herds generally correspond with known herd foundation and augmentation histories, combined with the expected effects of genetic drift. Results indicate that three bison herds currently have observed heterozygosity levels (H_o) close to 0.50, a value identified with an increased risk of inbreeding depression and as a threshold for triggering genetic augmentation.

Results of simulation models for individual bison herds (Chapter 3) project that all herds will lose genetic diversity over the next 200 years under current management conditions without additional gene flow. Herd size was the most important driver of genetic diversity loss, though the effect of herd size could be modulated by the effect of the removal strategies used to manage herd abundances. Overall, larger herds (>500 animals) lost modest amounts of genetic diversity (3-7% decrease) over time, while small herds (<100 animals) lost considerable diversity (34-81% decrease) over

time, with correspondingly large increases in mean inbreeding levels. After 200 years under current management conditions eight herds were projected to have heterozygosity levels < 0.50, with mean inbreeding coefficient levels similar to those shown to impact the reproduction and survival of bison reported by other studies. Increasing the size of herds can reduce rates of genetic diversity loss due to genetic drift, as can removal strategies that maintain even sex ratios, target younger age classes instead of adults during removals, or target genetically overrepresented animals (e.g., bison most closely related to the rest of the herd).

Results of simulation models for individual bison herds indicate that 15 of the 18 herds in this study have a >99% probability of persisting for the next 200 years without additional gene flow. Three of the smallest herds (<100 individuals) are projected to be vulnerable to extinction (>10% probability of extinction) if maintained at current abundance levels without additional gene flow.

We identified logistical, biological, or political issues that could limit particular herds from acting either as a source or as a recipient for translocations, then modeled 25 metapopulation management scenarios in which we altered the criteria used to select source herds for translocations, the frequency of translocations, and the number of animals moved per translocation. We modeled four general scenarios for the selection of source herds for translocations: 1. Source herd must be the genetically least-related herd to the recipient herd; 2. Source herd must be genetically similar to the recipient herd; 3. Source herd must be systematically rotated at every translocation (in order from least-related to most-related to the recipient herd); 4. Source herd must be the geographically closest herd to the recipient herd. For each source herd scenario, we varied the number of bison transferred from two to eight bison, and frequency of transfers from five, eight, or 10-year intervals.

Results of our metapopulation management models (Chapter 4) indicate that translocation management strategies vary considerably in their efficacy. In particular, the criteria used to select potential source herds for translocations, and interactions between criteria used to select source herds and the size and initial levels of genetic diversity of recipient herds, strongly affected the efficacy of translocations to increase or maintain genetic diversity within herds. Using genetically least-related herds as sources for translocations resulted in the largest gains in genetic diversity for almost all herds. However, the less information-intensive strategy of systematically rotating source herds every translocation (in order of least- to most-related) led to almost identically large and consistent increases in the genetic diversity of recipient herds.

If a uniform translocation management strategy were to be adopted for all herds in the bison metapopulation, then a strategy of smaller, less frequent translocations (e.g., 2 bison every 10 years, 3 every 7 years) using either least-related herds as source populations or systematically rotating source herds at every translocation would be adequate for increasing the genetic diversity of most herds while also minimizing the loss of diversity at the metapopulation level. However, our results suggest that individual herds differ in their management needs, and that exploring a more tailored, herd-specific translocation strategy may be most beneficial. In particular, smaller herds benefit from more frequent translocations, larger herds require fewer and less frequent translocations, and herds with low initial levels of diversity are likely to benefit from any translocation.

In summary, this study confirms that management of DOI bison herds in isolation promotes the loss of genetic diversity within all herds. More importantly, this study demonstrates that increased herd size and targeted removal strategies can reduce rates of diversity loss, and that adopting a Departmental metapopulation strategy through facilitated periodic movement of modest numbers of bison among DOI herds (i.e., restoring effective gene flow) can substantially reduce the negative impacts of geographic isolation. Analyses of an array of scenarios for practical bison translocations indicates that the selection of appropriate source herds and numbers of animals to translocate must be considered carefully to most effectively conserve genetic diversity and ensure the long-term population persistence of bison. Long-term monitoring of genetic diversity, both at the individual herd level and across the metapopulation, will be essential to refine the implementation of an appropriate metapopulation management approach to maximize benefit to the species.

Based on these results, we recommend that the DOI Bison Working Group, as chartered under the DOI Bison Conservation Initiative (2008), initiate and oversee a technical task force to develop a comprehensive bison metapopulation management strategy for use by DOI agencies. This comprehensive management strategy must include explicit consideration of genetics, wildlife health, cattle introgression, data management, local unit management issues, partner/stakeholder engagement (Chapter 5). As we complete this project, the DOI Bison Working Group is concurrently working to finalize a bison health report that will describe considerations and issues for management of healthy DOI bison populations, and recommendations for coordination among DOI management units to better support bison health. This forthcoming DOI bison health report, in conjunction with the results of this project, will be key to informing a bison metapopulation strategy. Addressing the complexity of managing bison for conservation purposes will call for new and sustained levels of coordination and communication between DOI agencies and other bison conservation stakeholders, and traditional management models at the individual herd or even bureau level will need to be adapted to encompass broad species conservation goals that support continental conservation across multiple jurisdictions while respecting the variations in local management purpose and capacity.

The next several years offer unprecedented opportunity to capitalize on active engagement and partnerships to make meaningful, impactful, and durable gains in the conservation of bison in North America. With an articulated vision, sound scientific foundations, and committed internal and external partnerships, DOI bureaus are now well equipped to implement a new approach to bison conservation: a cooperative, multi-scaled stewardship model to preserve and protect our national bison heritage and to promote ecological and cultural restoration of bison to North America.

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Acronyms

BADL: Badlands National Park (South Dakota)

BLM: Bureau of Land Management

BOOK: Book Cliffs (Utah)

CHIC: Chickasaw National Recreation Area (Oklahoma)

CPSG: Conservation Planning Specialist Group

DOI: The US Department of the Interior

ELK: Elk Island National Park (Canada)

FTN: Fort Niobrara National Wildlife Refuge (Nebraska)

FWS: US Fish and Wildlife Service

GRASS: Grasslands National Park (Canada)

GRCA: Grand Canyon National Park (Arizona)

HEMO: Henry Mountains (Utah)

NER/GRTE: National Elk Refuge / Grand Teton National Park (Wyoming); abbreviated in figures and tables as “NER”

IUCN: International Union for Conservation of Nature

NBR: National Bison Range (Montana)

NPS: National Park Service

NSM: Neal Smith National Wildlife Refuge (Iowa)

NWR: National Wildlife Refuge

RMA: Rocky Mountain Arsenal National Wildlife Refuge (Colorado)

SH: Sully’s Hill National Wildlife Refuge (North Dakota) (note that Sully’s Hill was renamed White Horse Hill in December, 2019)

TAPR: Tallgrass Prairie National Preserve (Kansas)

THROn: Theodore Roosevelt National Park North Unit (North Dakota)

THROs: Theodore Roosevelt National Park South Unit (North Dakota)

WICA: Wind Cave National Park (South Dakota)

WM: Wichita Mountains Wildlife Refuge (Oklahoma)

WRST: Wrangell-St. Elias National Park and Preserve (Alaska)

YELL: Yellowstone National Park (Wyoming/Montana/Idaho)

Glossary

allele: alternative form of a gene. The term is used in this report in reference to variation in short tandem repeat segments of deoxyribonucleic acid (DNA), rather than coding regions relating to phenotype.

allelic diversity: a measure of genetic diversity based on the average number of alleles per locus present in a population.

allelic richness: a measure of the number of alleles per locus; allows comparison between samples of different sizes by using various statistical techniques (e.g., rarefaction).

gene: a segment of DNA whose nucleotide sequence codes for protein or ribonucleic acid (RNA), or regulates other genes.

gene identity (J_{xy}): the average probability that alleles are shared between populations.

genetic bottleneck: the loss of genetic variation experienced by populations that undergo a marked reduction in effective population size.

genetic drift: random changes in allele frequencies in populations between generations due to binomial sampling of genes during meiosis. Genetic drift is more pronounced in small populations.

genetic swamping: the loss of locally adapted alleles or genotypes caused by the constant immigration and gene flow.

Hardy-Weinberg equilibrium: the principle that allele and genotype frequencies will reach equilibrium, defined by the binomial distribution, and remain constant in the absence of evolutionary forces (migration, selection, mutation, or non-random mating).

heterozygosity (H): a measure of genetic variation that accounts for either the observed (H_0) or expected (H_e) proportion of individuals in a population that are heterozygotes.

inbreeding depression: the reduction in fitness of progeny from matings between related individuals compared to progeny from unrelated individuals.

introgression: the incorporation of genes from one population to another through hybridization that results in fertile offspring that further hybridize and backcross.

lethal equivalents (LE): the number of deleterious alleles in an individual whose cumulative effect is the same as that of a single lethal allele.

locus: the position on a chromosome of a gene or other marker.

mean kinship: the average of the pairwise kinships between all individuals in population A to all individuals in population B.

metapopulation: a collection of spatially divided subpopulations that experience a degree of gene flow among them (Allendorf and Luikart 2007). More specifically, these subpopulations are genetically, demographically, and evolutionarily connected, even though individual populations may be geographically separated most of the time. Within a metapopulation, each local population functions largely independently, and there is some degree of movement of individuals from one local population to others.

metapopulation (DOI bison): U.S. Department of the Interior (DOI) bison metapopulation refers to the concept of bison conservation herds (local populations) managed by the DOI for the primary purpose of bison genetic conservation, within which some degree of movement of individuals is facilitated by managers to enable gene flow to improve or maintain genetic diversity of local populations and the overall metapopulation (i.e., to minimize inbreeding and loss of genetic diversity due to drift). Though some movement of bison presently occurs on an ad hoc basis, a formal DOI bison metapopulation, founded on conservation science and operated under a strategic plan, does not presently exist.

microsatellite: tandemly repeated DNA consisting of short sequences of one to six nucleotides repeated between approximately five and 100 times.

outbreeding depression: the reduction in fitness of hybrids compared with parental types.

population viability analysis (PVA): the general term for the application of models that account for multiple threats facing the persistence of a population to access the likelihood of the population's persistence over a given period of time. PVA helps identify threats faced by a species, plan research and data collection, prioritize management options, and predict the likely response of a species to management actions.

population viability: the probability that enough individuals in a population will survive to reproductive age to prevent extirpation of the population.

viability: the probability of the survival of a given genotype to reproductive maturity or of a population to persist through a certain time interval.

1. Introduction

The iconic American plains bison (*Bison bison bison*), represented on the National Park Service (NPS) arrowhead and the Department of the Interior (DOI) seal, is a symbol of strength and resilience and is our national mammal. Prior to European settlement, plains bison had the largest original distribution of any native large herbivore in North America, ranging from the desert grasslands in northern Mexico to the plains of central Canada. As large grazers, they shaped the grassland ecosystems they occupied, influencing fire regimes and soil nutrient cycling, increasing landscape heterogeneity, and ultimately driving patterns of biodiversity within plant and animal communities (Fuhlendorf et al. 2006; Knapp et al. 1999). Since humans first occupied the continent more than 12,000 years ago, bison have also played a pivotal role in shaping the traditions, diets, and economies of human cultures across North America (Gates et al. 2010).

Once estimated to number in the tens of millions (Shaw 2000), a combination of commercial hunting, introduced diseases, and habitat destruction throughout the 1800s drove bison to the brink of extinction (Coder 1975; Isenberg 1992; Isenberg 2000). By the end of the 1800s only an estimated 1,000 animals remained (Hornaday 1889; Isenberg 2000). As bison numbers dwindled, a handful of private citizens from Texas to Manitoba captured remaining plains bison to save the subspecies from extinction (Dratch and Gogan 2010; Freese et al. 2007). Historical accounts indicate that all plains bison today may be descendants of only 30 to 50 individuals from six captive herds (Hedrick 2009), along with the estimated 25 wild bison remaining in Yellowstone National Park (Meagher 1973). Through the combined efforts of private individuals, private organizations, and federal, state, and tribal governments, several small protected populations were established, allowing bison to emerge from this devastating genetic bottleneck and putting the species on a path to recovery (Coder 1975; Dary 1989; Dratch and Gogan 2010).

A century of conscientious stewardship efforts successfully increased bison numbers, and by 2017 there were an estimated 334,000 bison in North America (Plumb and Sucec 2006; Redford et al. 2009). The vast majority of these bison, about 303,000, are privately owned and managed using domestic and/or commercial livestock husbandry practices (U.S. Department of Agriculture National Agricultural Statistics Service 2019; Statistics Canada 2017). These bison are often managed using artificial selection strategies to promote better growth rates for meat production (Gates et al. 2010; Halbert and Derr 2008), or to favor more docile animals less challenging to handle as livestock. While these bison have important economic, cultural, and nutritional values, many commercial bison herds are not exposed to conditions and natural selection pressures that shaped their ancestors' wild nature.

The ecological recovery and stewardship of bison as wildlife has been more challenging. According to the IUCN Red List Assessment (Aune et al. 2017) there are approximately 31,000 total bison in 68 conservation herds in North America. These include about 20,000 plains bison and 11,000 wood bison (*Bison bison athabascae*), a subspecies with a range farther north than plains bison (Aune et al. 2017). Herds managed for conservation purposes are typically small (<400) and widely dispersed, with little to no natural movements between subpopulations. Only two large herds (>4,000 bison) of wild bison in North America range unfenced on protected public lands in the Greater Wood Buffalo Park Area (Canada) and the Greater Yellowstone Area (Aune et al. 2017; Gates et al. 2010). While extinction is no longer an imminent threat, substantial work remains to more fully restore the species to its ecological and cultural role on appropriate landscapes within its historical range (DOI 2014; Gates et al. 2010).

The DOI is the primary federal entity responsible for the ongoing recovery and conservation of plains bison in the United States. The DOI oversees the stewardship of ~11,000 plains bison in 19 herds on 4.6 million acres of NPS, US Fish and Wildlife Service (FWS) and Bureau of Land Management (BLM) lands in 12 states (Figure 1.1), making up approximately half of all plains bison managed for conservation in North America. Most of these herds are fenced, have less than 600 individuals, and lack native predators such that herds are subjected to selective removals (e.g.,culling) to maintain herd sizes at or below carrying capacity (DOI 2014). Many herds also show some evidence of low levels of cattle gene introgression from early 19th century crossbreeding with cattle. Despite these constraints, the DOI bison herds are an irreplaceable resource for the long-term recovery of North American plains bison (DOI 2014; Dratch and Gogan 2010).

Because most DOI bison herds were founded with a small number of individuals (Halbert and Derr 2008) and have been restricted in size and geographic range with limited genetic exchange, the genetic health of DOI bison is a significant concern for long-term subspecies survival (Dratch and Gogan 2010; Hedrick 2009). In particular, it has long been

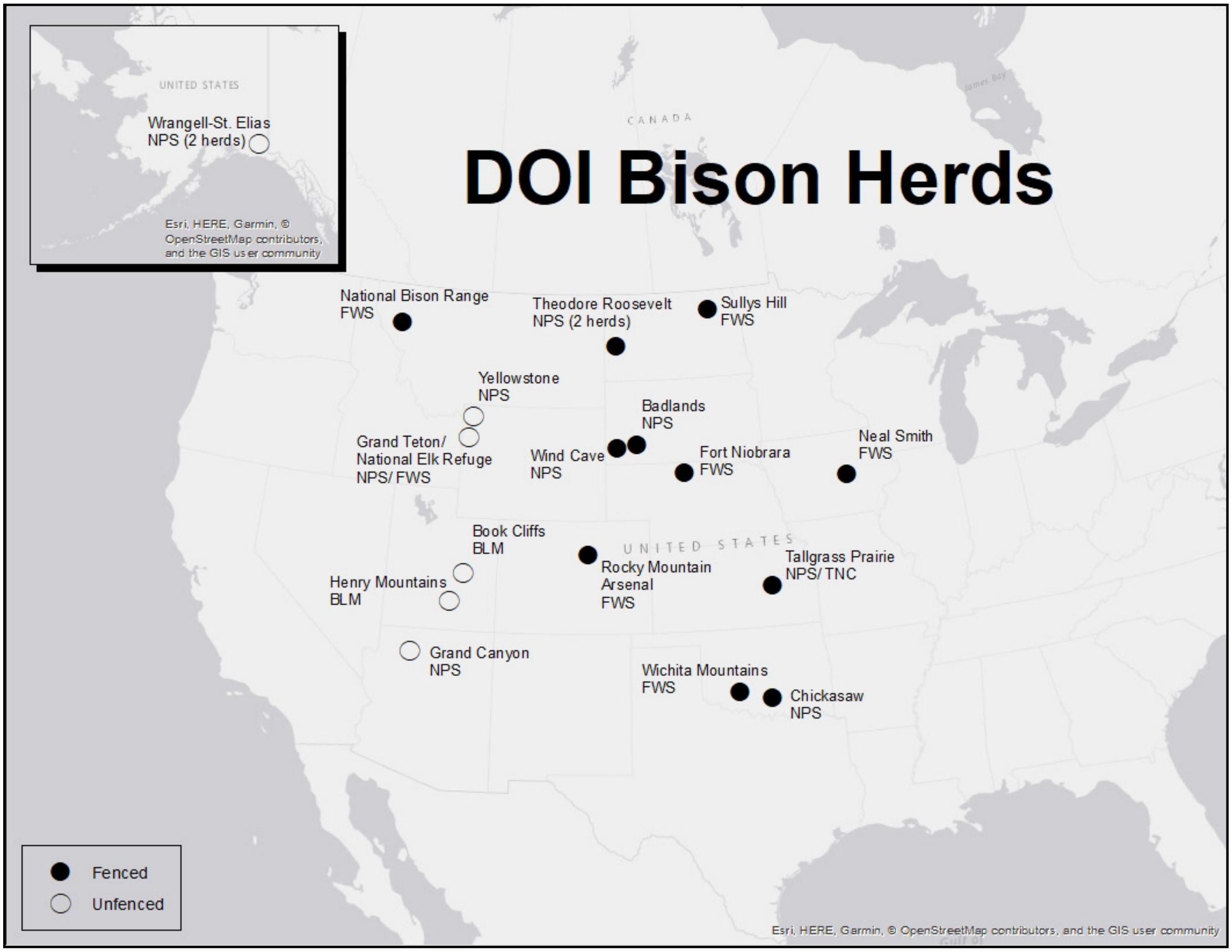

Figure 1.1. Map of all DOI plains bison herds.* Open circles indicate unfenced herds; shaded circles fenced herds. *The Book Cliffs herd is managed cooperatively by the BLM, Utah Division of Wildlife Resources, and the Ute Indian Tribe Fish and Wildlife Department; the Henry Mountains herd is managed cooperatively by the BLM and the Utah Division of Wildlife Resources; and the Wrangell-St. Elias herds are managed cooperatively by the NPS and the Alaska Department of Fish and Game.

recognized that small, isolated populations have a greater risk of extirpation due to random catastrophic events (Lande 1993; MacArthur and Wilson 1967) and lose genetic diversity more quickly through the process of genetic drift, the random loss of genetic material from generation to generation (Allendorf et al. 2013).

Loss of genetic diversity can have detrimental effects on both the short- and long-term viability of a population or species. In the short-term, diversity loss due to drift increases the risk of inbreeding depression – a reduction in fitness in the offspring of closely related parents relative to offspring of unrelated parents (Allendorf et al. 2013). Inbreeding depression has been widely documented among animal species and can result in reproductive failure, poor recruitment, and reduced disease resistance (Hedrick and Kalinowski 2000; Keller and Waller 2002). The lower survival and reproductive rates typical of inbred individuals in turn lead to declines in population growth rates, thereby further increasing the risk of population extirpation (Gilpin and Soulé 1986; Mlot 2015; Soulé and Mills 1998; Westemeier et al. 1998). Such severe consequences of genetic drift resulting in inbreeding depression have been well documented in the population decline of the Texas state bison herd (Halbert et al. 2004; Halbert et al. 2005).

In the long-term, reductions in genetic diversity ultimately decrease the ability of populations or species to evolutionarily adapt to changing or novel environmental conditions (Fisher 1930; Reed and Frankham 2003), such as increased climatic variability or the emergence of novel diseases (Reed et al. 2003; Siddle et al. 2007). Conservation of genetic diversity provides the foundation for adaptive capacity on the evolutionary pathway of bison and is essential for conservation, especially when the existing evolutionary forces of selection may be limited on some DOI landscapes. Combined with periodic population reductions of range-restricted DOI bison to maintain balance with available ecological resources, careful management is essential to ensure long-term bison conservation (Gates et al. 2010; Hedrick 2009).

In 2008, the Secretary of the Department of the Interior chartered the DOI Bison Conservation Initiative to improve DOI bison conservation efforts. One of the first outcomes of the Initiative was the Bison Conservation Genetics Workshop (Dratch and Gogan 2010), where biologists and population geneticists convened to develop guidance for the genetic management of federal bison herds. Participants established basic tenets of genetic management for DOI herds and discussed tactics for meeting those goals. Key recommendations from the workshop included establishing standard measures of genetic health for DOI bison; using precautions regarding translocations of bison in herds with cattle gene introgression into herds with no evidence of cattle gene introgression; and establishing science-based strategies for conserving the genetic health of DOI herds, including managing for large population sizes and maintaining age structure and sex ratios that facilitate breeding competition. Since many DOI bison herds are restricted to landscapes that cannot accommodate more than 1,000 animals, managing smaller satellite herds together as a larger metapopulation was also recommended to conserve the genetic health of DOI bison (Dratch and Gogan 2010).

In response to these recommendations, the NPS, in partnership with the FWS and the Wildlife Conservation Society (WCS), launched a multi-year, multi-agency project in 2015 to further develop scientific guiding principles to support the long-term conservation of bison as a wildlife managed by DOI agencies. Specific objectives of this project included the following:

1. Engage collaborators and build relationships for shared stewardship of bison within DOI agencies and with State, Tribal, and private partners.

2. Collect and analyze standardized genetic data for all DOI bison herds, and synthesize and update data on current management practices and herd demographics.

3. Develop and parameterize population viability analysis (PVA) models to assess the long-term population viability and genetic diversity of DOI bison herds given current herd genetics, demographics, and management approaches.

4. Use PVA to assess the effects of potential, alternate metapopulation management strategies (i.e., translocations between herds to facilitate gene flow) on the long-term population persistence and genetic diversity of DOI bison.

5. Use PVA modeling results to inform management recommendations for DOI bison conservation strategies, including metapopulation management approaches as appropriate.

The project also included education and outreach tasks, which were completed separately from the analytical portions of the project and are not discussed in this technical report.

Assessing the long-term genetic and demographic viability of bison requires knowledge of current genetic health, including levels of genetic diversity within herds and the degree of genetic differentiation between herds. While past research efforts have offered important, pioneering insights into the genetic health of a subset of individual DOI bison herds (Dratch and Gogan 2010; Halbert and Derr 2007; Halbert and Derr 2008; Hedrick 2009), in this study we set out to collect and analyze standardized genetic data and up-to-date information on the management practices and herd population structure of most DOI bison herds. Because conservation at a continent-wide scale would further benefit bison, we also partnered with managers of public bison herds in Canada (Elk Island National Park, Grasslands National Park) with a historic genetic relationship to DOI bison to sample and analyze these herds.

To estimate the long-term viability of herds under current management conditions, and under a suite of alternate translocation management scenarios, we used the genetic, demographic, and management data collected from each herd to develop and parameterize a suite of genetically explicit PVA. Models used for PVA typically incorporate genetic, demographic, stochastic, and specific management parameters to assess the probability of extinction of a population. Such simulation models are valuable and versatile tools for quantitatively assessing the variables affecting population growth as they allow for the exploration of interacting natural and anthropogenic factors that influence population persistence (Beissinger and Westphal 1998; DeAngelis and Mooij 2005; Hoban et al. 2012; Lacy 2019). We developed translocation scenarios based on direct input from NPS and FWS bison managers. Scenarios were constructed to evaluate a range of possible management actions, with variation in frequency and number of translocations, as well as genetic and logistical (distance) variables.

To evaluate the relative success of each potential DOI bison management strategy, herd managers and management leads developed quantitative measures to evaluate model performance. These herd managers and leads collectively stated that modeled bison management scenarios would be considered successful if model results met the following conditions:

- All DOI bison herds must have a high probability of survival, defined as a 99% probability of each DOI herd surviving for 200 years, and maintaining currently established abundance objectives;
- Existing genetic diversity is maintained or improved within each individual bison herd;
- Existing genetic diversity is maintained within the DOI metapopulation; and
- Genetic redundancy is retained within the DOI metapopulation, such that the loss of any one DOI bison herd does not substantially reduce the genetic diversity of DOI herds as a whole.

This report details the analysis of population persistence and genetic health within and across 16 DOI and two Parks Canada plains bison herds. We evaluate the genetic differentiation and population structure of these 18 herds, project their long-term viability under current management conditions, and explore alternative management scenarios. While each DOI unit may have some differences in mission and management strategies, all are unified in shared stewardship of bison based on best science and partnerships. DOI bison contribute to human and environmental health, support Tribal historical and cultural values, and provide a foundation for long-term ecological restoration of this subspecies. This project provides a science-based framework from which DOI bison management strategies may be developed, and on which future partnerships may be based to benefit conservation of bison as wildlife over large, diverse landscapes (Sanderson et al. 2008).

2. Assessing the Current Genetic, Demographic, and Management Status of Department of Interior Bison Herds

2.1 Introduction

Evaluating the long-term genetic and demographic viability of bison under current and alternate management scenarios requires data on existing levels of genetic variation within and between herds and on factors known to influence the genetic diversity and the probability of persistence of each herd (Soulé and Mills 1998). In particular, data on existing levels of genetic diversity within each herd can be used to assess risks of inbreeding depression (Allendorf et al. 2013). Developing effective genetic management strategies to increase genetic diversity and prevent the accumulation of inbreeding within herds requires data on the genetic differentiation between herds (Frankham et al. 2017).

Herd abundance through time, removal strategies to maintain herd abundance levels, and the age-structure and sex ratio of individuals within each population also influence the probability of population persistence and genetic variation within bison herds. In particular, removal strategies that maintain an even sex ratio, and that randomly remove animals from young age classes, or use mean kinship values to remove genetically over-represented animals have all been shown to minimize genetic diversity loss compared to other strategies (Giglio et al. 2016; Giglio et al. 2018; Gross and Wang 2005).

In this study we set out to gather and analyze up-to-date, standardized genetic, demographic, and management data on 16 of 19 DOI herds, as well as from two Parks Canada herds. While previous researchers have offered important, pioneering insights into the genetic health (Dratch and Gogan 2010; Halbert and Derr 2007; Halbert and Derr 2008; Hedrick 2009; Wilson and Strobeck 1999), herd demographics, and general management strategies of a subset of individual DOI bison herds, in this study we collected and analyzed standardized genetic data across the largest portfolio of DOI bison herds to date.

2.2 Methods

Collection of Demographic and Management Data

To gather up-to-date, standardized demographic and management data for each herd, we devised and sent electronic surveys to bison managers in July 2016 (see Appendix A for survey details). In the survey, bison managers were asked to provide information on their most recent estimates of herd size, the estimated number of males and females in each age class, any known information on the survival and reproductive rates of each sex and age class, as well as estimates of the biological carrying capacity of the herds' habitat (the number of animals that could be supported in the existing habitat in concert with the management of other species) and information on any known or suspected threats to the herd. Bison managers were also asked to provide their target or management-imposed maximum herd size (how many bison were deemed "acceptable" for each herd based on factors other than ecological carrying capacity) and details on their herd size control strategy. This included any criteria for frequency and number of bison removed, and age and sex ratios of those removals. Survey results were followed up by a workshop in August 2016, in which bison managers, ecologists, and geneticists met to review, discuss, and amend survey results and to provide additional herd-specific data.

Collection of Genetic Samples and DNA Extraction

Sample Collection

To assess the existing genetic diversity of bison on DOI lands and to evaluate the population structure of these herds, we partnered with State and Agency biologists to gather and analyze recently collected DNA samples (hair, tissue, or whole blood) from bison in each of the herds currently on DOI lands. Because conservation at a continent-wide scale would further benefit bison, we also partnered with managers of bison herds in Canada with a historic genetic relationship to DOI bison to sample and assess the viability of their herds under current management, and to determine how continent-wide management would affect the conservation of genetic diversity.

We collected hair, blood, and biopsy dart samples through capture and handling operations, hunter submitted samples, field biopsy collection efforts, and the use of recently collected archived samples. For herds that undergo regular capture, we gathered tail hair and whole blood samples while the animal was briefly restrained in the handling facility during routine capture operations. A minimum of 20 tail hairs was collected from each animal using forceps or pliers to remove hair with attached follicles. Hair samples were sealed in individual bags and stored at room temperature until submission to the laboratory. Blood samples were collected using jugular or tailhead venipuncture and were placed on Whatman® FTA nucleic acid preservation cards and stored at room temperature until submission to the laboratory. For herds that were not handled regularly, we collected tissue samples in the field using remotely delivered tissue biopsy darts. Samples collected through biopsy darting that were not part of normal management operations were accomplished under Institutional Animal Care and Use Committee (IACUC) protocol "MWR.IMR.AKR_THRO.CHIC.GRCA.WRST_Bison_2016.A3." Samples obtained as part of management actions were collected ancillary to operations and exempt from IACUC review. Animals were temporarily marked with paint to prevent duplicate sampling, as needed. We recovered darts and tissue within an hour of sample collection and tissue samples were stored frozen until submission to the laboratory. For herds managed through hunting, hunters were asked to collect tail hair with follicles and/or nucleic acid preservation cards upon successful harvest. Samples were returned to the appropriate agency and stored as described above prior to submission to the laboratory. Sample collection efforts are detailed in Table 2.2.1.

DNA Extraction

Based on microsatellite panels developed at Texas A&M University (Halbert and Derr 2007; Halbert and Derr 2008) of which a subset was adopted as a standard measure of genetic diversity and integrity by DOI in 2010 (Dratch and Gogan 2010), the University of California Davis Veterinary Genetics Laboratory (UCD-VGL) extracted DNA from all samples and provided genotypes for 52 microsatellites optimized for evaluation of genetic diversity, and 15 microsatellites and 1 mtDNA marker to detect cattle introgression (table with loci in Appendix B).

Genetic Analyses

Each individual sample was assigned a unique population identification to signify its herd of origin, and subsequent data analyses were carried out to evaluate the genetic diversity within herds and for the all sampled bison populations as a whole, and to determine the genetic differentiation between individual herds and of the entire metapopulation. All analyses were carried out in R (R Core Team 2018). Because missing data (e.g., due to allelic dropout) have been

Table 2.2.1 Summary of the 1,895 genetic samples collected and analyzed from 16 DOI and two Parks Canada bison herds for this project. Number of samples analyzed is the total number of samples collected minus samples dropped from analyses due to duplicated individuals or missing data.

Herd	Years Sampled	Estimated Herd Size at Time of Sampling	# of Samples Analyzed	% of Herd Analyzed
BADL	2014, 2015	900	100	11
BOOK	2017	540	38	7
CHIC	2016	10	10	100
ELK	2017	470	84	18
FTN	2015	357	330	92
GRCA	–	–	–	–
GRASS	2017	346	125	36
HEMO	2011-2013*	400	84	21
NBR	2015	302	259	86
NER/GRTE	2009	936	100	11
NSM	2015	53	51	96
RMA	2015	71	69	97
SH	2015	22	20	91
TAPR	2016	89	43	48
THROn	2016	280	100	36
THROs	2016	335	87	26
WM	2015	576	270	47
WICA	2015	350	100	29
WRST	2017, 2018	181	25	14
YELL	–	–	–	–

* Archived samples accessed from the American Natural History Museum, Ambrose Monell Cryo Collection, originally collected between 2011-2013 by Ranglack et al. (2015)

shown to skew the results of genetic analyses (Pompanon et al. 2005; Taberlet et al. 1999) we excluded any individual samples from analyses that contained missing data from five or more loci.

Genetic Diversity

We used the package hierfstat (Goudet and Jombart 2015) to calculate observed (H_O) and expected (H_e) heterozygosity (Nei 1987), the average number of alleles per locus for the entire metapopulation and for each individual herd, and the allelic richness (A_r) for each individual herd (El Mousadik and Petit 1996). Allelic richness and expected heterozygosity are unbiased estimators of the observed number of alleles per locus and heterozygosity, respectively, which minimize differences due to sample size variances. Because estimates of allelic richness are rarefied in accordance with the smallest sample of all populations being compared, our estimates of allelic richness were based on the sample size from the Chickasaw herd (10 individuals). We tested for deviations from Hardy-Weinberg equilibrium (HWE) for each population-marker combination using Fisher's exact test with sequential Bonferroni correction for multiple comparisons in the package pegas (Paradis 2010). We also estimated F_{IS} as ($1-H_o/H_e$), a test of non-random mating within each herd (Hedrick 2000).

Introgression

We tested for the presence of nuclear cattle alleles using a panel of 15 microsatellite markers developed from five common breeds of cattle (table with loci in Appendix B; Halbert and Derr 2007), and by testing for the presence of cattle mitochondrial DNA (mtDNA). Due to the small number of loci in this panel, this measure is appropriate for testing for the presence of introgression at a herd level, but is less useful at detecting introgression in individual animals (Dratch and Gogan 2010).

Genetic Differentiation and Population Structure

We assessed the population structure of DOI bison using two complementary methods: differentiation indices and Discriminant Analysis of Principal Components (DAPC) (Jombart et al. 2010; Jombart and Ahmed 2011). A variety of differentiation indices have been developed for identifying population structure from genetic markers, each with advantages and disadvantages (Jost et al. 2018; Meirmans and Hedrick 2011). We calculated three different indices to assess levels of genetic differentiation within the DOI metapopulation: Nei's F_{ST} (Nei 1987), Hedrick's $G_{ST'}$ (Hedrick 2005), and Jost's D (Jost 2008). F_{ST} and $G_{ST'}$ are both measures of fixation within a subdivided population, which compare expected heterozygosity within and between subpopulations. These measures are meant to take values of one when all subpopulations are fixed for a single allele (Meirmans and Hedrick 2011) indicating that populations have drifted apart due to lack of genetic interchange, and values of zero when all subpopulations are far from fixation. We use Nei's F_{ST} as it has traditionally been the most widely used measure and therefore allows comparison to previous studies on bison and other species. However, values that Nei's F_{ST} can take are restricted by the measured levels of existing variation within the population, meaning that F_{ST} typically underestimates the actual level of differentiation between subpopulations (Hedrick 2005; Jost 2008; Ryman and Leimar 2008). $G_{ST'}$ corrects for this bias by standardizing F_{ST} for the actual maximum levels of diversity within the population. In contrast to the above fixation indices, Jost's D measures levels of allelic differentiation between subpopulations within a sub-divided population. Jost's D takes a value of zero if all alleles are equally represented in all subpopulations, and a value of 1 if each subpopulation has a unique, different set of alleles.

We used the package hierfstat to estimate global values of F_{ST}, $G_{ST'}$ and Jost's D and bootstrapped 95% confidence intervals for each estimate to test for evidence of significant differentiation within the DOI bison population (if 95% CI do not include zero, significant genetic differentiation is supported). We then used package adegenet to estimate pairwise values of F_{ST}, and package mmod (Winter 2012) to estimate pairwise values of $G_{ST'}$ and D, between all sets of herds to determine specifically which herds were genetically differentiated from one another.

We used discriminate analyses of principal components (DAPC) to assess the genetic structure of the DOI bison metapopulation. DAPC is a multivariate method using synthetic variables (discriminant functions) to identify and maximize genetic variation within and between selected groups, thereby identifying clusters of genetically related individuals (Jombart et al. 2010; Jombart and Ahmed 2011). We carried out our DAPC analyses in the adegenet package (Jombart 2008) using a two-step process. First, we used the find.clusters function to identify the number of distinct genetic clusters that best describes all genetic data collected from the DOI bison herds. Find.clusters uses a K-means clustering algorithm that assesses data by lumping it sequentially in 1 to N distinct clusters then assesses how well results fit the data using Bayesian Information Criterion (BIC), with the lowest score indicating best-fit model. We then used DAPC to transform the data into synthetic variables that best describe variation between clusters, while also minimizing with-in cluster variance, to assign each individual genetic sample to a genetic cluster. We plotted the resultant clusters in a scatterplot of the first and second linear discriminates of DAPC for a visual representation of the genetic structure of the DOI bison metapopulation.

2.3 Results

Demographic and Management Data

Seven FWS, five NPS, and two state (managing bison on BLM lands) managers responded to the 2016 survey (Appendix A), providing detailed qualitative and quantitative information for 16 DOI bison herds and two Canadian herds. Table 2.3.1 summarizes respondents' estimates of herd size, ecological (K_{eco}) and management (target herd size, K_{man}) carrying capacity, factors influencing management carrying capacity, and removal strategies, including information about how often animals are removed and the ages of animals typically removed. Reported herd sizes accounted for time of year/season the count was conducted (e.g., before or after spring calves were born, before or after management removal activities) and level of certainty (e.g., exact count or census, an adjusted population estimate, or a range), with herds ranging from 11 (CHIC) to 1,222 (BADL) bison (YELL did not participate).

Differences in reported management carrying capacity (target herd size) and estimated ecological carrying capacity revealed two herds were being managed below the estimated ecological carrying capacity, 10 herds were being managed for target herd sizes equal to the estimated ecological carrying capacity, and, in seven cases, reported estimated ecological carrying capacity was reported as either "unknown" or not stated. Herd managers listed a variety of factors influencing the management carrying capacities for each herd, including ecological integrity, wildlife and hunting advocates, livestock and grazing associations, and habitat quality.

To maintain herd numbers at or below management carrying capacity, five herds were managed via annual hunts. For two of the five hunted herds, 85% of annual hunting permits targeted bulls and 15% targeted cows, while the respondents for the other three hunted herds did not specify age and sex classes targeted for annual harvest.

Most herds (14) were being managed via capture and removal operations. Eight of these herds were managed via annual removals; in six of these herds, managers removed yearlings and occasionally 2 or 3-year-olds determined to be the most closely related to the rest of the herd, to minimize mean kinship or relatedness within the herd. The largest herd was managed via annual capture operations focused on removing a random selection of yearlings to 2.5-year-olds, while the smallest herd, managed as a display herd, removed yearlings, bison over 10 years old, or bison that were sick or injured annually. Three herds were managed with removals every other year, primarily taking yearlings and pre-reproductive juveniles (<2 years old) along with some older adults in two herds (>5 years old in one herd; >10 years old in another herd). A fourth herd was managed via removals every other year, primarily taking yearlings and some 2-year-olds if no animals from that age class had been removed as yearlings.

Genetic Sampling

We gathered 1895 usable samples from 18 herds (Table 2.2.1), with the number of samples representing approximately 7% to 100% of individuals sampled per herd. Herds undergoing capture and handling operations yielded the largest sample sizes, while free-roaming and remote herds yielded smaller sample sizes due to the logistical difficulties and costs of sampling such herds. Three herds were not sampled: YELL, GRCA, and the Chitina herd at WRST. GRCA and the Chitina herd at WRST could not be sampled due to the logistical difficulties of sampling these remote, wild herds. YELL did not provide samples for this study, and pre-existing alternative sources of randomly collected YELL genetic samples could not be located.

Genetic Analyses

Genetic Diversity

Global estimates for observed and expected heterozygosity within herds were 0.592 (sd=0.106), 0.598 (sd=0.088), respectively, and total expected heterozygosity (HT) for the entire sampled bison metapopulation was 0.698 (sd=0.10). We detected no global deviations from Hardy-Weinberg equilibrium using the exact test (detailed results given in Appendix C).

Within herd estimates of heterozygosity and allelic richness varied considerably between herds (Table 2.3.2; Figure 2.3.1). Observed heterozygosity varied from a low of 0.503 (WRST; sd=0.01) to a high of 0.650 (WICA; sd=0.01), while expected heterozygosity ranged from a low of 0.480 (CHIC; sd=0.03) to a high of 0.662 (WICA; sd=0.01). The allelic richness of individual herds ranged from an estimated mean of 2.60 (CHIC; sd=0.8) to 4.14 (BOOK; sd=1.1) alleles per locus (Table 2.3.2; Figure 2.3.1).

Results of our analysis of cattle introgression revealed that eight herds had evidence of nuclear cattle alleles (Table

Table 2.3.1. Herd demographic and management data summarized from the survey responses of herd managers.

Herd	N	Ecological K (K_{eco})	Management K (K_{man})	Removal Strategy	Removal Schedule	Age Class Removed
BADL	1222 (with calves)	dry years 473; wet years 946	Herd not managed to meet human-imposed carrying capacity	randomly selected	annually	Yearlings and 2.5-year-olds
BOOK	est. 250 (~425 w/Ute bison)	unknown	450 post-season; 600-650 pre-season	hunter selected (85% bull; 15% cow)	annually	All age classes
CHIC	11	6-10	6-10	–	annually	Yearlings; >10-year-olds; sick/injured
ELK (Canada)	470	not stated	350 adults (>2+ years old)	mixture of ages	every other year	Primarily yearlings and juveniles (<2 years old); and some older adults (>5 years old)
FTN	412	350	350	minimize mean kinship	annually	Primarily yearlings; sometimes 2 or 3-year-olds
GRASS (Canada)	346 in 2018	398-511	400-500	mixture of ages	every other year	Juveniles (<2 years old) and some older adults (>10 years old)
HEMO	444	450	325	hunter selected (85% bull; 15% cow)	annually	All age classes except calves
NER/ GRTE	666	unknown	500	hunter selected animals	annually	All age classes*
NBR	359	285	285	minimize mean kinship	annually	Primarily yearlings; occasionally a few in the 2 and 3-year-old age classes
NSM	63	55	55	minimize mean kinship	annually	Yearlings
RMA	90	90	currently 90; or up to 200 when bison on full 12,000 acres)	Minimize mean kinship	annually	Yearlings;
SH	27	20	18	Minimize mean kinship	annually	Yearlings
TAPR	89	100	100	No removals yet (in 2016)	no removals yet (in 2016)	–
THROn	280	unknown	300	Randomly selected	every 4-5 years or as population approaches 300	Proportional removal of calves, yearlings, breeding cows, breeding bulls
THROs	335 (in 2014)	500	500	Randomly selected	every 4-5 years or as population approaches 500	Proportional removal of calves, yearlings, breeding cows, breeding bulls
WICA	400-425	not stated	350-500	Randomly selected	as needed; typically every 1-2 years	Yearlings; sometimes 2 or 3-year-olds
WM	682	650	650	Minimize mean kinship	annually	Yearlings;
WRST Chitina	57	unknown	minimum 50 adults	Hunter removal	annually	All age classes
WRST Copper R.	181	unknown	minimum 60 adults	Hunter removal	annually	All age classes

* See https://wgfd.wyo.gov/Hunting/Wild-Bison-Hunting-Information

2.3.2), though the proportion of cattle alleles detected within each of these herds was <2%. Only one herd (BOOK) had evidence of cattle mtDNA. For cattle introgression in herds which had not been previously reported, we found no evidence of introgression within ELK and GRASS, and we found very small levels within BOOK and WRST. For herds that have previously been tested for introgression, we did not identify significant differences compared to previously published values (Halbert and Derr 2008).

Population Structure

Global tests of genetic differentiation indicated significant differentiation within the DOI bison metapopulation, with values of 0.144 (95% CI: 0.369-0.380), 0.375 (95% CI: 0.369-0.380), and 0.269 (95% CI: 0.260-0.268) for F_{ST}, $G_{ST'}$, and Jost's D, respectively. Pairwise comparisons between herds revealed relatively high values of genetic differentiation between most individual herds (Tables 2.3.3, 2.3.4, Appendix D). with the lowest levels of genetic differentiation between newly created herds and their source herds (e.g., ELK and GRASS). The highest levels of differentiation were found between the smallest and/or most geographically distant herds (e.g., CHIC and WRST: pairwise $G_{ST'} = 0.597$), while some larger established herds also displayed high levels of genetic

Table 2.3.2. A summary of results from our analyses of the genetic diversity of 16 DOI bison herds and two Parks Canada herds, and for the presence of nuclear cattle alleles or mtDNA in each herd (published data for YELL is included for comparison). "Estimated N at sampling" indicates the estimated abundance for each herd when samples were collected; "Sample Size" is the number of genetic samples collected from each herd; "H_e" and "H_o" are the expected and observed heterozygosity; "A_r" is the estimated allelic richness; "MNA" is the uncorrected mean number of alleles per locus; and F_{IS} tests for non-random mating within herds.

Herd	Sample Size	H_e (sd)	H_o (sd)	A_r (sd)	MNA (sd)	F_{IS}	Nuclear Cattle Alleles	Cattle MtDNA
BADL	100	0.596 (0.02)	0.584 (0.01)	3.73 (1.1)	4.50 (1.4)	0.02	yes	no
BOOK	38	0.657 (0.02)	0.630 (0.01)	4.14 (1.1)	4.83 (1.4)	0.04	yes	yes
CHIC	10	0.480 (0.03)	0.550 (0.02)	2.60 (0.8)	2.60 (0.8)	-0.15	no	no
ELK	84	0.634 (0.02)	0.626 (0.01)	4.00 (0.9)	4.79 (1.4)	0.01	no	no
FTN	357	0.637 (0.02)	0.615 (0.01)	4.04 (1.0)	5.46 (1.7)	0.03	yes	no
GRASS	125	0.621 (0.02)	0.609 (0.01)	3.87 (1.0)	4.77 (1.4)	0.02	no	no
HEMO	85	0.556 (0.02)	0.544 (0.01)	3.22 (0.8)	3.73 (1.1)	0.02	no	no
NBR	302	0.647 (0.02)	0.642 (0.01)	4.08 (1.1)	5.04 (1.6)	0.01	yes	no
NER	100	0.526 (0.02)	0.515 (0.01)	2.97 (0.8)	3.75 (1.2)	0.02	no	no
NSM	53	0.642 (0.02)	0.647 (0.01)	3.96 (1.0)	4.54 (1.5)	-0.01	no	no
RMA	71	0.650 (0.02)	0.643 (0.01)	4.12 (1.0)	5.04 (1.5)	0.01	no	no
SH	22	0.544 (0.02)	0.557 (0.02)	3.37 (1.0)	3.71 (1.3)	-0.02	no	no
TAPR	43	0.662 (0.01)	0.647 (0.01)	4.07 (0.9)	4.63 (1.2)	0.02	no	no
THROn	100	0.531 (0.03)	0.529 (0.01)	3.09 (0.9)	3.48 (1.0)	0	yes	no
THROs	87	0.585 (0.02)	0.569 (0.01)	3.64 (0.9)	4.19 (1.2)	0.03	yes	no
WM	576	0.597 (0.02)	0.588 (0.01)	3.76 (1.0)	4.87 (1.3)	0.02	yes	no
WICA	100	0.660 (0.01)	0.650 (0.01)	4.04 (0.9)	4.69 (1.3)	0.02	no	no
WRST	24	0.524 (0.02)	0.503 (0.01)	3.04 (0.8)	3.31 (1.0)	0.04	yes	no
YELL	–	0.615[A]	0.625[A]	4.15[A]	4.84[A]	-0.02	no[B]	no[B]

[A] Summary statistics for YELL from Halbert and Derr (2008)

[B] Introgression data for YELL from Halbert and Derr (2007) differentiation: WM and BADL had a pairwise $G_{ST'}$ of 0.405, and WM and HEMO had a pairwise $G_{ST'}$ of 0.534.

Results from our K-means clustering analysis suggest that there are currently 10-13 distinct genetic clusters (k) within the sampled bison populations (Figure 2.3.2). Figure 2.3.2 shows a clear decrease in BIC with increasing values of k, up to a k-value of approximately 10 to 11 clusters, after which BIC stabilizes, then begins to increase again. Ideally, the optimal number of distinct clusters to retain to best describe the data should correspond to the lowest BIC. However, in practice, BIC values may continue to decrease for values of k greater than the true k value (Jombart et al. 2010). Jombart and Collins (2015) suggest that the most parsimonious value of k is often indicated by an elbow in the curve of BIC values as a function of k. We therefore fit our DAPC analyses with the number of unique genetic clusters in the DOI populations set to either 10 or 11, the approximate values at which BIC ceases to decrease in value.

When the number of genetic clusters in the DOI bison population is set to 10, results of our DAPC analysis revealed that these 10 genetic clusters generally correspond to individually managed herds and their affiliated satellite herds (Figure 2.3.3). One notable exception is that individual samples from FTN are divided among 2 separate genetic clusters (clusters

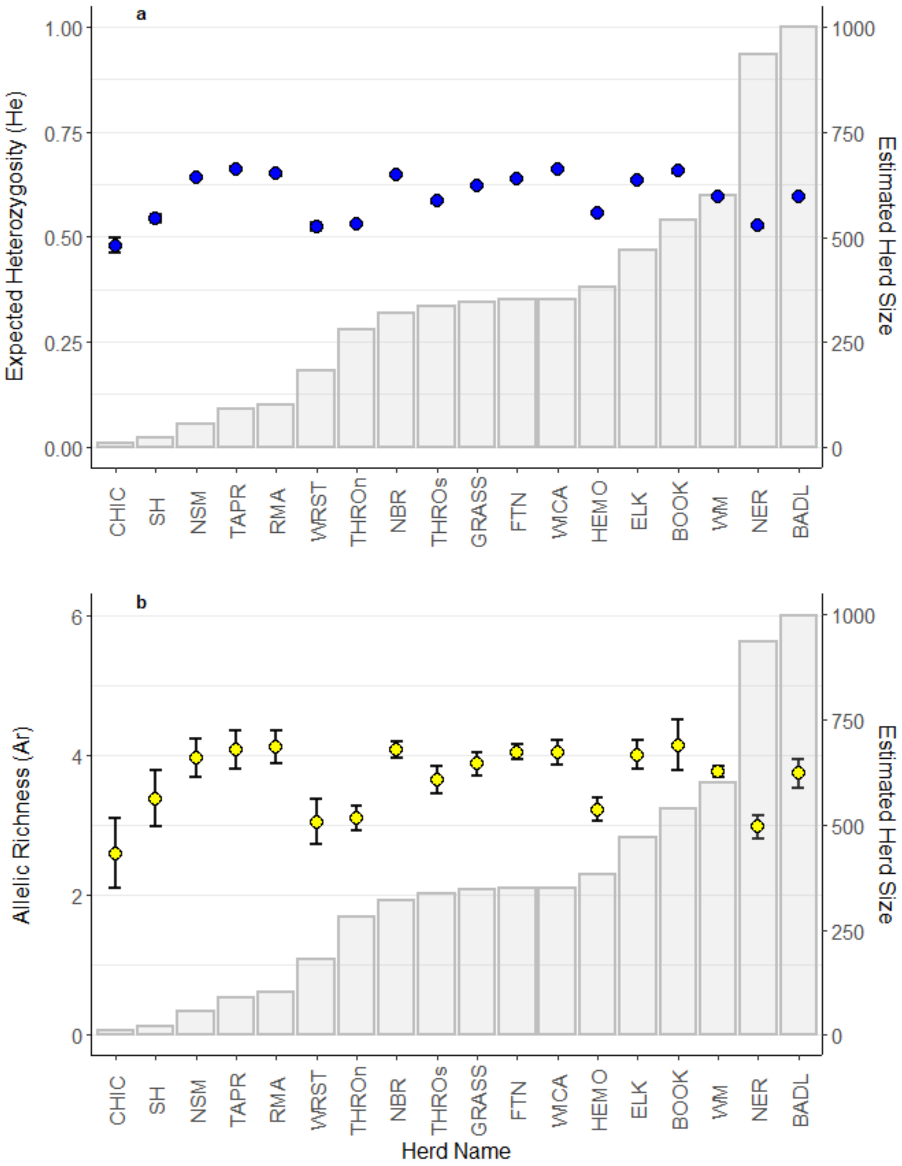

Figure 2.3.1. a) Expected heterozygosity (H_e); and b) allelic richness (A_r) of each of 16 DOI bison herds and two Parks Canada herds sampled in this study. Shaded bars denote the estimated herd size at the time of sampling. Error bars denote standard error.

labeled #2 and #7 in Figure 2.3.3), suggesting strong genetic differentiation between individuals within this herd. This is an expected result, with the recent combination of two separate historic herds onto one management unit. Otherwise individual samples from each herd tended to be found only within one cluster, with a few individuals from BOOK, RMA, FTN, and BADL assigned to other clusters, indicating either errors in assignment probabilities or traces of transfers between herds in previous years (e.g., one WICA-origin bull was moved to RMA in 2010 with confirmed offspring in 2011). The scatter plot in Figure 2.3.3 shows the degree of similarity (or differentiation) between the identified genetic clusters along the discriminant function axes, which are linear combinations of alleles emphasizing the largest between-group variance and the smallest within-group variance.

Fitting DAPC models with 11 distinct genetic clusters led to a split within NBR and its satellite herds (NSM, RMA, SH, and WRST). In this scenario, approximately half of all samples from NBR, RMA, and NSM were assigned to one genetic cluster, while the other half of samples from these herds were separated out into another distinct cluster along with SH and WRST. This sorting does not have support from historic movements between herds and is therefore unlikely to represent the actual number of distinct genetic clusters in the DOI bison population, suggesting that 11 clusters leads to an overfitted model. Hence, a threshold of 10 clusters was selected as most appropriate for interpretation.

2.4 Discussion

A primary question regarding the current levels of genetic diversity within and between herds is the extent to which these results have been shaped by natural selection versus human decisions and management actions during the recovery of

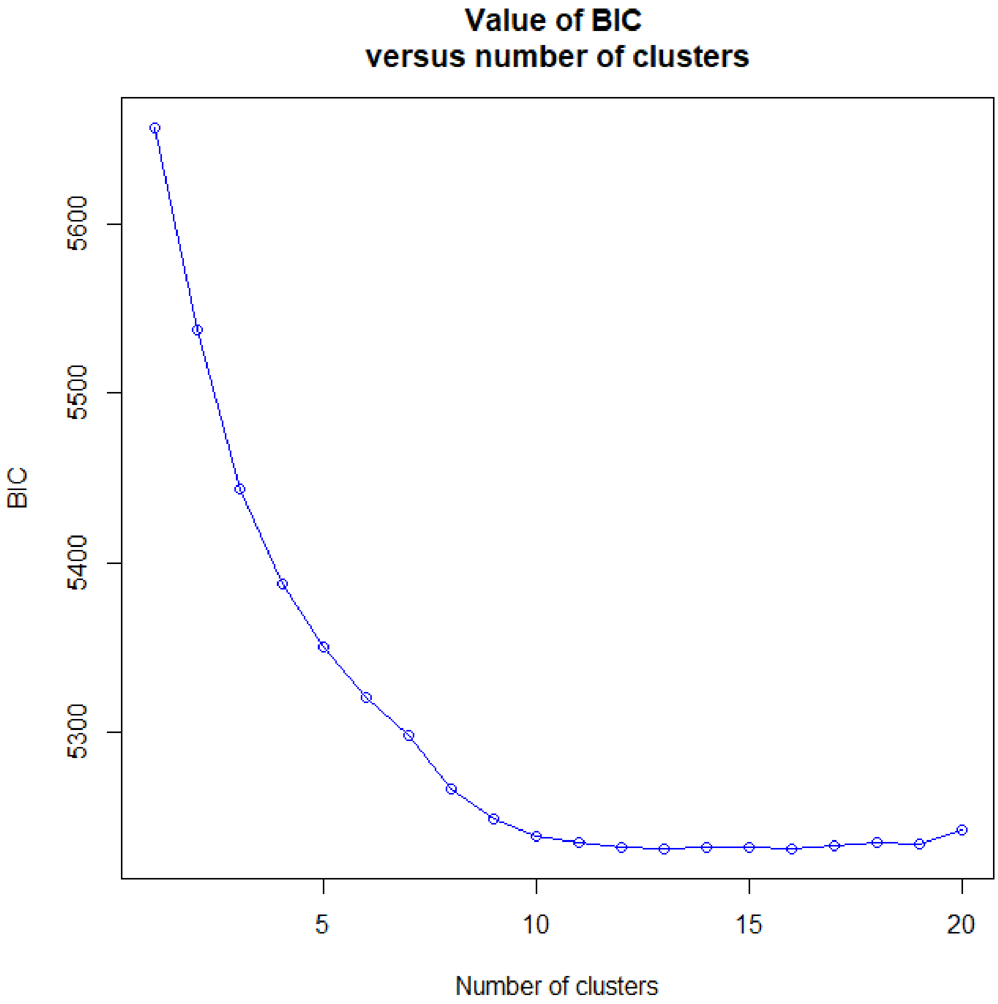

Figure 2.3.2. Bayesian Information Criterion (BIC) values for the fit of genetic data sampled from 16 DOI and two Parks Canada herds to models with increasing numbers (k; from 1 to 20) of distinct genetic clusters. Lower BIC scores indicate a better fit of the model to the data.

Table 2.3.3. Pair-wise F_{ST} values indicating levels of genetic differentiation between the 16 DOI and two Parks Canada herds sampled in this project. Shaded values denote herds that are not significantly differentiated from one another (i.e., 95% bootstrapped CI values include zero or have a lower confidence limit ≤ 0.01). Bootstrapped 95% CI values given in Appendix D.

Site	**BADL**	**BOOK**	**CHIC**	**ELK**	**FTN**	**GRASS**	**HEMO**	**NBR**	**NER**	**NSM**	**RMA**	**SH**	**TAPR**	**THROn**	**THROs**	**WM**	**WICA**
BADL	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BOOK	0.092	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CHIC	0.254	0.235	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ELK	0.144	0.101	0.238	–	–	–	–	–	–	–	–	–	–	–	–	–	—
FTN	0.045	0.073	0.225	0.114	–	–	–	–	–	–	–	–	–	–	–	–	–
GRASS	0.155	0.110	0.238	0.011*	0.123	–	–	–	–	–	–	–	–	—	–	–	–
HEMO	0.193	0.036	0.316	0.157	0.161	0.163	–	–	–	–	–	–	–	–	–	–	–
NBR	0.143	0.087	0.214	0.087	0.103	0.098	0.15	–	–	–	–	–	–	–	–	–	–
NER	0.129	0.122	0.293	0.176	0.115	0.187	0.198	0.178	–	–	–	–	–	–	–	–	–
NSM	0.153	0.095	0.24	0.097	0.117	0.11	0.156	0.009*	0.184	–	–	–	–	–	–	–	–
RMA	0.144	0.085	0.200	0.086	0.100	0.098	0.149	0.016*	0.17	0.028	–	–	–	–	–	–	–
SH	0.205	0.141	0.279	0.138	0.154	0.153	0.209	0.054	0.232	0.061	0.071	–	–	–	–	–	–
TAPR	0.133	0.082	0.218	0.091	0.101	0.095	0.142	0.1	0.179	0.111	0.088	0.159	–	–	–	–	–
THROn	0.082	0.130	0.324	0.179	0.085	0.189	0.232	0.187	0.162	0.197	0.188	0.235	0.164	–	–	–	–
THROs	0.045	0.100	0.255	0.15	0.056	0.154	0.204	0.15	0.126	0.155	0.142	0.201	0.132	0.077	–	–	–
WM	0.164	0.152	0.102	0.155	0.132	0.152	0.226	0.133	0.22	0.156	0.119	0.194	0.129	0.225	0.17	–	–
WICA	0.136	0.084	0.215	0.101	0.103	0.104	0.143	0.108	0.185	0.121	0.097	0.169	0.003*	0.169	0.137	0.123	–
WRST	0.224	0.173	0.298	0.157	0.189	0.167	0.231	0.11	0.261	0.109	0.122	0.153	0.169	0.259	0.225	0.226	0.178

*Shaded values denote herds that are not significantly differentiated from one another (i.e., 95% bootstrapped CI values include zero or have a lower confidence limit ≤ 0.01). Bootstrapped 95% CI values given in Appendix D.

Table 2.3.4. Pair-wise Hedrick's G_{ST} ($G_{ST'}$) values (above the diagonal), and pair-wise Jost's D values (shaded, below the diagonal) between 16 DOI and two Parks Canada herds sampled in this project. $G_{ST'}$ values indicate levels of genetic differentiation between herds and scale from 0 to 1, with a pair-wise value of 0 indicating low differentiation with both herds far from fixation (high levels of past gene flow), and values of 1 indicating high levels of differentiation, with both herds at fixation for all loci sampled. Jost's D values indicate levels of allelic differentiation between herds and scale from 0 to 1, with a pair-wise value of 0 indicating that two herds share all sampled alleles in common, and 1 indicating herds have no sampled alleles in common.

Site	**BADL**	**BOOK**	**CHIC**	**ELK**	**FTN**	**GRASS**	**HEMO**	**NBR**	**NER**	**NSM**	**RMA**	**SH**	**TAPR**	**THROn**	**THROs**	**WICA**	**WM**	**WRST**
BADL	–	0.248	0.55	0.374	0.119	0.395	0.455	0.381	0.294	0.401	0.381	0.477	0.359	0.189	0.11	0.366	0.405	0.511
BOOK	0.169*	–	0.545	0.285	0.206	0.305	0.093	0.253	0.299	0.272	0.245	0.354	0.242	0.319	0.265	0.246	0.408	0.425
CHIC	0.399*	0.411*	–	0.538	0.51	0.529	0.656	0.493	0.587	0.547	0.46	0.57	0.509	0.654	0.544	0.499	0.219	0.597
ELK	0.262*	0.191*	0.394*	–	0.314	0.029	0.389	0.242	0.419	0.268	0.24	0.338	0.258	0.428	0.385	0.286	0.402	0.375
FTN	0.045*	0.147*	0.375*	0.228*	–	0.332	0.399	0.291	0.275	0.325	0.281	0.378	0.287	0.205	0.145	0.293	0.345	0.454
GRASS	0.278*	0.21*	0.369*	0.016*	0.24*	–	0.396	0.269	0.439	0.3	0.269	0.369	0.264	0.445	0.388	0.289	0.389	0.392
HEMO	0.303*	0.053*	0.543*	0.249*	0.278*	0.257*	–	0.38	0.431	0.389	0.376	0.465	0.364	0.508	0.476	0.366	0.534	0.504
NBR	0.277*	0.173*	0.346*	0.158*	0.223*	0.178*	0.252*	–	0.434	0.025	0.047	0.135	0.29	0.458	0.393	0.314	0.355	0.268
NER	0.115*	0.171*	0.375*	0.297*	0.122*	0.313*	0.212*	0.299*	–	0.444	0.412	0.499	0.442	0.344	0.283	0.454	0.502	0.551
NSM	0.293*	0.172*	0.391*	0.179*	0.249*	0.201*	0.239*	0.016*	0.277*	–	0.079	0.15	0.321	0.476	0.402	0.346	0.41	0.264
RMA	0.27*	0.163*	0.322*	0.153*	0.208*	0.178*	0.24*	0.031*	0.268*	0.049*	–	0.177	0.257	0.458	0.37	0.28	0.317	0.298
SH	0.329*	0.221*	0.382*	0.203*	0.268*	0.241*	0.288*	0.099*	0.334*	0.1*	0.119*	–	0.402	0.507	0.462	0.426	0.452	0.33
TAPR	0.262*	0.166*	0.394*	0.169*	0.205*	0.169*	0.236*	0.2*	0.315*	0.221*	0.172*	0.266*	–	0.407	0.35	0.008	0.349	0.417
THROn	0.06*	0.198*	0.525*	0.282*	0.074*	0.304*	0.3*	0.346*	0.08*	0.336*	0.328*	0.151*	0.27*	–	0.175	0.416	0.515	0.55
THROs	0.054*	0.168*	0.35*	0.256*	0.069*	0.255*	0.3*	0.283*	0.116*	0.27*	0.248*	0.295*	0.233*	0.061*	–	0.362	0.416	0.507
WICA	0.279*	0.171*	0.382*	0.193*	0.224*	0.19*	0.239*	0.222*	0.334*	0.245*	0.19*	0.299*	0.004*	.301*	0.252*	–	0.331	0.439
WM	0.277*	0.299*	0.137*	0.274*	0.244*	0.26*	0.385*	0.239*	0.356*	0.287*	0.205*	0.316*	0.25*	0.396*	0.278*	0.233*	–	0.516
WRST	0.342*	0.258*	0.347*	0.242*	0.322*	0.261*	0.32*	0.164*	0.28*	0.147*	0.179*	0.127*	0.28*	0.208*	0.283*	0.305*	0.373*	–

*pair-wise Jost's D values (shaded, below the diagonal)

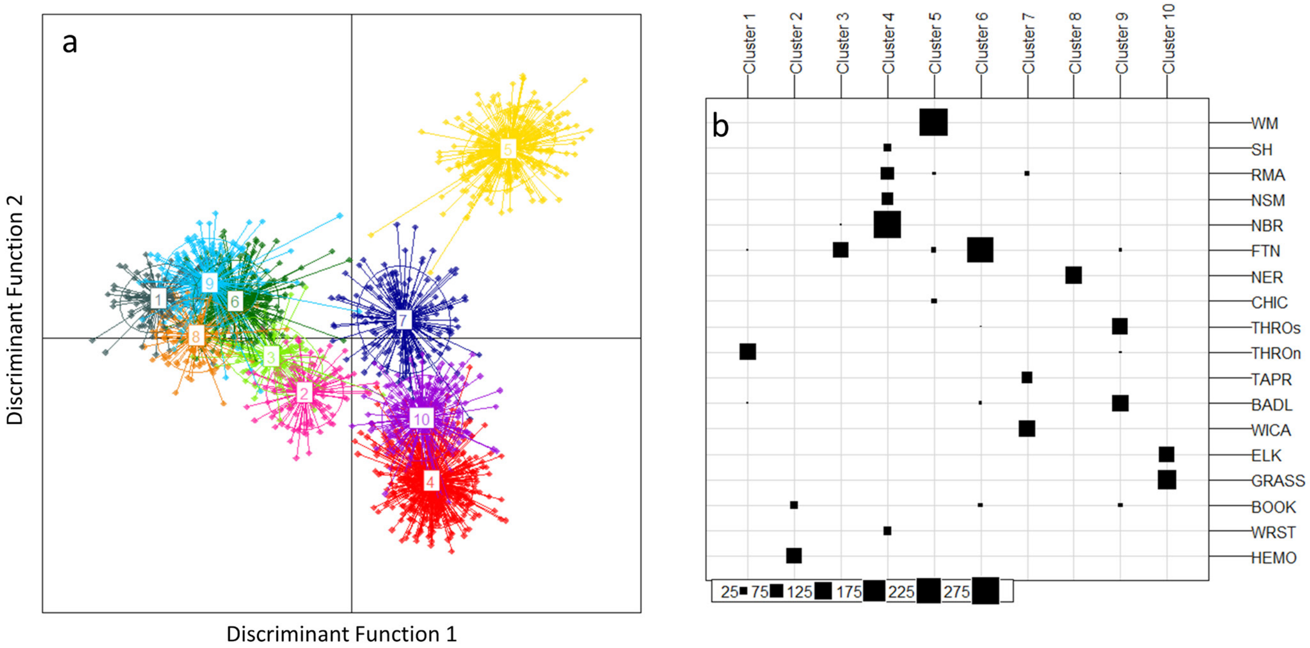

Figure 2.3.3. a) The genetic structure of 16 DOI and two Parks Canada herds sampled in this analysis. Points represent individual bison samples, and the numbered circles represent the 10 unique genetically differentiated clusters in the bison data; b) the relative number of individual samples from each herd assigned to each genetic cluster.

the plains bison. To better understand that relationship, we must consider the levels of genetic diversity and differentiation observed in this study in light of the establishment and augmentation history of existing herds, and prior genetic analyses.

Hedrick (2009) estimated that all extant plains bison in North America descend from an effective founding number of <100 individuals across seven described herds in the late 1800s to early 1900s. A review of foundation herds and animal transfers described by Coder (1975), Halbert and Derr (2007), and DOI records reveals that most existing herds were admixed at establishment or have been augmented over time with animals from multiple sources, some of which are unknown (Table 2.4.1). Therefore, most DOI herds have had at least some level of historic gene flow or mixing since their founding, with only ELK and GRASS known to originate from a single foundation herd described in the literature (Coder 1975; Parks Canada 2017).

Our analyses revealed considerable variation in the level of genetic diversity within the DOI and Parks Canada herds in this study. Measures of heterozygosity and allelic richness generally correspond with known herd foundation and augmentation histories, combined with the expected effects of genetic drift. Our results indicate that three bison herds (GRTE/NER, THROn, and WRST) currently have observed heterozygosity levels (H_o) close to 0.50, a value identified as a threshold for triggering genetic augmentation by Dratch and Gogan (2010). A further two herds (HEMO and CHIC) are just above this threshold with H_o estimates ~ 0.55. A sequential series of bottlenecks may partially explain the progressive decrease in genetic diversity observed from FTN to THROs to THROn, as THROs was founded with individuals from FTN, and THROn was founded with individuals from THROs (Table 2.3.2). The relatively small population size and isolation since its founding in 1950 likely explains the very low genetic diversity in the WRST Copper River herd. Founder effect, a history of small herd size, and long-term isolation likely explain the low diversity observed at HEMO. The low diversity level of NER is likely due to multiple founder effects, in which a very small, possibly already inbred herd, went through a bottleneck due to culling to prevent the spread of brucellosis.

In contrast, recently founded or augmented herds had relatively high levels of genetic diversity. The high levels of H_e and A_r in the BOOK herd revealed by our analysis likely reflect its recent foundation through HEMO and more recent admixture from intermingling with bison managed by the Ute Tribe. Additionally, six FWS herds are managed to conserve diversity within each herd using mean kinship

Table 2.4.1. A summary of the founding source, numbers, and subsequent augmentations for herds in this study, compiled from Coder (1975) and Halbert and Derr (2007).

Herd (Abbreviation)	Year	n	Foundation/Augmentation Source
Badlands National Park (BADL)	1963	3	Fort Niobrara National Wildlife Refuge
	1963	25	Theodore Roosevelt National Park (South)
	1983	20	Colorado National Monument[A]
Book Cliffs (BOOK)	2009	30	Henry Mountains
	2009	14	Northern Ute herd[B]
	2010	40	Henry Mountains
Grasslands National Park (GRASS)	2005	71	Elk Island National Park
Fort Niobrara National Wildlife Refuge (FTN)	1913	6	J.W. Gilbert Friend, NEA (multiple origin private herd)
	1913	2	Yellowstone National Park
	1935	4	Custer State Park, SD (Philip herd)
	1937	4	Custer State Park, SD (Philip herd)
	1952	5	National Bison Range
	2010	39	Original Sully's Hill National Game Preserve[C]
	2010	1	Wind Cave National Park (via American Prairie Reserve)
	2011	8	Wichita Mountains Wildlife Refuge
Grand Teton NP / National Elk Refuge (GRTE/NER)	1948	9	Yellowstone National Park
	1964	12	Theodore Roosevelt National Park (South)
Elk Island National Park (ELK)	1907	40-70	Pablo-Allard Herd
Henry Mountains (HEMO)	1941	18	Yellowstone National Park
	1942	5	Yellowstone National Park
National Bison Range (NBR)	1909	36	Conrad herd (Pablo-Allard herd origin), Kalispell, MT
	1909	1	Goodnight herd, TX
	1910	3	Corbin herd (multiple origin private herd)
	1939	2	7-Up Ranch, MT[A]
	1952	4	Fort Niobrara NWR
	1953	2	Yellowstone National Park
	1984	4	Maxwell State Game Refuge, KS (Jones herd origin)
Neal Smith National Wildlife Refuge (NSM)	2006	39	National Bison Range
	2014	2	Rocky Mountain Arsenal[D]
Rocky Mountain Arsenal (RMA)	2007	16	National Bison Range
	2008	2	Sully's Hill National Game Preserve display herd[D]
	2009	10	National Bison Range
	2010	1	Wind Cave National Park (via American Prairie Reserve)
	2011	3	Wichita Mountains Wildlife Refuge
Sully's Hill National Game Preserve (SH)[D]	2006	7	National Bison Range (to establish new display herd)
	2014	3	Rocky Mountain Arsenal
Tallgrass Prairie National Preserve (TAPR)	2009	13	Wind Cave National Park
	2014	10	Wind Cave National Park
Theodore Roosevelt National Park South Unit (THROs)	1956	29	Fort Niobrara National Wildlife Refuge
Theodore Roosevelt National Park North Unit (THROn)	1962	20	Theodore Roosevelt National Park (South Unit)
Wichita Mountains Wildlife Refuge (WM)	1907	15	New York Zoological Society Park[B]
	1940	4	Fort Niobrara National Wildlife Refuge
Wind Cave National Park (WICA)	1913	14	New York Zoological Society Park[B]
	1916	6	Yellowstone National Park
Wrangell-St. Elias, Copper River (WRST)	1950	50	Delta AK herd[E]
Yellowstone National Park (YELL)	1902	23	Remaining wild herd
	1902	3	Goodnight herd, TX
	1902	18	Pablo-Allard herd

[A] Origins unknown

[B] Multi-origin herd

[C] Multi-origin herd, including a private herd from Ravalli, MT; WICA; THRO; FTN; NBR

[D] National Bison Range origin

[E] Delta herd founded in 1928 with 23 bison from NBR to identify highly related individuals in the herd for removal during the annual capture and population management operation. Using mean kinship as a selection tool improves genetic diversity conservation over random removal in small, isolated bison populations (Giglio et al. 2016, Giglio et al. 2018). Recognizing the negative impacts of managing small populations in isolation and the need to facilitate gene flow, FWS bison managers identified conservation of genetic diversity in National Wildlife Refuge System bison as a priority in 2007, such that some FWS herds have been recently augmented genetically by translocation of animals with confirmed offspring production. This two-tiered management strategy to conserve diversity both within and across FWS managed herds supports the high levels of genetic diversity identified in this study.

Halbert and Derr (2008) completed an extensive analysis of genetic variation for 11 DOI herds, although sample sizes were small for some herds in their study. Differences in measures of within-herd genetic diversity between the results of our study and those previously published from samples collected 1997-2002 (Halbert and Derr 2008) are likely due to differences in sample size, changes in herd management including augmentation, and genetic drift that may have occurred in the time between studies. Examples include increased diversity in the FTN herd due to augmentation from other herds that is reflected in the assignment of individuals to multiple clusters from which those augmentations were made (SH, WM, and WICA) (Table 2.4.1; Figure 2.3.3), and increased diversity found in WM due to a significant increase in sample size over the previously published values. However, even accounting for sampling error, three herds in this study appear to have lower levels of genetic diversity than has been reported previously (NER/GRTE, THROn, THROs). Excluding herds with small samples sizes (BOOK and WRST) and herds managed at extremely small sizes (CHIC and SH), our study suggests a measurable loss of diversity in some herds compared to previously published values.

The absence of YELL and the inclusion of ELK, GRASS, BOOK, and HEMO in our analysis precludes direct comparison of our results to those previously published by Halbert and Derr (2008), but both studies identified significant levels of differentiation among herds. Halbert and Derr (2008) found support for eight unique genetic clusters out of the 11 herds they studied and identified a primary split between what they termed the “Fort Niobrara lineage” (including FTN and herds with a FTN foundation, including BADL, THROn, THROs) and a NBR, WICA, WM, and YELL grouping, with individuals from other herds generally split among the two groups. We also identified distinct genetic clusters associated with NBR and WICA, as well as separation of the FTN-origin herds. In our analysis, BOOK and HEMO herds generally occupy the space between FTN lineages and the other groups. Furthermore, our inclusion of a sufficient sample size from WM suggests that it separates completely from all other herds except for CHIC, which has regularly received WM animals (Table 2.2.1, Figure 2.3.3). The WM herd originates from the New York Zoological Park bison herd, which included an admixture of animals from multiple sources. A combination of founder effects and subsequent isolation from all other DOI herds may have resulted in its apparent level of differentiation.

Identification of 10 genetic clusters from the 18 herds evaluated here is supported by the known foundation and augmentation histories of these herds and is also in general agreement of the genetic differentiation measures calculated independently of the DAPC (Tables 2.3.3-2.3.4). Though consensus does not exist for threshold values of F_{ST} to differentiate populations, pairwise values > 0.05 are generally considered to signify genetic differentiation between populations (Balloux and Lugon-Moulin 2002). By this standard, our F_{ST} measurements generally support DAPC assignments with a few exceptions between foundation herds and herds more recently established from that foundation (Table 2.3.3). For example, both our DAPC and pairwise F_{ST} analyses support the known parent-child relationships for satellite herds (ELK-GRASS, NBR-NSM, NBR-RMA, WICA-TAPR). Further, groups most separated in our DAPC analysis (Clusters 1, 4, and 5) correspond to the largest pairwise herd F_{ST} values measured, typically > 0.2 (Table 2.3.3; Figure 2.3.3a). Likewise, for G_{ST}, and Jost’s D measures, there is no consensus threshold for interpretation of closely related herds established from a common foundation. However, our calculations for these statistics generally follow the pattern observed for F_{ST}, though scaling along a continuum of 0 to 1 is amplified for both values (Tables 2.3.4).

Despite the absence of YELL and GRCA in our analysis, we can still make inferences from herd establishment and augmentation histories. For instance, Pablo Allard lineage associations and subsequent transfers may explain some of the observed x-axis separation of clusters in the DAPC plot. ELK and GRASS (Cluster 10) emanate solely from this source, and the Pablo Allard herd was also the primary source for the initial NBR herd (Coder 1975; Halbert and Derr 2007). The WRST and modern RMA, NSM, and SH satellite herds were also established with NBR founders, explaining their inclusion with NBR in Cluster 4. The Pablo Allard lineage may have also contributed to WICA and WM herds through transfers of founders from the New York Zoological Park, although these relationships may be confounded by the fact that the New York Zoological Park conservation herd comprised animals from multiple other sources (Coder 1975). YELL was also augmented from the Pablo Allard herd in 1902, prior to distributing animals to FTN (1913), HEMO (1941), and NER/GRTE (1948), all of which fall left of center in the DAPC plot (Figure 2.33a). The addition of the original SH herd to FTN in 2010, and the observed social separation for several years after this addition (L. Jones, personal communication), likely explains the split of FTN genotypes across Clusters 3 and 6 in our analysis.

Both our analysis and that of Halbert and Derr (2008) illuminate the genetic signature of founder effects and past management on DOI bison herds. These effects have been exacerbated by genetic drift in some herds. Together these processes have led to the genetic divergence of bison herds into the statistically differentiated populations evidenced in this study (Table 2.3.3-2.3.4, Figure 2.3.3), despite their shared ancestry (Table 2.4.1). Our results also indicate a measurable loss of diversity from previous studies, likely due to continued isolation and drift, and ongoing loss will continue without intervention. Therefore, metapopulation management must be considered on a broader scale within DOI, in tandem with satellite herd establishment, genetic monitoring, and adaptive management.

3. Assessing the Viability of DOI Bison Under Current Management Conditions

3.1 Introduction

Ecological, social, and political limitations currently restrict the geographic distribution and abundance of bison herds on DOI lands (DOI 2014). As a consequence of these limitations, many DOI herds remain geographically isolated from one another with little natural movement between herds, and the majority of herds are actively managed to maintain population size of fewer than 500 animals on range-restricted landscapes. The isolation and relatively small sizes of many of these herds has led to concerns about their long-term population and genetic viability (Dratch and Gogan 2010; Hedrick 2009). In particular, it has long been recognized that small, isolated populations have a greater risk of extirpation due to random catastrophic events (Lande 1993; MacArthur and Wilson 1967) such as disease outbreaks (Smith et al. 2006), extreme weather events (Ameca y Juarez et al. 2012; Tyler 2010) or wildfire (Potvin et al. 2017). Small isolated populations also lose genetic diversity more quickly through the process of genetic drift (Hartl and Clark 2007), with detrimental effects on both the short- and long-term viability of the population.

The loss of genetic diversity due to random genetic drift increases the risk of inbreeding depression, the reduction in fitness in offspring of closely related parents relative to the offspring of unrelated parents (Allendorf et al. 2013). Inbreeding depression has been widely documented among animal species and can result in a broad range of fitness effects, including high infant mortality, skewed sex ratio, reduced adult survival, increased health problems, and infertility (Hedrick and Kalinowski 2000; Hogg et al. 2006; Keller and Waller 2002). The lower survival and reproductive rates typical of inbred individuals in turn lead to declines in population growth rates, thereby increasing the risk of population extirpation (Gilpin and Soulé 1986; Mlot, 2015; Soulé and Mills 1998; Westemeier et al. 1998). Reductions in genetic diversity also ultimately decrease the ability of populations or species to evolutionarily adapt to changing or novel environmental conditions (Fisher 1930; Reed and Frankham 2003), such as increased climatic variability or the emergence of novel diseases (McCallum and Jones 2010; Reed et al. 2003).

Characteristics of a population influence the rate at which genetic diversity is lost due to drift. These include the number of reproductive adults in the population, the ratio of breeding males to breeding females, and the level of gene flow into the population, i.e., the number of migrants from outside the population that enter the breeding pool and successfully reproduce (Hartl and Clark 2007). Characteristics of a species' life history also influence its vulnerability to drift: in particular, its breeding system and mean generation time (Allendorf et al. 2013). Generally speaking, small populations lose genetic diversity more quickly than large populations, and species with short generation times lose diversity more quickly than those with long generation times. The degree to which diversity loss due to drift increases inbreeding risk in an isolated population will also depend on initial levels of genetic diversity within that population.

Our genetic analyses of 16 DOI herds and two Parks Canada herds revealed considerable variation in the existing genetic diversity across herds. Given the variable levels of genetic diversity in these herds, current restrictions on herd size and gene flow, and the inevitable loss of genetic diversity due to drift, concerns have been raised about the long-term viability and evolutionary adaptability of these herds (Dratch and Gogan 2010; Gross and Wang 2005; Hedrick 2009). In particular, 5-6 herds (CHIC, HEMO, NER/GRTE, SH, THROn, WRST) already have relatively low levels of genetic heterozygosity and allelic diversity respectively, potentially increasing the risk of inbreeding depression for individuals in these herds if they remain isolated. To ensure the long-term population and genetic viability of these herds, it is critical to understand how management interacts with genetic diversity within each herd to affect risks of inbreeding and extinction and how these risks can be mitigated through changes in management practices. In particular, it is imperative to know which herds are likely to attain dangerously high levels of inbreeding, if any herds are at risk of extinction, and what factors drive these risks.

In this study we developed a population viability model to evaluate the long-term demographic and genetic status of each of the 18 plains bison herds for which we have standardized, up-to-date genetic and management data (16 DOI herds and two Parks Canada herds). Specifically we used an individual-based, genetically explicit simulation model to estimate four measures of population and genetic viability over the next 200 years: 1) the risk of extinction for each herd (defined as only one sex remaining), 2) final levels of genetic diversity for each herd and for the metapopulation as a whole, 3) levels of accumulated inbreeding for each herd, and 4) rates of genetic diversity loss for each herd and for the entire bison metapopulation.

3.2 Methods

Model Description

The stochastic, individual-based population model was developed using the VORTEX 10.2.7 (Lacy and Pollak 2017) software program. VORTEX is a Monte Carlo simulation that models the effects of demographic rates, environmental variability, and genetic stochastic events on populations (Lacy 1993; Lacy 2000; Lacy et al. 2017). VORTEX simulates population dynamics as discrete sequential events in which events such as breeding success, number of offspring per reproductive cycle, sex at birth, and survival are determined based upon designated probabilities that incorporate both demographic stochasticity and annual environmental variation.

The model developed for this study was based upon previous PVA work by the International Union for the Conservation of Nature Species Survival Commission (IUCN SSC) Conservation Breeding Specialist Group (now Conservation Planning Specialist Group, or CPSG) in 2016 to inform the revised Red List assessment for wild bison populations by the IUCN SSC American Bison Specialist Group (Aune et al. 2017; Traylor-Holzer 2016). In this study, we parameterized each herd with its herd-specific demographic, management, and genetic data collected in Chapter 2. We ran the model for 200 years, for 500 iterations (replicates), and we examined the mean and range of probable demographic and genetic outcomes for each herd and for the metapopulation as a whole.

Model Parameterization

Initial Population Demographic Parameters

Estimated herd sizes used as starting values in the model were obtained from the 2016 managers surveys (Chapter 2) or in subsequent workshops and communications. Current age and sex structure of each herd were based upon survey data when available and otherwise were assumed to be at a stable age and sex distribution for a herd's given size and demographic rates at the onset of simulations.

Management of Herd Size

Bison managers were asked to provide their target or management-imposed maximum herd size (K_{man}) along with details on their current herd size control strategy. This included any criteria for implementation, schedule, number of bison removed, and age and sex ratios of those removals (Table 3.2.1). In particular, many of the DOI bison herds are managed to slow the process of genetic drift, including targeting younger age classes (yearlings and 2-year-olds) for removals to lengthen the mean generation time of the herd or targeting genetically over-represented yearlings and 2-year-olds for removal as estimated by available population-wide genotypic data (mean kinship-based removals). We included all removals as 'harvest' in the VORTEX model, which permanently removes these bison from the multi-herd metapopulation (the fate of these individuals is not tracked in this model). To implement mean kinship-based removals, the mean kinship of each individual to all individuals in the herd was calculated by the model, and individuals (typically yearlings) chosen for removal were selected in order from highest to lowest mean kinship values. This results in the removal of individuals that are most genetically redundant in the population (Ballou and Lacy 1995).

We used survey responses to estimate the ecological carrying capacity (K_{eco}) for the area available to each herd in order to set a maximum allowable herd size in the model. If herd size exceeds K_{eco} at the end of the simulation year, VORTEX truncates the herd to ~K_{eco} via probabilistic removals. This could occur if harvests were insufficient to bring the herd down to its maximum size. The default method is to apply the risk of removal equally to each animal across all age and sex classes. For some herds, only certain age and sex classes were subjected to removal to simulate additional non-random removals or losses (Table 3.2.1).

Dispersal and Gene Flow

For this PVA, we assumed all herds were isolated with no exchange of bison with the exceptions of two herds: CHIC and BOOK. In CHIC's current management plan, herd abundance is maintained at 10 individuals, but the herd is required to have at least one adult male and one adult female. If one or both are lost, a replacement is translocated from WM.

BOOK is an unfenced, free-roaming herd in close proximity to another free-roaming herd owned by the Northern Ute tribe. These two herds are known to co-mingle, and the detection of cattle mtDNA in BOOK (Table 2.3.2) suggests that they have had genetic exchange. Because we do not have genotypic data from the Northern Ute herd, we approximated this gene flow in our models by assuming that two female yearlings with genotypes derived from THROs's alleles entered the BOOK population every year.

Demographic Rates

Age- and Sex-Specific Mortality Rates

We applied the mean annual age- and sex-specific mortality rates listed in Table 3.2.2 probabilistically to each individual each year. These rates are base line mortality rates and assume no density dependence and do not include effects

Table 3.2.1. Removal management parameters for each herd in VORTEX, based on managers' responses to a survey of management practices in use as of 2016. The table summarizes the frequency at which removal events occur; the threshold abundance (K_{man}) that determines whether a removal event will occur (removal is triggered if abundance > K_{man}); and the number of yearlings (1 to 2-year-olds), 2-year-olds (2 to 3-year-olds) and adults (>3-year-olds) removed from the population during a removal event. "N" denotes the total population abundance for a given year.

Herd	Frequency of removals[A]	Threshold abundance for removals	Number of yearlings removed (Female)	Number of yearlings removed (Male)	Number of 2-year-olds removed (Female)	Number of 2-year-olds removed (Male)	Number of adults removed (Female)	Number of adults removed (Male)
BADL	Every year	>600	Either 60% (37.5% chance) or 80% (62.5% chance) of ALL yearlings are removed (1:1 sex ratio)	Either 60% (37.5% chance) or 80% (62.5% chance) of ALL yearlings are removed (1:1 sex ratio)	none	none	none	none
BOOK	Every year[B]	>450 bison (not counting yearlings)	0.06*(N-460)	0.14*(N-460)	0.016*(N-460)	0.045*(N-460)	0.224*(N-460)	0.515*(N-460)
CHIC	Every year	>10	N-10 (1:1 sex ratio), provided at least 1 adult of same sex is present and retained	N-10 (1:1 sex ratio), provided at least 1 adult of same sex is present and retained	none	none	1 adult > 9 years old (1:1 sex ratio); no removal if there is only 1 adult of the selected sex	1 adult > 9 years old (1:1 sex ratio); no removal if there is only 1 adult of the selected sex
ELK	Every other year	>350	0.20*(N-350)	0.20*(N-350)	0.20*(N-350)	0.20*(N-350)	0.10*(N-350) [C]	0.10*(N-350) [C]
FTN[D]	Every year	>350	0.48*(N-350)	0.42*(N-350)	0.06*(N-350)	0.04*(N-350)	3-year-olds removed (with 1:1 sex ratio) only if not enough yearlings & 2-year-olds available to reach target size (N=350)	3-year-olds removed (with 1:1 sex ratio) only if not enough yearlings & 2-year-olds available to reach target size (N=350)
GRASS	Every other year	>400	0.25*(N-400)	0.25*(N-400)	0.20*(N-400)	0.20*(N-400)	0.05*(N-400) [C]	0.05*(N-400) [C]
HEMO	Every year	>375	none	none	0.047*(N-375)	0.053*(N-375)	0.423*(N-375)	0.477*(N-375)
NBR[D]	Every year	>285	0.48*(N-285)	0.42*(N-285)	0.06*(N-285)	0.04*(N-285)	none	none
NER/GRTE	Every year[B]	>500	0.075*(N-500)	0.075*(N-500)	0.14*(N-500)	0.06*(N-500)	0.46*(N-500)	0.19*(N-500)
NSM[D]	Every year	If N>55 AND >1 adult male AND >1 adult female	0.50*(N-55)	0.50*(N-55)	2-year-olds only removed (with 1:1 sex ratio) if not enough yearlings available to reach target size (N=55)	2-year-olds only removed (with 1:1 sex ratio) if not enough yearlings available to reach target size (N=55)	none	none
RMA[D]	Every year	>200	0.48*(N-200)	0.42*(N-200)	0.06*(N-200)	0.04*(N-200)	3-year-olds only removed (with 1:1 sex ratio) if not enough yearlings & 2-year-olds available to reach target size (N=200)	3-year-olds only removed (with 1:1 sex ratio) if not enough yearlings & 2-year-olds available to reach target size (N=200)
SH[D]	Every year	If N>15 AND >1 adult male AND >1 adult female	0.50*(N-15)	0.50*(N-15)	none	none	none	none

Table 3.2.1. Continued. Removal management parameters for each herd in VORTEX, based on managers' responses to a survey of management practices in use as of 2016. The table summarizes the frequency at which removal events occur; the threshold abundance (K_{man}) that determines whether a removal event will occur (removal is triggered if abundance > K_{man}); and the number of yearlings (1 to 2-year-olds), 2-year-olds (2 to 3-year-olds) and adults (>3-year-olds) removed from the population during a removal event. "N" denotes the total population abundance for a given year.

Herd	**Frequency of removals**[A]	**Threshold abundance for removals**	**Number of yearlings removed (Female)**	**Number of yearlings removed (Male)**	**Number of 2-year-olds removed (Female)**	**Number of 2-year-olds removed (Male)**	**Number of adults removed (Female)**	**Number of adults removed (Male)**
TAPR	Every year	>75	50% of ALL yearlings	50% of ALL yearlings	40% of ALL 2-year-olds (1:1 sex ratio)	40% of ALL 2-year-olds (1:1 sex ratio)	none	0.2*(# of male 3-year-olds in herd)
THROn	Every year[E]	>300	90% of ALL yearlings (1:1 sex ratio)	90% of ALL yearlings (1:1 sex ratio)	90% of ALL 2-year-olds (1:1 sex ratio)	90% of ALL 2-year-olds (1:1 sex ratio)	10% of ALL 3-year-olds (1:1 sex ratio)	10% of ALL 3-year-olds (1:1 sex ratio)
THROs	Every year[E]	>500	90% of ALL yearlings (1:1 sex ratio)	90% of ALL yearlings (1:1 sex ratio)	90% of ALL 2-year-olds (1:1 sex ratio)	90% of ALL 2-year-olds (1:1 sex ratio)	20% of ALL 3-year-olds (1:1 sex ratio)	20% of ALL 3-year-olds (1:1 sex ratio)
WM[D]	Every year	>650	0.38*(N-650)	0.32*(N-650)	0.17*(N-650)	0.13*(N-650)	3 yo.s only removed (with 1:1 sex ratio) only if not enough yearlings & 2 yo.s available to reach target size (N=650)	3 yo.s only removed (with 1:1 sex ratio) only if not enough yearlings & 2 yo.s available to reach target size (N=650)
WICA	Every other year	>400	80% of ALL yearlings (1:1 sex ratio)	80% of ALL yearlings (1:1 sex ratio)	80% of ALL 2-year-olds (1:1 sex ratio)	80% of ALL 2-year-olds (1:1 sex ratio)	10% of ALL 3-year-olds (1:1 sex ratio)	10% of ALL 3-year-olds (1:1 sex ratio)
WRST	Every year[B]	>60 bison (not counting yearlings)	none	none	0.05 *(# of 2-year-olds in herd)	0.1*(# 2-year-olds in herd)	0.05*(# adults in herd)	0.1*(# adults in herd)

[A] Removals can occur through organized capture operations or hunter harvests.

[B] Removal is administered through hunter harvests.

[C] Only adults in >10 age classes are removed.

[D] Removals based on mean kinship values such that genetically overrepresented individuals are selected for removal.

[E] Removals typically take place every other year, but growth rates of modeled populations required more frequent culling to maintain target herd sizes.

of disease epidemics or managed removals. These mortality rates were based on rates used for YELL and ELK herds in the 2016 PVA (Traylor-Holzer 2016), which in turn were derived in part on Brodie (2008) and Geremia et al. (2014). Based on the knowledge and experience of herd managers, these rates were then further revised for the DOI herds in this study (Traylor-Holzer 2017), resulting in three sets of potential mortality rates (Table 3.2.2). Maximum lifespan was set at 25 years for females and 20 for males. Annual variation in the mean mortality rate was applied through environmental variation (EV), with a standard deviation of 20% of the mean rate (coefficient of variation=20%). Sex-specific survival curves for the three sets of mortality rates used in this study are shown in Figure 3.2.1.

Female Age-Specific Reproduction

Females are considered to be reproductive starting between ages 2-3 and throughout the rest of their lives. Female reproductive rates (% adult females producing a calf in a given year) were derived from a fitted logistic function for ELK herd (Wilson et al. 2002; Figure 3.2.2a). These rates were either applied directly or modified by the herd managers and experts to increase reproduction in younger and older females (Figures 3.2.2 b & c). Annual variation in the mean female reproductive rate was applied through EV, with a standard deviation of 10% of the mean rate (coefficient of variation = 10%) except BOOK, HEMO, and WRST herds, which were assumed to have a standard deviation of 20% of the mean rate (COV = 20%), due to their relatively harsh and/or variable environments. All births were assumed to be single calves (no twins) born at a 50:50 sex ratio (Brodie 2008). Reproduction was assumed to be independent of population density.

Male Age-Specific Reproduction

Males were considered to be reproductive (i.e., able to impregnate a female) starting between age 2-3 and throughout the rest of their lives. The mating system was set as long-term polygyny, with a limitation of a maximum of 10 female mates in a given year. Parameterization of male reproductive success was based on information in Berger and Cunningham (1995), Wilson et al. (2002) and Mooring and Penedo (2014). In the model, males have a chance of being in the breeding pool (i.e., available to breed) in a given year, a subsequent chance of siring a calf with each female, and a chance of guaranteed mating with that female the subsequent year. Prime age bulls were given a higher probability of being in the breeding pool (92% for bulls age 4-9 years; Figure 3.2.3); all adult males were included in the breeding pool for herds under 20 bison. Unproven males (i.e., those with no offspring) in the breeding pool had a 90% chance of being rejected as the sire, whereas proven males had 100% acceptance. Males had a 10% chance of automatically mating with the same female in the subsequent year. These model attributes led to a model in which males may sire up to 10 calves in a year, with 73% producing no offspring in a given year and successful males typically producing 1 to 7 calves per year (mean = 3).

Table 3.2.2. Annual mortality probabilities used in models. Probabilities in a) and c) are derived from survival rates estimated for the Yellowstone and Elk Island herds, while probabilities in b) are estimates derived from information given by herd managers.

Age class	Standard (a) Female	Standard (a) Male	Alternate (b) Female	Alternate (b) Male	Elk Island (c) Female	Elk Island (c) Male
0	0.20	0.24	0.15	0.15	0.30	0.33
1	0.05	0.06	0.03	0.05	0.10	0.11
2-3	0.03	0.036	0.03	0.05	0.05	0.08
4-5	0.03	0.036	0.03	0.05	0.05	0.08
6-8	0.03	0.036	0.03	0.05	0.05	0.08
9	0.03	0.036	0.03	0.05	0.05	0.08
10	0.03	0.036	0.03	0.05	0.05	0.08
11-12	0.03	0.036	0.03	0.05	0.40	0.40
13	0.03	0.036	0.03	0.05	0.40	0.40
14-15	0.03	0.036	0.03	0.05	0.40	0.40
16-19	0.25	0.30	0.18	0.20	0.40	0.40
20	0.25	1.0	0.33	1.0	0.40	1.0
21-24	0.50	–	0.33	–	0.50	–
25	1.0	–	1.0	–	0.50	–

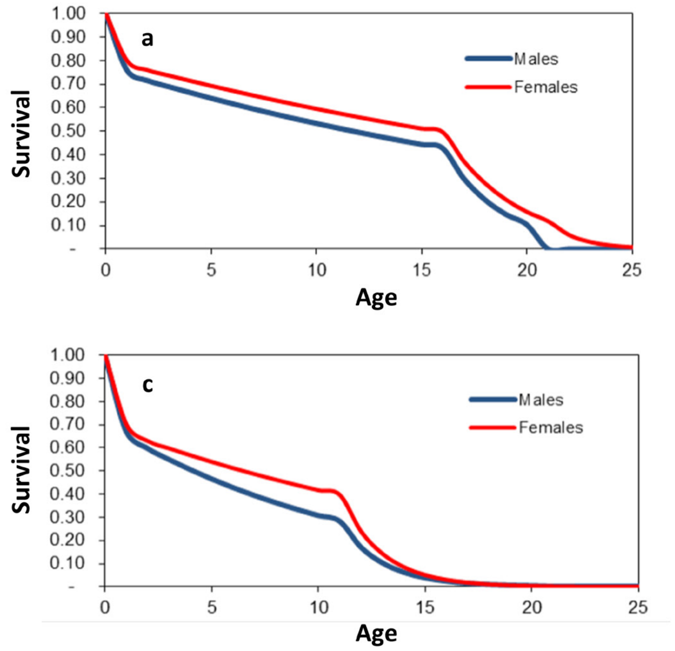

Figure 3.2.1. Survival curves (L_x) derived from mortality rates (a-c) given in Table 3.2.2.

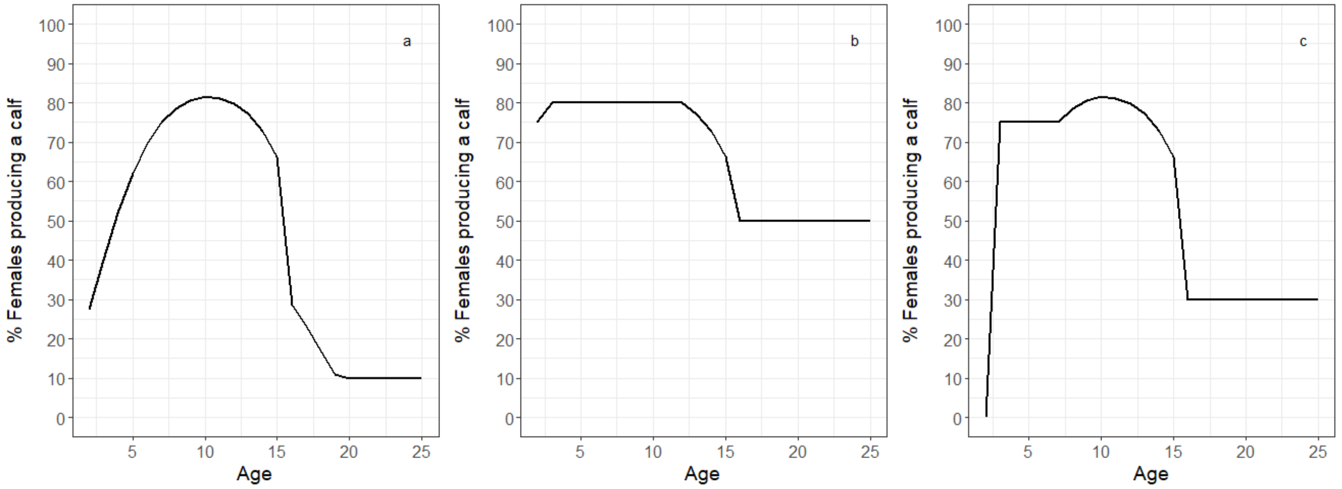

Figure 3.2.2. Mean female reproductive rates as a function of female age (percent of adult females producing a calf in a given year) used in models. Percentages in a) are derived from a fitted logistic function for ELK; while b) and c) are modifications that include higher reproductive rates for younger and older females based on information given by individual herd managers.

Intrinsic Growth Rate

The various combinations of different reproductive and mortality rates result in different deterministic intrinsic growth rates (r) across the 18 herds. Rates varied from r = 0.08 and generation time (T) of ~8 years for ELK under relatively wild conditions (and similar to the estimate for the YELL herd by Fuller et al. 2007) to r = 0.15-0.19 and T = ~9-10 years for herds under less predation pressure. These rates reflect growth if demographic rates are exactly realized and with no stochastic effects such as annual variation in environment conditions or inbreeding effects. Observed (stochastic) growth rates will be lower, especially for smaller herds.

These values indicate the potential for rapid growth in bison populations and the resulting need to manage herd size in the absence of predation and other mortality factors.

Variation in Vital Rates

Demographic rates vary over time due to various stochastic processes. Three sources of variation in reproductive and survival parameters are included in the model.

Demographic variation (chance variation in rates due to small population size) is an inherent property of the model and is implemented through a random number generator that determines the specific fate of each individual each year (e.g., sex determination, survival, reproduction, number of offspring per reproductive cycle).

Environmental variation (EV) is the annual variation in reproduction and survival due to random variation in environmental conditions. The bison model assumes a relatively stable environment (i.e., small fluctuations in mean vital rates between 'good' and 'bad' years), and used a coefficient of variation for EVmortality=20% and coefficient of variation for EV% females breeding=10%. EV for reproduction was based on annual breeding success data from the Wind Cave bison herd (2003-2009; unpublished data), for which EV was partitioned out of the observed variation in success. EV for survival was estimated based on moderately stable environmental conditions for these bison herds. EV for reproduction and survival were correlated in the model. EV determines the distribution from which the mean rate is selected for a given year, around which demographic stochasticity then acts as described above.

A generic catastrophe (outlier event in vital rates) was included in the model. Reed et al. (2003) examined 88 vertebrate populations and found the risk of severe population decline (>50% decline in one year) to be about 14% per generation. In the absence of specific catastrophe data, the extrapolation of this recommended level of risk of catastrophic events for bison populations would be about 1.5% per year (i.e., once per 7.5 generations), with a severity factor of 50% reduction in survival in a catastrophic year. It was decided to include this risk in the model, as not all catastrophic events can be foreseen, and it represents an intensity and rate of occurrence demonstrated across a variety of taxa, habitats, and circumstances.

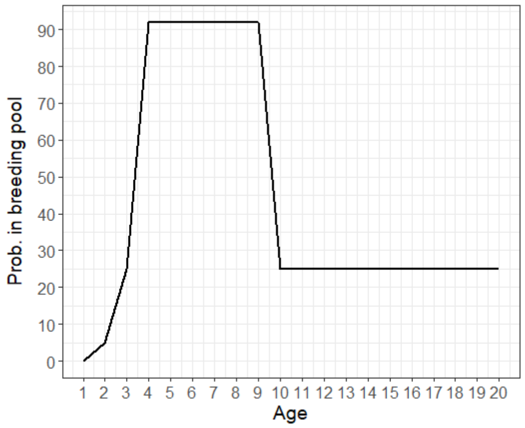

Figure 3.2.3. Probability of male being a member of a population's breeding pool as a function of age.

Sensitivity Analyses

We explored sensitivity of model results to uncertainty in demographic input values by varying mean survival and female reproduction by +10% for a herd of 400 bison. Model results indicated that variation in prime age (age 2-15) adult female survival and reproductive rates had a modest impact on population growth, while calf, yearling, and adult male survival had little impact. All input values tested led to a positive annual growth rate of at least 5% and no risk of extinction. While lower adult male survival has no demographic impact, it did lead to female-biased adult populations (62% female with 10% reduction in adult male survival) and more rapid loss of heterozygosity. Varying combinations of the reproductive rates (A-C) and mortality rates (a-c) used in models did affect stochastic growth rates, but growth rates remained strongly positive (>11%) across all models with little other impact on population viability (Traylor-Holzer 2017). Overall, model results were not highly sensitive to uncertainty in demographic rates within the ranges tested.

Genetic Factors

Genetic Variation

Genetic analysis of samples from each herd by the University of California Davis-Veterinary Genetics Laboratory provided allele frequencies for 52 microsatellite loci common for all herds. We used herd-specific allele frequencies to probabilistically assign two alleles for each of these 52 loci to each individual bison in the initial population. We modeled these loci as neutral loci subject to genetic drift via gene drop simulations and used them to evaluate the relatedness among herds and to track genetic diversity over time.

Initial Kinships

VORTEX uses estimates of kinship to assess inbreeding levels for individuals (i.e., the inbreeding coefficient F) as well to simulate non-lethal effects of inbreeding on the survival and reproduction of individuals (Lacy and Pollack 2017). Given the historical bottlenecks for bison and the subsequent re-establishment of herds from a small number of founders, it is appropriate to assume some initial level of relative relatedness (i.e., inbreeding) of bison within each herd at the start of simulations. VORTEX allows users to input mean kinship values within and between herds. To estimate initial mean kinships within and between herds for model initiation, we used the package related (Pew et al. 2015; Wang 2011a) in R (R Core Team 2018) to estimate relatedness (Θ_{ij}) from the microsatellite marker data of all sampled individuals (both within and between herds), then transformed these values to mean kinship (mk_{ij}) as $mk_{ij} = \Theta_{ij}/2$ (Wang 2011b).

The package related offers a number of estimators to estimate relatedness between individuals based on microsatellite data, each with particular advantages and disadvantages based on the type and quantity of data available (Wang 2014). To determine which estimator was the most appropriate estimator for our bison microsatellite data, we first tested the relative performance of each estimator on our bison data by simulating individuals of known relationships from our data (i.e., parent, offspring, sib, half-sib, and unrelated) and correlated estimates of relatedness generated by each estimator to known relatedness (relatedness results and mean kinship estimates given in Appendix E). Simulation results indicated that all estimators performed well in estimating relatedness values within our dataset, but that the Wang estimator performed the best (correlation coefficient between observed and expected values of 0.94; Appendix E). We therefore used the Wang estimator to estimate relatedness values between all individuals within our sampled bison population and mean relatedness values for individuals within each herd and between all pairwise sets of herds. These values were used to set initial within- and between-herd kinships in the model, which determined initial individual inbreeding coefficients and kinships among individuals.

Inbreeding Depression

VORTEX provides the option to simulate the impacts of inbreeding on survival and reproduction, implemented by default as lower juvenile survival rates in inbred individuals. The degree of inbreeding impact is measured as the number of 'lethal equivalents' (LE), which is the genetic load of recessive genes in a heterozygous state that if in a homozygous state would cause death or carry a risk of death. O'Grady et al. (2006) concluded that 12.29 lethal equivalents spread across survival and reproduction is a realistic estimate of inbreeding depression for wild populations. In the absence of species- or population-specific data, the default value suggested for use in VORTEX is to incorporate 6.29 LE in the model as a conservative estimate, 50% of which are assigned to lethal alleles and subject to purging.

Inbreeding depression is difficult to document without extensive multi-generational pedigree and fitness data but has been observed in at least one bison conservation herd (Texas State Bison Herd, or TSBH). Hedrick (2009) calculated the approximate level of accumulated inbreeding to be F~0.367, which was associated with sperm abnormalities, lower reproductive rate, and higher first-year mortality. We used reproductive and survival data for TSBH and for other large bison herds (as a relatively non-inbred control) to calculate a genetic load of ~ 6 LE in TSBH after purging and ~6.6 LE before purging of a portion of lethal alleles. This estimate includes inbreeding effects on male and female fertility, gestation, and survival from birth to one year and was calculated as described by Kalinowski and Hedrick (1998) using the probability of producing a living calf from time of mating to yearling (1-year-old) as 0.178 for TSBH (inbred) and 0.536 for non-inbred herds. Given the lack of herd-specific data for bison, we decided to use the default of 6.29 LE to implement inbreeding impacts in the model, assuming that initial genetic loads were similar among herds and that a modest amount of purging may have already occurred. These LE impacts were distributed in the model as 50% due to lethal alleles (modeled via gene dropping) and 50% based on non-lethal recessive allele impacts (based on individual inbreeding coefficients tracked through the pedigree from the starting kinships).

Output and Analysis

We ran the model for 200 years, for 500 iterations (replicates). We assessed the probability of extinction in 200 years for individual herds as the proportion of runs (iterations) in which the herd became extinct (defined as only one sex remaining). To assess how current management practices are expected to affect the genetic diversity of each individual herd and the bison metapopulation as a whole we assessed absolute and proportional changes in mean genetic diversity at the start and end of simulations (year 0 and year 200). Genetic diversity was measured as both heterozygosity (gene diversity) and allelic diversity (mean number of alleles per locus). Note that because models have perfect knowledge of the genotype of every simulated individual in every population, there is no need to correct these measures for sampling error (i.e., to use expected heterozygosity or allelic richness). We assessed mean inbreeding levels within herds at the start and end of simulations using inbreeding coefficients (F) calculated by VORTEX. VORTEX estimates of inbreeding coefficient of each individual as the kinship value between the individual's parents (Lacy and Pollak 2017) based on initial kinships and subsequent additional inbreeding over the 200-year simulation.

To assess the degree of genetic redundancy currently existing across herds, we ran simulations in which we sequentially excluded a herd from the metapopulation and compared the pooled allelic diversity from simulations with all herds included in the metapopulation to the pooled allelic diversity of the reduced metapopulation. A substantial decrease in allelic diversity resulting from the loss of any one herd would suggest a low degree of genetic redundancy across herds, whereas a small loss in diversity may suggest a high degree of genetic redundancy across herds. To assess redundancy, we chose to exclude four herds with relatively high differentiation from each other: BADL, FTN, NBR, and WM. NBR and FTN are both approximately 300 animals; WM and BADL are both herds with >500 animals.

The way in which we measure genetic redundancy corresponds to the number of unique alleles in each herd, but it does not account for the evenness of alleles across herds. For example, allele A may occur at a frequency of 60% in Herd 1, and at a frequency of 0.1% in a Herd 2. If Herd 1 is extirpated, allele A still persists in the metapopulation, and therefore we would assume we have genetic redundancy across herds, though there has been a considerable decrease in the abundance of the allele. We therefore also examine how the genetic structure of the metapopulation (patterns of genetic differentiation and similarity between herds) changes over time as a second method for inferring genetic redundancy.

To assess how the genetic structure of the entire bison population (all 18 herds in this study) changes over time, we simulated individual genotypes from each herd at the end of simulations and analyzed these genotypes using discriminant analysis of principal components (DAPC; Jombart et al. 2010). At the end of simulations, VORTEX outputs the mean allele frequencies at each locus for each herd (averaged across all runs). To create individual diploid genotypes from each herd, we randomly selected two alleles from each locus, with probabilities of selection weighted by the allele frequencies for that locus. We used these simulations to create 1000 individual genotypes from every herd, then

Table 3.2.3 Input parameters for model. "Initial N" is the starting abundance for each herd, "Target N" is the abundance to which herds are managed throughout simulations, "K_{eco}" is estimated ecological carrying capacity, "Initial H_e" and "MNA" refer to starting levels of heterozygosity and mean number of alleles per locus, respectively.

Herd	**Initial N**	**Target N (K_{man})**	**K_{eco}**	**Repro.[A] Rate**	**Mortality[B] Rate**	**Initial H_e**	**Initial MNA**
BADL	1000	600	1342	B	a	0.593	4.50
BOOK[C]	540	550	700	A	a	0.648	4.83
CHIC[C]	10	10	11	A	a	0.434	2.50
ELK	470	400	800	A	c	0.630	4.79
FTN	350	350	350	C	b	0.635	5.27
GRASS	346	400	500	A	c	0.617	4.76
HEMO	400	~400	600	A	b	0.552	3.73
NBR	285	285	285	C	a	0.651	5.01
NER/GRTE	900	500	800	A	a	0.523	3.75
NSM	55	55	55	C	a	0.633	4.53
RMA	100	200	200	C	a	0.642	4.95
SH	20	15	18	C	b	0.518	3.51
TAPR	89	100	100	C	a	0.651	4.60
THROn	280	300	400	A	a	0.527	3.48
THROs	335	500	700	A	a	0.580	4.19
WICA	350	350-500	600	C	a	0.655	4.69
WM	650	650	650	C	a	0.596	4.84
WRST	181	> 90	250[D]	A	c	0.514	3.31

[A] Reproductive rate codes refer to respective rate from Figure 3.2.2.

[B] Mortality rate codes refer to respective rate from Table 3.2.2.

[C] BOOK intermixes with the Northern Ute Tribe's bison herd; CHIC receives genetic reinforcement from WM as part of its current management.

[D] The biological carrying capacity of the WRST Copper River herd is unknown, value is an estimate.

randomly selected N genotypes from each herd where N is the number of genetic samples originally collected from that herd to match the structure of our original genetic dataset (Table 2.1). All genotypes were created in R, and analyzed with package adegenet (Jombart 2008; Jombart and Ahmed 2011) as in section 2.2.

3.3 Results

Population Persistence and Growth

Given the current (2016) demographic and genetic structure of herds, herd size restrictions, and current management, our models projected that the four smallest herds in the bison metapopulation had a non-zero probability of going extinct over the next 200 years. Extinction probabilities for these four herds were: SH = 0.96, WRST = 0.85, CHIC = 0.11, and NSM = 0.01 (Table 3.3.1). All other DOI bison herds had zero probability of extinction in our models. Although CHIC represents the smallest herd (K~10) expected to be at the most risk, its persistence is promoted through reinforcement from WM.

Most herds show essentially no long-term growth or decline (r ~ 0.00) due to significant removal operations to maintain herds at target size (K_{man}). Modeled removal strategies appear to be effective at controlling herd size in the model; otherwise stochastic growth results would be positive, with herd size further controlled in the model through truncation to K subsequent to the calculation of r. The only herds with distinguishable decline are those with extinction risk > 12% (SH and WRST) and BADL. The negative growth rate estimate for BADL is likely a result of the large number of removals required to reach this herd's target abundance (600 animals) from its initial abundance of 1000 animals.

Genetic Diversity

All herds were predicted to lose genetic diversity (heterozygosity and allelic diversity) over the next 200 years due to small population size insufficient to balance genetic drift with mutation. Small herds lost genetic diversity faster than larger herds, and the two herds supported with gene flow (BOOK and CHIC) lost genetic diversity slower than those without gene flow (Figure 3.3.1; Figure 3.3.2; Table 3.3.1). Correspondingly, our models projected SH (smallest herd with no gene flow) to have the largest proportional decreases in genetic diversity, with a 63.5% in allelic diversity and an 81.1% decrease in heterozygosity without gene flow. The two largest herds, WM and BADL, were projected to have, respectively, a 10.3% and 9.1% decrease in allelic diversity, and a 3.1% and 4.5% decrease in heterozygosity. CHIC, the smallest herd in the metapopulation, received gene flow in the form of translocations of animals from WM as part of its management plan. This additional gene flow mitigated the effects of drift resulting in relatively little allelic diversity and heterozygosity loss for a herd of its size (1.2% and 7.2% decrease, respectively). In total, 8 herds were projected to have heterozygosity levels <0.5 by the end of simulations (CHIC, HEMO, NER/GRTE, NSM, SH, TAPR, THROn, and WRST).

Despite the overarching association between herd size and rates of diversity loss, the proportion of genetic diversity lost varied considerably between herds and between the diversity measures used (heterozygosity versus allelic diversity; Table 3.3.1). Differences in the proportion of heterozygosity lost within herds was modulated both by herd size and by the removal strategy used to meet abundance thresholds set by management (Figure 3.3.3). Management strategies targeting younger animals for removal (yearlings with the highest mean kinship values or randomly selected yearlings) resulted in lower levels of heterozygosity being lost within herds compared to removal strategies targeting older animals (mixed age removals or adult-biased harvest). In particular, using mean kinship to select animals for removal consistently led to the smaller heterozygosity losses compared to other removal strategies, while using adult-biased harvest led to the largest losses in heterozygosity.

The proportion of allelic diversity lost within herds was modulated by herd size, initial levels of allelic diversity, and removal strategy (Table 3.3.1). Consistent with Giglio et al. (2018), we found that herds with high initial levels of allelic diversity tended to lose a higher proportion of that diversity over time than herds with low initial levels of allelic diversity. For example, THROn had an initial allelic diversity of 3.48 alleles per locus, was maintained at a target abundance of 300 individuals, and lost approximately 10% of its allelic diversity over the course of 200 years. While NBR herd had an initial allelic diversity of 5.01 alleles per locus, was maintained at a target abundance of 300 individuals, and lost approximately 16% of its allelic diversity over the course of 200 years.

The projected loss in genetic diversity across all herds was mirrored by a projected increase in mean inbreeding coefficients (F) across all herds (Figure 3.3.4). In particular, under management without gene flow our models predicted three herds (NSM, SH, WRST) to reach inbreeding coefficient levels equivalent to that of the Texas State bison herd (TSBH) when it suffered decreased reproductive rates and yearling survival due to inbreeding depression (F= 0.367; Halbert et al. 2004; Hedrick 2009).

Our models predicted no loss of heterozygosity (0% change) for the combined bison population (all 16 DOI and two Parks Canada herds) as a whole under current management conditions, but predicted a 7.4% decrease in allelic diversity after 200 years (Table 3.3.1).

Genetic Redundancy

Our test of genetic redundancy suggested that the allelic diversity of the combined DOI bison population was not overly sensitive to the loss of any one herd, with only minor changes to the allelic diversity of the metapopulation with the loss of any one herd (Table 3.3.2). The loss of WM

Table 3.3.1. Summary of simulation results for each herd simulated forward 200 years under current (2016) management practices. N denotes abundance, r_s denotes stochastic population growth, P(E) denotes the probability of extinction, H denotes heterozygosity, MNA denotes mean number of alleles per locus, and META are results estimated for the entire metapopulation.

Herd	**r_s**	**r_s 95% CI**	**P(E)**	**Initial H**	**Initial MNA**	**Final H**	**Final MNA**	**Proportional Change H**	**Proportional Change MNA**
BADL	-0.003	-0.004, -0.002	0	0.593	4.5	0.566	4.09	-0.045	-0.091
BOOK*	0.003	0, 0.006	0	0.648	4.83	0.617	4.61	-0.048	-0.046
CHIC*	0.003	0.002, 0.003	0.114	0.434	2.5	0.403	2.47	-0.072	-0.012
ELK	-0.002	-0.006, 0.002	0	0.630	4.79	0.572	3.96	-0.092	-0.173
FTN	0.001	0, 0.001	0	0.635	5.27	0.600	4.33	-0.055	-0.178
GRASS	0	-0.003, 0.003	0	0.617	4.76	0.568	3.94	-0.08	-0.172
HEMO	0	-0.001, 0	0	0.552	3.73	0.493	3.15	-0.107	-0.155
NBR	0.001	0, 0.001	0	0.651	5.01	0.603	4.2	-0.073	-0.162
NER/GRTE	-0.003	-0.01, 0.003	0	0.523	3.75	0.488	3.06	-0.068	-0.184
NSM	0.006	0.005, 0.006	0.008	0.633	4.53	0.415	2.57	-0.344	-0.433
RMA	0.005	0.004, 0.007	0	0.642	4.95	0.581	3.97	-0.095	-0.198
SH	-0.019	-0.021, -0.018	0.964	0.518	3.51	0.098	1.28	-0.811	-0.635
TAPR	0	0, 0.001	0	0.651	4.6	0.464	2.89	-0.287	-0.372
THROn	0.001	-0.005, 0.006	0	0.527	3.48	0.483	3.11	-0.084	-0.106
THROs	0.002	-0.005, 0.008	0	0.580	4.19	0.549	3.87	-0.053	-0.076
WICA	0.003	-0.005, 0.011	0	0.655	4.69	0.621	4.28	-0.052	-0.087
WM	0.001	0, 0.001	0	0.596	4.84	0.578	4.34	-0.031	-0.103
WRST	-0.03	-0.032, -0.029	0.858	0.514	3.31	0.264	1.83	-0.487	-0.447
META	0.005	0.003, 0.007	0	0.691	6.87	0.691	6.36	0	-0.074

* BOOK and CHIC experience gene flow from other herds as part of their current management.

Table 3.3.2. Results of our genetic redundancy analysis, showing the differences in allelic diversity of the metapopulation when BADL, FTN, NBR, or WM are excluded. Allelic diversity is measured as the mean number of alleles/locus, standard deviation in parentheses.

Diversity	**All Herds Extant**	**BADL Extirpated**	**FTN Extirpated**	**NBR Extirpated**	**WM Extirpated**
Allelic Diversity	6.36 (0.05)	6.33 (0.05)	6.34 (0.05)	6.29 (0.05)	6.24 (0.06)

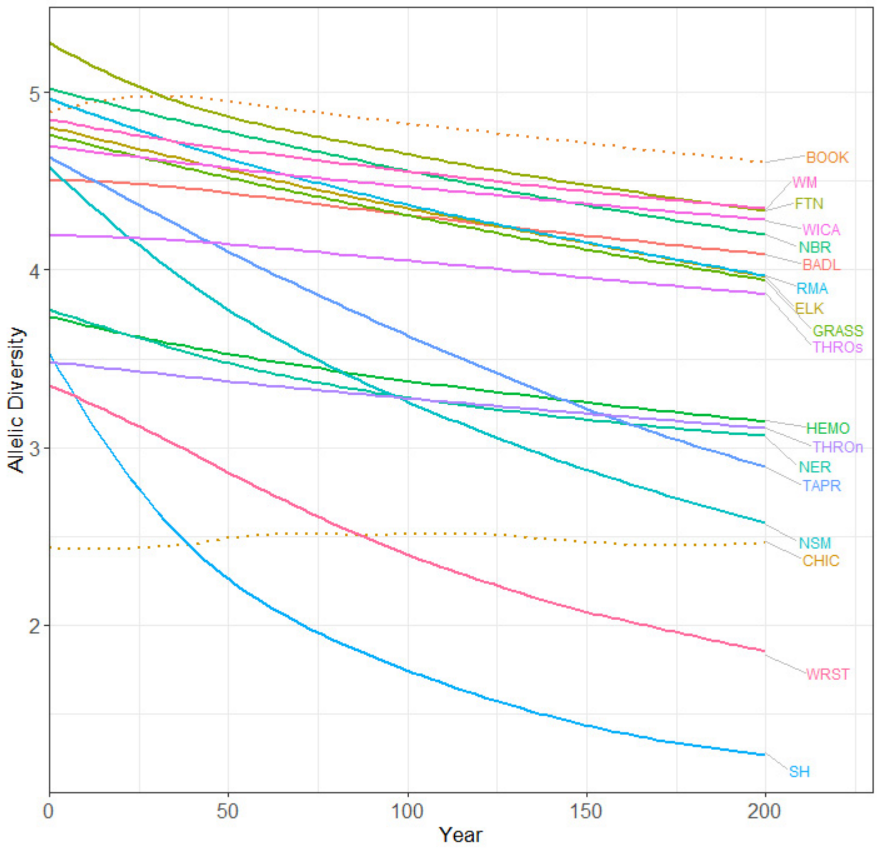

Figure 3.3.1. Decrease in the allelic diversity over time for each of the 18 herds in our analysis, demonstrating differences in the rate of loss of allelic diversity between herds. Dotted lines denote herds that currently experience gene flow (BOOK, CHIC), solid lines denote herds without gene flow. Initial and final values of allelic diversity (mean number of alleles/loci) for each herd are given in Table 3.3.1.

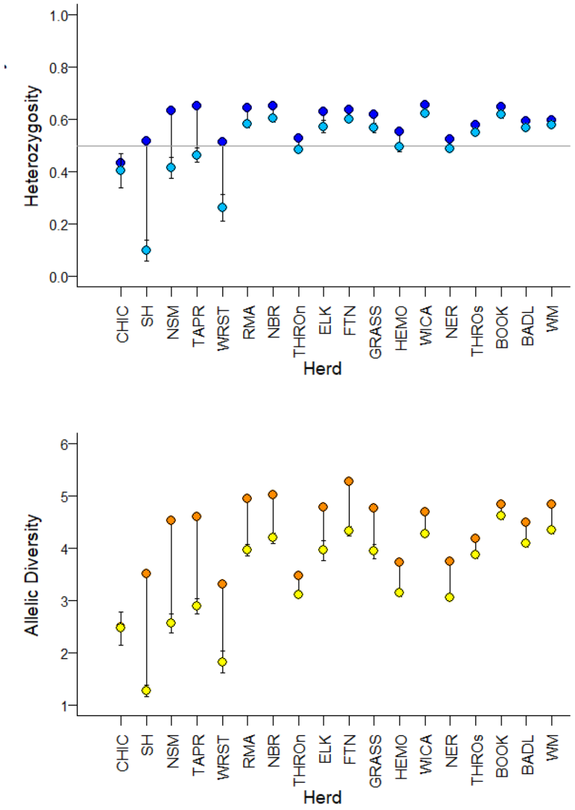

Figure 3.3.2. Total change in (top) heterozygosity and (bottom) allelic diversity for each of the 18 herds in our model. Dark blue and orange symbols are the initial levels of heterozygosity and allelic diversity in each herd, respectively, and light blue symbols and light-yellow symbols are the predicted heterozygosity and allelic diversity levels 200 years into the future. Herds are ordered by target herd size, from smallest (CHIC =10) to largest (WM = 650). Error bars denote standard deviation. Note: BOOK and CHIC experience gene flow from other herds as part of their current management.

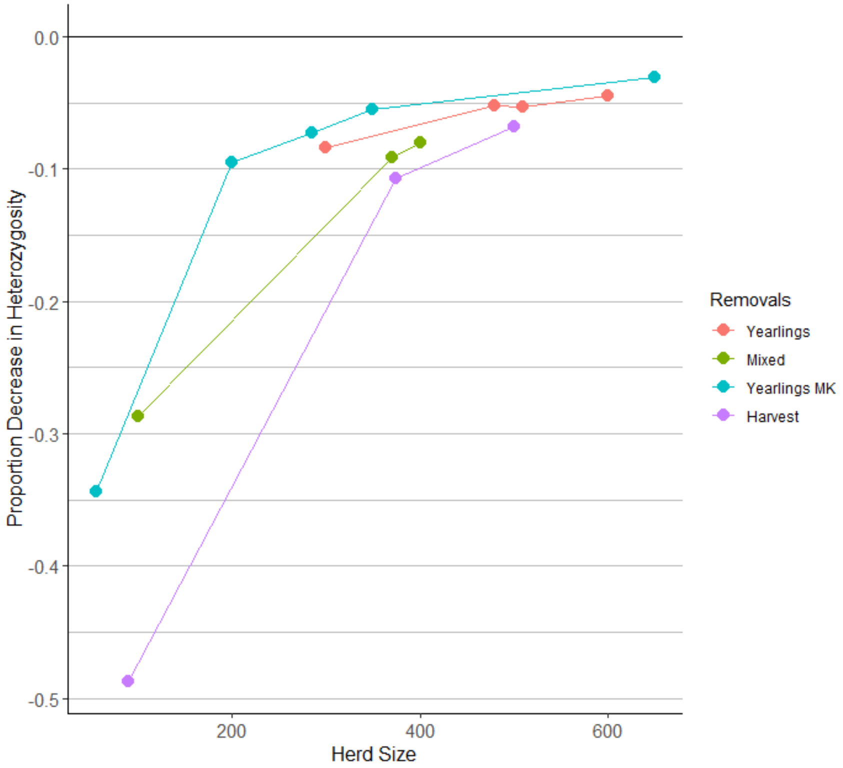

Figure 3.3.3. Projected proportional decreases in heterozygosity for each herd as a function of that herd's target size and removal strategy. Removal strategies include: "yearlings" = most animals targeted for removal are randomly selected yearlings; "yearlings mk" = most animals targeted for removal are yearlings with the highest mean kinship values; "mixed" = randomly selected animals targeted for removal include all age classes; "harvest" = animals are removed through hunter harvest, with a bias toward the removal of older age classes.

resulted in the loss of the most unique alleles, translating to a mean loss of 0.12 alleles per locus, followed by a mean loss of 0.07 alleles/locus when NBR was extirpated. The loss of BADL and FTN resulted in very little change in the mean number of alleles per locus in the metapopulation, indicating that these two herds have fewer unique alleles, as expected based on their foundation histories.

Examining the projected genetic structure of all 18 bison herds at the end of simulations, we see that herds are projected to become more dissimilar over time under current management, as expected from genetic drift resulting from managing small herds in isolation. Figure 3.3.5 shows how the genetic structure of the metapopulation is expected to change after 200 years of current management practices, with increasing distances between genetic clusters, most notable in the increased distance of clusters from the discriminant function axes. Our model predicts that the two unique genetic clusters currently found in the FTN herd will become integrated into one genetically similar cluster as social integration between the two combined herds continues, while the herds currently making up the NBR lineage will become further differentiated into two distinct genetic clusters as a result of genetic drift. In particular the frequency and identity of alleles of WRST and SH are currently indistinguishable from that of NBR, but our models project that the identity and frequency of alleles in these herds will become genetically distinct from NBR after 200 years of isolation.

3.4 Discussion

Our model projected that 15 of the 18 herds in this study have a >99% probability of persisting for the next 200 years without additional gene flow. Only three herds, SH, WRST, and CHIC, had a >1% probability of extinction within 200 years, but our model projected that all 18 herds will lose genetic diversity over time without additional gene flow. Herd size was the primary driver of diversity loss across all herds, though the effect of herd size was modulated by the effect of the removal strategies used to manage herd abundances, and by initial levels of allelic diversity within herds. Overall, larger herds (>500 animals) lost modest amounts of genetic diversity over time (3% - 7% decrease), while small herds (<100 animals) lost considerable diversity over time (34% - 81% decrease), with correspondingly large increases in mean inbreeding level. Indeed, after 200 years under current man-

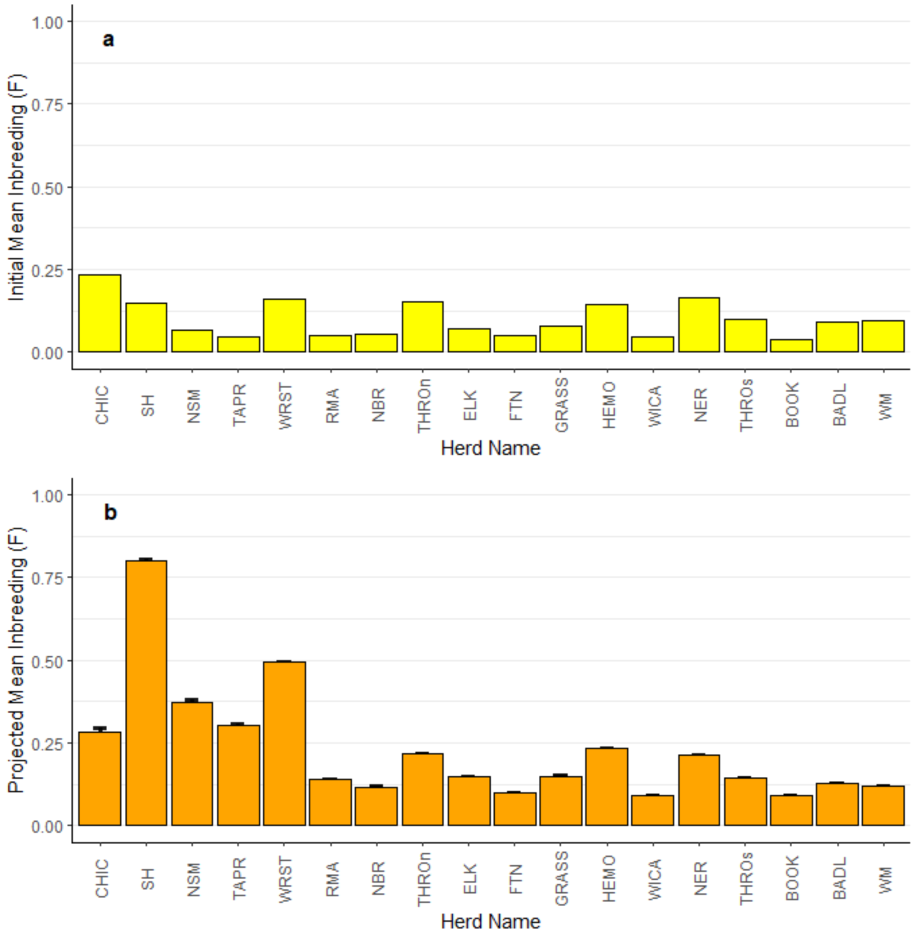

Figure 3.3.4. a) Initial; and b) projected mean inbreeding coefficients (F) after 200 years under current management conditions. Herds are ordered by target size, from smallest (CHIC = 10) to largest (WM = 650). Error bars denote standard deviation. Note: BOOK and CHIC experience gene flow from other herds as part of their current management.

agement conditions eight herds were projected have heterozygosity levels < 0.5 and to attain mean inbreeding coefficient levels similar to those shown to impact the reproduction and survival of bison (Halbert et al. 2004; Hedrick 2009).

Small populations typically have a higher risk of extinction than larger populations (Lande 1993; MacArthur and Wilson 1967), yet despite their relatively small sizes, most of the herds modeled in this study had no risk of extinction. This can be attributed to the high stochastic growth rates prior to removals (i.e., high reproduction, low mortality), which provide demographic resilience against demographic stochastic processes. The low extinction risk for herds in this study is consistent with PVA results for four large North American plains bison herds considered to be 'functioning as wild,' which projected low PE (<0.01) over 200 years, even in the presence of predation pressure and disease risk (Traylor-Holzer 2016). Sensitivity testing of herd size and severity of inbreeding impacts (i.e., lethal equivalents) using this 2016 plains bison model suggested that the impact of population size on bison herd viability may occur primarily through genetic effects (i.e., more rapid accumulation of inbreeding and its impacts), with inbreeding having significant impacts on growth rate and extinction risk on populations under a few hundred animals. Stochastic growth rates approached zero when mean inbreeding levels reached 20% (assuming 6.29 lethal equivalents) (Traylor-Holzer 2016).

In our models of the16 DOI and two Parks Canada herds, eight herds were predicted to attain mean inbreeding coefficients of ≥20% over 200 years, yet only the four smallest herds in this study had a non-zero probability of extinction. These 4 herds attained mean inbreeding coefficients between 25-80%. In both our models and those developed for the 2016 study, juvenile mortality rates increased as a function of an individual's estimated inbreeding coefficient and to the same degree (6.29 lethal equivalents). The difference in the impact of inbreeding for herds in this study compared to those in the 2016 PVA is likely due to the lower mortality and higher reproductive rates in this study (Tables 3.2.2; Fig ure

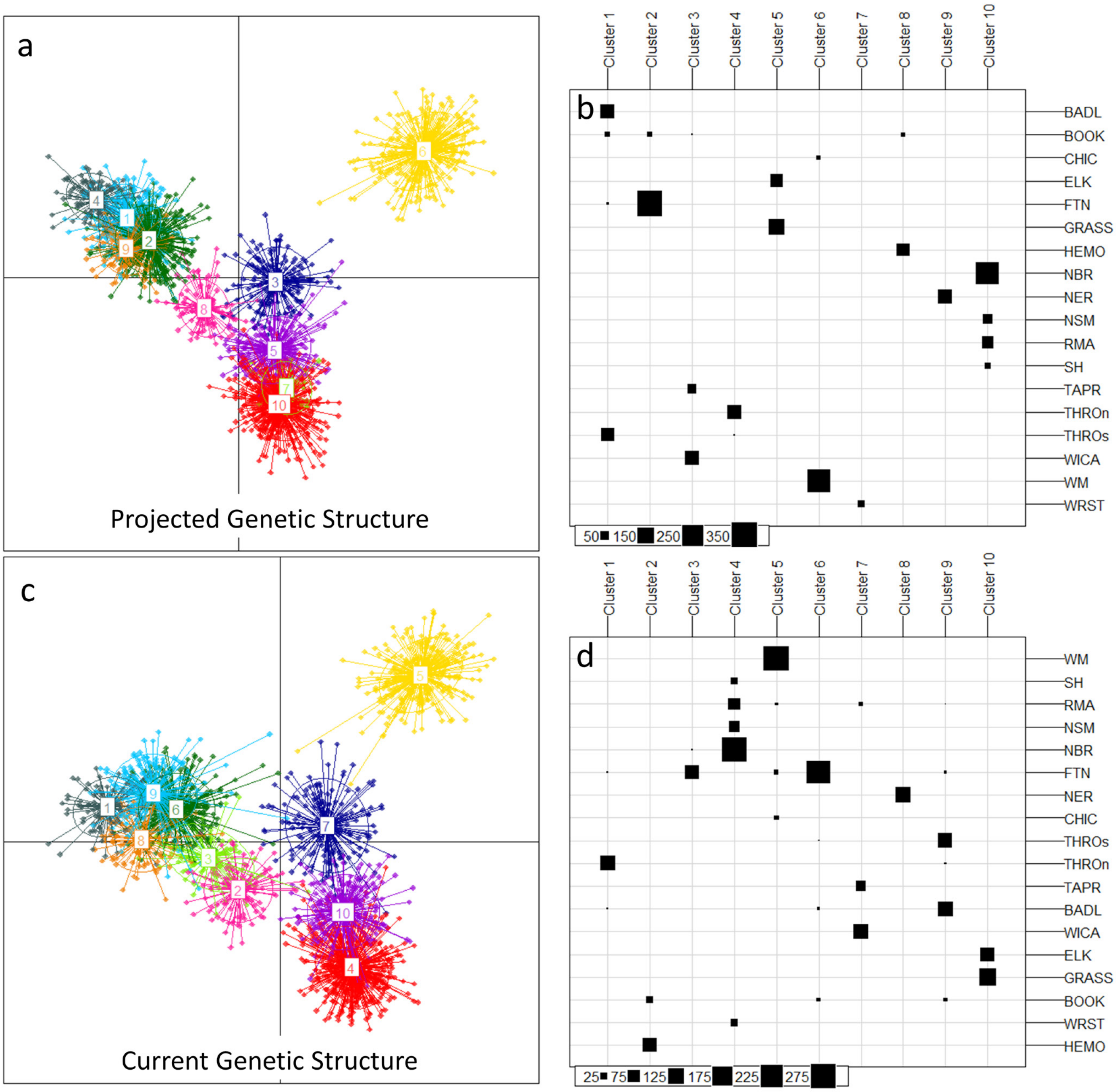

Figure 3.3.5. Plots a) and b) show the DAPC results projected for bison herds after 200 years. Symbols in a) represent individual bison samples, and circles with numbers represent the 10 unique genetically differentiated clusters in the bison data; b) shows the number of individual samples from each herd assigned to each genetic cluster. Plots c) and d) show the current genetic structure of herds today. Note: Colors and ID numbers associated with each cluster are assigned randomly by the DAPC algorithm, and thus are not comparable between plots a) and c).

3.2.2). Compared to the 'functioning as wild' herds modeled in the 2016 PVA, most of the herds in this study are managed to ensure consistent natural forage availability and are free from predation pressures. The resulting higher growth rate is able to offset the impact of inbreeding effects (i.e., higher juvenile mortality) such that most herds in our model demonstrated positive population growth rates under modeled conditions, greatly reducing the probability of extinction.

Many of the input values in our model are best estimates informed by expert opinions and values reported in the literature (e.g., Berger and Cunningham 1995 [BADL]; Brodie 2008 [ELK]; Mooring and Penedo 2014 [FTN]; Pyne et al. 2010 [BADL]). Mean annual survival and reproductive rates may be lower for some herds or may vary more due to extreme environmental conditions. Our models also included only one particular type of short-lived "catastrophe" in our models (1 year in duration with a 50% increase in mortality rates). We did not include periodic, multi-year decreases in survival or reproduction that might occur with an extended drought or disease outbreak. Inbreeding has been shown to act as an amplifier of negative environmental conditions across several species, rendering individuals more susceptible to parasites, diseases, or extreme conditions that lower survival or reproductive rates. (Acevedo-Whitehouse et al. 2003; Armbruster and Reed 2005; Coltman et al. 1999; Fox and Reed 2011). The interactive effect of longer duration catastrophes with increases in mean inbreeding levels predicted for the bison herds in this study remains unknown. Despite the continued positive population growth with increasing inbreeding levels projected for some herds in our model, the projected levels of inbreeding for the herds in this study should be cause for concern, particularly under changing environmental conditions

Decreases in genetic diversity could ultimately decrease the ability of the herds in this study to adapt to novel or changing environmental conditions (Ralls et al. 2018; White et al. 2015; Willi and Hoffman 2009; Willi et al. 2006). Increasingly, conservation biologists are recognizing that the genetic management of populations and species requires not just staving off the worst effects of inbreeding, but also maintaining the evolutionary resiliency of populations and species (Ralls et al. 2018; Weeks et al. 2011). Evolutionary resiliency – the ability to adapt to changing environmental conditions – is proportional to the heterozygosity of a population (Frankham 2015; Ralls et al. 2018), and even small decreases in genetic diversity are predicted to decrease the ability of populations or species to evolutionarily adapt to changing or novel environmental conditions (Fisher 1930; Reed and Frankham 2003), such as increased climatic variability or the emergence of novel diseases (McCallum and Jones 2010; Reed et al. 2003).

Herd size had the strongest effect on the rate of genetic diversity loss across all herds. However, this effect of herd size on diversity loss was modulated by the removal strategy used to manage herd abundance and by initial levels of allelic diversity within herds. Overall, management strategies aimed at removing younger age classes (yearlings and 2-year-olds) resulted in lower rates of heterozygosity loss compared to strategies targeting older age classes. This result is expected, as the removal of older age classes within a herd reduces the mean generation time of that herd, thereby increasing rates of genetic drift (Gross and Wang 2005). As has been demonstrated in other studies (Giglio et al. 2016, Giglio et al. 2018), we found that removal strategies targeting genetically over-represented yearlings and 2-year-olds (i.e., those with high mean kinship values to other individuals in their herd) was an effective strategy to slow rates of heterozygosity loss, though this strategy is data-intensive.

In contrast, rates of allelic diversity loss across herds appeared to be more strongly influenced by initial levels of diversity within a herd. Similar results have been noted by other researchers (e.g., Giglio et al. 2018) and is likely due to the allelic make up of high and low diversity herds. Herds with high levels of allelic diversity tend to have many alleles per locus, some of which exist only at low frequencies. While low diversity herds tend to have fewer alleles per locus, each may occur at relatively high frequencies. Subsequently, rates of allelic diversity loss as a result of drift are expected to be most rapid in highly diverse herds, as rare or low frequency alleles are probabilistically more likely to be lost to drift than common alleles (Giglio et al. 2018).

Final predicted levels of genetic diversity within each herd at the end of simulations were also a function of each herd's initial level of genetic diversity. For example, NER/GRTE and THROn are predicted to have final heterozygosity levels of between 0.48-0.49, corresponding to final mean inbreeding levels of approximately 20%. These two herds are managed to have moderate to large abundances (approximately 500, 300 respectively) and are predicted to lose relatively little diversity over time (6.8% and 8.4% loss in heterozygosity over 200 years, respectively). However, even with small losses in diversity over time, their low current levels of genetic diversity put them at increased risk of inbreeding effects. Ultimately, eight herds (CHIC, HEMO, NER, NSM, SH, TAPR, THROn, WRST) with some combination of either small herd size, adult-biased removal strategies, and/or low initial levels of diversity attained mean inbreeding levels of approximately 20% or greater at the end of simulations without gene flow. Of these herds, CHIC was modeled with regular gene flow into the population from WM; however, these supplementations were still not enough to counteract the effects of drift in this tiny display herd, with a target size of 10.

Our model projects that the heterozygosity of the entire bison population (all 18 herds combined) will be maintained at current levels for the next 200 years under current management conditions but that allelic diversity will decrease by 7.4%. The disparity in results between heterozygosity and allelic diversity at the metapopulation level is expected. As heterozygosity decreases within herds as a result of allele loss due to drift, the differentiation between herds increases, meaning that heterozygosity levels measured across the entire metapopulation can remain unchanged. In contrast, the loss of alleles always decreases global genetic diversity. The decrease in allelic diversity within the entire metapopulation in our model is likely a combination of the loss of alleles through genetic drift within each herd and the increased probability of extinction for small herds. Subsequently, retaining allelic diversity within the entire metapopulation requires slowing the rate of genetic drift within each herd.

As identified by others (Gross and Wang 2005), we found that herd size is the most important driver of genetic diversity loss in bison over time under isolated herd management strategies. Although opportunities to increase the size of existing herds are limited, these opportunities should be thoroughly explored. Any effort to increase herd sizes must also ensure that healthy landscapes that support the character of wild bison are maintained and that the resource needs of other species are met. Establishment of satellite herds can provide some protection against losses due to drift, especially when genetic exchange occurs across the satellites, by managing the satellites together as a single larger population. Using population management strategies that maintain even sex ratios, target younger age classes instead of adults for removal, or that target genetically over-represented animals for removal can contribute to mitigating the effects of diversity loss in individual herds.

4. Evaluating the Effects of Metapopulation Management on the Genetic Diversity and Population Viability of DOI Bison

4.1 Introduction

Our population viability modeling results for the 16 DOI and two Parks Canada herds sampled in this study suggest that all herds are expected to lose genetic diversity over the next 200 years under management conditions without gene flow between herds. In particular, smaller herds and herds with low initial levels of genetic diversity are projected to become increasingly inbred. Indeed, while a total of eight herds were projected to reach inbreeding levels shown to reduce population growth rates in challenging environmental conditions (Traylor-Holzer 2016), three of the smallest herds were projected to reach inbreeding levels equivalent to those known to negatively impact survival and reproduction in bison (Halbert et al. 2004; Hedrick 2009) greatly increasing their risk of extinction. These results imply that management aimed at maintaining or restoring genetic diversity within herds will be needed to ensure the population persistence of the smallest herds, and the long-term evolutionary adaptability of all herds within the combined DOI bison population.

Preventing or reversing the loss of genetic diversity in fragmented or isolated populations, and the negative consequences of such loss, can be achieved by re-establishing or increasing gene flow (Frankham 2015; Tallmon et al. 2004; Whiteley et al. 2015). New alleles brought into a population via gene flow increase genetic diversity and decrease the effects of inbreeding (Frankham 2015). Gene flow can be restored either by restoring natural movement between populations or through the translocation of animals (or gametes) between populations. Translocation of animals or gametes is often referred to as genetic augmentation (Frankham et al. 2017) and has been used successfully as a conservation strategy to reverse the effects of inbreeding depression for a wide variety of species (greater prairie-chickens: Bouzat et al. 2009; bighorn sheep: Hogg et al. 2006; Florida panthers: Johnson et al. 2010; adders: Madsen et al. 1999; lions: Trinkel et al. 2008; mountain pygmy possums: Weeks et al. 2017. Fewer studies have examined the ability of translocations to restore historic levels of genetic diversity within isolated populations with the aim of restoring or maintaining the evolutionary adaptability of populations (but see: Bouzat et al. 2009), though there is increasing recognition of the importance of evolutionary adaptability in rapidly changing and increasingly uncertain environments (Hoffman et al. 2015; Ralls et al. 2018; Weeks et al. 2011; Willi and Hoffman 2009).

While the power of translocations to increase gene flow into isolated populations is increasingly recognized and used in conservation (Frankham et al. 2017; Whiteley et al. 2015), it is not a strategy without genetic risks. In particular, translocating too few animals too infrequently or using genetically related or inbred populations as a source for translocations may result in no appreciable increases in the genetic diversity of recipient herds (Frankham et al. 2017). In contrast, translocating large numbers of animals too often can swamp out local rare alleles (i.e. genetic swamping), ultimately decreasing the allelic diversity across all populations (Allendorf et al. 2013; Hufford and Mazer 2003). In extreme cases, if populations are strongly adapted to their local environmental conditions and environmental conditions differ between populations, establishing gene flow between populations could result in outbreeding depression (Edmands 2007).

Outbreeding depression is defined as a reduction in the fitness of offspring relative to either parent resulting from the crossing of individuals from genetically divergent populations or from different sub-species (Allendorf et al. 2013). Crossing two individuals that are adapted to their local environments can disrupt beneficial gene complexes of either individual (Allendorf et al. 2001; Lynch 1991). The risk of outbreeding depression resulting from crosses of individuals from two isolated populations depends on the length of time the populations have been separated, differences in local selection pressures, and the degree of genetic divergence between the populations (Frankham et al. 2017). To date, evidence of outbreeding depression in natural populations has been relatively rare, especially in mammals (McClelland and Naish 2007; Whitlock et al. 2013). Nonetheless, the risk of outbreeding depression remains a concern when restoring gene flow to manage the genetics of small, isolated populations (Edmands 2007; Hedrick 1995; Odell et al. 2018).

In light of the potential trade-offs associated with genetic augmentation, Frankham et al. (2017) developed a decision tree to help managers assess whether genetic augmentation should be considered in the genetic management of fragmented and isolated populations (Figure 4.1.1). This guide consists of a series of conditional questions, three of which are relevant to the bison herds included in this study. Below we discuss each question as it relates to the genetic management of DOI bison.

First, is the population suffering from genetic erosion? Genetic erosion describes the process whereby small, isolated

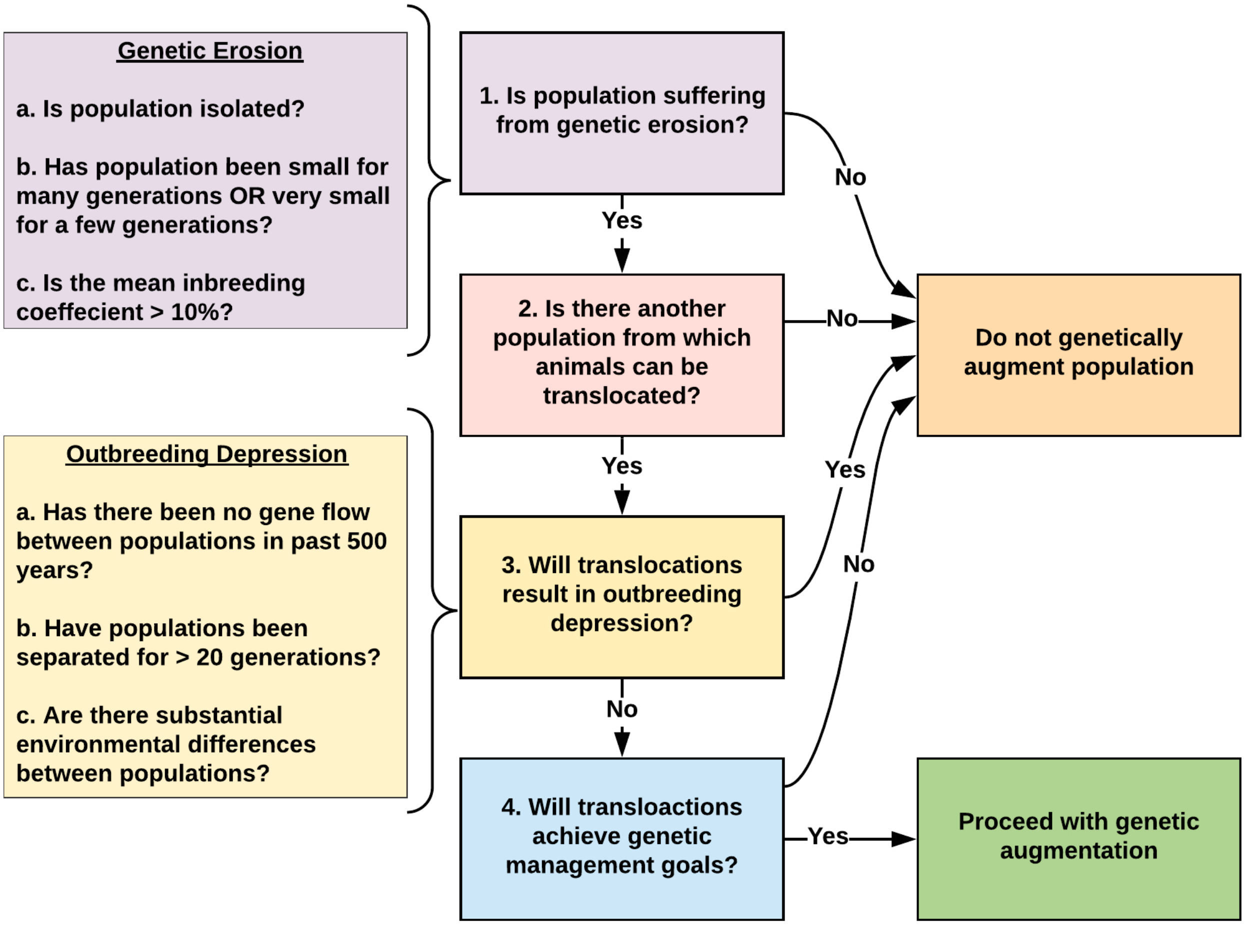

Figure 4.1.1. A conceptual model to help guide decision-making as to whether genetic augmentation (i.e., translocations between populations) should be considered as a component of long-term population management (modified from Frankham et al. 2017).

populations lose genetic diversity due to the process of genetic drift and become increasingly inbred, eventually resulting in decreased population viability through inbreeding depression, reduced adaptive potential, with a subsequent increase in extinction risk (Frankham et al. 2017). For well-studied populations such as plains bison, Frankham et al. (2017) suggest a number of indicators to assess whether a population is suffering from genetic erosion (Figure 4.1.1). These include evaluating information about the current and historic size of the population, its degree of isolation, and whether the known or inferred mean inbreeding coefficient (F) of the population exceeds 0.1.

Figures 4.1.2a shows the current estimated mean inbreeding coefficients for each bison herd sampled in this study as estimated by VORTEX. Currently nine herds are estimated to have mean F ≥ 10% at the time of sampling (BADL, CHIC, HEMO, NER/GRTE, SH, THROn, THROs, WM, and WRST). After 200 years, our model (Chapter 3) projected all herds to have F values ≥ 10% without gene flow (Figure 4.1.2 b). Therefore, a number of DOI bison herds included in this study meet the diversity erosion criterion.

The second question relevant to the bison metapopulation is whether translocations between populations will result in outbreeding depression. Without direct evidence of outbreeding depression (e.g., from crossing experiments), Frankham et al. (2017) suggest assessing the potential for outbreeding depression by evaluating information about the length of time the proposed source and recipient populations have been isolated from one another and whether substantial differences in natural selection pressures exist between source and recipient populations. For the bison herds in this study, gene flow has occurred more recently than 500 years (Figure 4.1.1), but several of the herds have been separated since their founding in the early 20th century, approximately 100-120 years ago. The generation time of wild plains bison herds has been estimated to be between 7-8

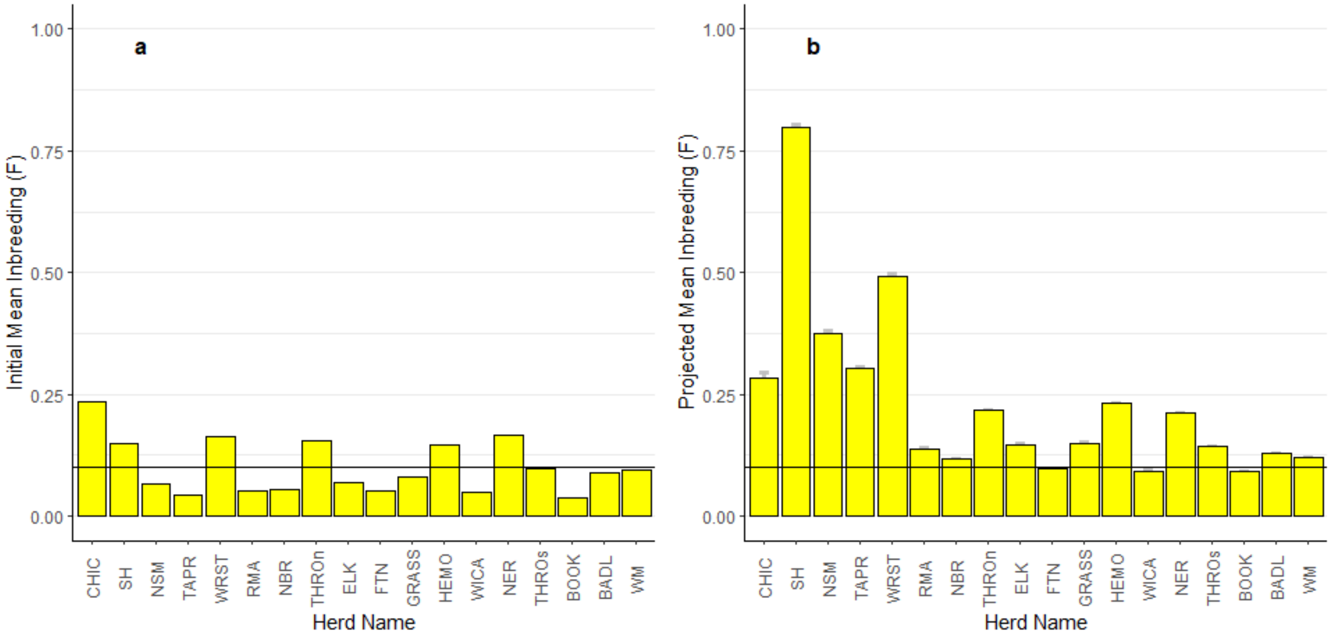

Figure 4.1.2. a) Initial estimates of inbreeding coefficients (F) for each of the 18 bison herds included in this study; and b) the projected mean inbreeding coefficients for those herds after 200 years under current management. Horizontal lines indicate F = 10%, the suggested threshold for evaluating the risk of genetic erosion. Error bars denote standard errors. Inbreeding coefficient of individuals was estimated as the kinship between its parents.

years (Fuller et al. 2007; Hedrick 2009; Traylor-Holzer 2016), indicating that some herds have been isolated for at least 12 generations.

Assessing whether substantial environmental differences exist between herds is more difficult, given the range of potential selection pressures (e.g., forage type and quality, presence of natural predators, differences in climatic conditions, differences in disease exposure). Additionally, it remains unknown whether any of these selection pressures are strong enough to counteract the effects of genetic drift and founder effects on the allelic diversity and make-up of the relatively small bison herds in this study (Hereford 2009; Mills 2013). However, it is important to recognize that the management required to maintain restricted herd sizes likely represents the most significant current selection pressure in each of these managed DOI bison herds, with removals constituting the vast majority of losses of individual animals to the herd. While there does appear to be strong genetic differentiation between many of the herds sampled in this study, it remains unknown whether this differentiation in neutral markers corresponds to differences in adaptive genetic variation in bison. However, given the origins and relatively recent history of successful admixture of many of the herds in this study (see section 2.4), the potential for outbreeding depression in DOI bison is likely to be low. Additionally, as discussed in section 2.4 of this report, the genetic differences among DOI bison herds are most likely artifacts of human-mediated herd establishment and subsequent management.

Finally, we must determine whether and how much gene flow in the form of translocations will achieve our genetic management objectives for the population. This final question is the objective of this study. Ultimately the genetic benefits or risks of translocations will be modulated by the life history of the species or population in question, including its mating system, its probability of surviving to reach reproductive maturity, and its mean reproductive output and success (Lowe and Allendorf 2010; Spies et al. 2018; Vucetich and Waite 2000). In this study, we determine whether establishing gene flow between the 16 DOI and two Parks Canada herds through a process of translocations ensures we meet the management goals for the long-term viability of plains bison and explore and compare the effects of varying the frequency and number of animals moved during translocations, and of using alternate criteria for selecting source herds for translocations. Specifically, we develop genetically explicit population models to explore which management scenarios best maintain or increase genetic diversity of individual herds, increase the genetic redundancy across herds, and maintain or increase the genetic diversity in the bison metapopulation overall.

4.2 Methods

Developing Metapopulation Management Scenarios

Herds Included in Metapopulation Management Scenarios

Before developing management scenarios, we first identified logistical, biological, or political issues that could limit herds in the bison metapopulation from acting either as a source or as a recipient for translocations, thereby precluding it from either giving or receiving translocated animals in our metapopulation models. We identified issues that might preclude a herd from participating in translocations. These included disease risk, geographic remoteness, logistical difficulty, levels of known cattle introgression, and management goals of individual units. Herds affected by a disease of concern (such as brucellosis in NER/GRTE) were excluded as donors due to the significant risk to the recipient herd from potential disease translocation associated with animal translocation. Although vaccination and individual animal diagnostic testing for some diseases can reduce this risk, a few diseases are difficult to detect such that risk outweighs any potential genetic benefit to the recipient herd. Logistical challenges and remote locations make inclusion of a few herds (WRST) impractical, while two herds (CHIC and SH) are designated as display herds and are too small to contain diversity sufficient to augment recipient herds. Genetic resources of these two display herds are more appropriately sourced from the original founder herds, WM and NBR, respectively. Finally, herds with higher levels of cattle introgression, especially in the mitochondria with the potential for metabolic effects (BOOK), were excluded as source herds to protect the genetic integrity of recipient herds (Table 4.2.1). This resulted in 13 herds identified as both potential donors and potential recipients.

Source Herd Scenarios

During workshop discussions with herd managers and agency leads, we identified four general strategies for selecting source herds for translocations most likely to meet the stated management goals of a proposed DOI bison metapopulation while also addressing the management and logistical concerns of DOI bison stakeholders. These strategies included 1. Source herd must be the genetically least-related herd to the recipient; 2. Systematic and sequential rotation of source herd at every translocation, in order from least-related to most-related; 3. Source herd must be genetically similar to the recipient; 4. Source herd must be the geographically closest herd to the recipient. From these strategies we developed five source herd modeling scenarios.

Source Herd Scenario 1 – Genetically Least-Related

If the goal of a translocation is to increase the genetic diversity of the recipient herd, then choosing a source herd that is highly genetically differentiated from the recipient herd should produce the best results, as the benefits of gene flow to genetic diversity increases with increasing differences in the allele frequencies between populations (Falconer and MacKay 1996). In particular, evidence from modeling and captive breeding programs suggest that selecting individuals or populations with the lowest mean kinship to the recipient population produces the largest increases in genetic diversity (Ballou and Lacy 1995; Ballou et al. 2010; Fernandez et al. 2004;). For this translocation management scenario, we used gene identity values (J_{xy}) estimated from our allelic data on each herd to approximate mean kinship values between herds. Gene identity (J_{xy}) is the average probability that alleles are shared between populations (Toro et al. 2014). In this scenario, animals selected for translocations into the recipient herd must originate from the herd with the lowest mean J_{xy} value to the recipient herd, requiring that the allelic composition of every herd is known at each scheduled translocation.

Source Herd Scenario 2 – Sequential Rotation of Source Herd at Every Translocation ('Alternating')

Selecting a source herd that is the genetically least-related to the recipient herd at every scheduled translocation would entail regular sampling and analysis of herd genetics, as herds that exchange animals will become genetically more similar over time. Consequently, the network of genetic relatedness between herds (values of J_{xy}) will change as a result of translocations. Because sampling and analyzing the genetics of all herds during every translocation would be costly and logistically difficult, we tested whether a regular exchange of animals between all herds, based on our current knowledge of the DOI bison genetics, would yield similar results as the more precise scenario 1. In this scenario (hereafter referred to as: 'alternating'), we used our current knowledge of the genetic relatedness between herds to schedule sequential translocations for each herd in which source herds were ordered from least related to most related (lists of source herds for each recipient herd given in Appendix F). For example, as measured by our current genetic data, the most distantly related herd to ELK is WM, and second most distantly related herd is BADL, and the most related herd is GRASS. Therefore, the first scheduled translocation into ELK would select animals from WM, during the second scheduled transloca-

Table 4.2.1. A list of herds considered for inclusion in metapopulation management models, whether herds were included or excluded from models, whether herds were included or excluded from acting as a donor or as a recipient during simulated translocations, and reasons for exclusion.

Herd	**Included in Models**	**As Donor**	**As Recipient**	**Reasons for exclusion**
BADL	Y	Y	Y	N/A
BOOK	Y	N	N	mtDNA cattle introgression
CHIC	Y	N	N	Small display herd unable to maintain long-term diversity; is already a regular recipient from WM
ELK	Y	Y	Y	N/A
FTN	Y	Y	Y	N/A
GRCA	N	N	N	Lack of standardized data
GRASS	Y	Y	Y	N/A
HEMO	Y	Y	Y	N/A
NBR	Y	Y	Y	N/A
GRTE/NER	Y	N	N	Disease risk due to brucellosis
NSM	Y	Y	Y	N/A
RMA	Y	Y	Y	N/A
SH	Y	N	N	Small display herd unable to maintain long-term diversity; receives augmentation to maintain herd size
TAPR	Y	Y	Y	N/A
THROn	Y	Y	Y	N/A
THROs	Y	Y	Y	N/A
WICA	Y	Y	Y	N/A
WM	Y	Y	Y	N/A
WRST - Chitina	N	N	N	Logistical difficulty, remoteness
WRST – Copper River	Y	N	N	Logistical difficulty, remoteness
YELL	N	N	N	Lack of standardized genetic data, disease risk due to brucellosis

tion animals would be sourced from BADL, and on down the list until GRASS is used as a source herd. The model then repeatedly used this same sequence of source herds for translocations into ELK throughout each 200-year run.

Source Herd Scenario 3 – Geographically Closest Herd Within Lineage

While one of our given management goals is to maintain or increase genetic diversity within individual herds, some researchers have suggested that bison should ideally only be transferred between satellite or related herds to reduce the risk of outbreeding depression, as well as to reduce threats to the existing genetic uniqueness and identity of herds due to the loss or dilution of rare or unique alleles (Dratch and Gogan 2010). Subsequently, workshop discussions with herd managers and agency leads identified a management strategy to be included as a modeling scenario in which translocations only occur between groups of closely related herds. In this scenario, translocations would only occur between herds within groups of genetically similar herds as identified by our DAPC analysis (Chapter 2), i.e., herds that cluster together along the two discriminant function axes in the DAPC analysis of DOI bison allelic data (Figure 4.2.1; Table 4.2.2). We hereafter refer to these groups of genetically similar herds as lineages for the sake of brevity.

Lineage 1 consists of BADL, FTN, HEMO, NER/GRTE, THROn, and THROs (Table 4.2.2; Figure 2.3.3b). Lineage 2 consists of ELK, GRASS, NBR, NSM, RMA, SH, TAPR, WICA, and WRST. Lineage 3 consists of WM and CHIC. The herds at BOOK and RMA are made up of individuals that belong to multiple genetic clusters, but the majority of animals at BOOK cluster with lineage 1, and the majority of animals at RMA cluster with lineage 2, so we included these herds in these respective lineages.

In this scenario source herds used for any translocation were simply the geographically closest herd that is in the same lineage as the recipient herd (Table 4.2.2; Figure 4.2.2). Geographic distances between herds was measured as the driving distance (in miles, obtained from Google Maps; Appendix G) to represent the actual transport of bison via highway.

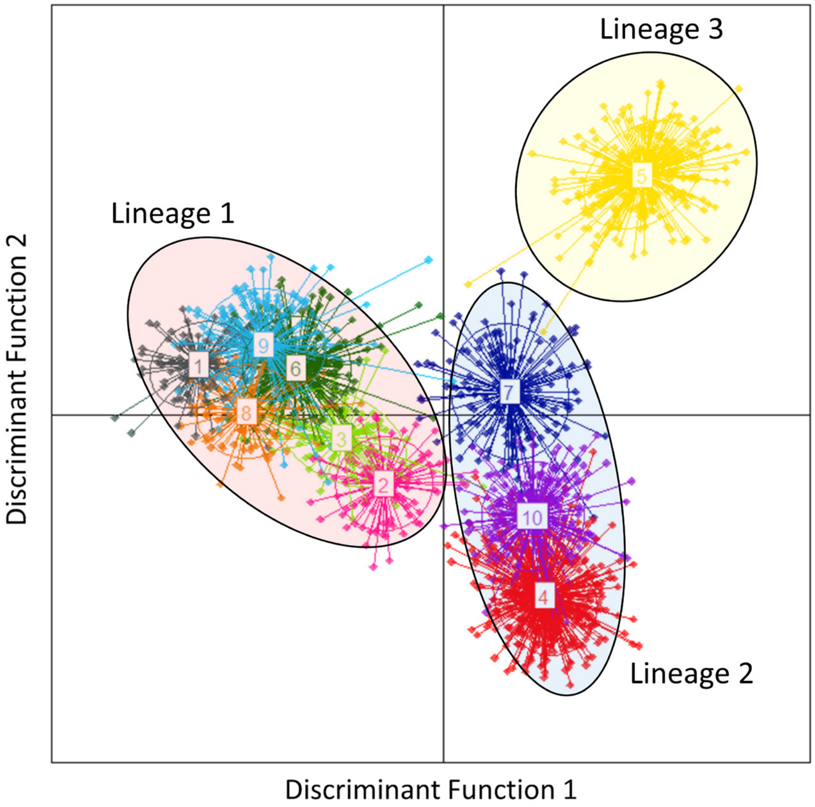

Figure 4.2.1. Scatter plot depicting the 10 unique genetic cluster identified in our DAPC analysis (see section 2.2 and Figure 2.3.2 for details). Axes represent discriminant functions, synthetic variables that are linear combinations of alleles with the largest between-group variance and the smallest within-group variance. Shaded areas encompass genetically similar clusters, hereafter referred to as lineages.

Source Herd Scenario 4 – Genetically Least-Related Within Lineage

Scenario 3 is a static scenario, in which each recipient herd receives animals from the same source during all translocations. We also wanted to explore the effects of dynamic exchange of alleles between all herds within each identified lineage. In this scenario, during each translocation the model assessed the genetic relatedness between all herds (as in scenario 1) in each lineage (Figure 4.2.1; Table 4.2.2) and chose the herd least related to the recipient herd to be a source. As in scenario 1, the genetic relatedness of herds will change as a result of genetic management, and so the source herds used in translocations for any one recipient herd may change through time.

Source Herd Scenario 5 – Geographically Closest

We also tested a logistically simple and cost-effective scenario in which the source herd used for translocations is simply the herd that is geographically closest to the recipient herd based on driving distance (Appendix G).

Table 4.2.2. List of herds within each group of genetically similar herds as identified by our DAPC analyses (Section 2.2). Hereafter we refer to these groups as lineages.

Herds	**Lineage 1**	**Lineage 2**	**Lineage 3**
Herds included in metapopulation management scenarios	BADL FTN HEMO THROn THROs	ELK GRASS NBR NSM RMA TAPR WICA	WM
Herds included in metapopulation management scenarios	BOOK NER/GRTE	SH WRST	CHIC

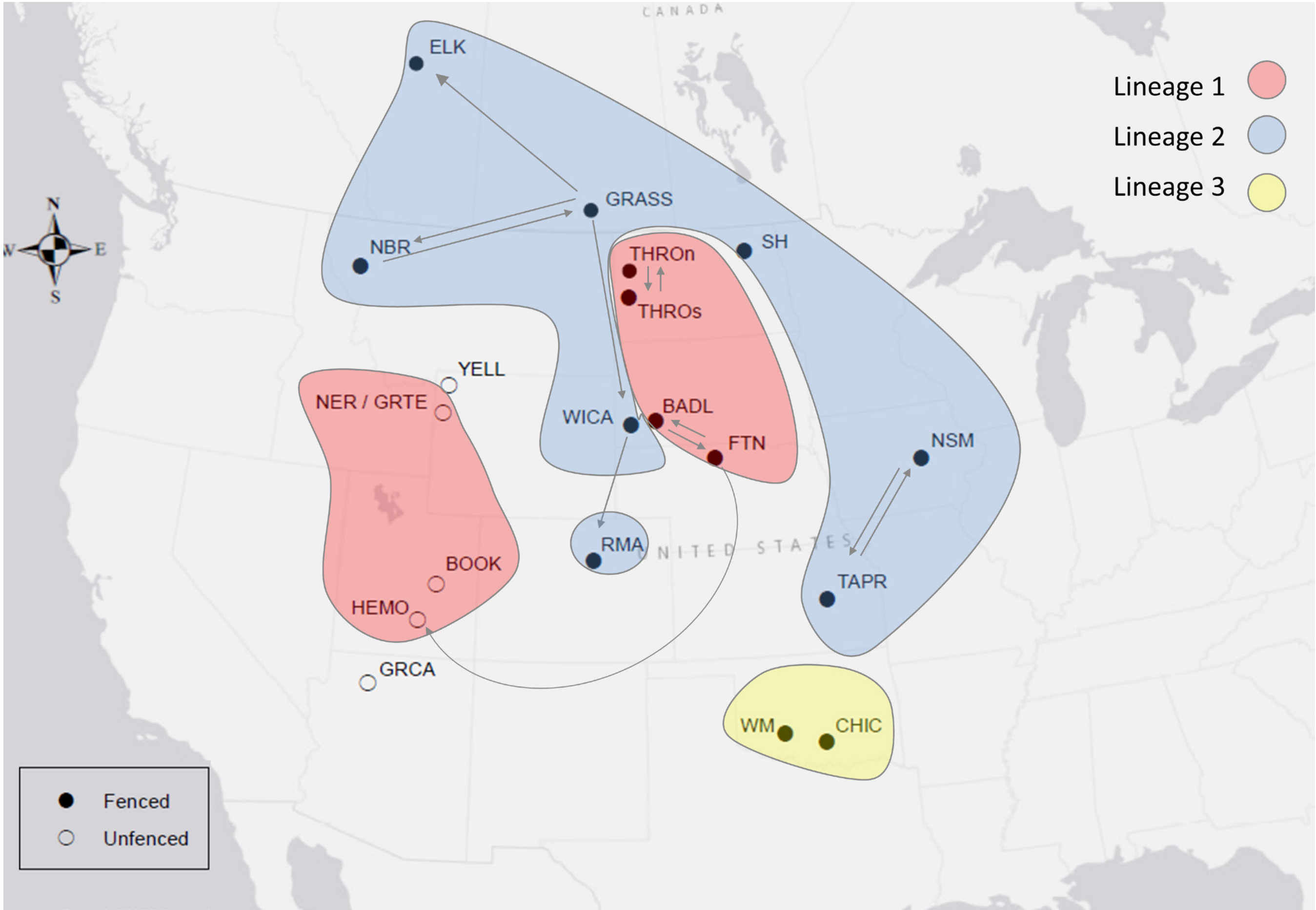

Figure 4.2.2. Map showing directional translocations between 13 DOI and Parks Canada herds undergoing translocations, when translocations occur between the geographically closest herds within lineages. Shaded areas indicate the three lineages identified in Figure 4.2.1: Lineage 1 is shaded in red, lineage 2 is shaded in blue, lineage 3 is shaded in yellow. Arrows indicate the direction of translocations, from source to recipient. Note that due to differing geographical distances and degree of isolation between herds, not all translocations will be reciprocal. Herds without arrows are not included in metapopulation management in this scenario.

Size and Frequency of Translocations

A number of considerations must be made during translocations to make these movements safe for bison and their handlers both on the journey and in their new home, as well as to increase the probability of successful social integration into the recipient herd to result in breeding (and therefore gene flow). Experience in recent translocations suggests that the gregarious nature and social structure of bison is important, and moving more than one animal is likely to reduce stress and increase success. Younger bison are safer to handle and transport, and they more easily and quickly integrate socially into a recipient herd. Moving small numbers of animals more frequently benefits diversity more than large, infrequent batches, and the cost and logistics of transporting small numbers of bison in a Park- or Refuge-personnel driven trailer instead of a large commercial transport are optimized.

We therefore incorporated these considerations into our management scenarios models. For each source herd scenario, we simulated five different translocation scenarios that meet these criteria: moving 2 animals every 10 years, 3 animals every 7 years, 3 animals every 5 years, 8 animals every 7 years, and 8 animals every 5 years. Bison selected for translocations were yearlings (between 1 and 2 years old), and consisted of a roughly 50:50 sex ratio (Table 4.2.3).

Simulation Modeling

All simulations were carried out using VORTEX, as described in Chapter 3, in which individual bison herds were simulated concurrently as a metapopulation (for 200 years, 500 iterations). However, in these management scenarios, individual animals were selected and moved between herds on a given time schedule based on the specified individual and herd-level characteristics detailed in Table 4.2.5. For source herd scenarios 1 and 4, the mean gene identity (J_{xy}) was estimated between each herd and every potential donor herd within the metapopulation during each year, with animals transferred from the least-related donor herd into the recipient herd during scheduled translocations. To ensure that no one herd would experience excessive demands for animals in any given year, translocations were staggered across years. Translocated bison were assumed to have the same age- and sex-specific survival and reproductive rates as resident bison. Translocated bison were assumed to be marked in NPS herds, and therefore tracked to prevent their removal during management operations once in their new herd. Translocation bison were assumed not to be tracked in FWS herds or in HEMO, where translocated bison could be removed during management operations or harvested by hunters.

Model Outputs and Analysis

For each source herd and translocation scenario we assessed the probability of extinction for individual herds as the proportion of runs (iterations) in which the herd became extinct. We assessed changes in the genetic diversity for each individual herd and for the metapopulation as a whole as the absolute and proportional change in both allelic diversity and heterozygosity between the start (year 0) and final year (year 200) of simulations.

To assess how alternate management scenarios change the genetic structure of the bison metapopulation, we simulated individual genotypes from each herd at the end of simulations and analyzed these genotypes using discriminant analysis of principal components (DAPC; Jombart et al. 2010). At the end of simulations, VORTEX outputs the mean allele frequencies at each locus for each herd (averaged across all iterations). To create individual diploid genotypes from each herd, we randomly selected two alleles at each locus, with probabilities of selection weighted by the allele frequencies for that locus. We used these simulations to create 1000 individual genotypes from every herd, then randomly selected N genotypes from each herd where N is the number of genetic samples originally collected from that herd (Table 2.2.1) to match the structure of our original genetic dataset. All genotypes were created in R and analyzed with package adegenet (Jombart 2008; Jombart and Ahmed 2011) as in section 2.2.

To assess how each of our alternate management scenarios affected the degree of genetic redundancy across herds, we sequentially simulated the extinction of selected herds from the metapopulation at year 30 of each simulation and compared the resultant pooled allelic diversity after 200 years to simulations in which no herds are lost from the metapopulation. As in the models from section 3.2, we only modeled the loss of BADL, FTN, NBR, and WM. After a selected herd becomes extinct (in year 30), the source herd selection for all other herds was adjusted to account for the loss (e.g., in the geographically closest source herd scenario, BADL is a source for WICA; when BADL is removed, WICA's source herd becomes the next closest herd, THROs).

4.3 Results

Source Herd Scenario 1 – Genetically Least-Related

Changes to Within-Herd Genetic Diversity

Selecting the genetically least-related herd as a source for translocations yielded the largest increases in genetic diversity across all herds, both in terms of heterozygosity and in terms of allelic diversity (Table 4.3.1, Figure 4.3.1). Increases

Table 4.2.3. A summary of all combinations of source herd criteria, size of translocations, frequency of translocations and sex ratio of animals moved in each of our modeled management scenarios. A total of 25 translocation scenarios were modeled.

Source Herd	Number and Frequency	Identity of Animals Moved
Genetically Least Related	2 every 10 years 3 every 7 years 3 every 5 years 8 every 7 years 8 every 5 years	Yearlings (1 male; 1 female) Yearlings (2 males; 1 female) Yearlings (2 males; 1 female) Yearlings (4 males; 4 females) Yearlings (4 males; 4 females)
Alternating	2 every 10 years 3 every 7 years 3 every 5 years 8 every 7 years 8 every 5 years	Yearlings (1 male; 1 female) Yearlings (2 males; 1 female) Yearlings (2 males; 1 female) Yearlings (4 males; 4 females) Yearlings (4 males; 4 females)
Geographically Closest Within Lineage	2 every 10 years 3 every 7 years 3 every 5 years 8 every 7 years 8 every 5 years	Yearlings (1 male; 1 female) Yearlings (2 males; 1 female) Yearlings (2 males; 1 female) Yearlings (4 males; 4 females) Yearlings (4 males; 4 females)
Genetically Least Related Within Lineage	2 every 10 years 3 every 7 years 3 every 5 years 8 every 7 years 8 every 5 years	Yearlings (1 male; 1 female) Yearlings (2 males; 1 female) Yearlings (2 males; 1 female) Yearlings (4 males; 4 females) Yearlings (4 males; 4 females)
Geographically Closest	2 every 10 years 3 every 7 years 3 every 5 years 8 every 7 years 8 every 5 years	Yearlings (1 male; 1 female) Yearlings (2 males; 1 female) Yearlings (2 males; 1 female) Yearlings (4 males; 4 females) Yearlings (4 males; 4 females)

in allelic diversity were the largest (up to 65%) for herds with low initial levels of allelic diversity (HEMO, THROn). Large herds such as BADL, WM, and WICA also had considerable gains in allelic diversity, with increases ranging between approximately 10-30%. Small herds experienced smaller gains, ranging from a 1% to 20% increase in allelic diversity. Only TAPR was predicted to lose allelic diversity under this source herd scenario (0.4% decrease) and only then in the scenario with the smallest, least frequent translocations (two animals every 10 years). Changes in heterozygosity as a result of translocations followed the same pattern, though small, infrequent translocations (two every 10 years) tended to decrease heterozygosity in smaller herds.

Changes to Population Structure

Translocations between herds in which the source herds were always the least-related to recipient herds greatly decreased the genetic differentiation between most of the herds within the metapopulation. After 200 years, results of our DAPC analysis suggests that only seven distinct genetic clusters remained in the metapopulation, with each cluster consisting of individuals from almost every herd involved in translocations (Figure 4.3.2). In contrast, herds excluded from translocations (NER/GRTE, SH, WRST) became increasingly differentiated from those participating in translocations.

Source Herd Scenario 2 - Sequential Rotation of Source Herd at Every Translocation ('Alternating')

Changes to Within-Herd Genetic Diversity

Results from models in which source herds alternated at every scheduled transfer were almost identical to those for scenario 1 (genetically least-related), with genetic diversity increasing across all herds (Figure 4.3.3; Table 4.3.2). Again, allelic diversity increased the most in herds with low initial levels of diversity and in larger herds, and it increased the least in smaller herds. The only exception to this pattern was TAPR, which again was predicted to slightly lose allelic diversity when only 2 animals are translocated into the herd every 10 years.

Changes to Population Structure

After 200 years of translocations in which source herds alternate during each translocation, genetic differentiation decreased between most of the herds within the metapopulation. As with Source Herd Scenario 1, only seven distinct genetic clusters remained in the metapopulation, with each

Table 4.3.1. The absolute and proportional change in allelic diversity (measured as MNA) for each herd and for the entire DOI bison metapopulation ("META") after 200 years of translocations, given varying sizes and frequencies of translocations when source herds are chosen to be the genetically least-related to the recipient herd.

Herd	Target N	Initial MNA	Final MNA (proportional change in MNA) when translocate 2 every 10 years	Final MNA (proportional change in MNA) when translocate 3 every 5 years	Final MNA (proportional change in MNA) when translocate 3 every 7 years	Final MNA (proportional change in MNA) when translocate 8 every 5 years	Final MNA (proportional change in MNA) when translocate 8 every 7 years
BADL	600	4.5	5.09 (0.131)	5.52 (0.227)	5.35 (0.189)	5.84 (0.298)	5.73 (0.273)
BOOK*[+]	550	4.83	4.82 (-0.002)	5.08 (0.052)	5 (0.035)	5.3 (0.097)	5.22 (0.081)
CHIC*[+]	10	2.5	2.78 (0.112)	2.83 (0.132)	2.77 (0.108)	2.85 (0.14)	2.82 (0.128)
ELK	400	4.79	4.86 (0.015)	5.34 (0.115)	5.24 (0.094)	5.67 (0.184)	5.59 (0.167)
FTN	350	5.27	5.38 (0.019)	5.67 (0.074)	5.59 (0.059)	5.81 (0.1)	5.77 (0.093)
GRASS	400	4.76	4.86 (0.021)	5.38 (0.13)	5.27 (0.107)	5.72 (0.202)	5.64 (0.185)
HEMO	~400	3.73	4.98 (0.335)	5.54 (0.485)	5.45 (0.461)	5.73 (0.536)	5.68 (0.523)
NBR	285	5.01	5.3 (0.058)	5.61 (0.12)	5.54 (0.106)	5.75 (0.148)	5.7 (0.138)
NER[+]	500	3.75	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)
NSM	55	4.53	4.58 (0.011)	5.07 (0.119)	4.82 (0.064)	5.37 (0.183)	5.15 (0.137)
RMA	200	4.95	5.17 (0.042)	5.5 (0.111)	5.41 (0.093)	5.65 (0.139)	5.58 (0.127)
SH[+]	15	3.51	1.26 (-0.641)	1.28 (-0.635)	1.28 (-0.635)	1.27 (-0.638)	1.28 (-0.635)
TAPR	100	4.6	4.58 (-0.004)	5.2 (0.13)	5.09 (0.107)	5.51 (0.198)	5.46 (0.184)
THROn	300	3.48	4.83 (0.388)	5.44 (0.563)	5.3 (0.523)	5.75 (0.652)	5.66 (0.626)
THROs	500	4.19	5 (0.193)	5.51 (0.315)	5.39 (0.286)	5.83 (0.391)	5.74 (0.37)
WICA	350-500	4.69	5.11 (0.09)	5.52 (0.177)	5.36 (0.143)	5.82 (0.241)	5.7 (0.215)
WM	650	4.84	5.52 (0.14)	5.8 (0.198)	5.73 (0.184)	5.93 (0.225)	5.89 (0.217)
WRST[+]	> 90	3.31	1.84 (-0.444)	1.81 (-0.453)	1.83 (-0.447)	1.87 (-0.435)	1.85 (-0.441)
META	–	6.87	6.31 (-0.082)	6.30 (-0.083)	6.31 (-0.082)	6.32 (-0.081)	6.31 (-0.082)

*Though not included in metapopulation management, BOOK and CHIC experience gene flow from the Northern Ute and WM herds, respectively, as part of their current management practices.

[+] Herd values in highlighted text are not included in translocation management.

cluster consisting of individuals from almost every herd included in translocations (Figure 4.3.4). Herds excluded from translocations (NER/GRTE, SH, WRST) became increasingly differentiated from those participating in translocations.

Source Herd Scenario 3 – Geographically Closest Herd Within Lineage

Changes to Within-Herd Genetic Diversity

The majority of herds lost diversity when source herds used for translocations were the geographically closest herd within the recipient herd's lineage (Table 4.3.3; Figure 4.3.5). Regardless of the number of bison translocated or the frequency of translocations, the allelic diversity of eight herds always decreased in this scenario (ELK, GRASS, FTN, NBR, NSM, TAPR, THROs, WM). The largest decreases in allelic diversity were projected for the smallest herds, NSM and TAPR, with projected decreases in allelic diversity ranging from 23-50% and 22-49% respectively, depending on the number of animals moved and frequency of translocations. In contrast, allelic diversity for the two herds with the lowest initial levels of allelic diversity (HEMO, THROn) always increased under this management scenario regardless of the number of animals moved or the frequency of translocations, with the largest increases projected for HEMO (15-26%). Results were mixed for BADL and RMA. For BADL, our models predicted small increases in allelic diversity (< 5% increase) for translocations greater in number or frequency than 2 every 10 years. For RMA our models predicted small increases in allelic diversity (< 0.05%) with large or frequent translocation scenarios (when 8 animals were translocated into the herd, regardless of frequency, or 3 animals every 5 years), but decreased when translocations consisted of either 3 animals every 7 years or 2 animals every 10 years.

Changes to Population Structure

Limiting gene flow to occur only within lineages resulted in

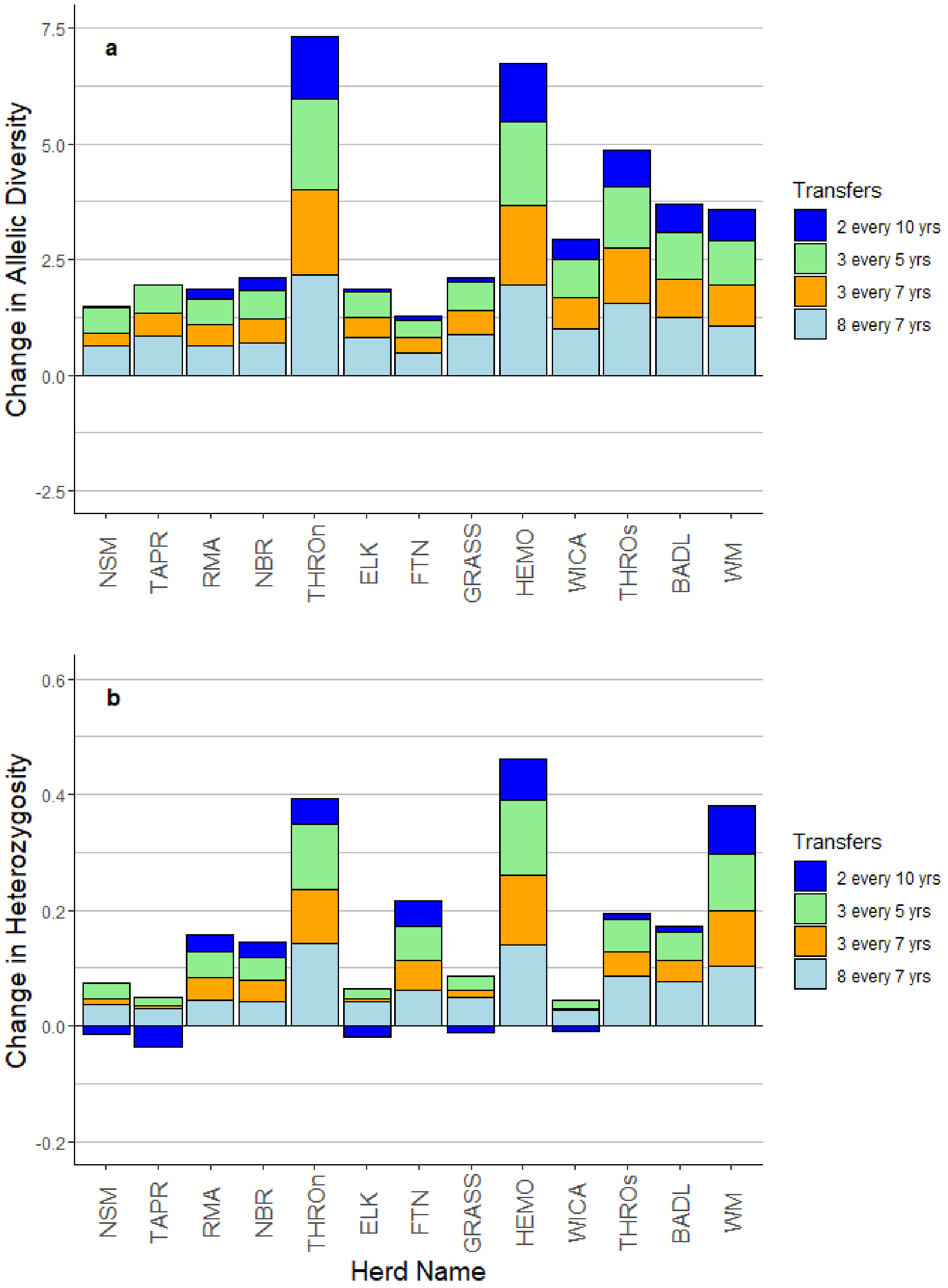

Figure 4.3.1. Stacked bar plots showing the change in a) allelic diversity and b) mean heterozygosity when the source herd for all translocations is the genetically least-related herd to the recipient herd. Colored segments represent the total change in diversity (allelic diversity or heterozygosity) corresponding to each transfer scenario (see Table 4.3.1 for values). Herds excluded from translocations are not shown. Herds are ordered by target abundance: left to right, smallest to largest.

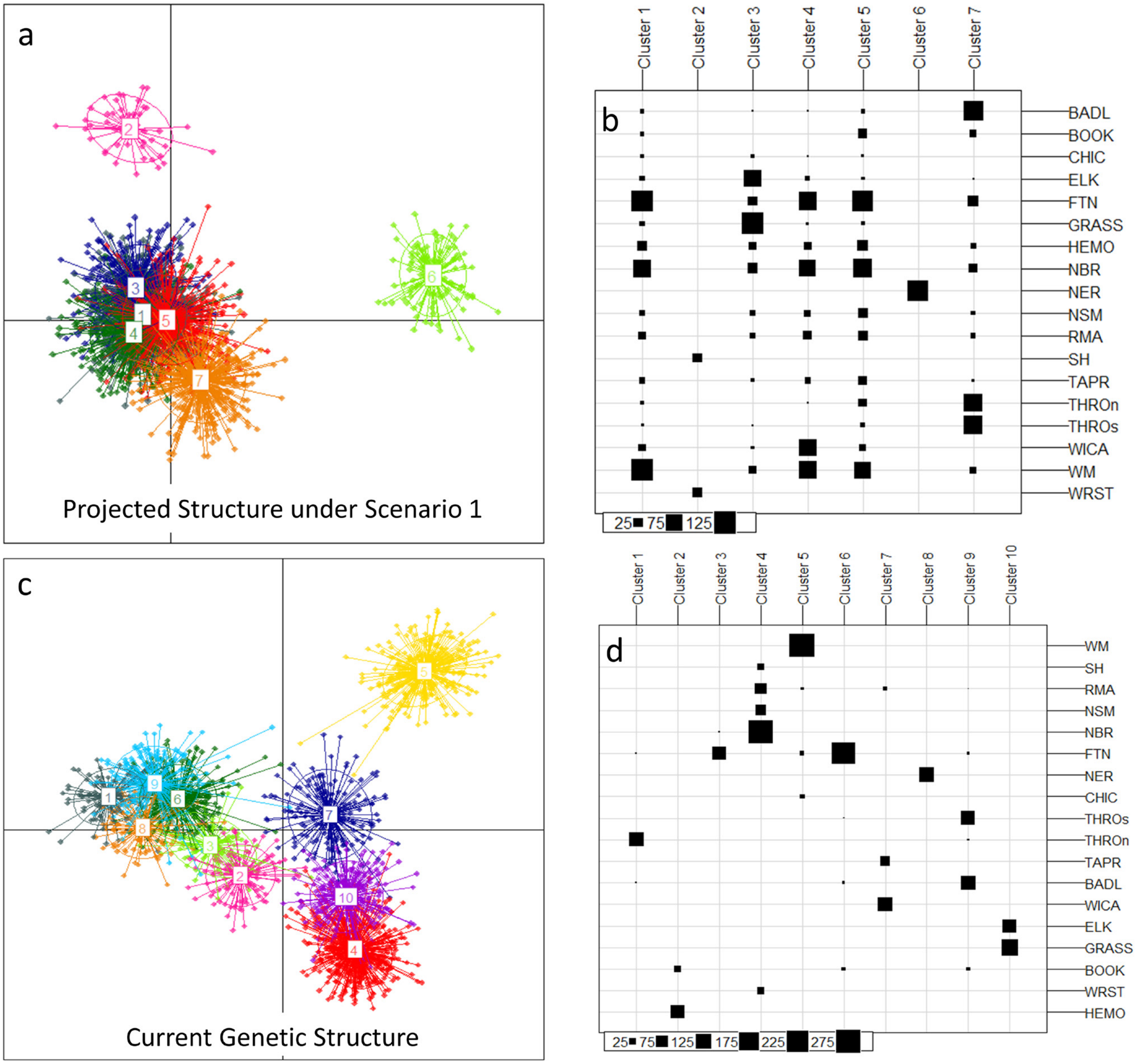

Figure 4.3.2. Plots a) and b) show DAPC results after 200 years of genetic augmentation management when 3 animals are moved every 5 years, and the source herd was always the genetically least-related to the recipient herd. Symbols in a) represent individual bison samples, and circles with numbers represent the seven unique genetically differentiated clusters in the bison data and b) show the number of individual samples from each herd assigned to each genetic cluster. Plots c) and d) show the current genetic structure of herds today. Note: Colors and ID numbers associated with each cluster are assigned randomly by the DAPC algorithm, and thus are not comparable between plots a) and c).

related herds becoming increasingly homogenized with one another, while increasing differentiation from all other herds (Figure 4.3.6). As a result, after 200 years of translocations only five distinct genetic clusters remained in the metapopulation. All herds participating in translocations segregated out into three clusters, while the remaining two clusters represented herds excluded from translocations (SH, NER/GRTE, and WRST).

Source Herd Scenario 4 – Genetically Least-Related Within Lineage

Changes to Within-Herd Genetic Diversity

Scenarios in which source herds were always the genetically least-related herd within the recipient herd's lineage yielded mixed results (Table 4.3.4; Figure 4.3.7). The direction and magnitude of changes in allelic diversity for each recipient herd under this scenario were related to the number and genetic diversity of the other herds (potential sources) within

Table 4.3.2. The absolute and proportional change in allelic diversity (measured as MNA) for each herd and for the entire DOI bison metapopulation ("META") after 200 years of translocations, given varying sizes and frequencies of translocations, when source herds alternated at each translocation.

Herd	**Target N**	**Initial MNA**	**Final MNA (proportional change in MNA) when translocate 2 every 10 years**	**Final MNA (proportional change in MNA) when translocate 3 every 5 years**	**Final MNA (proportional change in MNA) when translocate 3 every 7 years**	**Final MNA (proportional change in MNA) when translocate 8 every 5 years**	**Final MNA (proportional change in MNA) when translocate 8 every 7 years**
BADL	600	4.5	5.16 (0.147)	5.57 (0.238)	5.39 (0.198)	5.88 (0.307)	5.76 (0.28)
BOOK*+	550	4.83	4.8 (-0.006)	5.02 (0.039)	4.94 (0.023)	5.26 (0.089)	5.18 (0.072)
CHIC*+	10	2.5	2.77 (0.108)	2.82 (0.128)	2.8 (0.12)	2.79 (0.116)	2.84 (0.136)
ELK	400	4.79	4.84 (0.01)	5.36 (0.119)	5.25 (0.096)	5.69 (0.188)	5.63 (0.175)
FTN	350	5.27	5.38 (0.019)	5.67 (0.076)	5.59 (0.059)	5.84 (0.106)	5.78 (0.095)
GRASS	400	4.76	4.86 (0.021)	5.4 (0.134)	5.3 (0.113)	5.73 (0.204)	5.67 (0.191)
HEMO	~400	3.73	4.97 (0.332)	5.53 (0.483)	5.44 (0.458)	5.75 (0.542)	5.7 (0.528)
NBR	285	5.01	5.22 (0.042)	5.59 (0.116)	5.5 (0.098)	5.75 (0.145)	5.7 (0.138)
NER+	500	3.75	3.07 (-0.181)	3.06 (-0.184)	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)
NSM	55	4.53	4.54 (0.002)	5.05 (0.115)	4.8 (0.06)	5.39 (0.19)	5.14 (0.135)
RMA	200	4.95	5.14 (0.036)	5.52 (0.115)	5.42 (0.095)	5.68 (0.147)	5.59 (0.129)
SH+	15	3.51	1.24 (-0.646)	1.28 (-0.634)	1.33 (-0.621)	1.26 (-0.641)	1.29 (-0.632)
TAPR	100	4.6	4.56 (-0.011)	5.18 (0.126)	5.06 (0.1)	5.49 (0.191)	5.41 (0.176)
THROn	300	3.48	4.81 (0.382)	5.43 (0.56)	5.3 (0.523)	5.78 (0.661)	5.69 (0.635)
THROs	500	4.19	5.02 (0.198)	5.52 (0.317)	5.4 (0.289)	5.85 (0.396)	5.76 (0.375)
WICA	350-500	4.69	5.22 (0.113)	5.6 (0.194)	5.44 (0.16)	5.87 (0.252)	5.76 (0.228)
WM	650	4.84	5.54 (0.145)	5.84 (0.207)	5.77 (0.192)	5.98 (0.236)	5.95 (0.229)
WRST+	> 90	3.31	1.82 (-0.45)	1.82 (-0.45)	1.87 (-0.435)	1.81 (-0.453)	1.81 (-0.453)
META	–	6.87	6.32 (-0.08)	6.31 (-0.082)	6.31 (-0.08)	6.32 (-0.08)	6.32 (-0.082)

*Though not included in metapopulation management, BOOK and CHIC experience gene flow from the Northern Ute and WM herds, respectively, as part of their current management practices.

+Herd values in highlighted text are not included in translocation management.

the recipient herd's lineage. For herds in lineage 1 (ELK, GRASS, NBR, NSM, RMA, TAPR, WICA) allelic diversity mostly increased (increases ranging between 1-16%, though four herds lost diversity when only 2 animals were moved every 10 years (ELK, GRASS, NSM, TAPR). In lineage 2 (BADL, FTN, HEMO, THROn, THROs) the two herds with the lowest initial levels of diversity (HEMO, THROn) experienced the largest increases (between 19-42%), while the most diverse herd (FTN) always lost diversity (decreases of up to 9%). Lineage 3 only consisted of one herd: WM (excluding CHIC, which did not participate in translocations). As a result, WM always lost diversity in this scenario as it was excluded from receiving translocations.

Changes to Population Structure

As in scenario 3, limiting gene flow to only occur within lineages resulted in the herds within these lineages becoming increasingly homogenized with one another, while increasing differentiation from all other herds (Figure 4.3.8). As a result, after 200 years of translocations only five distinct genetic clusters remained in the metapopulation. All herds participating in translocations segregated out into three clusters, while the remaining two clusters represented herds excluded from translocations (SH, NER/GRTE, and WRST).

Source Herd Scenario 5 – Geographically Closest

Changes to Within-Herd Genetic Diversity

The majority of herds lost allelic diversity when the source of translocations was always the herd geographically closest to the recipient herd (Table 4.3.5; Figure 4.3.9). Only six herds gained allelic diversity in this scenario (BADL, HEMO, TAPR, THROn, WICA, WM). Herds that increased allelic diversity under this scenario were again those with low initial levels of

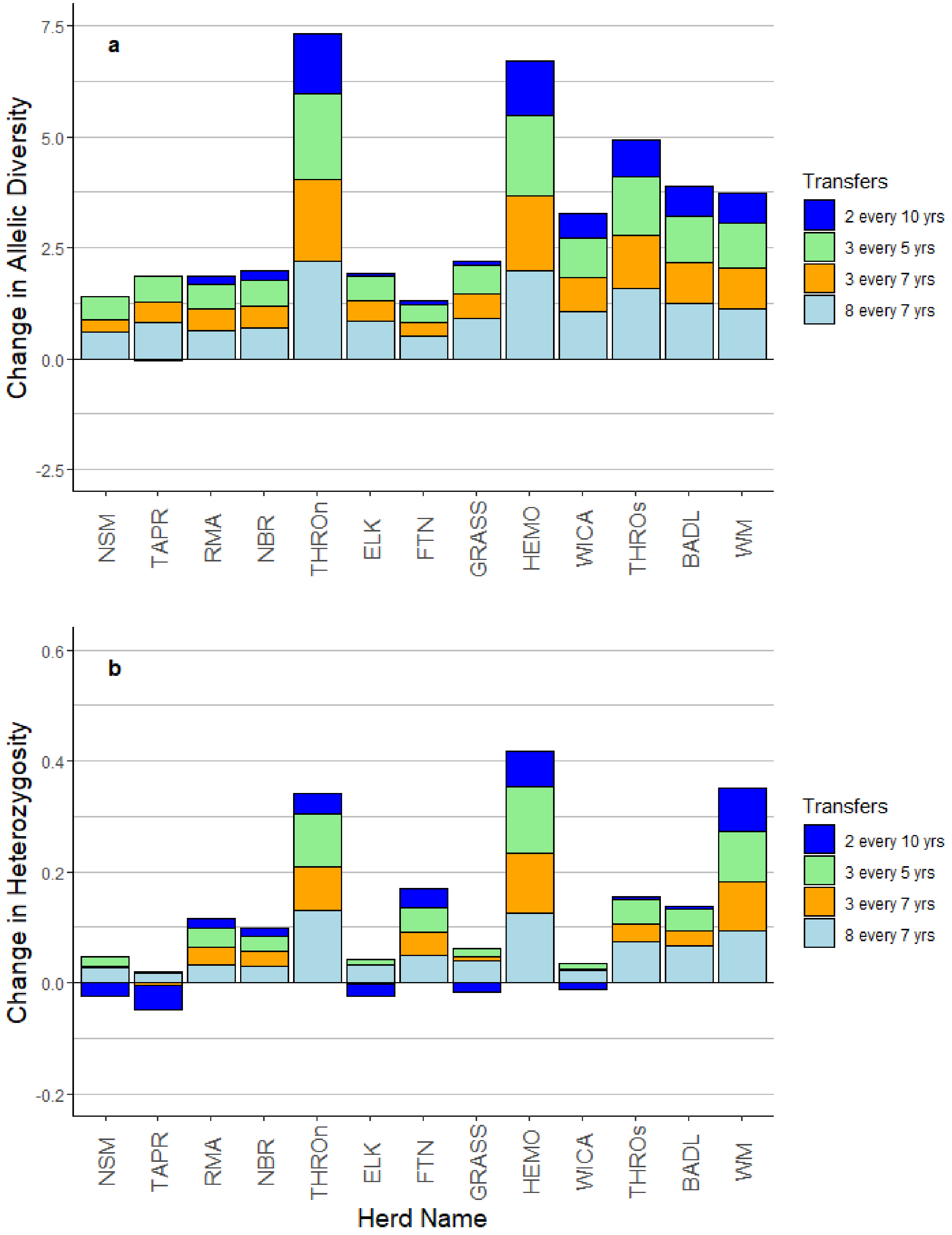

Figure 4.3.3. Stacked bar plots showing the change in a) allelic diversity and b) mean heterozygosity when source herds alternated at each translocation. Colored segments represent the total change in diversity (allelic diversity or heterozygosity) corresponding to each transfer scenario (see Table 4.3.2 for values). Results for herds excluded from translocations are not shown. Herds are ordered by target abundance: left to right, smallest to largest.

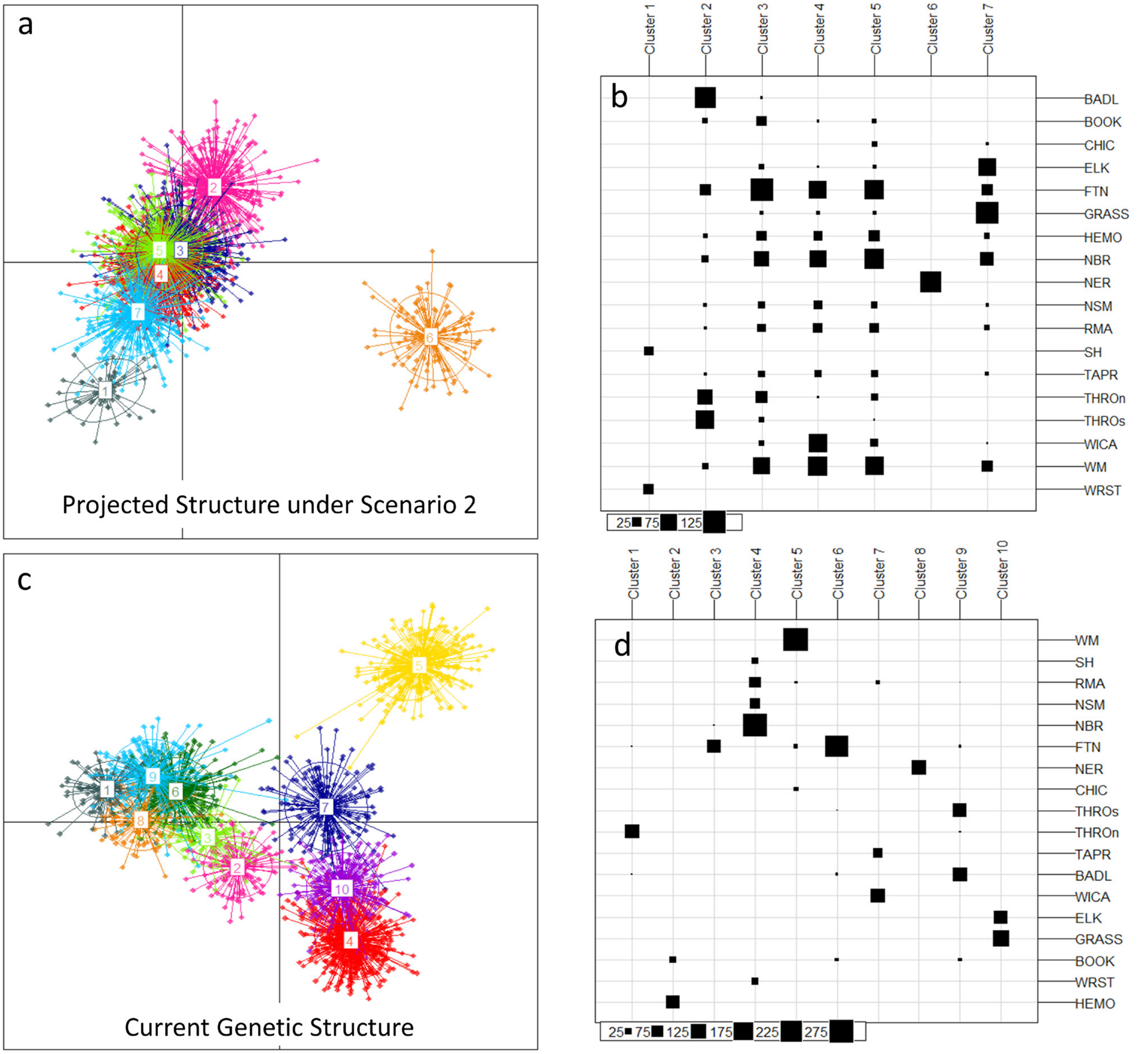

Figure 4.3.4. Plots a) and b) show DAPC results after 200 years of genetic augmentation management when 3 animals are moved every 5 years, and the source herd alternated at each translocation. Symbols in a) represent individual bison samples, and circles with numbers represent the seven unique genetically differentiated clusters in the bison data and b) show the number of individual samples from each herd assigned to each genetic cluster. Plots c) and d) show the current genetic structure of herds today. Note: Colors and ID numbers associated with each cluster are assigned randomly by the DAPC algorithm, and thus are not comparable between plots a) and c).

allelic diversity (HEMO, THROn), and herds that were closest neighbors to large or genetically diverse herds (BADL, TAPR, WICA, WM). The allelic diversity of most of the small herds or herds with small or genetically depauperate neighbors decreased in this scenario.

Changes to Population Structure

Genetic differentiation decreased within the metapopulation when translocations always came from the herd geographically closest to the recipient (Figure 4.3.10), with a reduction from the current 10 unique genetic cluster to only sevdistinct genetic clusters within the metapopulation after 200 years of translocations. Genetic exchanges under this scenario resulted in herds undergoing regular genetic exchange with one another becoming increasingly genetically similar (e.g., NBR, GRASS, and ELK).

Projected Changes to Genetic Diversity at the Metapopulation Level

Heterozygosity levels of the entire metapopulation either remained the same or increased for the majority of management scenarios tested (Figure 4.3.11a). The exceptions were scenarios in which 8 animals were moved during translocations, and in which translocations came from the same source year after year (Scenario 3 – geographically closest within recipient herd's lineage and Scenario 5 – geographically closest), both of which led to a decrease in heterozygosity within the entire metapopulation. In contrast, the allelic diversity of the metapopulation decreased in all scenarios (Figure 4.3.11b). With translocations, the allelic diversity of the metapopulation decreased between approximately 7.9-10% after 200 years, depending on the source herd scenario and number of animals moved. The largest decreases occurred in scenarios in which 8 animals were moved during translocations and when translocations always occurred between the same source and recipient (Scenario 3 – geographically closest within recipient herd's lineage and Scenario 5 – geographically closest), providing evidence that moving large numbers of individuals during translocations can result in some genetic swamping of the recipient herd's genetics. Results from our simulation model projecting the population viability and genetic diversity of all herds under current management conditions (with no translocations; see Chapter 3) predicted that allelic diversity of the entire bison population would decrease by approximately 7.4% after 200 years.

Figure 4.3.12 demonstrates that the effects of genetic swamping on allelic diversity are typically small, but can become more pronounced with time depending on the scenario. In particular, for smaller and less frequent translocations (2 every 10; 3 every 7), any negative effects of translocations on the allelic diversity of the entire bison metapopulation typically only manifest after 50-100 years, or between five to

Table 4.3.3. The absolute and proportional change in allelic diversity (measured as MNA) for each herd and for the entire DOI bison metapopulation ("META") after 200 years of translocations, given varying sizes and frequencies of translocations, when source herds are selected to be the geographically closest herd within the same lineage as the recipient herd. Herd values in highlighted text are not included in translocation management.

Herd	**Target N**	**Initial MNA**	**Final MNA (proportional change in MNA) when translocate 2 every 10 years**	**Final MNA (proportional change in MNA) when translocate 3 every 5 years**	**Final MNA (proportional change in MNA) when translocate 3 every 7 years**	**Final MNA (proportional change in MNA) when translocate 8 every 5 years**	**Final MNA (proportional change in MNA) when translocate 8 every 7 years**
BADL	600	4.5	4.47 (-0.007)	4.6 (0.022)	4.55 (0.011)	4.68 (0.04)	4.65 (0.033)
BOOK*+	550	4.83	4.63 (-0.041)	4.64 (-0.039)	4.64 (-0.039)	4.64 (-0.039)	4.64 (-0.039)
CHIC*+	10	2.5	2.48 (-0.008)	2.44 (-0.024)	2.46 (-0.016)	2.48 (-0.008)	2.46 (-0.016)
ELK	400	4.79	4.22 (-0.119)	4.51 (-0.058)	4.43 (-0.075)	4.45 (-0.071)	4.59 (-0.042)
FTN	350	5.27	4.56 (-0.135)	4.61 (-0.127)	4.6 (-0.129)	4.64 (-0.121)	4.63 (-0.123)
GRASS	400	4.76	4.42 (-0.071)	4.62 (-0.029)	4.59 (-0.036)	4.58 (-0.038)	4.67 (-0.019)
HEMO	~400	3.73	4.3 (0.153)	4.59 (0.231)	4.54 (0.217)	4.7(0.26)	4.7(0.26)
NBR	285	5.01	4.69 (-0.064)	4.75 (-0.052)	4.74 (-0.054)	4.71 (-0.062)	4.74 (-0.054)
NER+	500	3.75	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)	3.06 (-0.184)
NSM	55	4.53	3.51 (-0.227)	3.49 (-0.23)	3.5 (-0.227)	2.3 (-0.492)	3.1 (-0.316)
RMA	200†	4.95	4.74 (-0.042)	4.98 (0.006)	4.9 (-0.012)	5.17 (0.044)	5.15 (0.038)
SH+	15	3.51	1.29 (-0.632)	1.31 (-0.627)	1.32 (-0.624)	1.28 (-0.635)	1.29 (-0.632)
TAPR	100	4.6	3.56 (-0.226)	3.54 (-0.23)	3.57 (-0.224)	2.75 (-0.402)	3.22 (-0.3)
THROn	300	3.48	3.72 (0.069)	3.9 (0.121)	3.87 (0.112)	3.96 (0.138)	3.96 (0.138)
THROs	500	4.19	3.98 (-0.05)	4 (-0.045)	4 (-0.045)	4 (-0.045)	4 (-0.045)
WICA	350-500	4.69	4.94 (0.053)	5.2 (0.109)	5.1 (0.087)	5.34 (0.139)	5.31 (0.132)
WM	650	4.84	4.34 (-0.103)	4.34 (-0.103)	4.34 (-0.103)	4.31 (-0.11)	4.3 (-0.112)
WRST+	> 90	3.31	1.86 (-0.438)	1.78 (-0.462)	1.85 (-0.441)	1.86 (-0.438)	1.83 (-0.447)
META	–	6.87	6.33 (-0.079)	6.32 (-0.08)	6.32 (-0.08)	6.26 (-0.089)	6.3 (-0.083)

*Though not included in metapopulation management, BOOK and CHIC experience gene flow from the Northern Ute and WM herds, respectively, as part of their current management practices.

+Herd values in highlighted text are not included in translocation management.

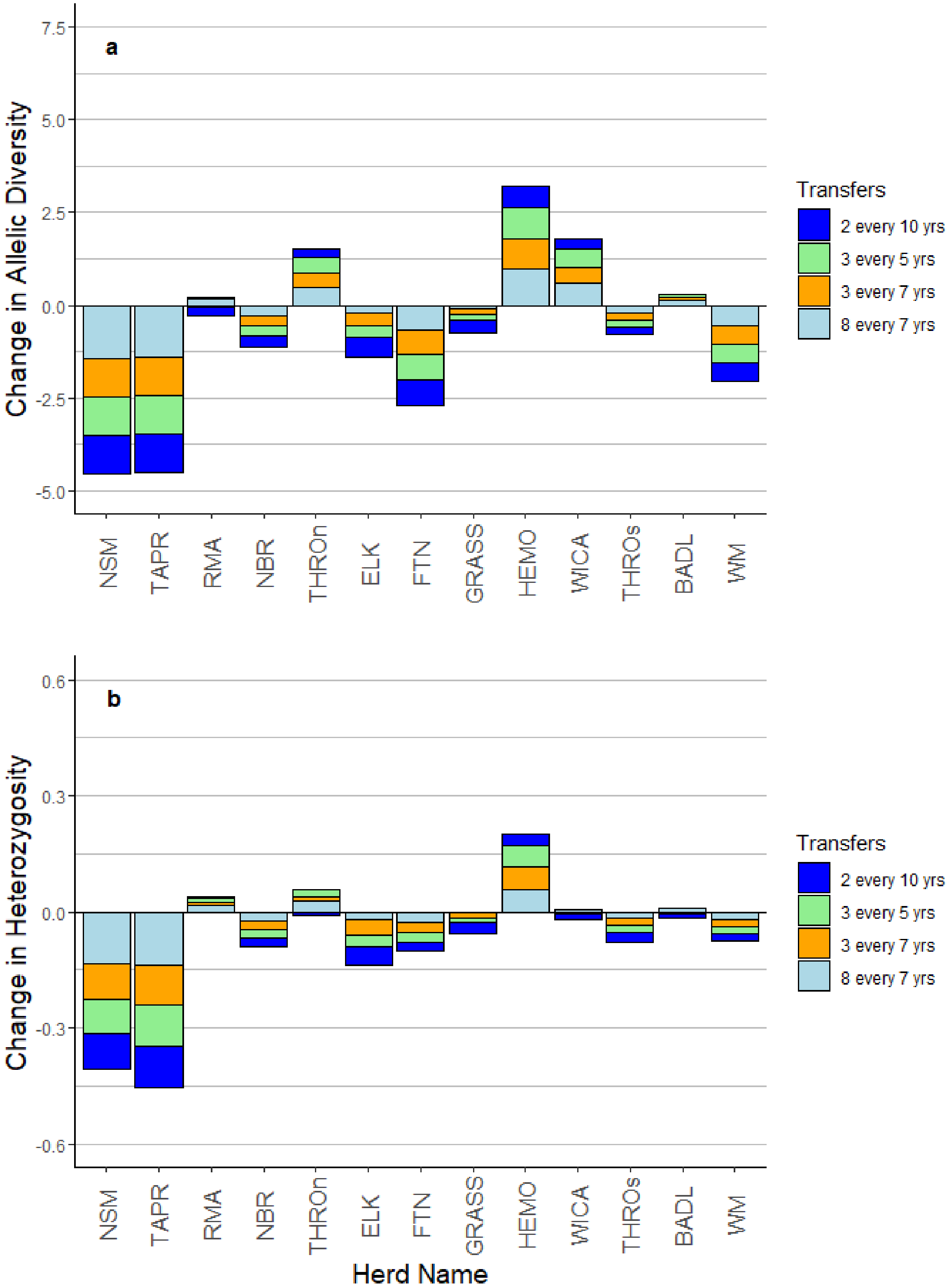

Figure 4.3.5. Stacked bar plots showing the change in a) allelic diversity and b) mean heterozygosity when the source herd for all translocations is the geographically closest herd within the same lineage as the recipient herd. Colored segments represent the total change in diversity (allelic diversity or heterozygosity) corresponding to each transfer scenario (see Table 4.3.3 for values). Herds are ordered by target abundance: left to right, smallest to largest.

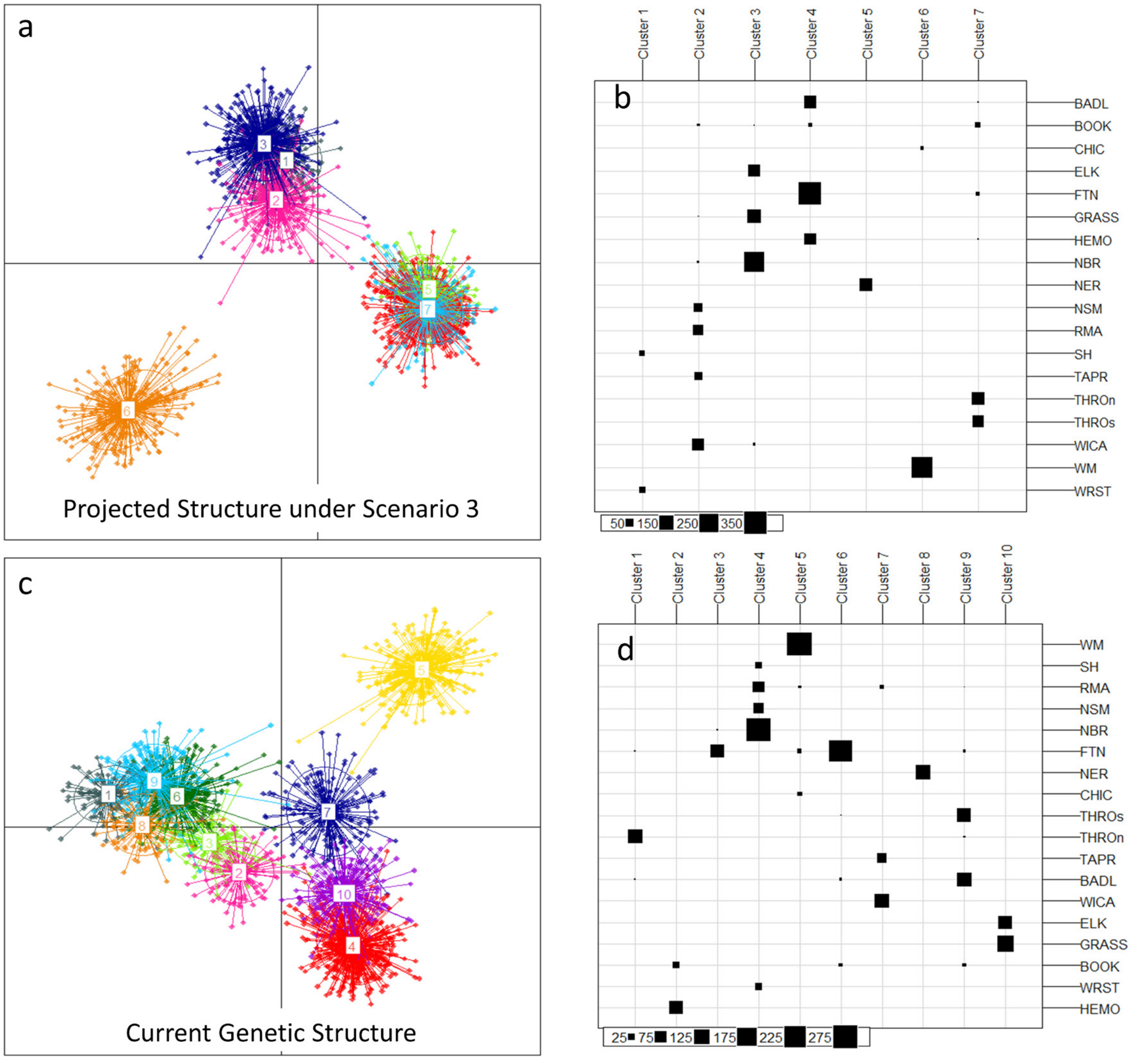

Figure 4.3.6. Plots a) and b) show DAPC results after 200 years of genetic augmentation management when 3 animals are moved every 5 years, and in which the source herd for all translocations is the geographically closest herd within the same lineage as the recipient herd. Symbols in a) represent individual bison samples, and circles with numbers represent the seven unique genetically differentiated clusters in the bison data and b) show the number of individual samples from each herd assigned to each genetic cluster. Plots c) and d) show the current genetic structure of herds today. Note: Colors and ID numbers associated with each cluster are assigned randomly by the DAPC algorithm, and thus are not comparable between plots a) and c).

20 translocations, depending on the scenario. With larger translocations (8 every 7 years) the effects of genetic swamping on allelic diversity can be detected earlier, even after six translocations for some scenarios.

Evaluating Genetic Redundancy across Herds

Our measure of genetic redundancy indicates that translocations did not reduce the impacts of herd extirpation on the allelic diversity of the metapopulation, but rather tended to slightly increase the mean number of alleles lost when a herd was extirpated (Table 4.3.6), though typically only by 0.5-3%. Regardless of the herd extirpated, all translocation source herd scenarios led to the loss of slightly more alleles than scenarios without translocations. This measure of redundancy is comparing the presence (and loss) of rare, low frequency alleles in each of the four herds. These rare alleles are more likely to be lost from any herd due to drift and less likely to be selected for translocation in any source herd scenario.

Another way to assess how translocations affect the genetic redundancy of the bison metapopulation is to compare changes to the genetic structure of the metapopulation with and without translocations (Figure 4.3.2 – 4.3.10). In partic-

Table 4.3.4. The absolute and proportional change in allelic diversity (measured as MNA) for each herd and for the entire DOI bison metapopulation ("META") after 200 years of translocations, given varying sizes and frequencies of translocations, when source herds are selected to be the genetically least related herd within the same genetic group as recipient herds.

Herd	Target N	Initial MNA	Final MNA (proportional change in MNA) when translocate 2 every 10 years	Final MNA (proportional change in MNA) when translocate 3 every 5 years	Final MNA (proportional change in MNA) when translocate 3 every 7 years	Final MNA (proportional change in MNA) when translocate 8 every 5 years	Final MNA (proportional change in MNA) when translocate 8 every 7 years
BADL	600	4.5	4.64 (0.031)	4.89 (0.087)	4.8 (0.067)	5.03 (0.118)	4.97 (0.104)
BOOK*+	550	4.83	4.66 (-0.035)	4.74 (-0.019)	4.71 (-0.025)	4.84 (0.002)	4.8 (-0.006)
CHIC*+	10	2.5	2.44 (-0.024)	2.46 (-0.016)	2.44 (-0.024)	2.44 (-0.024)	2.44 (-0.024)
ELK	400	4.79	4.69 (-0.021)	5.05 (0.054)	4.97 (0.038)	5.33 (0.113)	5.28 (0.102)
FTN	350	5.27	4.82 (-0.087)	4.91 (-0.07)	4.88 (-0.076)	4.97 (-0.059)	4.95 (-0.063)
GRASS	400	4.76	4.73 (-0.006)	5.11 (0.074)	5.02 (0.055)	5.38 (0.13)	5.33 (0.12)
HEMO	~400	3.73	4.42 (0.185)	4.77 (0.279)	4.7 (0.26)	4.92 (0.319)	4.88 (0.308)
NBR	285	5.01	5.09 (0.016)	5.28 (0.054)	5.24 (0.046)	5.4 (0.078)	5.37 (0.072)
NER+	500	3.75	3.06 (-0.184)	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)	3.06 (-0.184)
NSM	55	4.53	4.39 (-0.031)	4.79 (0.057)	4.57 (0.009)	5.07 (0.119)	4.86 (0.073)
RMA	200	4.95	4.95 (0)	5.19 (0.048)	5.14 (0.038)	5.32 (0.075)	5.28 (0.067)
SH+	15	3.51	1.28 (-0.635)	1.3 (-0.63)	1.27 (-0.638)	1.24 (-0.647)	1.27 (-0.638)
TAPR	100	4.6	4.4 (-0.043)	4.91 (0.067)	4.83 (0.048)	5.19 (0.126)	5.15 (0.117)
THROn	300	3.48	4.22 (0.213)	4.71 (0.353)	4.6 (0.322)	4.94 (0.42)	4.88 (0.402)
THROs	500	4.19	4.47 (0.067)	4.8(0.146)	4.72 (0.126)	4.99 (0.191)	4.94 (0.179)
WICA	350-500	4.69	4.98 (0.062)	5.25 (0.119)	5.14 (0.096)	5.48 (0.168)	5.4 (0.151)
WM	650	4.84	4.33 (-0.105)	4.32 (-0.107)	4.33 (-0.105)	4.3 (-0.112)	4.3 (-0.112)
WRST+	> 90	3.31	1.82 (-0.45)	1.79 (-0.459)	1.8 (-0.456)	1.8 (-0.456)	1.86 (-0.453)
META	–	6.87	6.33 (-0.079)	6.32 (-0.08)	6.32 (-0.08)	6.33 (-0.08)	6.33 (-0.079)

*Though not included in metapopulation management, BOOK and CHIC experience gene flow from the Northern Ute and WM herds, respectively, as part of their current management practices.

+Herd values in light text are not included in translocation management.

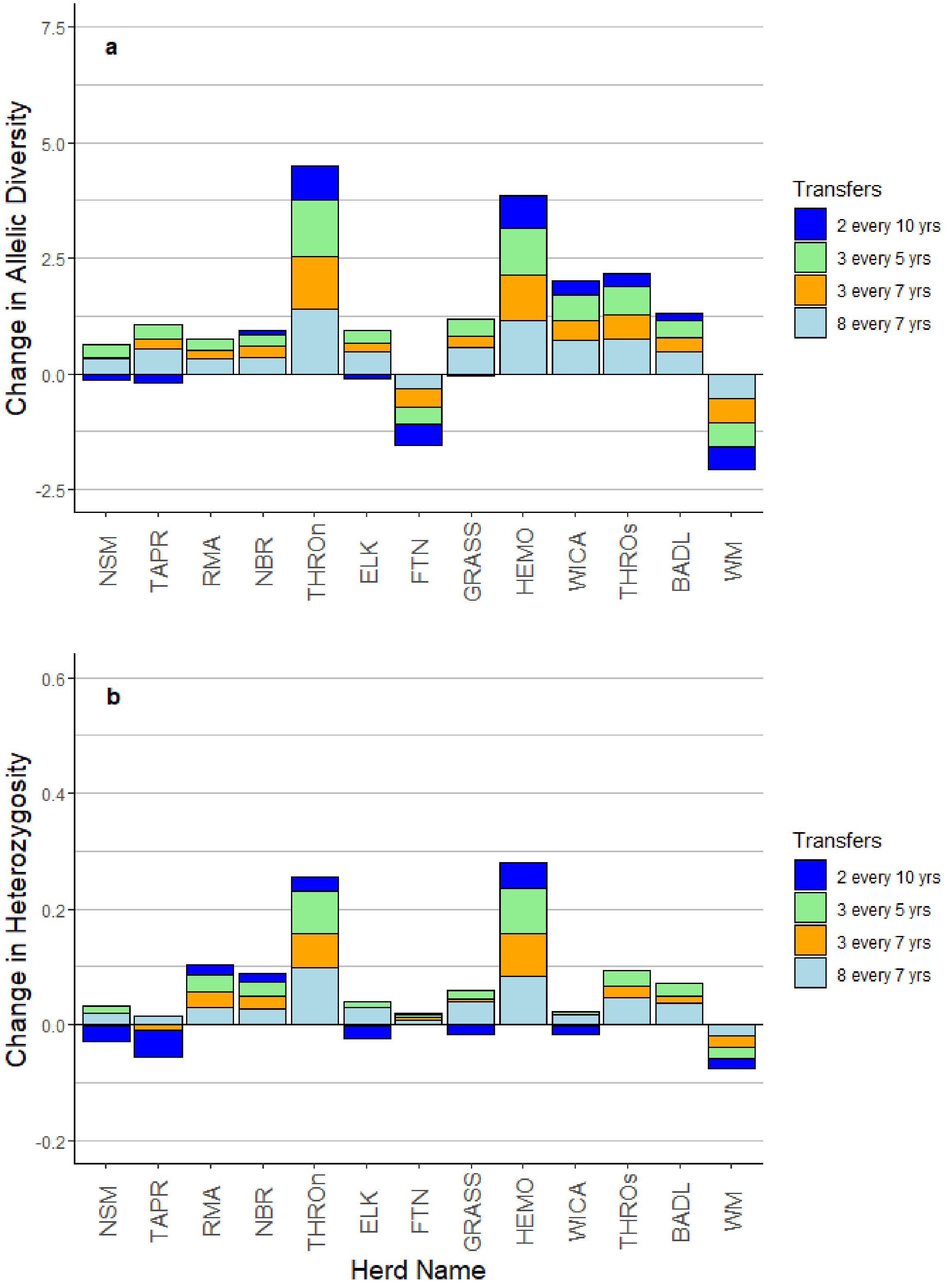

Figure 4.3.7. Stacked bar plots showing the change in a) allelic diversity and b) mean heterozygosity when the source herd for all translocations is the genetically least-related herd in the same lineage as the recipient herd. Colored segments represent the total change in diversity (allelic diversity or heterozygosity) corresponding to each transfer scenario (see Table 4.3.4 for values). Herds are ordered by target abundance: left to right, smallest to largest.

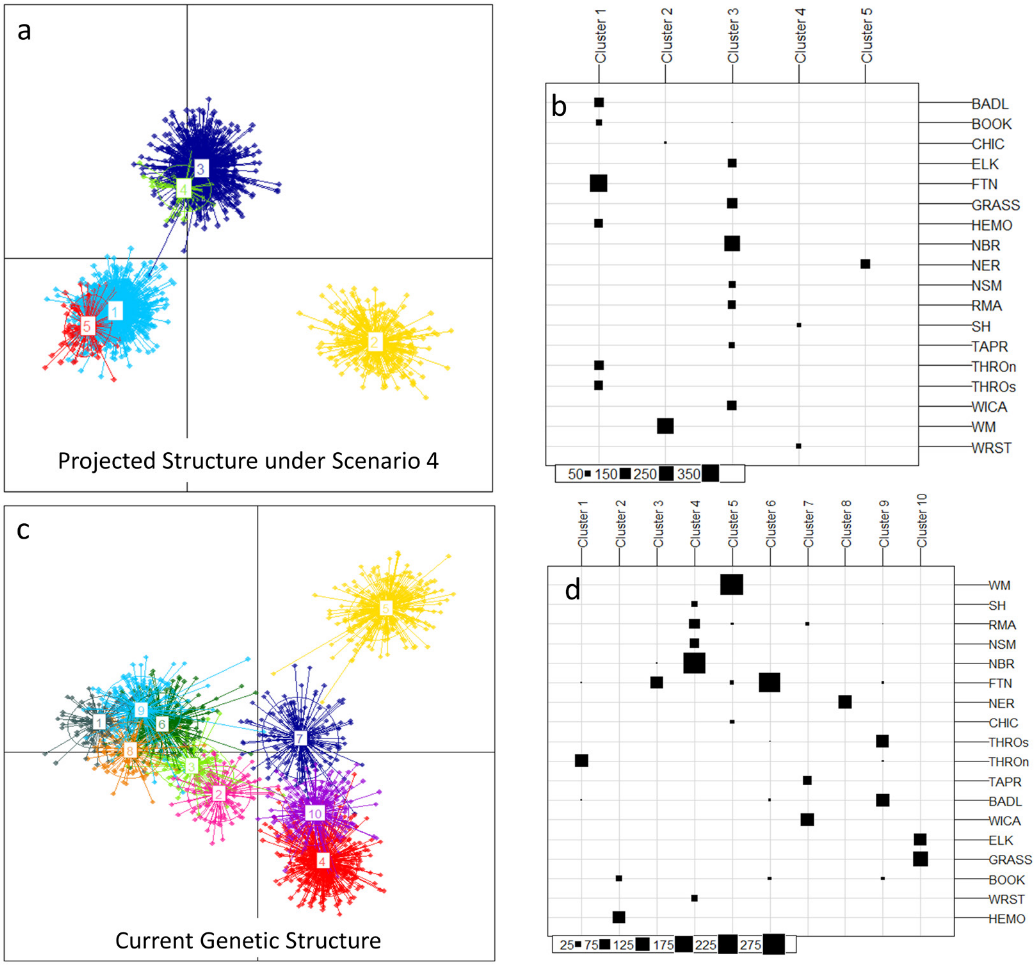

Figure 4.3.8. Plots a) and b) show DAPC results after 200 years of genetic augmentation management when 3 animals are moved every 5 years, and in which when the source herd for all translocations is the genetically least related herd in the same lineage as the recipient herd. Symbols in a) represent individual bison samples, and circles with numbers represent the five unique genetically differentiated clusters in the bison data and b) show the number of individual samples from each herd assigned to each genetic cluster. Plots c) and d) show the current genetic structure of herds today. Note: Colors and ID numbers associated with each cluster are assigned randomly by the DAPC algorithm, and thus are not comparable between plots a) and c).

ular, we see that translocations using Source Herd Scenario 1 or 2 (genetically least-related or alternating) result in almost all of the unique genetic clusters within the metapopulation being represented across all herds participating in translocations. After translocation under these two source herd scenarios, if WM were to be lost to a catastrophe, the unique genetic clusters found within WM (e.g., clusters 1,3,4,5,7 in Figure 4.3.2) would also be represented in almost all other herds participating in translocations. In contrast, scenarios in which translocations only occur between herds in our designated lineages (Figure 4.3.6, 4.3.8) resulted in genetic redundancy only within the herds within those lineages.

4.4 Discussion

Our results suggest there is considerable variability in the efficacy of translocation management strategies to increase or maintain genetic diversity within the 16 DOI and two Parks Canada bison herds sampled in this study. In particular, the criteria used to select potential source herds for translocations, and interactions between the identity of source herds and the size and initial levels of genetic diversity of recipient herds, strongly affected the efficacy of translocations to increase or maintain genetic diversity within herds. In general our results indicate that, with respect to the genetic diversity within herds, (1) scenarios in which the source of translocations varied from year to year resulted in considerably greater increases in genetic diversity than scenarios in which source herds used for translocations remained static over the years; (2) larger and less diverse herds required fewer and less frequent translocations to maintain or increase diversity; and

Table 4.3.5. The absolute and proportional change in allelic diversity (measured as MNA) for each herd and for the entire DOI bison metapopulation ("META") after 200 years of translocations, given varying sizes and frequencies of translocations, when source herds are those geographically closest to recipient herds.

Herd	Target N	Initial MNA	Final MNA (proportional change in MNA) when translocate 2 every 10 years	Final MNA (proportional change in MNA) when translocate 3 every 5 years	Final MNA (proportional change in MNA) when translocate 3 every 7 years	Final MNA (proportional change in MNA) when translocate 8 every 5 years	Final MNA (proportional change in MNA) when translocate 8 every 7 years
BADL	600	4.5	4.86 (0.08)	4.98 (0.107)	4.94 (0.098)	5.02 (0.116)	5.01 (0.113)
BOOK*+	550	4.83	4.62 (-0.043)	4.64 (-0.039)	4.64 (-0.039)	4.64 (-0.039)	4.64 (-0.039)
CHIC*+	10	2.5	2.61 (0.044)	2.76 (0.104)	2.73 (0.092)	2.73 (0.092)	2.75 (0.1)
ELK	400	4.79	4.26 (-0.111)	4.67 (-0.025)	4.57 (-0.046)	4.59 (-0.042)	4.79 (0)
FTN	350	5.27	4.71 (-0.108)	4.96 (-0.061)	4.9 (-0.07)	5.06 (-0.042)	5.06 (-0.04)
GRASS	400	4.76	4.58 (-0.038)	4.77 (-0.002)	4.74 (-0.004)	4.52 (-0.05)	4.71 (-0.011)
HEMO	~400	3.73	4.65 (0.247)	5.03 (0.349)	4.99 (0.338)	5.08 (0.362)	5.11 (0.37)
NBR	285	5.01	4.81 (-0.04)	5.03 (0.004)	4.99 (-0.004)	5.02 (0.002)	5.07 (0.012)
NER+	500	3.75	3.06 (-0.184)	3.07 (-0.181)	3.07 (-0.181)	3.07 (-0.181)	3.06 (-0.184)
NSM	55	4.53	3.95 (-0.128)	4.5 (-0.007)	4.32 (-0.048)	4.56 (0.007)	4.56 (0.007)
RMA	200†	4.95	4.75 (-0.042)	4.91 (-0.01)	4.87 (-0.018)	4.94 (-0.002)	4.98 (0.006)
SH+	15	3.51	1.26 (-0.64)	1.3 (-0.63)	1.26 (-0.641)	1.3 (-0.63)	1.27 (-0.638)
TAPR	100	4.6	4.03 (-0.126)	4.7 (0.022)	4.65 (0.011)	4.86 (0.057)	4.91 (0.067)
THROn	300	3.48	3.71 (0.066)	3.9 (0.121)	3.88 (0.115)	3.95 (0.135)	3.95 (0.135)
THROs	500	4.19	3.97 (-0.053)	4 (-0.045)	4 (-0.045)	4 (-0.045)	4 (-0.045)
WICA	350-500	4.69	4.85 (0.034)	4.96 (0.058)	4.93 (0.051)	5.01 (0.068)	4.99 (0.064)
WM	650	4.84	4.85 (0.002)	5.28 (0.091)	5.22 (0.079)	5.45 (0.126)	5.41 (0.118)
WRST+	> 90	3.31	1.81 (-0.453)	1.83 (-0.447)	1.82 (-0.45)	1.82 (-0.45)	1.75 (-0.471)
META	–	6.87	6.31 (-0.082)	6.27 (-0.087)	6.29 (-0.084)	6.18 (-0.1)	6.22 (-0.095)

*Though not included in metapopulation management, BOOK and CHIC experience gene flow from the Northern Ute and WM herds, respectively, as part of their current management practices.

+Herd values in light text are not included in translocation management.

(3) smaller herds typically required larger and more frequent transfers to maintain or increase genetic diversity.

Of the three source herd scenarios in which the source of translocations varied from year to year, using the least-related herd as a source for translocations (Scenario 1) resulted in the largest gains in heterozygosity and allelic diversity for almost all herds and translocation scenarios considered. However, the less information-intensive strategy of systematically rotating source herds every translocation (in order of least- to most-related; Scenario 2) led to almost identically large and consistent increases in the genetic diversity of recipient herds. In contrast, when translocations always came from the same source herd into the same recipient herd, year after year (Scenarios 3 & 5), most herds lost allelic diversity. The efficacy of such "static" translocation scenarios to increase allelic diversity depended on the size and initial diversity of the source herd, and how genetically divergent the source was from the recipient. For example, HEMO and THROn, herds with low initial levels of genetic diversity, were always projected to gain diversity from an input of new alleles under any scenario. While WICA and BADL, two diverse genetically divergent herds that were geographically close to one another, also gained diversity in these scenarios when only exchanging individuals with one another. Otherwise, most herds were predicted to lose allelic diversity under the two static scenarios unless larger numbers of individuals were moved.

Our results indicate that scenarios in which animals were only exchanged between genetically closely related herds (i.e., herds within the same lineage; Scenarios 3 & 4) maintained or increased genetic diversity within some herds, but it was not an effective strategy universally. In particular, the efficacy of this strategy depended on the number and diversity of the herds within each lineage. In the largest lineage

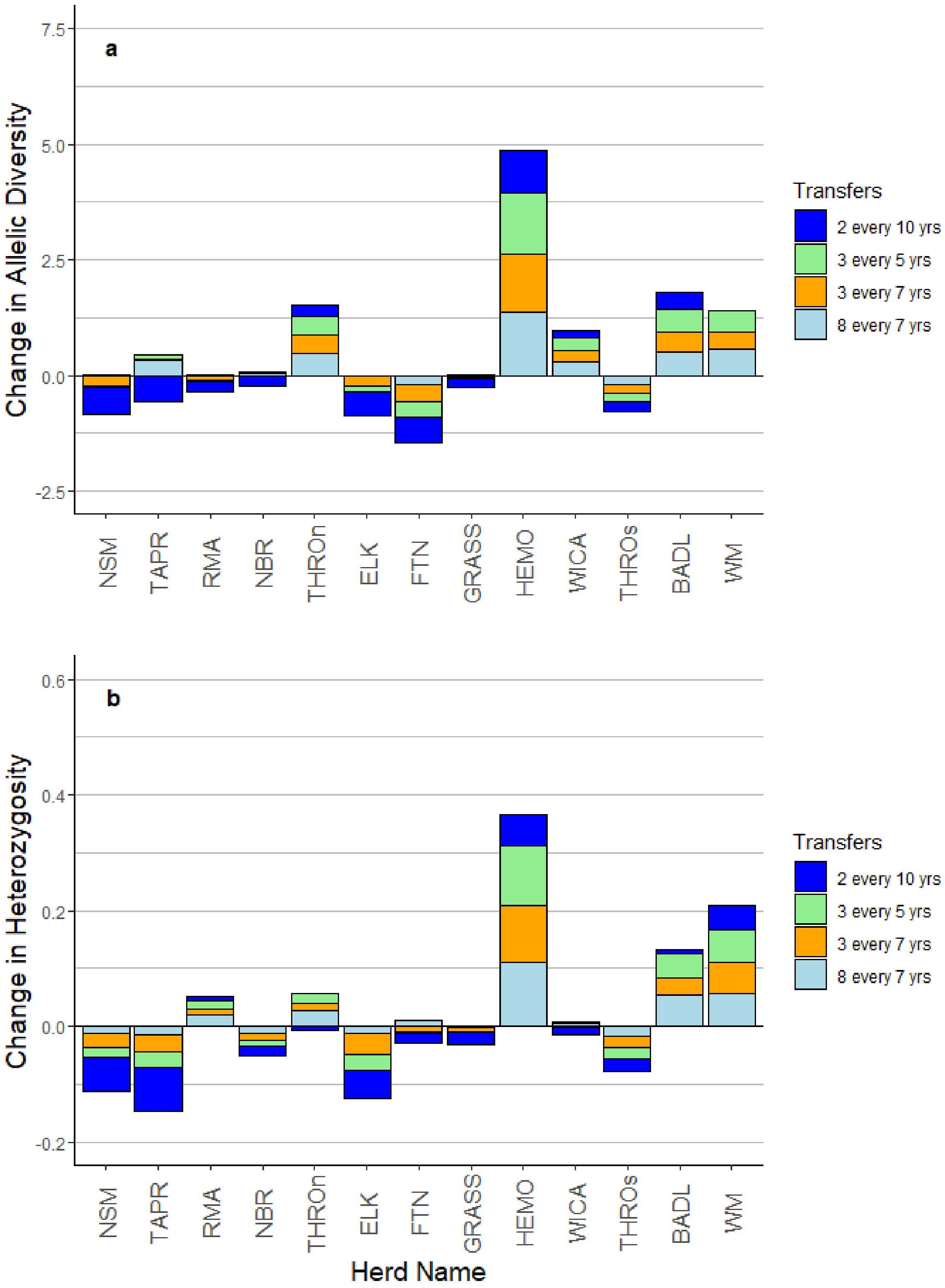

Figure 4.3.9. Stacked bar plots showing the change in a) allelic diversity and b) mean heterozygosity when the source herd for all translocations is the herd geographically closest to the recipient herd. Colored segments represent the total change in diversity (allelic diversity or heterozygosity) corresponding to each transfer scenario (see Table 4.3.2 for values). Herds are ordered by target abundance: left to right, smallest to largest.

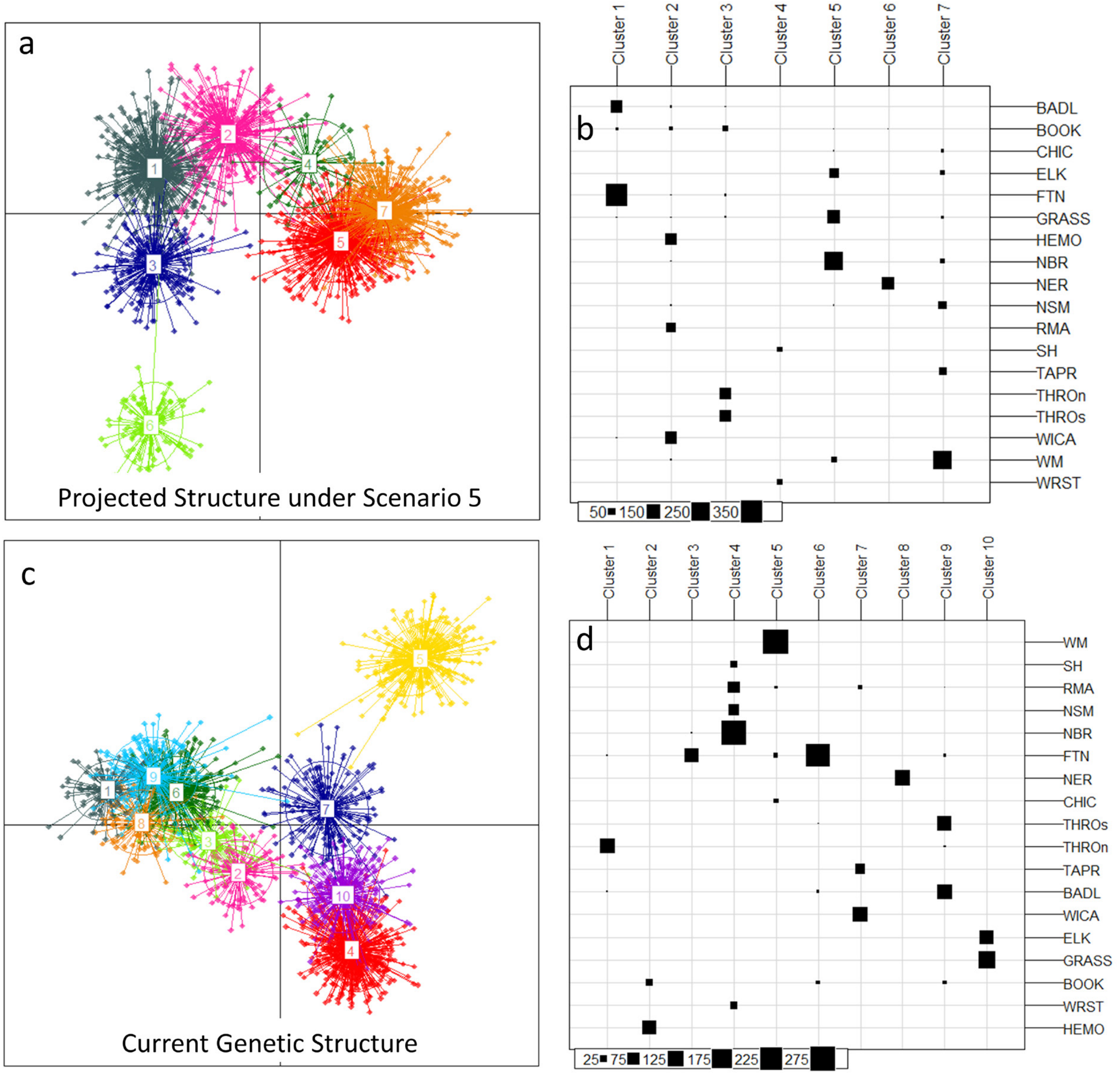

Figure 4.3.10. Plots a) and b) show DAPC results after 200 years of genetic augmentation management when 3 animals are moved every 5 years, and in which the source herd for all translocations is the herd geographically closest to the recipient herd. Symbols in a) represent individual bison samples, and circles with numbers represent the 5 unique genetically differentiated clusters in the bison data b) show the number of individual samples from each herd assigned to each genetic cluster. Plots c) and d) show the current genetic structure of herds today. Note: Colors and ID numbers associated with each cluster are assigned randomly by the DAPC algorithm, and thus are not comparable between plots a) and c).

(the NBR/WICA lineage), selecting source herds to be the least-related within the recipient's genetic lineage maintained or increased the allelic diversity of all herds within that lineage. In the smaller FTN lineage, herds with initially low levels of allelic diversity (THROn and HEMO) also increased. However, restricting translocations to only occur within each lineage was detrimental to the long-term genetic diversity of FTN, the most diverse herd in the FTN lineage, and to , which was isolated in these scenarios.

Gene flow in the form of translocations can only effectively move alleles and increase allelic diversity within source herds if translocated animals survive and successfully reproduce with animals in their new herd. In our models, we assumed that there were no fitness costs for translocated individuals, i.e., that translocated bison had the same mean survival and reproductive rates as other individuals in the recipient herd. This may not be the case. Results from management scenarios modeled, the numbers and frequencies of translo-

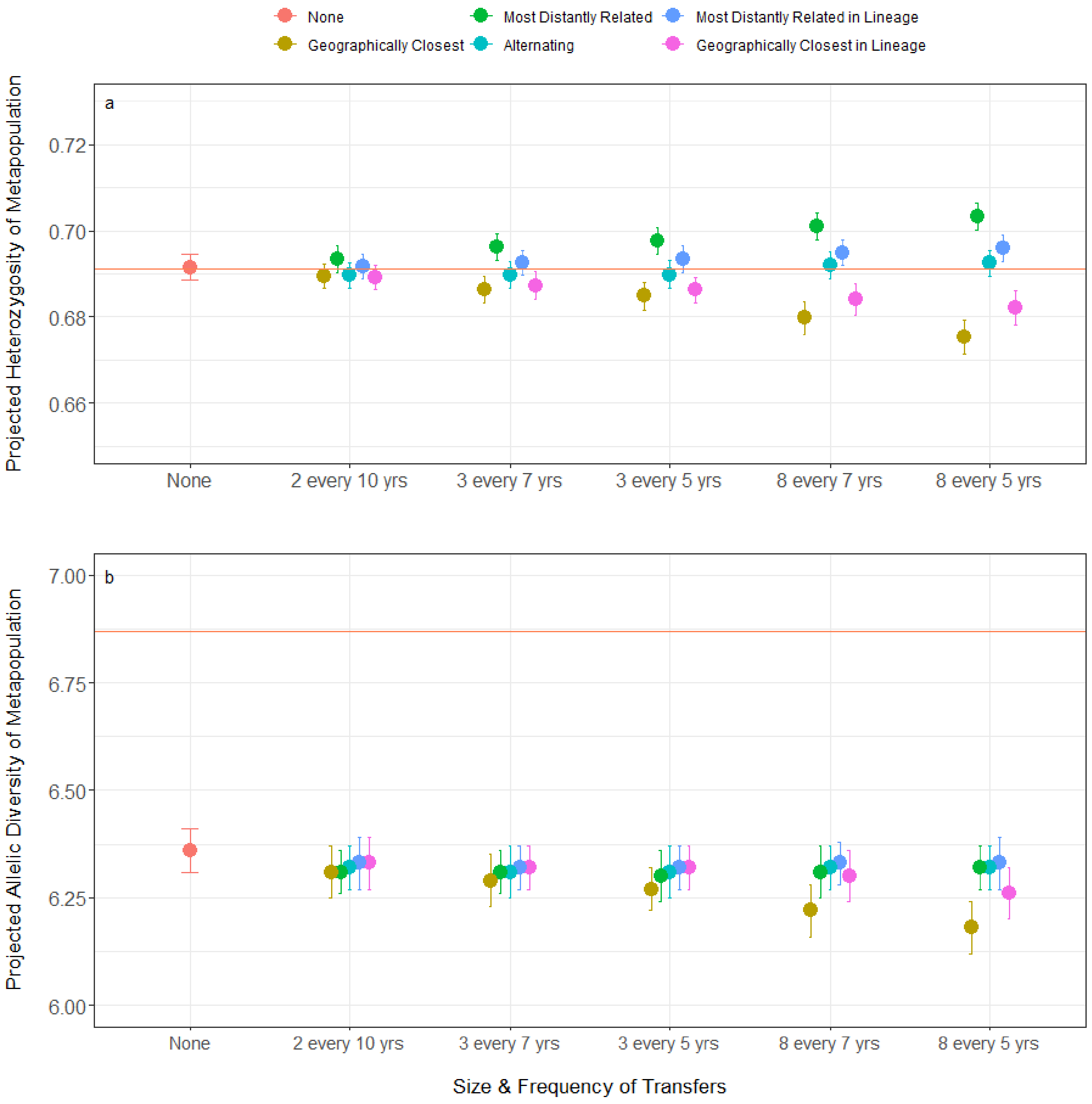

Figure 4.3.11. Projected change in a) heterozygosity and b) allelic diversity within the bison metapopulation under current management, and under each modeled translocation scenario. Point colors represent each source herd scenario, with orange points representing current management (no translocations), and the orange horizontal line in each plot represents current existing levels of each diversity measure within the bison metapopulation, as estimated by our genetic sampling and analyses in this study.

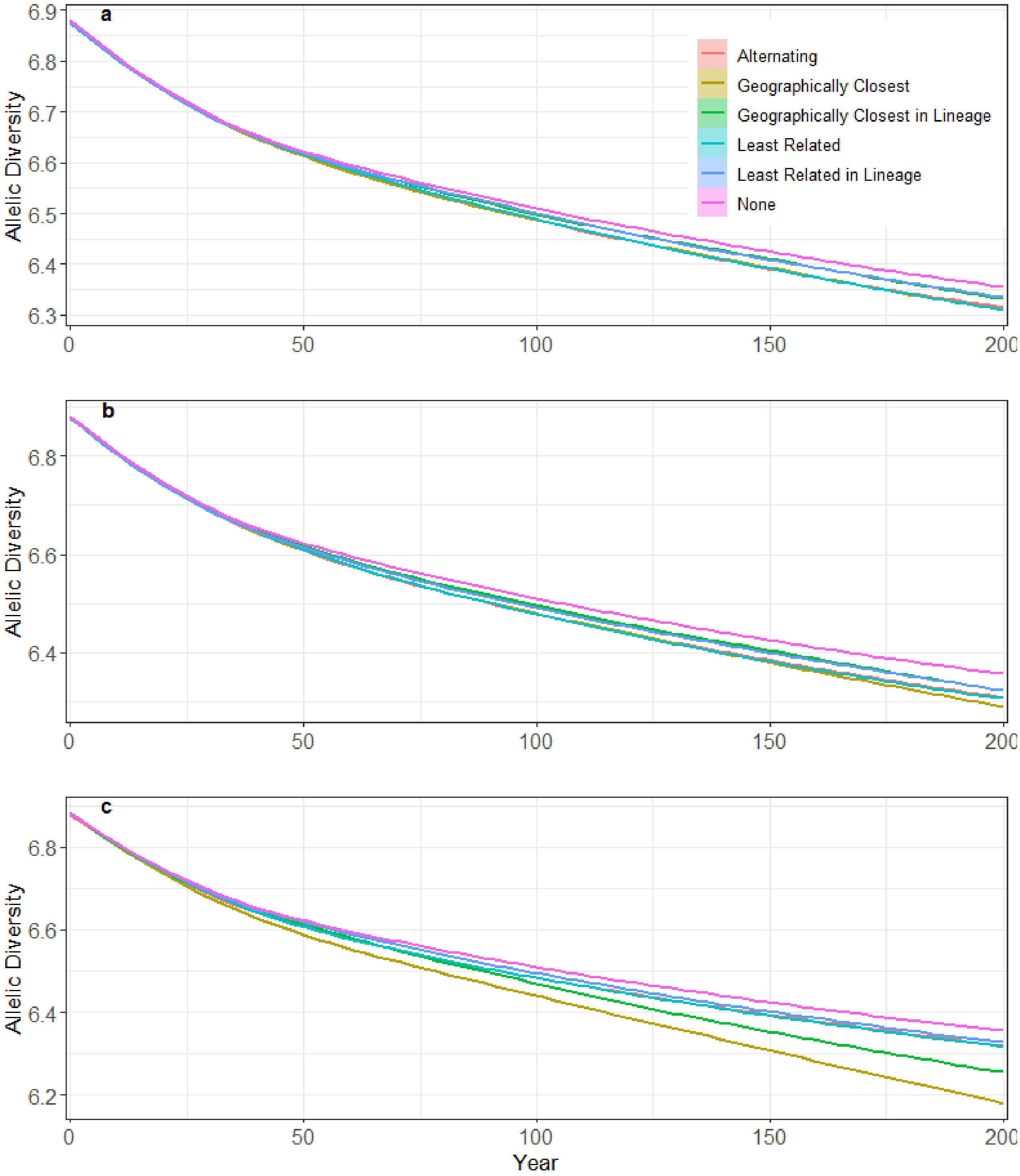

Figure 4.3.12. Allelic diversity of the entire modeled bison metapopulation as a function of time for each source herd scenario when a) 2 animals are translocated every 10 years; b) 3 animals are translocated every 7 years; and c) 8 animals are translocated every 5 years. Differences in the loss of allelic diversity between source herd scenarios were small and only became notable after approximately 50 years of translocations.

Table 4.3.6. Results of simulations testing how the extirpation of any one herd affects the allelic diversity of the metapopulation (measured as the mean # alleles/locus) under each source herd scenario when 3 animals are moved every 5 years. Herds were extirpated during year 30 of each simulation.

Extirpated Herd	**Source Herd Scenario None**	**Source Herd Scenario 1**	**Source Herd Scenario 2**	**Source Herd Scenario 3**	**Source Herd Scenario 4**	**Source Herd Scenario 5**
BADL	6.33	6.26	6.27	6.24	6.3	6.28
FTN	6.34	6.27	6.3	6.26	6.3	6.3
NBR	6.29	6.26	6.27	6.21	6.27	6.26
WM	6.24	6.23	6.22	6.17	6.19	6.18
None	6.36	6.3	6.31	6.32	6.32	6.27

cations that best increase genetic diversity within herds, are a function of our model assumptions. If translocated bison have lower probabilities of surviving or reproducing in their new herd, more animals may need to be moved to increase the probability of gene flow occurring. Likewise, if translocated bison have higher reproductive success than other individuals within their new recipient herd, fewer individuals could be moved or translocations could occur less frequently to achieve the same results. In FWS herds to date, translocations of animals aged 2 years and younger has resulted in consistent confirmed social integration and offspring production. while translocating adults has resulted in mixed success (L. Jones, unpublished data).

One of the management goals set forth by herd managers and agency leads to be assessed by our models was to determine if, and which, translocation scenarios increased genetic redundancy within the entire bison metapopulation. Assessing changes in genetic structure of the bison metapopulation at the end of simulations compared to the currently observed structure (Figures 4.3.2, 4.3.4, 4.3.6, 4.3.8, 4.3.10), indicated that this goal was best achieved when source herds were always the least-related to the recipient herd (Scenario 1) or when source herds were alternated at each translocation (Scenario 2). In particular, our results suggested that under these two source herd scenarios, after 200 years of translocations, individuals from each unique genetic cluster were distributed across almost all herds participating in translocations. In contrast, scenarios in which translocations only occurred between herds within specified genetic lineages resulted in redundancy only within those lineages but in strongly increased genetic differentiation between herds from different lineages.

Another metapopulation management goal identified by herd managers and agency leads was to identify management scenarios that maintained current levels of allelic diversity within the entire metapopulation. Our models indicate that the translocation scenarios modeled in this study alone cannot achieve this goal. Indeed, our models suggest that under some source herd scenarios the entire metapopulation lost allelic diversity faster with translocations between herds than without translocations. This is evidence of genetic swamping, an increased loss or dilution of rare alleles in recipient populations due to a large or constant influx of new alleles (Allendorf et al. 2013). This effect is strongest when eight or more animals are used in translocations, and it is weakest when two to three animals are used in translocations. Criteria used to select source herds also affected the degree to which swamping occurs: the effect of swamping decreases when the source herd alternates every translocation or is genetically related to the recipient herd (i.e., when translocations only occur within lineages).

At the metapopulation level, alleles can only be rearranged through the movement and reproduction of animals or extinguished through the process of genetic drift or inappropriate removal methods. Without translocations, the loss of rare or low frequency alleles occurs within each herd due to genetic drift, often resulting in the loss of those alleles from the entire modeled bison population. In our translocation management models, alleles are still being lost within each herd due to drift but are being replaced with new alleles brought in by each translocated individual. In some cases, the new alleles arriving through translocation may be the same as those lost, effectively replacing the lost alleles, or they may be novel alleles that had not previously occurred in the recipient herd. If the alleles lost due to drift were unique to the recipient herd, and if they are lost to drift, they are then permanently lost from the metapopulation and cannot be replaced through translocations. Overall, the decrease in allelic diversity at the metapopulation level appears to be due to a decrease in the frequency of four to five rare alleles within some herds, with translocations increasing the probability of these alleles being lost due to drift.

The only way to maintain rare alleles unique to particular herds is to mitigate the rate of genetic drift within individual populations. Reducing rates of diversity loss due to genetic drift can be achieved by increasing the effective population size of each herd. Consequently, opportunities to increase herd size should be explored as the most effective way to conserve diversity in DOI bison. Maintaining an even sex ratio within herds, using management strategies that target young animals for removal, or using mean kinship to select animals for removal can also help mitigate diversity loss to some extent.

The apparent loss of allelic diversity at the metapopulation level in our models may also be exacerbated by the exclusion of the Yellowstone herd (YELL). YELL is a large (>3000 individuals), relatively genetically diverse herd (Halbert and Derr 2008) that likely loses allelic diversity slowly. Some of the rare alleles lost in our smaller herds may be maintained in YELL and may be able to be replaced through translocations with YELL. Although YELL did not participate in this study, satellite herds established from brucellosis-free Yellowstone bison on the Fort Peck Indian Reservation, the Soapstone Prairie Natural Area in Colorado, and Turner Enterprise's Green Ranch in Montana could be used for future transfers.

Although this project did not include cattle introgression as a factor in any of the metapopulation management translocation scenarios due to the lack of a sensitive individual animal test at the time of analysis, most managers wish to avoid either introducing novel segments of cattle introgression or increasing the amount of existing introgression in a recipient herd. Given the differing missions of each agency and unit, further consideration of health and introgression issues may be required before translocations can take place. New, more sensitive technologies to detect cattle introgression are expected to become available in the future, allowing for even more refinement of metapopulation management to benefit conservation of DOI bison.

Our results suggest that if a uniform strategy is to be adopted for all herds in the bison metapopulation, then a strategy of smaller, less frequent translocations (e.g., 2 every 10 years, 3 every 7 years) using either least-related herds as source populations or alternating source herds at every translocation would be adequate for increasing genetic diversity within most individual herds while minimizing the loss of diversity at the metapopulation level. However, the variability in success of alternate translocation scenarios with respect to the size and initial level of genetic diversity of recipient herds also suggest that exploring a more tailored, herd-specific translocation strategy may be most beneficial. In particular, smaller herds benefit from more frequent translocations, larger herds require fewer and less frequent translocations, and herds with low initial levels of diversity are likely to benefit from any translocation. Alternate translocation scenarios not included in this study may prove to be superior at maximizing benefit to both individual herds and the metapopulation, and they could also be explored to reduce the potential for genetic swamping identified at the 50 to100-year mark in this study.

Given the importance of maintaining or increasing the genetic diversity of individual herds – staving off inbreeding effects and ensuring evolutionary adaptability (Ralls et al. 2018; Willi and Hoffman 2009) – it is clear that re-establishing some level of gene flow is essential to the long-term conservation of bison. Long-term monitoring of genetic diversity, both at the individual herd level and across the metapopulation, will be essential to fine tune the implementation of an appropriate metapopulation management approach to maximize benefits to plains bison.

5. Management Implications and Recommendations

DOI agencies have understood, conceptually, the potential benefits of a coordinated metapopulation strategy for some time (DOI 2014; Dratch and Gogan 2010; NPS 2006). Results of this project build on previous work to rigorously and quantitatively describe risks of an isolated herd management strategy and expected benefits of a metapopulation management strategy. Based on our results, we recommend that the DOI Bison Working Group, as chartered under the DOI Bison Conservation Initiative in 2008, initiate and oversee a technical task force to develop a comprehensive metapopulation management strategy for DOI agencies. This comprehensive management strategy must include explicit consideration of genetics, wildlife health, cattle introgression, local unit management issues, partner/stakeholder engagement, and data management.

Implementation of a metapopulation strategy will require active engagement at multiple management levels within each participating agency. Success will depend on unit-level engagement operating under a framework of support from the DOI Bison Working Group. Implementing this strategy will require new and sustained levels of coordination and communication, requiring a paradigm shift within DOI agencies and other jurisdictions such as states, tribes, etc. Traditional management models at the individual herd or even bureau level should be revised to encompass broad subspecies conservation goals to support continental conservation across multiple jurisdictions while respecting the complexity and variation in local management purpose and capacity. Implementing such a complex strategy is a challenging task, yet completion of this project represents significant progress toward the required paradigm shift. The project itself was informed – through multiple workshops – by bison managers and biologists who already recognize and advocate for increased coordination in bison conservation. The FWS already has an exceptionally strong technical backdrop to its refuge system herd management decisions, capture protocols, and selection of animals for removal. The FWS has already implemented genetic augmentation practices among refuge-system herds that contribute to the high levels of diversity found in this study. The NPS Midwest Region (DOI Unified Region 5) has active coordination across its five parks with bison. Both agencies have positive and long-standing partnerships with partner conservation organizations, as well as with both individual tribes and intertribal organizations for distribution of live bison to Native American herds and communities. The DOI Bison Working Group has engaged and committed representatives from the NPS, the FWS, the BLM, the USGS, and the BIA. In short, bison managers and agency leads have organically recognized and have already begun to act on the need for improved coordination and bison conservation.

One particularly important outcome of this project is that its completion required assembly of a common panel of neutral genetic markers across virtually all FWS and NPS herds. Beyond its importance to the analyses presented here, creation of this dataset represents a major accomplishment and substantial progress toward implementing a cohesive and well-coordinated DOI bison conservation strategy.

There is great opportunity – and even enthusiasm at multiple organizational levels to take on the task of developing and implementing a comprehensive DOI bison metapopulation strategy. Substantial progress in conservation is typically driven by either a groundswell from local levels or occasionally by top-down direction that presents a framework for an organizational shift in priorities. Convergence of both unit-level managers and agency science leadership upon a shared vision of what is needed to advance conservation provides unique potential for success. The next several years offer unprecedented opportunity to capitalize on active engagement and partnerships to make meaningful, impactful, and durable gains in the conservation of bison in North America.

General Principles for a DOI Metapopulation Strategy

Genetics

Initial Approaches to Size and Frequency of Movement

Our models identify an essential need to restore gene flow among DOI bison units, especially as genetic diversity loss is detectable in some herds over previous studies. However, a uniform strategy for all herds is not necessary, and customized translocation strategies should be considered. For most herds, conservation of diversity can be achieved through periodic translocation of smaller numbers of animals (2 or 3 animals every 5 to 10 years), and these kinds of translocations are also more logistically achievable. Small herds will need more frequent augmentation while larger and/or more diverse herds may need less frequent actions.

Short-term implementation strategies could include continuation of the FWS diversity conservation and translocation model, with additional translocations into the lowest diversity herds, including HEMO and THROn. WRST also has low levels of diversity, such that intervention may be required to prevent genetic diversity loss if the viability of this herd is a management priority, given that it is outside the range of plains bison. The GRTE/NER bison herd also has low levels of genetic diversity, even though it is thought to have very low level of gene flow from YELL as previously documented with radio telemetry. Introducing new animals into this herd may help offset the impacts of low levels of genetic diversity and of a hunting management strategy that is designed to restrict the size of this herd.

Consideration of Cattle Introgression

Our results reaffirm earlier positions by NPS and FWS (Dratch and Gogan 2010) that levels of cattle introgression in DOI herds are generally quite low and of less concern to the conservation of DOI bison than is maintenance of bison genetic diversity. Consistent with recommendations of multiple authors (Dratch and Gogan 2010; Gates et al. 2010; Halbert and Derr 2007; Hedrick 2009), managers must be sure to not increase introgression in any individual herd. Given the differing missions of each agency and unit, further consideration of health and introgression issues may be required before translocations can take place. Future technological advances may ultimately allow us to more precisely refine this recommendation, potentially incorporating introgression into the overall metapopulation management strategy.

Consideration of Individual Herd Lineage

Translocating individuals only among closely related herds (e.g., within lineages) to maintain current levels of genetic differentiation between herds is not generally advised. Some herds lost diversity in this modeled scenario. This strategy could be used for selecting source herds for translocations into some large, genetically diverse herds (WICA, BADL, NBR) as a first implementation step. However, given the increasingly rapid pace of environmental change, the driving paradigm of conservation genetics has shifted increasingly to protect the adaptive potential of species and populations to future change. This means prioritizing the overall adaptive genetic diversity of the plains bison over maintaining the isolation and current level of genetic differentiation of DOI herds (Weeks et al. 2011; White and Wallen 2012).

The Value of a Common DOI Panel of Genetic Markers

DOI agencies (and state partners managing herds on DOI-administered lands) previously identified and adopted a common panel of genetic markers used for evaluating herds and their potential for being a source, destination, or both for bison to/from other DOI herds (Dratch and Gogan 2010). Any future expansion of, or changes to, this standard panel should be considered for all DOI herds to maintain consistency. New markers should be evaluated in the peer-reviewed literature before being added to DOI bison management protocols.

Data Management

Effective data management will be fundamental to initial implementation, periodic assessment, and long-term success of a DOI metapopulation program. While each DOI agency currently has its own data management system, the specific content and structure of a data management system to support metapopulation management of DOI bison will be driven by (1) the information need and application, and (2) the nature of the data themselves.

Consistent with existing DOI IT requirements, data files for individual herds should be managed to current best practices for security/access, backup, and appropriate accessibility. More than that, any metapopulation strategy should identify a DOI data manager/database developer to assist with the conceptual development of required data systems prior to building and populating the system. This data management process would require a deliberative scoping effort to specify data application, required outputs/deliverables, workflow processes to produce each deliverable, the form of input data files required to supply a given workflow, and the process for getting raw data of different forms (spreadsheets, lab files, documents, photos, etc.) into the front end of the data management system. Development of such a system however, should start with defining information dissemination (specifying the information required for management, decision-making, and analysis), and working through development of the information/data repository, to the standards required for data acceptance into the database/repository, and ultimately to processes for the front end of data acquisition (Johnson and Moynahan 2008).

Future coordinated data management activities will need to assess what level of standards and quality control should be required – or only recommended – of parks and refuges participating as members of a DOI-wide metapopulation. Certain standards for collection, management, distribution, and analysis of genetics data, for example, will likely need to be rigorously prescribed and closely managed. Other data (e.g., unit-level physiological or demographic data from bison capture and handling events) may be appropriate for local or regional management.

All FWS units and a few NPS units are already using a single field data collection system. DOI level support of unit-led specification of a flexible data collection and management system could be accomplished prior to, and later fully integrated with, a more comprehensive metapopulation data management system.

Herd Size and Establishing New Herds

Opportunities to increase the size of individual herds and to establish new herds should be carefully considered, as an increase in the number of DOI bison can have a significant positive impact on conservation of genetic diversity. Opportunities to increase the size of existing herds are limited, but these opportunities should be thoroughly explored. However, any efforts to increase in bison herd sizes must ensure that healthy landscapes that support the character of wild bison are maintained and that the resource needs of other species are met.

New herds should be established with at least 15 founders, with subsequent augmentation in subsequent years. Until more sensitive introgression detection methods become available, establishing new satellite herds to replicate DOI herds that do not currently have satellites large enough to sustain diversity (such as WM) should be a high priority. New herd management should be balanced to maintain wild character and minimize diversity loss, depending on the specific establishment goals for the herd. It is important to consider that smaller, hunted herds may have higher rates of diversity loss than herds managed for diversity conservation and may require more frequent augmentation.

Key Research Needs

We envision several important lines of research and monitoring that will help inform whether or not a given metapopulation strategy is meeting DOI bison conservation goals. In particular, we encourage expansion of existing unit-level efforts to evaluate the social, behavioral, and demographic drivers affecting functional incorporation of moved bison into a recipient herd. While some DOI herd managers have observed little to no apparent functional incorporation of new genetics into existing herds through translocations, others have demonstrated high levels of success. One example of such research is the controlled study of bison translocated from BADL to THRO in which managers will quantitatively evaluate the degree of genetic incorporation of translocated bison. This type of research will be critical to inform and adapt a metapopulation strategy by increasing our understanding of bison behavioral ecology.

In addition to being identified as a priority in the Initiative, we echo the concerns of Dratch and Gogan (2010), noting that relatively little progress has been made in developing sensitive genetic analytical techniques to detect cattle introgression in individual bison.

Within the confines of recommendations to avoid exacerbating existing levels of cattle introgression in DOI herds, along with a recipient herd's genetic augmentation needs, most DOI herds could be eligible as source and/or recipient herds. These needs would be evaluated on a case-by-case basis using the molecular genetic techniques described here and as outlined in the structure of a DOI metapopulation strategy.

Wildlife Health

We note that the DOI Bison Working Group is, at the time of writing, concurrently working to finalize a bison health report. This report will describe considerations and issues for management of healthy bison populations, the overall approaches of both the NPS and the FWS to management of bison health, and recommendations for coordination among DOI management units to better support DOI bison health. This forthcoming report, to be published in the NPS Natural Resource Report series, will be the primary source for information regarding bison health management for DOI agencies.

Our work included modeled effects of a 1-year, generic catastrophic event that reduced the probability of survival by 50% but did not affect reproduction. In reality, such an event could, but not necessarily, manifest as a particular type of disease outbreak. While modeling a generic catastrophic event allowed us to incorporate one potential type of population level impact, wildlife disease often presents in complex ways that have multiple-level impacts on a population, including sub-lethal effects on disease resistance, reproductive success, and behavior. Presence of disease has the potential to significantly limit implementation of a metapopulation management strategy, as seen currently in herds with brucellosis. Our recommendations for consideration of wildlife health in the development of a metapopulation strategy are therefore similarly broad.

DOI agencies have long demonstrated a commitment to supporting wildlife and ecological health and to responding to emerging threats. Both the NPS and the FWS have established wildlife health programs with a wide range of expertise in ungulate health, including bison. Both programs include licensed veterinarians and both use a variety of partnerships and agreements to obtain specialized laboratory and diagnostic services. Both programs have a strong history of providing the specific expertise and personnel required to address wildlife health issues in bison. This existing commitment to actively supporting all wildlife health (including that of DOI-managed bison herds) is a clear indication that DOI agencies are already well prepared to incorporate wildlife health considerations into the development of a metapopulation strategy. However, the DOI may find that current expertise and resources are not fully adequate for developing a comprehensive strategy for a bison health strategy across constituent herds.

We recommend that DOI bureaus continue – and further develop – institutional framing and communication of disease issues as one part of a broader programmatic goal of supporting holistic wildlife health. Biologists and managers should continue to consider these issues at multiple scales in support of a DOI-wide conservation strategy. A DOI strategy must inherently include the requirements of testing, documentation, and coordination with state animal health agencies, in support of interstate transport of live bison, and it should also coordinate to deliver appropriate surveillance monitoring for specific pathogens that threaten bison health. Individual agencies, and even units within agencies (i.e., individual parks or refuges), may require different levels of resolution or breadth of surveillance depending on the surrounding health landscape, disease history of each herd, and capabilities of each bureau unit. Enabling legislation, policy, or staffing for each agency, indeed for individual parks and refuges, may allow or preclude certain activities, such as access to animals for necropsies, disposal of animals, administration of antibiotics or vaccinations, etc. A comprehensive strategy must address both common standards as well as local flexibility.

Local Management Issues

A metapopulation strategy must incorporate staffing levels, training, and technical capacity at parks and refuges. Managers of parks and refuges customarily enjoy a great deal of local autonomy in decision-making and priority-setting, within the bounds of enabling legislation and in coordination with regional and national guidance. This autonomy enables a great deal of flexibility and helps keep parks and refuges nimble and able to respond to local emerging issues. Through our multiple workshops with many bison managers of parks and refuges, we came to appreciate the importance of balance in maintaining local management flexibility while simultaneously pursuing a coordinated national strategy. In the case of bison conservation, it is our sense that bison managers are largely – perhaps completely – in agreement that managing in isolation is not a viable nor desirable strategy for the future, and FWS managers have already begun to implement genetic conservation management efforts to mitigate genetic diversity loss. We see no inherent conflict between managers' interest in preserving customary flexibility and their ability to actively partner in a coordinated DOI metapopulation strategy.

Movement toward a coordinated DOI bison metapopulation strategy must be made in consultation with local managers, regional managers, agency leadership, and the DOI Bison Working Group. Early communication regarding the scope and logistics of occasional bison movement will help ensure that all levels and all units are aware of the proposed translocation, allowing each to tailor the outreach and educational opportunity to capture the benefits of the coordinated management action. Implementation of a DOI metapopulation strategy could offer considerable management flexibility for bison managers. Having full representation of herd genetics at multiple sites may allow a unit to alter herd size in order to reduce grazing pressure, respond to fire or drought, or implement a study to emulate presumed historic range of interannual variation in bison use of a particular area. Similarly, one unit may be able to accept a temporary substantial increase in herd size to impose grazing pressure variation and also accommodate another unit that experienced a wildfire that burned a large portion of available forage. This type of dynamic management could preserve bison genetic variation and also allow for temporal variation in landscape use that is not typically practical.

Criteria for Assessing Metapopulation Partners

Although implementation and evaluation of a coordinated DOI bison metapopulation management strategy is the first priority, working with partners may provide additional opportunities not available within the DOI. Distinguishing between a conservation partner, where DOI bison may contribute to conservation partner goals, and a DOI bison metapopulation partner, where the goals of both DOI bison and the conservation partner are both met, will be essential. Previous work identified high levels of cattle introgression in many private herds, and bison managed under traditional production models have often been selected to remove wild character (Gates et al. 2010; Halbert and Derr 2007). Subsequently, augmenting DOI bison herds with animals from outside sources should be discouraged until sensitive new technologies have become available to confidently detect cattle introgression in individual animals.

Careful consideration of a partner's commitment to contribute to the conservation goals for DOI bison, including genetic diversity and integrity, along with maintaining wild character, is essential. However, genetically diverse DOI bison can meet the ecological, genetic, and cultural conservation goals of partners, and we encourage exploration of mutually beneficial relationships with a wide variety of willing partners. We especially encourage exploring relationships with partners that specifically seek to establish satellite herds of DOI bison in support of DOI bison conservation goals.

Partner and Stakeholder Engagement

The world of bison conservation in North America is broad, complex, and of great public interest. DOI agencies recognize that active, positive partnerships are developed by fostering trust and open communication. Although this study was conducted within the bounds of DOI jurisdiction, we had considerable engagement from State, Canadian, Tribal, and NGO partners.

Given its scope and objectives, this project has been necessarily technical and inward-looking in its approach. We recommend that DOI agencies collaborate on a public communication plan to brief partners and the general public on results and incremental progress toward development of a metapopulation strategy. Each agency has professional communication staff, as does DOI itself. Those communication professionals should be engaged as the DOI Bison Working Group takes next steps on development of a metapopulation strategy.

More specifically, a successful metapopulation strategy must communicate early and often with state partners, especially state agencies involved in the cooperative management of bison on DOI lands. Each state has a unique set of ecological, political, and social issues related to bison management. Some recognize bison as wildlife, others categorize bison as livestock; some states would have DOI agencies coordinate directly with their wildlife management agencies, others would have agencies coordinate with their departments of livestock.

Presently, both the NPS and the FWS partner extensively with conservation partners, as well as with both individual Tribes and the InterTribal Buffalo Council (ITBC) to distribute live bison from DOI units to Native American Tribes. ITBC is a chartered and federally recognized tribal organization that is an exceptionally effective partner in this regard. The FWS has developed a 'bison donation protocol' that guides its fulfillment of bison donation requests as an equitable and transparent mechanism to prioritize the limited numbers of bison that exceed ecological carrying capacity of refuges to the highest conservation purposes. The NPS anticipates preparing a similar guidance for its parks and regions to ensure a thoughtful prioritization of the diverse interests of multiple conservation partners.

Specifically, we recommend consideration of the Henry Mountain herd, managed by the Utah Division of Wildlife Resources (UTDWR) on BLM-administered lands, as a full partner to a DOI metapopulation program. The Henry Mountains herd is substantial in size and free-ranging, was initially founded with animals from the Yellowstone herd, and currently has low levels of heterozygosity due to maintained isolation. It thus is in need of genetic exchange and may be a disease-free source of YELL genetics. In addition, UTDWR has effective partnerships with the Uintah and Ouray Reservation.

We recommend that the DOI Bison Working Group continue discussions to describe the role and types of non-federal herds that could be identified as conservation partners to a DOI metapopulation strategy. The Bison Working Group and DOI agencies recognize that bison conservation within the DOI – while fundamental – is one part of a larger conservation landscape. States, Tribes, NGOs, and collaboratives of multiple partners are essential to bison conservation in their own right, but also as partners to DOI as it looks to preserve bison diversity, maintain wild character, broadly ensure wildlife health, and support the restoration of the ecological role of bison at the continental scale. The DOI can have a major role in supporting and co-leading development of a continental bison conservation strategy, in partnership with States, Tribes, NGOs, and the governments of Canada and Mexico.

The Trilateral Committee for Wildlife and Ecosystem Conservation and Management ("Trilateral") offers an appropriate venue for furthering partnership with Canada and Mexico on bison conservation in particular, and grassland ecosystem conservation in general. At the past two Trilateral meetings a bison discussion was convened at the conservation table. We encourage DOI agencies to continue to engage with Trilateral partners through the Trilateral annual meetings.

6. Conclusions

This report is the culmination of a decade of effort by a broad coalition of Department of the Interior agency administrators, natural resource managers, wildlife biologists, and scientists from national, regional, and unit levels, working closely with an array of new partners from Parks Canada, multiple state wildlife agencies, universities, and non-government organizations. The impetus of this project was the Department's assessment of bison genetics (Dratch and Gogan 2010) that recommended rigorous scientific assessment of how metapopulation management might alleviate otherwise inevitable genetic drift within individual herds managed in isolation.

This study confirms that management of DOI bison herds in isolation would promote the loss of genetic diversity over the long term. More importantly, this study demonstrates that adopting a DOI metapopulation strategy through facilitated periodic movement of modest numbers of bison among DOI herds (i.e., restoring effective gene flow) can substantially reduce the negative impacts of geographic isolation. Analyses of an array of scenarios for practical bison translocations indicate that the selection of appropriate source herds and numbers of animals to translocate must be considered carefully to most effectively conserve genetic diversity and ensure the long-term population persistence of bison. In the process of completing this work, we assembled the first-ever common panel of genetic data for nearly all DOI bison herds. Beyond the technical goals and objectives of the project, a principal intent was to address a priority of the DOI Bison Conservation Initiative (DOI 2008), namely, development of stronger interagency collaboration across the DOI and increasing the number of new partners for long-term bison conservation. Agency and partner leadership committed itself and its resources, providing funding and prioritizing work plans for innovative multi-year science investigations and team meetings. Integrated teams of managers, biologists, and scientists formed and worked closely together to design and execute robust scientific investigations.

This new approach for shared interagency bison conservation assessment and action may prove to be one of the most important advances in federal bison conservation since the establishment of herds during the past century. With an articulated vision, sound scientific foundations, and committed internal and external partnerships, DOI bureaus are now well equipped to implement a new approach to bison conservation: a cooperative, multi-scaled stewardship model to preserve and protect our national bison heritage and to promote ecological and cultural restoration of bison to North America.

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Appendix A. DOI Bison Herd Information Questionnaire

Survey sent to DOI bison herd managers in 2016 to gather standardized information on the environmental conditions, herd demographics, management, and known genetics of DOI bison herds.

DOI Bison Herd Information Questionnaire

Thank you for your assistance with this information request. This request is supported by your agency as part of an interagency collaborative effort to assess the current and future status of bison managed by the Department of the Interior (DOI). You have been identified as having expertise in and access to demographic, environmental/ecological, genetic and management information for (at least one of) the bison herds your agency manages.

Background

The DOI manages 19 bison herds comprising ~10,000 bison -- one-third of all bison managed for conservation in North America. The DOI Bison Conservation Initiative and the 2014 DOI Bison Report "Looking Forward" call for science-based strategies to evaluate current and future management of DOI bison for species recovery efforts. In response to this call, the National Park Service (NPS) partnered with the Wildlife Conservation Society (WCS) to implement a multi-year project to develop current science and facilitate collaborative discussions regarding the conservation status of DOI bison.

An objective of this project is to compile information and genetic data for each DOI bison herd that will be used in population viability analyses (PVAs). The goal of the PVAs is to predictively model the viability of bison herds at least 200 years into the future under current conditions and management as well as under potential alternative management scenarios. PVA results will

- Offer a comprehensive, standardized overview of variables associated with effective long-term management of bison under a variety of management scenarios;
- Provide managers with science-based information across all DOI bison herds that can inform discussions regarding current and future bison management goals and strategies; and
- Generate a rigorous baseline of quantitative outputs that can be used in an adaptive management framework to evaluate effects of potential future management and monitoring strategies in order to informatively adjust these strategies to ensure DOI bison conservation goals are achieved.

To accomplish this objective, we are requesting the following types of information BY FRIDAY APRIL 1st:
1. Current herd demographic, ecological/environmental, and management information; and

2. An assessment of existing bison genetic data and archived biological samples that may be used for genetic analyses; and your capacity and estimated timeline to collect and send bison genetic samples to a lab for genetic analyses (the project covers the lab costs for analyses).

You are not expected to be able to provide answers to every question. Please respond with the best available information and indicate when requested information is not available. You may be contacted later to discuss assumptions and inferences that may be drawn upon to address information gaps in the PVA model parameterization process.

Your assistance with this information request is important and appreciated - If you have any questions about this request, the DOI Bison Project or this questionnaire, please contact Amanda Hardy.

Respondent Contact Information and Bison Herd Name

Please complete an entire questionnaire for each herd for which you may have information to offer.

Please identify each herd with a unique herd name, complete an entire questionnaire for that herd, then repeat this process for other bison herds. For example, Theodore Roosevelt National Park manages bison independently in a "North Unit" and "South Unit"; therefore it would be appropriate to complete this questionnaire in its entirety for the "North Unit" herd, then repeat the process (using a new, unique link so you do not overwrite your answers) for the "South Unit" herd.

* 1. Please provide the following requested information for each questionnaire you fill out:

- ○ Your Name
- ○ Bison herd name
- ○ Agency
- ○ Unit (park, refuge, district)
- ○ Title/position
- ○ State/Province
- ○ ZIP/Postal Code
- ○ Email Address
- ○ Phone Number
- ○ Current Herd Population Size

* 2. What is the current population size of this bison herd? Please provide a POINT VALUE with a standard deviation or a RANGE. If you have an exact count (census), please indicate this in your answer below.

* 3. Are summer calves (born in spring 2015) included in this count? Please select one.

- ○ Yes
- ○ No
- ○ Do not know

* 4. When was this population count conducted? Please select all that apply.

- ○ post-rut, prior to winter
- ○ after winter, prior to 2016 calf influx
- ○ just prior to herd reductions for management just after herd reductions for management Other (please explain below)
- ○ If there are other considerations that may affect the count reported here, please explain:

* 5. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications, grey literature) supporting your answers provided above:

Current Age- and Sex-Structure of Herd

For the current herd (animals still living and residing in this herd), please quantify the number of males, females and undetermined sex for the following age classes:

* 6. For CALVES (born in 2015) in this herd. If you do not know the number, please enter "unknown."

- ○ Males
- ○ Females
- ○ Sex undetermined

* 7. For YEARLINGS (born in 2014) in this herd. If you do not know the number, please enter “unknown.”
  - ○ Males
  - ○ Females
  - ○ Sex undetermined

* 8. For NON-BREEDING AGE ADULTS (too young/old) in this herd. If you do not know the number, please enter “unknown.”
  - ○ Males
  - ○ Females
  - ○ Sex undetermined

* 9. For BREEDING AGE ADULTS in this herd. If you do not know the number, please enter “unknown.”
  - ○ Males
  - ○ Females
  - ○ Sex undetermined

* 10. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications, grey literature) supporting your answers provided above. If you are referring to a source that has been fully documented previously in your responses, you can abbreviate the citation (i.e., Hardy et al. 2006).

Herd Reproductive Rates
Age-specific reproductive rates used in the Red List Assessment were gleaned from bison herd data and are summarized in the figures below. Age-specific (3-20 years) probability of reproduction for female plains bison (a) is based on Brodie 2008. Relative age-specific probability of breeding (i.e., potential breeder) for males (b) is estimated based on multiple sources.

* 11. If the pattern of reproductive rates for males and females in this herd does not differ from the graphs presented above, please state “no substantial difference” in the block below.

OR

If the pattern of female and/or male reproduction for this herd differs substantially from the graphs above, please report annual female and male reproductive data.

If you have and are willing to share a spreadsheet with annual reproductive data for this herd, please indicate this below and email the file to Amanda Hardy at ahardy@wcs.org (data ownership will be respected).

* 12. Approximately what percent of females breed as yearlings and give birth to calves at age 2 years (if unknown, please enter “unknown”)?

* 13. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications, grey literature) supporting your answers provided above. If you are referring to a source that was fully documented previously in your responses, you can abbreviate the citation (i.e., Hardy et al. 2006).

Herd Mortality Rates
PLEASE BE AWARE that the mortality rates below refer to a baseline mean mortality and do NOT include culling or other management removals to control herd size, significant disease outbreaks or other catastrophic events, or years of extreme environmental conditions (you will have an opportunity to address these other factors in subsequent questions).

Age-specific mortality rates have been generated from data from several large bison herds (Brodie 2008, Geremia et al. 2014, and others) to produce appropriate age and sex structure and growth rate for large herds "functioning as wild" for use in the Red List Assessment and are given below. Also shown is sex-specific survivorship (lx) resulting from these mortality rates. Please refer to the table and figure to answer #15 below.

* 14. If the pattern of mortality rates for males and females in this herd does not differ from the information above, please state "no substantial difference" below.

OR

If the pattern of mortality for this herd differs substantially for females and/or males from the information above, please report annual female and male mortality rates for this herd.

If you have and are willing to share a spreadsheet with mortality data for this herd, please indicate this below and email the file to Amanda Hardy at ahardy@wcs.org (data ownership will be respected).

* 15. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications, grey literature) supporting your answers provided above. If you are referring to a source that was fully documented previously in your responses, you can abbreviate the citation (i.e., Hardy et al. 2006).

Interaction with other bison herds

These questions are intended to summarize current plans for anticipated FUTURE interactions between bison herds. Please do not summarize past transfers; only plans for future bison transfers into or out of this herd.

*Note: this DOI project will further explore and model the effects of possible movements of bison between herds but please do not speculate on those possible changes in management here. Please only report on current, existing plans for future anticipated transfers into or out of this herd.

* 16. Under current management, will bison move into or out of this herd (into other herds) or will this herd be isolated from other herds? Please select all that apply:

- ○ Bison from other herds are sometimes released INTO this herd.
- ○ Bison are sometimes transferred from this herd AND released into one or more other herds.
- ○ This herd is completely isolated from other bison herds and no bison are anticipated to be moved into or out of this herd into other herds.
- ○ Unsure if bison will be moved into this herd from other herds or transferred out of this herd to other herds. Bison can naturally immigrate or emigrate between this herd and other herds.
- ○ Other (please explain below)

* 17. Under current management plans, if bison are anticipated to be transferred into or out of this herd, please indicate:

- ○ Source herd(s):
- ○ Recipient herd(s):
- ○ Age and sex classes transferred
- ○ Other animal traits that influence which animals are moved:
- ○ Rate of transfer (# of animals and time interval):
- ○ Any other factors used to determine transfers:

* 18. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications,

grey literature) supporting your answers provided above. If you are referring to a source that was fully documented previously in your responses, you can abbreviate the citation (i.e., Hardy et al. 2006).

Environmental Conditions and Threats

Is this herd at risk for diseases of concern? For each disease listed below, please indicate:

- ○ Is it currently present in this herd?
- ○ What is the future risk of occurrence (expected # of occurrences in 100 years)?
- ○ What is the survival rate relative to unaffected years (0 to 1†)?
- ○ What is the reproductive rate relative to unaffected years (0 to 1†)?

†1.00 = no impact; 0.75 = 25% reduction; 0.00 = no survival/breeding that year

*19. Tuberculosis (TB) - If unknown, please enter "unknown."

- ○ Currently present (yes/no - or unknown)?
- ○ Future risk?
- ○ Survival rate (0 to 1†)?
- ○ Reproductive rate (0 to 1†)?

* 20. Brucellosis - If unknown, please enter "unknown."

- ○ Currently present (yes/no - or unknown)?
- ○ Future risk?
- ○ Survival rate (0 to 1†)?
- ○ Reproductive rate (0 to 1†)?

* 21. Anthrax (major outbreak) - If unknown, please enter "unknown."

- ○ Currently present (yes/no - or unknown)?
- ○ Future risk?
- ○ Survival rate (0 to 1†)?
- ○ Reproductive rate (0 to 1†)?

* 22. Anthrax (minor outbreak) - If unknown, please enter "unknown."

- ○ Currently present (yes/no - or unknown)?
- ○ Future risk?
- ○ Survival rate (0 to 1†)?
- ○ Reproductive rate (0 to 1†)?

* 23. Other

- ○ Name of disease:
- ○ Currently present? (yes/no - or unknown)
- ○ Future risk?
- ○ Survival rate?
- ○ Reproductive rate?

* 24. Other

- ○ Name of disease:
- ○ Currently present? (yes/no - or unknown)
- ○ Future risk?
- ○ Survival rate?
- ○ Reproductive rate?

* 25. Are there other types of catastrophes (extreme events, notable perturbations) that may impact this herd? If unknown, please enter "unknown."

- ○ Name of catastrophe:
- ○ Future risk?
- ○ Survival rate?
- ○ Reproductive rate?

* 26. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications, grey literature) supporting your answers provided above. If you are referring to a source that was fully documented previously in your responses, you can abbreviate the citation (i.e., Hardy et al. 2006).

Environmental Conditions and Threats

Ecological carrying capacity refers to the number of animals that could be supported in the existing habitat in concert with the management of other species.

The PVA model will assume that habitat is not fluctuating randomly in quality over time, or that annual variations in habitat quality are accounted for in the model by yearly variation in mortality and reproductive rates.

* 27. What is the ecological carrying capacity for this herd?

* 28. How many total acres of habitat are available to this herd?

* 29. Will habitat (ecological carrying capacity) be lost or gained over time? E.g., do you anticipate acquisition or loss of land? Or do you anticipate a change in habitat quantity or quality due to the effects of climate change?

- ○ Lost
- ○ Gained
- ○ No loss or gain
- ○ Uncertain/do not know
- ○ Other (please explain)

* 30. Over how many years will habitat be lost or gained? If you anticipate no change in carrying capacity, please enter "no change."

* 31. What percentage of habitat will be lost (please enter a negative number) or gained (positive number) each year during the time period specified in the previous question (#31)? If you anticipate no change in carrying capacity, please enter "no change."

* 32. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications,

grey literature) supporting your answers provided above. If you are referring to a source that was fully documented previously in your responses, you can abbreviate the citation (i.e., Hardy et al. 2006).

Environmental Conditions and Threats

Human-imposed carrying capacity refers to how many bison have been deemed "acceptable" in this herd based on factors other than habitat (i.e., based on factors other than ecological carrying capacity for the management of multiple species objectives).

* 33. What is the human-imposed carrying capacity for this herd? If not applicable, please enter "not applicable."

* 34. Please identify the factor(s) that influence this human imposed carrying capacity (please select all that apply):

○ Not applicable (herd is not managed for a human-imposed carrying capacity) Internal management plan
○ Local policy
○ State policy
○ Federal policy
○ Litigation
○ Neighboring private land owners
○ Neighboring federal land management agency
○ Neighboring state / local land management agency
○ Conservation easement terms on neighboring lands
○ Wildlife / hunting advocates
○ Livestock / grazing associations
○ Environmental or animal rights advocacy groups
○ Other (please explain)

* 35. Does this human-imposed carrying capacity result in the removal of (please select all that apply):

○ Herd is not managed/animals are not removed to meet human-imposed carrying capacity
○ Calves
○ Yearlings
○ Non-breeding females
○ Non-breeding males
○ Breeding cows
○ Breeding bulls
○ Hunter-selected animals (please describe in the text box below how hunting permits are issued for age/sex classes and if hunter- harvest data are collected)
○ Other (please explain)

* 36. How often are animals removed from this herd to meet human-imposed carrying capacity?

○ Herd is not managed/animals are not removed to meet human-imposed carrying capacity
○ Annually
○ Every 2 years
○ As needed (please describe how this is determined in the text box below)
○ Other (please explain)

* 37. Please cite your sources of information (e.g., peer-reviewed papers, reports, unpublished data, personal communications, grey literature) supporting your answers provided above. If you are referring to a source that was fully documented previously in your responses, you can abbreviate the citation (i.e., Hardy et al. 2006).

Genetic Sampling and Data

* 38. Have genetic samples been collected for animals assumed to be currently alive and still residing in this herd?

- ○ Yes
- ○ No
- ○ Do not know
- ○ Other (please explain)

* 39. If genetic samples have been collected, please answer the following questions (if uncertain, please enter "uncertain"):

- ○ When were samples collected?
- ○ How many samples were collected?

* 40. If genetic samples have been collected, how was the herd sampled (i.e., what do the samples represent)? Check all that apply.

- ○ All new animals (e.g., calves, first-time round-up animals) are sampled annually Random sampling within herd
- ○ Stratified (if so, please describe below; e.g., balanced sample across age/sex classes)
- ○ Selective sampling (if so, please describe below; e.g., hunted, culled, surplussed, disease-tested)
- ○ Unknown
- ○ Other (please describe below)

* 41. If genetic samples have been collected, what type(s) of biological samples were collected (check all that apply)?

- ○ Hair follicle (tail hair typically)
- ○ Blood card (or DNA card, Whitman DNA card)
- ○ Tissue biopsy (skin, muscle tissue)
- ○ Bone or tooth
- ○ Feces
- ○ Other (please specify)

* 42. If genetic samples have been collected, can you access these samples and their attributing data? Please select one.

- ○ Yes
- ○ No
- ○ Do not know
- ○ Not applicable (no samples available)
- ○ Other (please specify)

* 43. If genetic samples have been collected, were these samples sent to a lab for genetic analysis? Please select one.

- ○ Yes
- ○ No

- ○ Do not know
- ○ Not applicable (no samples were collected)
- ○ Other (please explain)

* 44. If genetic samples have been collected, are these samples archived? Please select one.

- ○ Yes (please identify where samples are archived below)
- ○ No
- ○ Do not know
- ○ Not applicable (no samples were collected)
- ○ Other (please explain)

* 45. If genetic samples have been collected but not yet analyzed, would you (or your staff) be able to organize and send these samples to a laboratory for analyses (packaging and shipping protocols will be provided)? Note: Shipping and lab costs are covered by this project. Please select one.

- ○ Yes
- ○ No
- ○ Uncertain (please explain below)
- ○ Other (please explain)

* 46. Have there been any resulting peer-reviewed publications that describe the sampling, lab methods, data interpretation and results? If so, please cite papers here. If not, please state “no publications”.

* 47. If genetic samples have been collected and analyzed, please answer the following questions:

- ○ What lab analyzed these samples?
- ○ What genetic markers were analyzed (e.g., mtDNA, nuclear DNA, SNPs)?

* 48. Are molecular data on allele frequencies available for import to establish the genetic composition of the current population? Please select one.

- ○ Yes
- ○ No
- ○ Do not know
- ○ Not applicable (no samples available nor analyzed)
- ○ Other (please specify)

* 49. If genetic samples have been collected and analyzed, what genetic information was yielded (please check all that apply)?

- ○ Cattle gene introgression
- ○ Parentage
- ○ Expected heterozygosity
- ○ Allelic richness
- ○ Other (please explain)

Genetic Sampling Feasibility Assessment

Please answer the questions below regarding the potential of obtaining samples from this herd this year regardless of whether existing genetic samples or data are available.

* 50. Do you have plans to handle bison in this herd in the next ~6 months? Please select one.

○ Yes (if so, please estimate when you anticipate handling bison in the text box below)
○ No
○ Unsure (please explain below)

* 51. If unable to handle bison in this herd, would you be willing to consider using biopsy darts to obtain samples for genetic analyses? Please select one.

○ Yes
○ No
○ Potentially, with support (e.g., logistical, methodological, financial support)
○ Other (please explain)

* 52. If able to collect samples from bison in this herd for genetic analyses, what sectors of the population would you be able to sample? Check all that apply

○ Unable to collect samples
○ All ages and sexes, randomly Calves only
○ Cows only Bulls only
○ Bison selected for culling/slaughter/surplus
○ Hunter-killed bison
○ Other (please specify)

* 53. When would be the best time of the year for you/your staff to collect genetic samples and why?

* 54. Please provide any additional relevant information regarding existing genetic samples or the potential to collect genetic samples. If you have no additional input, please enter “no additional input”.

Appendix B. Bison loci used in this study

Bison loci used for the 52-marker diversity panel and for the 15-marker cattle introgression panel.

Diversity Panel Loci

- AGLA232
- BL1036
- BM1225
- BM1706
- BM17132
- BM1824b
- BM1862
- BM2113b
- BM2830
- BM4028
- BM4107
- BM4311
- BM4440
- BM47
- BM6017
- BM711
- BM720
- BM757
- BMC4214
- BMS1001
- BMS1074
- BMS1117
- BMS1172
- BMS1315
- BMS1355
- BMS1675
- BMS1716
- BMS1747
- BMS1857
- BMS1862
- BMS2258
- BMS2639
- BMS410
- BMS510
- BMS527
- BMS528
- BMS601
- BMS812
- BMS911
- BMS941
- HUJ246
- IL4
- ILSTS102
- INRA037
- INRA133
- INRA194
- RM372
- SPS115
- TGLA122b
- TGLA44
- TGLA53b
- URB011

Introgression Panel Loci

- AGLA17
- AGLA293
- BM1314
- BM4307
- BM4513
- BM7145
- BMC3224
- BMS2270
- BMS4040
- CSSM36b
- CSSM42b
- RM185
- RM500
- SPS113b
- TGLA227b

Appendix C. Results of the Fisher's exact test

Table C.1. Results of the Fisher's exact test of the hypothesis that genotype frequencies follow the Hardy–Weinberg equilibrium (HWE) for each locus in the 52-marker diversity panel. Column values are locus ID, the X^2-value, the number of degrees of freedom, the associated p-value for each test, and an exact test based on Monte Carlo permutations of alleles. Values indicate none of the loci departed from HWE.

Locus	**X^2**	**df**	**p-value**	**Permuted p-value**
AGLA232	174.2228	21	0.00E+00	0
BL1036	224.8702	10	0.00E+00	0
BM1225	698.1511	66	0.00E+00	0
BM1706	161.6066	21	0.00E+00	0
BM17132	261.941	10	0.00E+00	0
BM1824b	194.0119	28	0.00E+00	0
BM1862	215.3441	15	0.00E+00	0
BM2113b	529.5877	28	0.00E+00	0
BM2830	208.9168	45	0.00E+00	0
BM4028	1107.885	15	0.00E+00	0
BM4107	251.1199	45	0.00E+00	0
BM4311	276.0223	15	0.00E+00	0
BM4440	164.1576	15	0.00E+00	0
BM47	63.75925	15	5.63E-08	0
BM6017	2854.207	28	0.00E+00	0
BM711	79.5594	10	6.13E-13	0
BM720	370.4799	45	0.00E+00	0
BM757	145.5455	28	0.00E+00	0
BMC4214	138.8853	15	0.00E+00	0
BMS1001	150.6249	10	0.00E+00	0
BMS1074	36.45215	10	7.04E-05	0
BMS1117	62.84977	10	1.04E-09	0
BMS1172	238.5028	21	0.00E+00	0
BMS1315	80.78292	10	3.52E-13	0
BMS1355	35.54869	6	3.37E-06	0
BMS1675	37.46502	6	1.43E-06	0
BMS1716	95.96707	15	7.55E-14	0
BMS1747	140.364	15	0.00E+00	0
BMS1857	436.2181	66	0.00E+00	0
BMS1862	379.5492	55	0.00E+00	0
BMS2258	436.2464	45	0.00E+00	0
BMS2639	288.8982	21	0.00E+00	0
BMS410	107.0355	21	1.61E-13	0
BMS510	66.62632	10	1.98E-10	0
BMS527	176.4658	28	0.00E+00	0
BMS528	179.5442	10	0.00E+00	0
BMS601	227.906	10	0.00E+00	0
BMS812	273.2446	28	0.00E+00	0
BMS911	2344.684	10	0.00E+00	0
BMS941	376.1091	10	0.00E+00	0
HUJ246	116.4882	10	0.00E+00	0

Locus	X^2	df	p-value	Permuted p-value
IL4	576.0595	66	0.00E+00	0
ILSTS102	51.99738	10	1.14E-07	0
INRA037	323.1823	15	0.00E+00	0
INRA133	339.0022	21	0.00E+00	0
INRA194	130.2551	10	0.00E+00	0
RM372	355.4382	45	0.00E+00	0
SPS115	268.7718	15	0.00E+00	0
TGLA122b	80.43052	21	6.84E-09	0
TGLA44	373.125	15	0.00E+00	0
TGLA53b	157.5498	15	0.00E+00	0
URB011	375.8077	28	0.00E+00	0

Appendix D. Bootstrapped 95% confidence intervals for pairwise F_{ST} values between herds.

Table D.1. Bootstrapped 95% confidence intervals for pairwise F_{ST} values between herds.

Site	**BADL**	**BOOK**	**CHIC**	**ELK**	**FTN**	**GRASS**	**HEMO**	**NBR**	**NER**	**NSM**	**RMA**	**SH**	**TAPR**	**THROn**	**THROs**	**WM**	**WICA**	**WRST**
BADL	–	0.08-0.11	0.20-0.27	0.12-0.16	0.03-0.06	0.13-0.17	0.16-0.22	0.12-0.17	0.10-0.15	0.13-0.19	0.12-0.17	0.16-0.23	0.10-0.16	0.07-0.10	0.03-0.06	0.14-0.19	0.10-0.16	0.18-0.26
BOOK	–	–	0.18-0.25	0.08-0.12	0.06-0.09	0.08-0.13	0.03-0.05	0.07-0.10	0.10-0.16	0.07-0.11	0.07-0.10	0.10-0.17	0.07-0.10	0.11-0.16	0.08-0.12	0.13-0.18	0.07-0.10	0.14-0.19
CHIC	–	–	–	0.18-0.26	0.17-0.23	0.18-0.25	0.26-0.35	0.16-0.21	0.24-0.33	0.19-0.24	0.15-0.21	0.23-0.31	0.16-0.23	0.28-0.37	0.20-0.27	0.07-0.12	0.16-0.22	0.24-0.34
ELK	–	–	–	–	0.90-0.13	0.01-0.01	0.12-0.18	0.07-0.10	0.15-0.21	0.07-0.12	0.07-0.10	0.10-0.15	0.07-0.11	0.16-0.20	0.13-0.17	0.13-0.18	0.08-0.12	0.12-0.18
FTN	–	–	–	–	–	0.10-0.14	0.13-0.19	0.08-0.13	0.09-0.13	0.09-0.15	0.08-0.12	0.12-0.18	0.08-0.12	0.07-0.10	0.05-0.07	0.11-0.15	0.08-0.13	0.14-0.21
GRASS	–	–	–	–	–	–	0.13-0.19	0.08-0.11	0.15-0.22	0.09-0.13	0.08-0.11	0.12-0.17	0.08-0.12	0.16-0.21	0.13-0.17	0.12-0.18	0.09-0.12	0.13-0.19
HEMO	–	–	–	–	–	–	–	0.12-0.17	0.16-0.23	0.13-0.19	0.13-0.18	0.16-0.26	0.13-0.17	0.19-0.28	0.17-0.24	0.19-0.25	0.13-0.17	0.19-0.27
NBR	–	–	–	–	–	–	–	–	0.15-0.20	0.01-0.01	0.01-0.03	0.03-0.06	0.08-0.12	0.15-0.20	0.13-0.17	0.11-0.15	0.08-0.12	0.08-0.12
NER	–	–	–	–	–	–	–	–	–	0.16-0.22	0.14-0.20	0.18-0.29	0.16-0.22	0.14-0.19	0.10-0.15	0.17-0.25	0.15-0.22	0.23-0.29
NSM	–	–	–	–	–	–	–	–	–	–	0.02-0.04	0.04-0.08	0.09-0.13	0.16-0.24	0.13-0.18	0.13-0.18	0.10-0.14	0.08-0.13
RMA	–	–	–	–	–	–	–	–	–	–	–	0.05-0.09	0.07-0.11	0.16-0.22	0.12-0.17	0.10-0.14	0.07-0.12	0.09-0.14
SH	–	–	–	–	–	–	–	–	–	–	–	–	0.12-0.18	0.20-0.27	0.16-0.24	0.15-0.22	0.13-0.18	0.12-0.19
TAPR	–	–	–	–	–	–	–	–	–	–	–	–	–	0.14-0.20	0.11-0.16	0.11-0.16	0-0.01	0.14-0.19
THROn	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.06-0.10	0.19-0.27	0.14-0.20	0.21-0.30
THROs	–	–-	–	–	–	–	–	–	–	–	–	–	–	–	–	0.14-0.20	0.11-0.16	0.19-0.25
WM	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.10-0.15	0.17-0.26
WICA	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.14-0.19
WRST	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Appendix E. Estimating Relatedness of Bison Herds Using Microsatellite Markers

The package *related* offers a number of estimators to estimate relatedness between individuals based on microsatellite data, each with particular advantages and disadvantages based on the type and quantity of data available (Wang 2014). To determine which estimator was most appropriate estimator for our bison microsatellite data, we first tested the relative performance of each estimator on our bison data by simulating individuals of known relationships from our data (i.e., parent, offspring, sib, half-sib, and unrelated; Figure E.1) and correlated estimates of relatedness generated by each estimator to known relatedness (Table E.1). Simulation results indicated that all estimators performed well in estimating relatedness values within our dataset (Figure E.1; Table E.1), but the Wang estimator performed the best (correlation coefficient between observed and expected values of 0.94). We therefore used the Wang estimator to estimate relatedness values between all individuals within our sampled bison population.

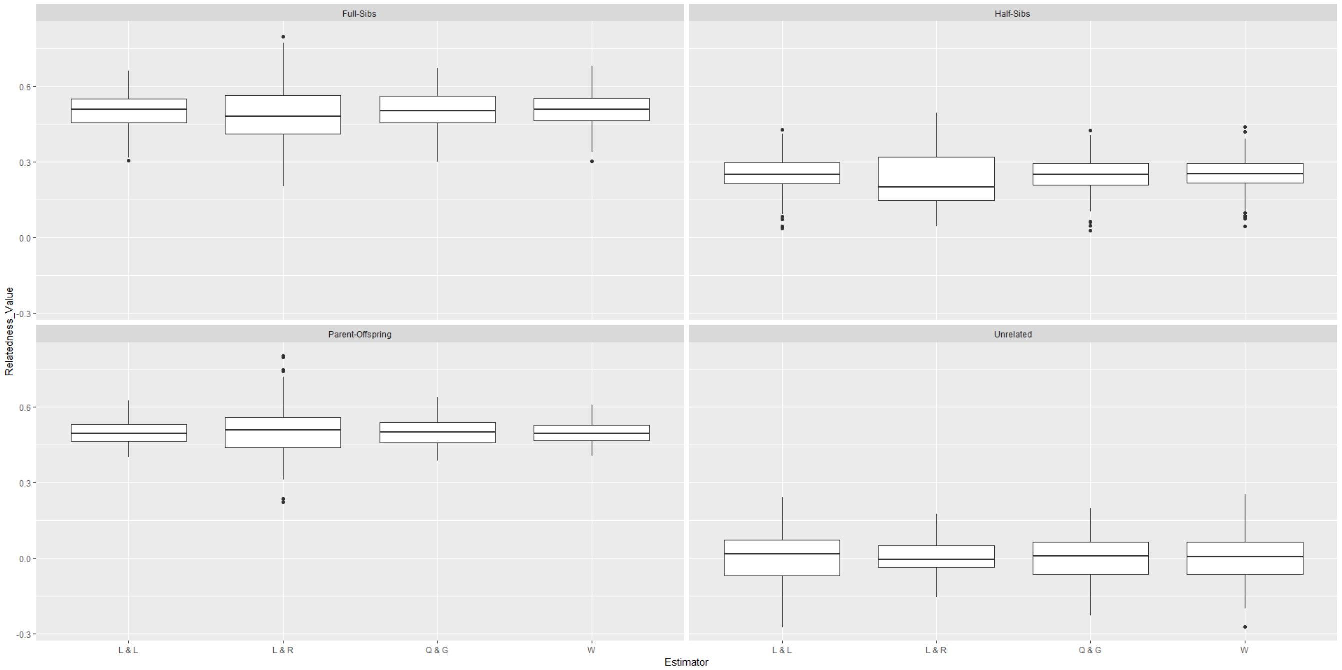

Figure E.1. Box plots comparing the accuracy of the estimated relatedness value generated by each estimator (L&L = Li et al. [1993], L&R = Lynch & Ritland [1999], Q&G = Queller & Goodknight [1989], W = Wang [2002]) for simulated individuals (full-siblings, half-siblings, parents and offspring, and unrelated individuals). The Wang estimator performed best overall.

Table E.1. Correlation between actual relatedness value of simulated individuals and estimated relatedness values generated by each estimator.

Estimator	**Correlation Coefficient**
Wang (2002)	0.944
Li et al. (1993)	0.942
Lynch & Ritland (1999)	0.883
Queller & Goodknight (1989)	0.941

Table E.2. Pairwise mean kinship (mk_{ij}) values used to initialize models. Mean kinship values were estimated as $mk_{ij} = \Theta_{ij}/2$, where Θ_{ij} is the mean relatedness between herds i and j.

Site	BADL	BOOK	CHIC	ELK	FTN	GRASS	HEMO	NBR	NER	NSM	RMA	SH	TAPR	THROn	THROs	WM	WICA	WRST
BADL	0.091	0	0	0	0.031	0	0	0	0.02	0	0	0	0	0.061	0.061	0	0	0
BOOK	0	0.037	0	0	0	0	0.06	0	0	0	0	0	0	0	0	0	0	0
CHIC	0	0	0.235	0	0	0	0	0	0	0	0	0	0	0	0	0.089	0	0
ELK	0	0	0	0.069	0	0.065	0	0	0	0	0	0	0	0	0	0	0	0
FTN	0.031	0	0	0	0.051	0	0	0	0.009	0	0	0	0	0.03	0.029	0	0	0
GRASS	0	0	0	0.065	0	0.08	0	0	0	0	0	0	0	0	0	0	0	0
HEMO	0	0.06	0	0	0	0	0.146	0	0	0	0	0	0	0	0	0	0	0
NBR	0	0	0	0	0	0	0	0.056	0	0.053	0.04	0.061	0	0	0	0	0	0.012
NER	0.02	0	0	0	0.009	0	0	0	0.166	0	0	0	0	0.026	0.028	0	0	0
NSM	0	0	0	0	0	0	0	0.053	0	0.065	0.036	0.062	0	0	0	0	0	0.013
RMA	0	0	0	0	0	0	0	0.04	0	0.036	0.053	0.042	0	0	0	0	0	0
SH	0	0	0	0	0	0	0	0.061	0	0.062	0.042	0.15	0	0	0	0	0	0.034
TAPR	0	0	0	0	0	0	0	0	0	0	0	0	0.045	0	0	0	0.044	0
THROn	0.061	0	0	0	0.03	0	0	0	0.026	0	0	0	0	0.154	0.069	0	0	0
THROs	0.061	0	0	0	0.029	0	0	0	0.028	0	0	0	0	0.069	0.099	0	0	0
WM	0	0	0.089	0	0	0	0	0	0	0	0	0	0	0	0	0.096	0	0
WICA	0	0	0	0	0	0	0	0	0	0	0	0	0.044	0	0	0	0.048	0
WRST	0	0	0	0	0	0	0	0.012	0	0.013	0	0.034	0	0	0	0	0	0.163

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Appendix F. Pairwise Gene Identity Values (J_{xy}) between Herds

Table F.1. The sequence of source herds used for translocations in Source Herd Scenario 2. Translocations from source herds were ordered from least-related to most-related. Relatedness was estimated as pairwise gene identity values (J_{xy} values given in parenthesis) from the allelic data for each herd. After the 12th translocation, the respective sequence of source herds for each recipient herd was repeated until the end of simulations (200 years).

Recipient herd	**1st donor**	**2nd donor**	**3rd donor**	**4th donor**	**5th donor**	**6th donor**	**7th donor**	**8th donor**	**9th donor**	**10th donor**	**11th donor**	**12th donor**
BADL	NSM (0.265)	WICA (0.265)	NBR (0.268)	TAPR (0.271)	GRASS (0.273)	HEMO (0.275)	ELK (0.275)	RMA (0.276)	WM (0.280)	FTN (0.342)	THROn (0.372)	THROs (0.372)
ELK	WM (0.272)	BADL (0.275)	WICA (0.281)	FTN (0.283)	THROs (0.283)	TAPR (0.289)	NSM (0.291)	HEMO (0.292)	THROn (0.292)	NBR (0.295)	RMA (0.301)	GRASS (0.367)
FTN	NSM (0.276)	WICA (0.278)	NBR (0.282)	TAPR (0.282)	GRASS (0.283)	ELK (0.283)	WM (0.284)	RMA (0.288)	HEMO (0.288)	BADL (0.342)	THROs (0.351)	THROn (0.360)
GRASS	BADL (0.273)	WM (0.278)	FTN (0.283)	WICA (0.286)	THROs (0.287)	NSM (0.287)	THROn (0.289)	HEMO (0.293)	NBR (0.293)	TAPR (0.294)	RMA (0.301)	ELK (0.367)
HEMO	WM 0.2557	BADL 0.2752	THROs 0.2806	NBR 0.2862	FTN 0.2879	TAPR 0.288	RMA 0.2887	WICA 0.2902	ELK 0.2919	NSM 0.2923	GRASS 0.2926	THROn 0.293
NBR	WICA 0.2626	BADL 0.2678	TAPR 0.2708	THROn 0.2726	THROs 0.2731	WM 0.2744	FTN 0.2816	HEMO 0.2862	GRASS 0.2931	ELK 0.2951	RMA 0.3378	NSM 0.3452
NSM	WM 0.2606	WICA 0.2615	BADL 0.2649	THROn 0.2677	TAPR 0.2689	THROs 0.2714	FTN 0.2757	GRASS 0.287	ELK 0.2907	HEMO 0.2923	RMA 0.3344	NBR 0.3452
RMA	WICA 0.2744	BADL 0.2762	TAPR 0.2804	THROn 0.281	FTN 0.2878	THROs 0.2881	HEMO 0.2887	WM 0.2915	GRASS 0.2931	ELK 0.2951	RMA 0.3378	NSM 0.3452
TAPR	NSM 0.2689	BADL 0.2708	NBR 0.2708	RMA 0.2804	WM 0.2811	FTN 0.2824	THROs 0.2841	HEMO 0.288	ELK 0.2894	THROn 0.2903	GRASS 0.2935	WICA 0.3351
THROn	NSM 0.2677	NBR 0.2726	WM 0.2751	RMA 0.281	WICA 0.2829	GRASS 0.2892	TAPR 0.2903	ELK 0.2924	HEMO 0.293	FTN 0.3597	BADL 0.3715	THROs 0.3962
THROs	NSM 0.2714	NBR 0.2731	WICA 0.2783	HEMO 0.2806	ELK 0.2834	TAPR 0.2841	WM 0.2853	GRASS 0.2868	RMA 0.2881	FTN 0.3513	BADL 0.3715	THROn 0.3962
WICA	NSM 0.2615	NBR 0.2626	BADL 0.2654	RMA 0.2744	FTN 0.2777	THROs 0.2783	WM 0.2798	ELK 0.281	THROn 0.2829	GRASS 0.2859	HEMO 0.2902	TAPR 0.3351
WM	HEMO 0.2557	NSM 0.2606	ELK 0.2718	NBR 0.2744	THROn 0.2751	GRASS 0.2777	BADL 0.2796	WICA 0.2798	TAPR 0.2811	FTN 0.2844	THROs 0.2853	RMA 0.2915

Appendix G. Pairwise Geographic Distances between Herds

Table G.1. Pairwise distances between herds (in miles). Geographic distances between herds was measured as the driving distance between units to represent the actual transport of bison via trailer trucks. Driving distances were obtained using Google Maps.

Site	**BADL**	**BOOK**	**CHIC**	**ELK**	**FTN**	**GRASS**	**HEMO**	**NBR**	**NER**	**NSM**	**RMA**	**SH**	**TAPR**	**THROn**	**THROs**	**WM**	**WICA**	**WRST**
BADL	–	754	856	1017	135	534	798	765	503	574	362	449	623	345	297	776	57	2880
BOOK	754	–	1047	1216	780	946	120	741	429	1072	395	1210	909	992	944	940	722	3005
CHIC	856	1047	–	1804	733	1406	1060	1693	1234	649	754	1023	316	1182	1134	171	905	3650
ELK	1017	1216	1804	–	1151	479	1304	581	841	1456	1238	839	1592	705	753	1844	1014	1796
FTN	135	780	733	1151	–	683	823	915	576	441	391	466	498	461	413	649	200	3000
GRASS	534	946	1406	479	683	–	1036	460	585	1046	763	423	1170	232	274	1390	530	2322
HEMO	798	120	1060	1304	823	1036	–	830	542	1116	439	1254	953	1036	988	918	765	3093
NBR	765	741	1693	581	915	460	830	–	435	1349	945	973	1459	640	671	1575	752	2304
NER	503	429	1234	841	576	585	542	435	–	1059	492	940	1008	678	652	1125	464	2631
NSM	574	1072	649	1456	441	1046	1116	1349	1059	–	683	669	345	865	817	663	695	3304
RMA	362	395	754	1238	391	763	439	945	492	683	–	860	521	645	597	615	342	3064
SH	449	1210	1023	839	466	423	1254	973	940	669	860	–	830	236	302	1039	519	2676
TAPR	623	909	316	1592	498	1170	953	1459	1008	345	521	830	–	1026	978	332	674	3440
THROn	345	992	1182	705	461	232	1036	640	678	865	645	236	1026	–	48	1104	345	2549
THROs	297	944	1134	753	413	272	988	671	652	817	597	302	978	48	–	1051	262	2597
WM	776	940	171	1844	649	1390	918	1575	1125	663	615	1039	332	1104	1051	–	805	3670
WICA	57	722	905	1014	200	530	765	752	464	695	342	519	674	345	262	805	–	2873
WRST	2880	3005	3650	1796	3000	2322	3093	2304	2631	3304	3064	2676	3440	2549	2597	3670	2873	–

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