A Population Viability Analysis for American Plains Bison (*Bison bison bison*) at American Prairie

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Contents

List of Acronyms

AP – American Prairie

CPSG - IUCN Species Survival Commission Conservation Planning Specialist Group

BLM – Bureau of Land Management

DOI – U.S. Department of the Interior

EINP – Elk Island National Park

PVA- Population Viability Analysis

YNP- Yellowstone National Park

Abbreviations and Definitions

We use the following abbreviations and definitions for model outputs:

Abbreviation /Term	**Description**
P(E)	Probability of extinction in 50 years (i.e. the # of extinct iterations/total # of iterations) across 1000 model iterations. Extinction was defined as no bison remaining. The highest probability of extinction is 1 and the lowest is 0.
N	Mean population size in 50 years, calculated across all 1000 model iterations (extant)
SD (N)	Standard deviation in mean population size in 50 years, calculated across all 1000 model iterations (extant)
Stoch-r	The mean stochastic growth rate of the population averaged across all 50 years. A growth rate greater than zero indicates a growing population, and a growth rate less than zero indicates a declining population.
SD(r)	The standard deviation in stochastic growth rate
Effective Population Size (N_e)	The size of an idealized population that would lose genetic diversity, become inbred, or experience genetic drift at the same rate as the actual population. This idealized population has no gene flow from other populations, random mating, no overlapping generations, and a constant number of breeding adults among other factors. This means that the effective size of a population is often far less than the census size of a population in the real world.
Gene Diversity Or Expected Heterozygosity (H_e)	The probability that two alleles randomly sampled from the same genetic locus across a population are not identical by descent. Gene diversity is calculated relative to a population's founders, which are assumed to be unrelated and not inbred, and is the proportional diversity retained by the current, descendant population.

Note that *N* and Stoch-*r* all have variability associated with them due to the stochastic nature of the model dynamics, and this variability conveys the range of possible future outcomes under a model scenario. See Appendix II, Table 1 summarizing all model results across all scenarios.

Executive Summary

While tens of millions of American bison (*Bison bison)* once roamed the Great Plains, the species was nearly hunted to extinction in the late 1800s. After significant effort to re-establish herds that are maintained for conservation purposes, the species is now listed as Near Threatened on the IUCN Red List but Critically Depleted on the Green List, highlighting the significant conservation work that remains to build more viable populations.

American Prairie (AP) is a non-profit focused on conserving the grasslands of the American West at a landscape scale across approximately 3.2 million acres. Key to AP's restoration goals is the return of plains bison (*B. b. bison*) to the landscape. Bison are a keystone species, and are critical for the restoration of functioning ecological communities in the Northern Great Plains. AP manages two growing bison herds, and were interested in evaluating the viability of these herds, strategies for translocations between herds, and the movement of animals in or out of their populations for genetic management.

We conducted a population viability analysis to assess whether AP's current management actions, constrained by regulatory barriers and available land, can support growth of AP bison herds toward a long-term target of 5,000 animals while maintaining a "natural" age structure and genetic health. Model results indicate that under current conditions, AP herds will experience robust growth with no probability of extinction. Extinction risk remains very low even in scenarios where the herd is severely impacted by *Mycoplasma bovis* outbreaks. If regulatory conditions improve and allow current AP herds to grow and a new herd to be started, bison herds could grow to around 5,000 animals in approximately 34 years.

Given projected growth rates, management actions including biennial exports to other conservation herds and continued hunter harvests are necessary to maintain herds at the target population size. If AP maintains the White Rock and Sun Prairie herds at their current sizes, and roundups and exports occur every two years, AP is projected to export a total of ~5,000 bison in the next 50 years. In model scenarios where AP herds grow towards a total size of 5,000 animals, a total of ~15,000 bison are projected to be exported over 50 years. Although hunter harvest removes far fewer animals than biennial exports, it still has an outsized influence on AP herd demographics. Model results show that even small shifts in the age or sex composition of the animals taken each year can markedly affect population structure and growth.

Genetic analysis indicate that the AP herds are genetically diverse and have low levels of inbreeding compared to other conservation herds. This finding, combined with our projections of gene diversity loss, means that without importing bison, the White Rock and Sun Prairie herds are in a good position to avoid inbreeding depression, at least for the model duration. However, maintaining the long-term evolutionary potential of the AP herds at their current sizes will require periodic importation of bison.

Finally, the current model does not incorporate density-dependent limits on population growth, in part because AP herds are managed below the expected ecological carrying capacity, and no empirical estimates of a bison-specific carrying capacity on AP properties exist. However, as herds grow, carrying capacity and density-dependent demographic effects will become important considerations, as these impacts have been observed in other bison populations.

Recommendations

1. **Consider the sex and ages of bison harvested in annual hunter harvests**
    a. Although hunter harvest removes far fewer animals than biennial exports, it still has an outsized influence on AP herd growth and structure
    b. Increasing annual hunter harvest of female bison can help to reduce the female bias in the AP herds.
    c. If managers want to increase growth rates in the population, harvesting fewer females or pausing harvests entirely could be effective management options.
2. **Consider the frequency of roundup and export events for future herd management**
    a. In our *Roundup Every Three Years* scenario, the population has a higher carrying capacity and more individuals are exported at each roundup event, but since roundups occur less frequently, the total number of bison exported is only marginally greater than in the *Baseline* model where roundups occur every two years.
3. **To maintain the long-term evolutionary potential for AP herds, import two to three bison every five to 10 years**
    a. Identifying the right source herd for these imports is critical:
        i. Import individuals from the least related herds
        ii. Vary the source herd between import events
        iii. Import males and females when possible
        iv. The Department of the Interior Bison Metapopulation Management Working Group and the Association of Zoos and Aquariums Bison SAFE program have the expertise and resources to help identify the right source herds
4. **To incorporate genetics from one of the unrepresented "five lineages" into AP herds, import 30 bison from that lineage.**
    a. Fewer individuals could be imported and achieve a similar result if any sex or age class other than male calves is imported.
5. **When starting a new herd from a small founder base, identify a founding group of bison that represents each of the unique lineages already found at AP**
    a. Minimize the number of direct relatives (e.g., siblings, parents, cousins) in the group
6. **Develop a standardized data-collection framework that supports estimation of survival rates for calf and yearling bison**
    a. Demographic rates will change if herds grow to approach the ecological carrying capacity or predation becomes a factor
    b. Developing a framework and collecting this data now will allow managers to assess the impacts of increased population size or predation in the future.

Introduction

Small and fragmented animal populations are vulnerable to extinction and often require human management interventions to survive. While tens of millions of American bison (*Bison bison)* once roamed the Great Plains, the species was nearly hunted to extinction in the late 1800s. After significant effort to re-establish herds that are maintained for conservation purposes, the species is now listed as Near Threatened on the IUCN Red List (Aune et al., 2017) but Critically Depleted on the Green List (Rogers et al., 2022), highlighting the significant conservation work that remains to build more viable populations.

American Prairie (AP) is a non-profit organization focused on conserving the grasslands of the American West at a landscape scale across 3.2 million acres. To achieve this goal, AP is focused on acquiring private land parcels, while also leasing adjoining public land managed by the Bureau of Land Management (BLM), in their project area in Northeast Montana adjacent to the Charles M. Russell National Wildlife Refuge and Upper Missouri River Breaks National Monument. Since 2004, AP has completed 43 land acquisition transactions that encompass a total of 603,657 acres (American Prairie, 2025). On this land, AP is focused on restoring the prairie ecosystem through active land management and rewilding.

Key to AP's restoration goals is the return of plains bison (*B. b. bison;* hereafter bison) to the landscape. Bison are a keystone species, and are critical for the restoration of functioning ecological communities in the Northern Great Plains. AP manages two growing bison herds, and are interested in evaluating the viability of these herds, strategies for translocations between herds, and the movement of animals in or out of their populations for genetic management. Specifically, they had the following questions:

1. How do imports and exports affect the genetic diversity of the AP bison herds?
2. How might the AP bison population grow if AP land acquisition plans are realized?
3. How would AP populations respond to unpredictable and emerging threats such as *Mycoplasma bovis* infection?

In 2024, AP contacted the IUCN SSC (Species Survival Commission) Conservation Planning Specialist Group (CPSG) headquarters to inquire about population viability analysis (PVA) practitioners who could build a PVA to address the questions above. AP also requested training to enable managers to update the PVA in the future to support ongoing management decisions. In March of 2025, AP staff and CPSG members had their first online meeting to kick off the PVA development process, and from May 21st to 23rd, 2025 CPSG and AP staff met at the American Prairie National Discovery Center in Lewistown, Montana for an in-person PVA workshop. Virtual meetings continued over the summer to refine model scenarios and validate initial model results, and on September 23rd and 24th CPSG returned to Lewistown to present final model results and train AP staff on the use of the Vortex based population model developed over the course of the year.

This report outlines the PVA developed to address the management questions noted above. After an overview of PVA and the software used, we describe the structure and function of the PVA model representing the AP bison herds and management system. We then summarize the model's input parameters. Finally, we summarize the analytical results, review major assumptions, and provide a set of conclusions to inform future bison management.

Criteria for Success

At the AP Bison PVA workshop on May 21st in Lewistown, Montana, participants envisioned successful herd management at 30 and 100 years into the future and identified criteria for measuring that success.

From this discussion, the PVA team defined criteria to evaluate model results and clarified the PVA's role in helping AP achieve these goals.

The PVA team identified five main criteria for success. In the next 30 years AP bison herds should:

1. Grow to a combined minimum size of ~5,000 bison
2. Be maintained in no more than three separate herds
3. Each herd should be managed to have a "natural" age and sex structure
4. AP bison herds should have all five unique bison genetic lineages represented

The role of this PVA is to focus on how AP's current management actions, constrained by regulatory barriers and available land, can facilitate the growth of the AP bison herd toward these criteria for success.

Herd History

AP reestablished bison on their property beginning with an initial import of 16 bison from Wind Cave National Park in the fall of 2005 (Fig. 1). Additional bison were brought in from Wind Cave in 2006 and 2007, and 10 animals from TNC's Broken Kettle Grasslands were added in 2008. From 2010 to 2014, AP imported 238 bison from Elk Island National Park (EINP) in Canada. Most recently, in 2023, AP acquired 65 YNP-lineage bison from several conservation herds. All bison currently on AP descend from these collective imports.

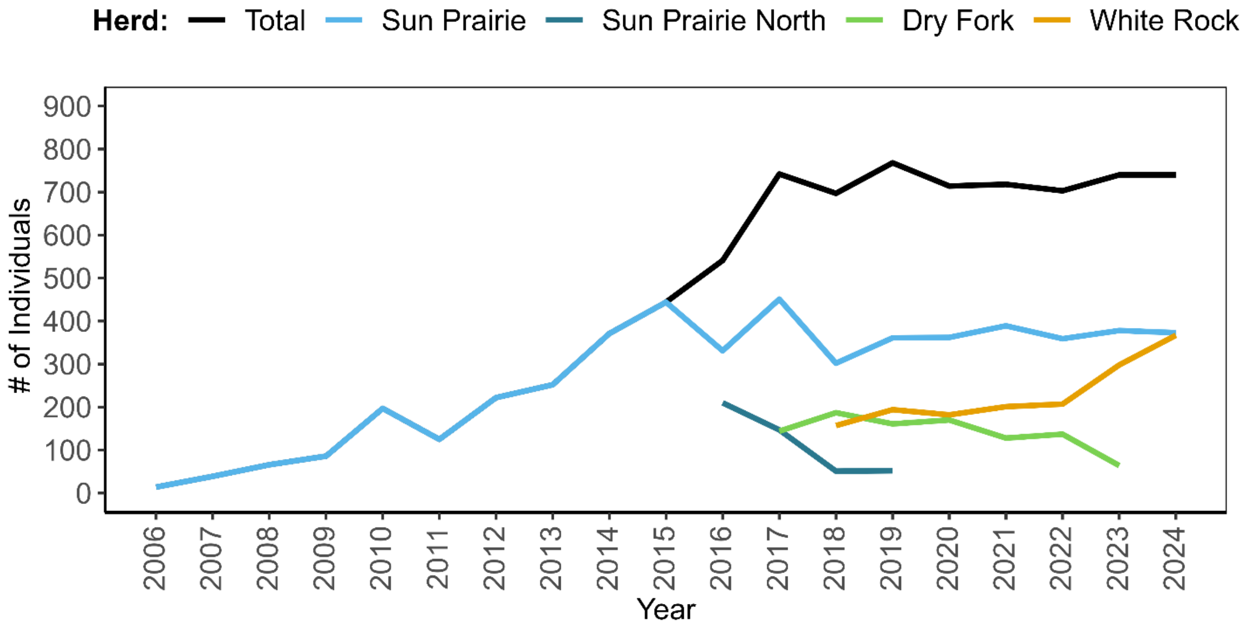

Figure 1. Spring census counts for AP bison herds from 2005 to 2024. AP first imported bison in the fall of 2005, so the first spring census count available is from the spring of 2006.

AP currently manages their bison in two separate herds, one herd at their Sun Prairie Unit and one herd at their White Rock Unit (hereafter Sun Prairie and White Rock). Bison have occupied Sun Prairie since AP's first import in 2005, while bison were established on White Rock in 2018. At times, AP also maintained herds in the Sun Prairie North and Dry Fork Units, but those animals were subsequently moved to Sun Prairie and White Rock. The herds at White Rock and Sun Prairie are maintained in fenced units and are geographically isolated from each other, meaning that bison cannot move from one unit to another on their own. AP owns and manages a number of other units across the region, and may establish bison herds on some of those units in the future.

AP staff have two main ways to manage herd size: exports and hunter harvests. The first export of bison from AP to outside partners occurred in 2018, when bison from Sun Prairie were moved to other conservation herds. Regular hunter harvests began at Sun Prairie in 2017, and have occurred every fall/winter since. Hunter harvests began at White Rock in 2020, but since the herd at White Rock is relatively new and still in its growth phase, regular exports have not started.

Methods

Modeling Approach

We developed a population model in Vortex (version 10.7.3.0), a widely used PVA modeling software package (Lacy & Pollak, 2025). For more detailed descriptions of Vortex and how it is applied in PVA, see Lacy (2000b, 2000a) and Lacy et al., (2021). The model is individual-based, meaning it tracks every animal (current and future) in a population over time. After being initiated with the starting population, the model steps through an annual event cycle (e.g., births, deaths, aging; *see* Appendix I, Fig. 1) for all individuals. It also includes multiple sources of stochasticity: 1) demographic stochasticity: the randomness in survival, reproduction, and birth sex ratios among individuals, which is especially important for small populations, 2) environmental stochasticity: the variability in demographic rates due to normal fluctuations in the environment as well as environmental catastrophes, and 3) genetic stochasticity: the randomness inherent in the transmission of alleles from parents to offspring. Due to this stochasticity, we run each model scenario many times, allowing us to determine the range of potential outcomes a population could experience under a given set of conditions.

Model inputs are the result of analyses of available data on the bison at AP, published research on bison maintained in conservation herds across North America, and our conversations within the PVA model team. As detailed below, the structure of the reproduction functions within the model was adapted from two previous bison PVAs created to assess the viability of bison herds managed by the U.S. Department of the Interior (DOI; Hartway et al., 2020) and evaluate the status of bison for the IUCN Red List of Threatened Species (Traylor-Holzer, 2016).

All model outputs were processed and plots created in R (R Core Team, 2025). Results are reported as the mean value (± SD).

Demographic and Genetic Input Data

General simulation characteristics

We ran each individual model scenario, defined by a unique set of input parameters, for 1,000 iterations. This iterative procedure is necessary as each replicate yields a different outcome resulting from random annual variation in expected rates of breeding and survival in the simulated population. Each scenario was projected forward for 50 years, a timeframe considered long enough to observe reliable trends in demographic and genetic performance under alternative management options.

Initial population size and structure

Bison life history centers around age and dominance, and we used Wes Olson's (2005) bison life stage categories to define the stage structure of AP herds throughout this report (Fig. 2).

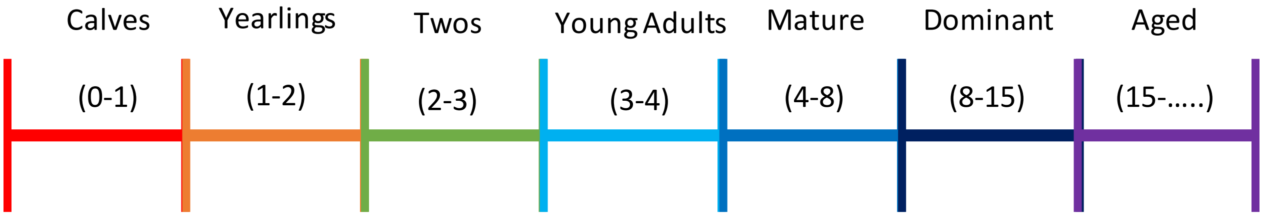

Figure 2. Stage classes for bison and the ages (years) for each stage (Olson, 2005).

AP staff maintain comprehensive records on the bison across their properties, including an individual database of bison handled and tagged during biennial roundups, and records from annual aerial census counts conducted in spring (pre-calving) and fall (post-calving). According to AP records, before calves began to drop in the spring of 2025, there were 888 bison at AP with 499 (245 males and 254 females) on the Sun Prairie unit and 389 (146 males and 243 females) on the White Rock unit. Ages for many of the bison at AP are known, but for animals that were imported from other herds or individuals that have never been brought in during a roundup, exact ages remain unknown and were estimated for this modeling effort. From AP records we were able to infer a comprehensive age structure for each herd (Fig. 3). The initial population size and the age and sex structure for each herd are read into the Vortex model via a studbook file.

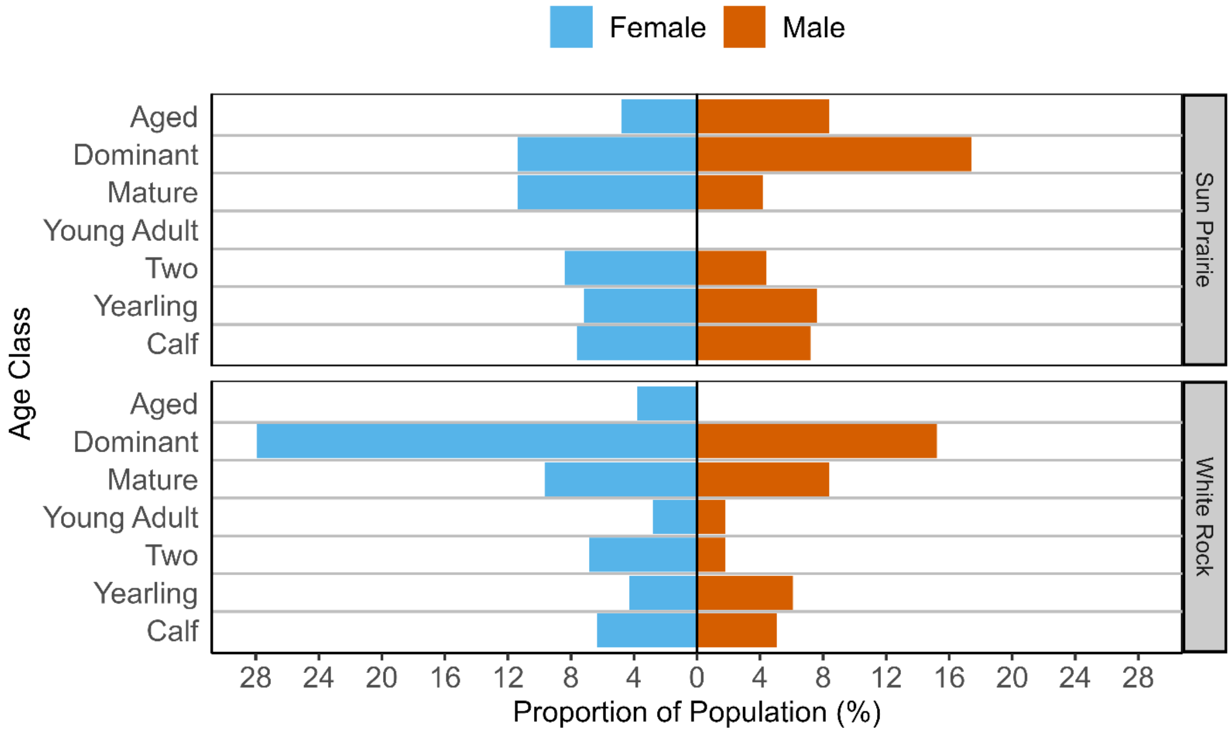

Figure 3. Proportional stage structure of the Sun Prairie and White Rock bison herds as of the winter of 2024.

Initial carrying capacity

AP bison units are comprised of a combination of properties owned by AP and adjoining public land managed by the BLM for which AP holds grazing rights. Each bison herd at AP is strictly managed to carrying capacities designated by the AP bison team which reflect the goals of the organization on deeded properties and the BLM-designated stocking rate for permitted lands. At Sun Prairie, the designated carrying capacity is 556 bison, and at White Rock the carrying capacity is 600 bison. These carrying capacities are likely well below the ecological carrying capacity of these properties.

Bison Management

Exports occur following biennial roundups, where AP staff attempt to round up all bison in a given herd. Currently, roundups occur every year on at least one AP property; one year at White Rock and the next year at Sun Prairie. Following this process, bison are chosen for shipment and moved to other conservation herds across the country.

Hunter harvests occur every fall on each property, with AP staff controlling the number of allowed harvests. The maximum number of animals harvested for the two current bison herds is around 30 per herd, and AP staff largely determine the sex and age class of animals to be harvested each year.

AP staff calculate the total number of animals to remove from each herd during biennial roundups. The central idea is to remove enough bison following a roundup so that the population does not exceed the carrying capacity before the next roundup occurs two years later (Fig. 4). At Sun Prairie, where the population is at carrying capacity and this system has been applied, managers have removed a combined (hunter harvest + exports) average of 161 (±40) bison from the property each roundup year (2016-2023).

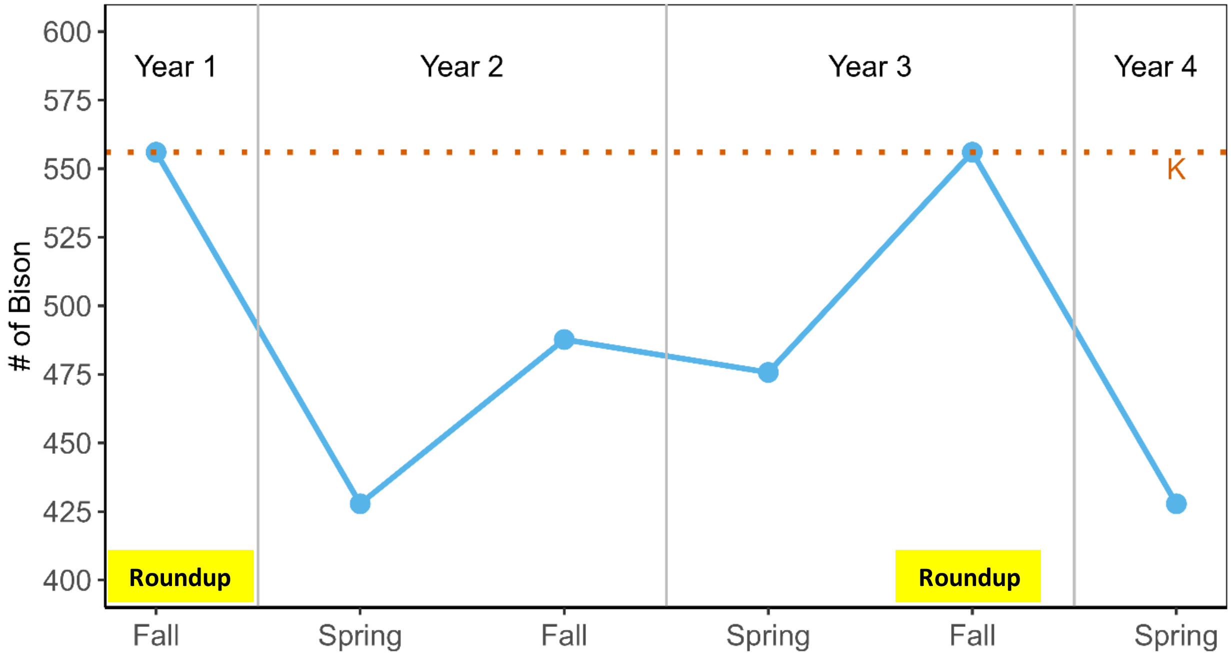

Figure 4. Idealized AP export schedule with the number of bison at fall and spring (pre-calving) censuses across four years of bison management. Roundups and bison removals occur every other year in the fall, in this case in years one and three. The orange dotted line represents the carrying capacity designated by managers.

We replicated this system with the following function in the "*Dispersal*" routine of Vortex which applies to each property on alternating years:

$$X=1-(K/[G^2*N])$$

Where X is the proportion of animals removed that year, K is the designated carrying capacity for the property, G is the mean intrinsic growth rate calculated from AP data on the Sun Prairie bison herd (geometric mean intrinsic growth rate (2007 -2024) = 19%), and N is the current number of bison in the herd. This function does not target specific age or sex classes for removal.

To simulate annual hunter harvest in Vortex, we used the "*Harvest*" routine to remove a set number of animals from each age and sex class (Table 1). These values were derived from the age/sex composition of 166 individuals harvested at Sun Prairie since annual hunter harvests began in 2018. We calculated the proportion of harvested animals in each class and applied those proportions to the maximum harvest quota for a property. For example, 17% of harvested animals at Sun Prairie (2018–2024) were male calves. Applying this proportion to the quota of 30 animals at Sun Prairie in the model results in the removal of five male calves a year (30*0.17=5).

Table 1. Proportion of the total number of individuals harvested annually by hunters from each age/sex class. Calculated from the 166 harvested individuals at Sun Prairie annual hunter harvests began in 2018.

	Proportion (%)	
Age Class	**Males**	**Females**
Calf	17	13
Yearling	29	10
Twos	1	2
Adults	25	4

Reproduction

Bison exhibit a polygynous mating system in which reproductive success is dictated by a social hierarchy based on an individual's age (Fig. 5) and condition.

Male Reproduction

Bulls establish dominance within the herd through combat, and dominant males then control access to females during the breeding season. Bulls achieve their maximum body weight at around seven to nine years of age (Berger & Peacock, 1988), correspondingly bulls over the age of seven are considered "dominant" and are responsible for the majority of successful copulations in a herd. Bulls of lower status may breed opportunistically later in a breeding season after dominant bulls tire and leave the herd (Wolff, 1998). This breeding system means that while males may be biologically able to reproduce at around two to three years, they typically do not breed until five to six years of age (Brodie, 2008). Peak reproductive output for males is between the ages of 8 and 14 (Wilson et al., 2002), after which a male's rank and reproductive output decline with age (Wolff, 1998).

The breeding function in our model follows Traylor-Holzer et al., (2016), where the proportion of bulls in the breeding pool is limited until the age of eight when 92% of males in each age class enter the pool

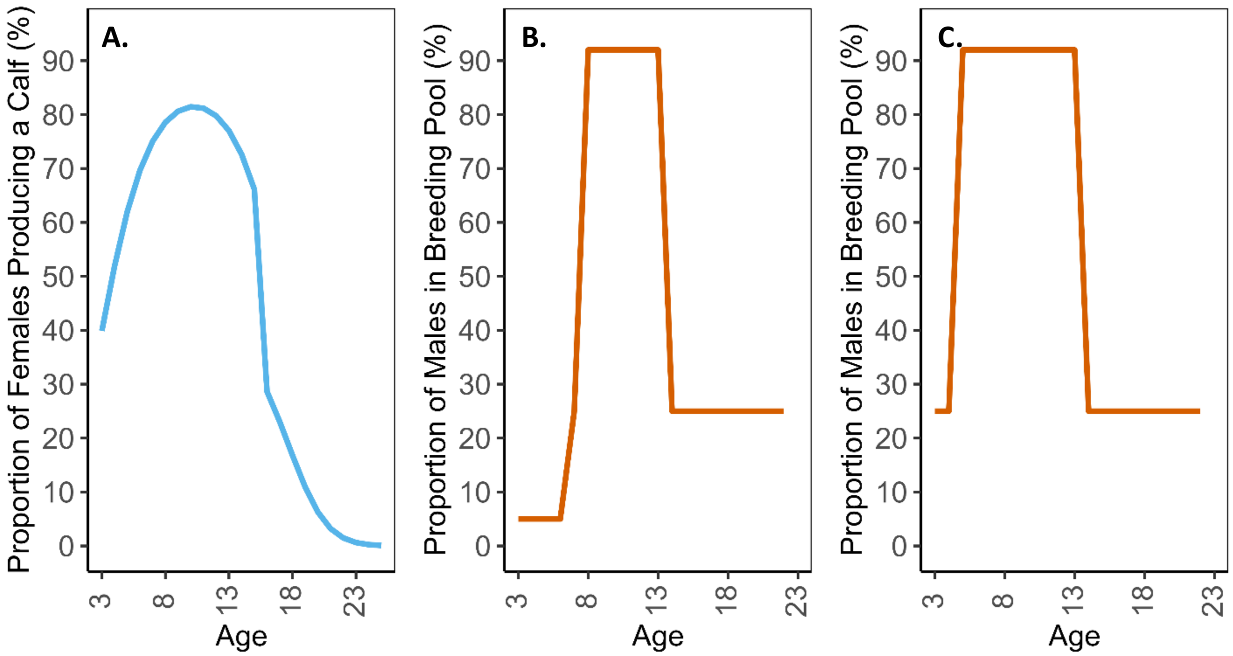

Figure 5. Mean proportion of females producing a calf per year by age (A), mean proportion of males in the breeding pool by age (B), and mean proportion of males in the breeding pool at low dominant male densities (C). Breeding functions adapted from Traylor-Holzer et al., 2016.

(Fig.5B). After the age of 14, only a quarter of males in each age class enter the breeding pool each year. There is no limit to how many females a single male can breed with, however, unproven males (i.e., that have not sired offspring) in the breeding pool have only a 10% chance of successfully pairing with a potential mate, compared to a 100% chance for proven males.

In draft versions of the model, this breeding system limited population growth when there were few bulls in the prime breeding age classes (8-14). According to the PVA team, when bulls in the prime breeding age classes are not available, younger bulls will compensate by breeding. To simulate this, we created a function in Vortex where a much higher proportion of younger males enter the breeding pool. If there are fewer than one male aged six or older for every 10 adult females in the population in a given year, 25% of three and four-year-old males, and 92% of males five to seven enter the breeding pool (Fig. 5C).

Under this breeding structure in our *Baseline* model, an average of 37% (±4%) of adult males sire an offspring each year. Annually, successful males sire an average of

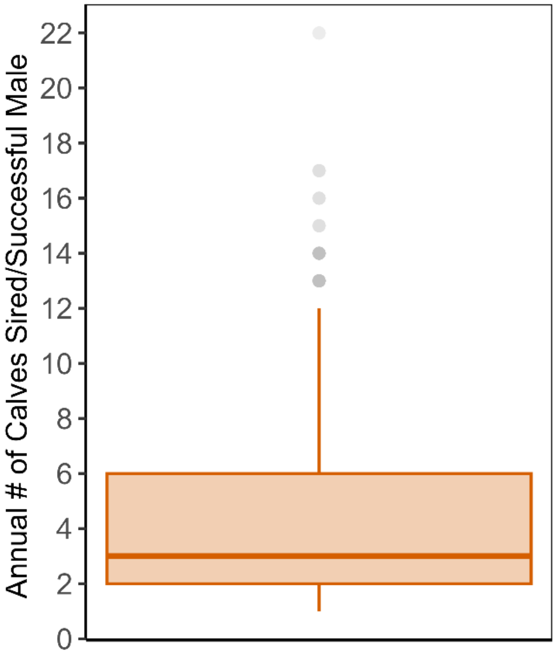

Figure 6. Boxplot showing the annual number of calves sired per year by successful males from a single iteration of the Baseline model. The box spans the interquartile range (IQR; 25th to 75th quartile), with the median (3 calves) indicated by the central line. Gray dots represent outliers, defined as values beyond 1.5 × IQR.

4.2(±2.8) calves (median = 3 calves), with some individuals siring as many as 22 (Fig. 6). This aligns with published estimates from wild bison herds where successful bulls sired an average of 1.67 (Wilson et al., 2002) to 5.8 (Wilson et al., 2006) calves a year, and individual bulls sired as many as 17 (Wilson et al., 2006).

Female Reproduction

While there is a social hierarchy among female bison and that hierarchy may affect reproductive success (Brodie, 2008), females have a significantly longer reproductive lifespan and a higher probability of producing a calf each year compared to males. We adapted the female reproductive function from Traylor-Holzer et al., 2016 (Fig. 5A), which is derived from the observed age specific probability of producing a calf for bison cows at EINP (Brodie, 2008; Wilson et al., 2002). Reproduction begins at age three, and as cows age they have an increasing probability of producing a calf each year until the age of 11 at which point over 80% of females produce a calf. After 11, the probability of producing a calf begins to decline, and a sharp drop off in reproduction occurs after the age of 15.

In the *Baseline* model scenario, ~63% of adult females produce a calf annually when a population is at equilibrium. AP staff do not directly track the number of calves at birth, instead the number of calves is estimated annually from fall aerial census counts. Based on estimates from Sun Prairie (2006-2024), 33% to nearly 100% of adult females produced a calf depending on the year (mean=52±18%). These estimates are influenced by major changes in herd size and structure across the years, as well as the application of contraception to some cows. For reference, the proportion of adult females pregnant annually in conservation herds varies widely, with published estimates ranging from 37% to 89% depending on the herd and study methodology (Brodie, 2008).

Contraception

From 2015 to 2019, a total of 192 females in AP herds were administered the immunocontraceptive vaccine porcine zona pellucida (PZP) in an effort to manage population growth. PZP prevents pregnancies by initiating the production of anti-PZP antibodies which alter the shape of the ovum thereby preventing the attachment of sperm (Duncan et al., 2013). PZP is broadly used in wild horses where managers administer multiple doses to prevent pregnancy; an initial primer dose, followed by a second inoculation before the onset of the breeding season, and then annual boosters in subsequent years to maintain infertility (Kirkpatrick & Turner, 2002). For horses, there are high rates of reversibility within four years of the last dose (~68%; Kirkpatrick & Turner, 2002), but reversibility rates appear to be significantly lower in

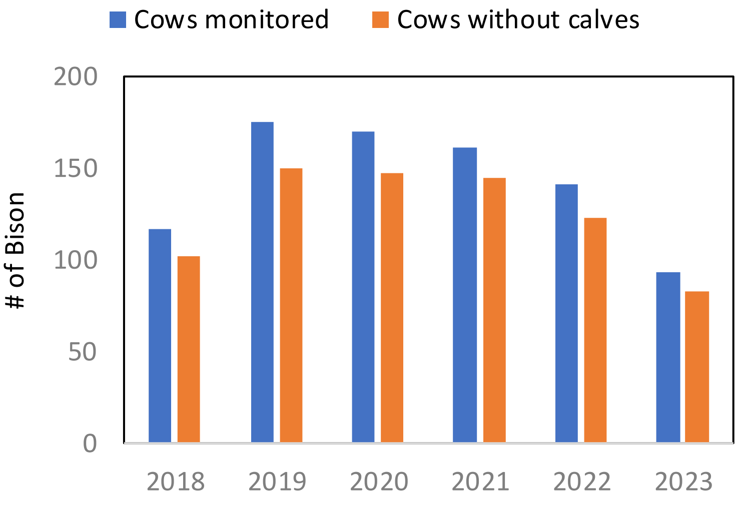

Figure 7. The number of PZP treated cows monitored (blue) and the number of those cows who failed to produce a calf by year (orange; 2018-2023). Note that the number of cows monitored is lower than the actual number of treated individuals. Figure courtesy of Ellen Anderson at AP.

bison. For instance, in the Catalina Island bison herd, following three to four years of annual PZP treatment for all cows in the herd, no calves were produced in the four to five years after the last dose was administered (Duncan et al., 2017).

At AP, bison cows received between one to three doses of PZP with the last cows receiving a dose in 2019. Today, six years after the last doses were administered, only 55 PZP treated cows are known to have produced a calf (55/192=28%). AP staff have monitored PZP treated females and their reproduction across the years and found that, on average, only 12% of treated cows produce a calf annually (2018-2023; Fig. 7). As of 2024, 153 PZP treated cows remain in the population with 131 of those in the White Rock herd. To simulate the impacts of PZP contraception on population growth we identified and marked the 153 cows treated with PZP in the studbook input file for the model. In the "*Distribution of broods per year*" field in Vortex we wrote a function that gives each of these females only a 12% chance of producing a calf if given the chance to breed (compared to a 100% chance for females with no history of contraception).

Survival

Since AP does not track all individual bison, carcasses are difficult to locate, and the herds have only recently been established, accurate age-specific mortality rates could not be calculated. Instead we relied on a combination of age-specific survival estimates from the National Bison Range (Peterson et al., 1991) and estimates from YNP and EINP adapted from Traylor-Holzer et al. (2016) bison PVA (Table 2). Decisions about which values to use for each age class were made by the PVA team based on their experience with the AP bison herds. We used the sex specific estimates of maximum longevity in bison (22 for males and 25 for females) from Jung (2021). Age specific survival estimates (Table 2) are meant to reflect the survival of bison without the effects of hunter harvest or management actions.

Table 2. Age and sex specific survival estimates and the sources for those estimates used in the AP Bison PVA.

Sex	Age Class (Age in Years)	Annual Survival (%)	Source
Males	Calves (0-1)	94	National Bison Range (Peterson et al., 1991)
	Yearlings (1-2)	97	YNP (Traylor-Holzer, 2016)
	Twos (2-3)	97	
	Young Adults (3-4)	97	
	Mature (4-8)	97	
	Dominant (8-15)	70	EINP (Traylor-Holzer, 2016)
	Aged (15-23)	50	National Bison Range (Peterson et al., 1991)
Females	Calves (0-1)	94	National Bison Range (Peterson et al., 1991)
	Yearlings (1-2)	97	YNP (Traylor-Holzer, 2016)
	Twos (2-3)	97	
	Young Adults (3-4)	97	
	Mature (4-8)	97	
	Dominant (8-15)	97	
	Aged (15-20)	75	
	Aged (20-25)	50	
	Aged (25-26)	25	No published data; Expert Judgement

We set the standard deviation due to environmental variation for mortality to the low fixed rate of 3% for all age classes. Given the low mortality of bison from yearlings through the mature stage classes, these stages sometimes experience nearly zero mortality in a given year.

Genetics

Before the early 1870s, tens of millions of bison could be found across North America from northern Mexico to just south of the Arctic Circle in Canada. By the 1880s, bison were nearly extinct, with just six small herds remaining, established from a combined total of less than 100 founder bison (Hedrick, 2009). Today, there are an estimated 20,000 bison maintained in conservation herds across North America, all of them descended from that initial small founder base (Hedrick, 2009).

Populations descended from small founder bases are susceptible to both inbreeding depression and the loss of genetic diversity through drift. The severity of these effects varies among populations, depending on factors such as demographic history and environment (Fox & Reed, 2011). For other small populations, inbreeding depression resulted in lower reproductive output (Keller & Waller, 2002), lower juvenile survival (Keller & Waller, 2002), and lower adult survival (Trask et al., 2021). In bison, similar effects are documented in the Goodnight herd, founded from only five animals in the 1880s, which shows reduced female calving rates and elevated calf mortality (Hedrick, 2009). More generally, the loss of genetic diversity is a loss of a population's adaptive potential, and a growing body of research has identified a linear relationship between population fitness and the loss of genetic diversity (Frankham et al., 2017).

In 2020 and 2021, researchers collected samples from bison in AP bison herds and quantified gene diversity (expected heterozygosity; H_e) and inbreeding based on genetic analysis using single nucleotide polymorphisms (SNPs; Zimmerman et al., 2026). The estimated mean gene diversity (H_e) for the combined AP herds is 0.233. A comparison of estimates of gene diversity and inbreeding levels at AP to other conservation bison herds established that the AP bison herds are among the most genetically diverse and have low levels of inbreeding (Zimmerman et al., 2026).

At the time of sampling, researchers collected samples from bison in the Sun Prairie and Dry Fork herds. Since that time, all animals from the Dry Fork herd were transferred into the Sun Prairie or White Rock herds; therefore, we used the combined gene diversity estimate for both herds to initialize our model. We set the initial gene diversity using the "*Start population with all inbreeding and kinships set to:*" field within the "Genetics" tab of Vortex. This approach initializes all individuals with a kinship value of 0.767, corresponding to a population gene diversity of 0.233 (1-0.767 = 0.233 population gene diversity). Setting gene diversity this way meant that all individuals were equally and highly related to each other, and we did not set an independent inbreeding level for the population. For this reason, inbreeding outputs are not tracked or reported for this model.

Finally, samples were collected before AP imported around 65 bison from the YNP lineage, so it is possible that gene diversity estimates are higher now than they were at the time of sampling.

Genetic Management Goals

Conservation biologists and managers of *ex-situ* populations have a couple benchmark goals for the retention of genetic diversity in a population to avoid the impacts of inbreeding and the loss of genetic diversity:

1. Wildlife populations maintained in *ex-situ* settings are often small and have relatively low rates of reproduction compared to wild populations. Managers of *ex-situ* populations often track parentage in a studbook database, which allows for easy estimation and tracking of rates of genetic diversity and inbreeding. For managers of *ex-situ* populations, a common genetic management goal is to retain 90% of the founding gene diversity for 200 (or 100) years (Soulé et al., 1986).

2. It is harder for managers to track the loss of gene diversity across a population in the wild. For these populations, estimates of effective population size (N_e), and the ratio of effective population size to the census size of a population can be used to set population goals. Effective population size is the size of an idealized population that would lose gene diversity, experience genetic drift, or become inbred at the same rate as the actual population under study. For example, while there are more than 7 billion people on earth, this population is estimated to have the same rate of gene diversity loss, genetic drift and inbreeding as an idealized population of 10-20,000 individuals (Charlesworth, 2009). Frankham et al. (2014) recommends maintaining an N_e greater than 100 individuals to avoid inbreeding depression in the short term (five generations), and an N_e of approximately 1,000 individuals to retain long-term evolutionary potential and population fitness.

If both the census size of a population and the ratio of effective to census size (N_e/N) is known, estimating the effective population size is a straightforward calculation. For conservation bison herds, effective population size to total population size ratios (Ne/N) have been estimated to range from 0.09 to 0.30 in the Witchita Mountains (Shull & Tipton, 1987) and 0.3 to 0.45 at Badlands National Park (Berger & Cunningham, 1994). At the low end of these estimates ($N_e/N = 0.09$), a bison herd would need to have more than 1,100 individuals to have an effective size of 100, or 11,100 individuals to have an effective size of 1,000. Frankham et al. (2014) recommends estimating the effective size of a population based on the Ne/N ratio of 0.1-0.14 based on several meta-analyses.

Currently, the bison herds at AP exist in a management state that falls between *ex-situ* populations and free-ranging wildlife, so we use both of the benchmarks above to assess the genetic health of the AP bison herd for this modeling effort.

PVA Results

Model Validation

We used a historical validation approach (*see* Lacy et al., 2021) to test whether the model accurately simulates AP's bison herd dynamics. We set our model to the size and age structure of the Sun Prairie herd when it was founded in 2005, and projected forward 18 years to the present, running the model for 1000 iterations using *Baseline* reproductive and mortality parameters. For the first 10 model years, we matched AP management by importing, harvesting, and exporting the exact number, age class, and sex of animals recorded annually for the Sun Prairie herd. After year 10, we applied the export function described in the "Bison Management" section for the remainder of the validation period. We then compared the mean projected population size, with error bars representing 95% of the distribution of individual iterations of the simulation, to the annual spring Sun Prairie census counts over the validation period (2006 to 2024).

A comparison of the projected mean population size to observed historical totals across the validation period showed a strong fit (Fig. 8). The model generally tracks the behavior of the Sun Prairie population with the exception of the period between 2014 and 2017. In these years, the growth of the real Sun Prairie population outstripped growth in the validation model, with around 100 more bison in the spring census of 2015 than in the validation model. This likely results from a difference in growth rates between the observed population whose annual intrinsic growth ranged between 0.18 and 0.36 from 2015 to 2017 (Appendix I, Fig. 2), and the model which produces a mean stochastic growth rate of 0.142 (±0.046) in a population free of management. Once the population approaches its carrying capacity and exports begin in the model (2016 to 2018), the effect of the differences in growth rate is less apparent. This finding is consistent with growth in other bison populations, characterized by high annual growth rates of 0.22–0.25 immediately after herd founding, followed by a decline once herds are established or management interventions occur (Brodie, 2008).

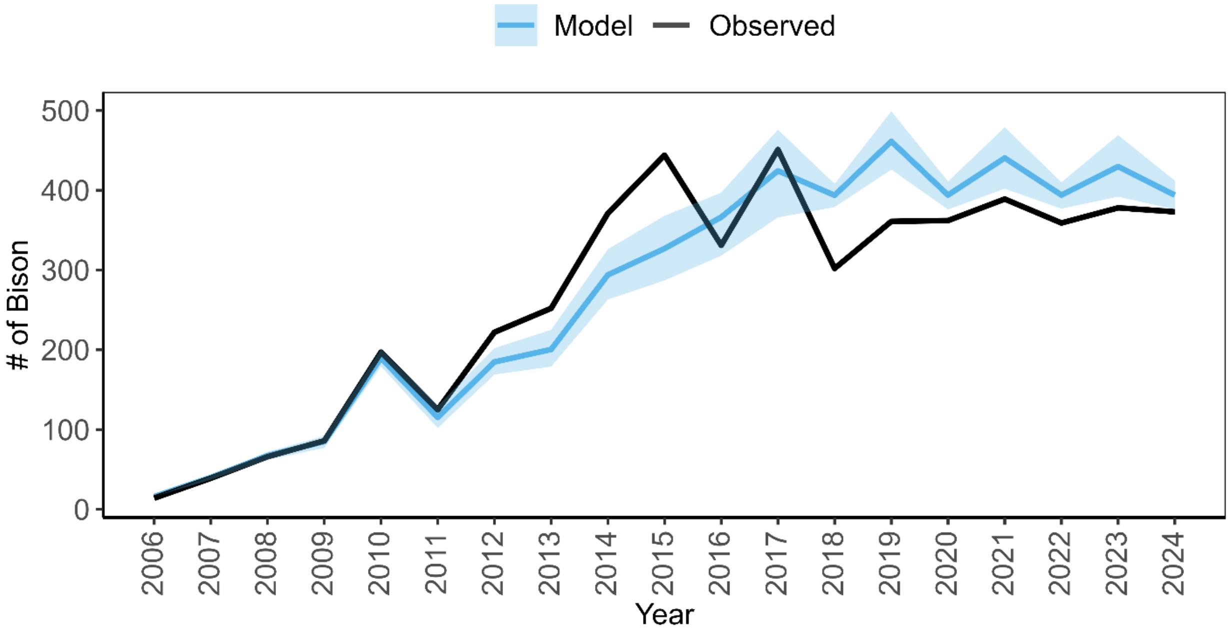

Figure 8. Observed spring census count size of the Sun Prairie herd (black) and the projected mean spring census size (blue; ±SD) from 2006 to 2024.

Sensitivity Analysis

Sensitivity analysis can be used to assess the relative impact of changes to demographic rates on indicators of population health (Mills & Lindberg, 2002). The results of sensitivity analysis can identify which rates are most important to the long-term persistence of a population, which may be targets for management intervention, or which are candidates for further research to understand the factors that influence that rate or to enable better estimates of that rate.

We did not conduct a sensitivity analysis for this PVA; however, Traylor-Holzer (2016), whose model we adapted for this effort, did perform such an analysis. In that study, the effects of varying five demographic rates (adult male survival, adult female survival, subadult survival, juvenile survival, and reproduction) by ±20% were evaluated for their influence on population growth. They found changes to adult female and juvenile survival rates had the largest impact on population growth. Conversely, changes in subadult or adult male survival had little impact. These results make sense in the context of this long-lived, polygynous species; males contribute less to overall reproductive output since a minority of males are responsible for the majority of reproduction.

Baseline Scenario

To evaluate the current population status and trajectory, we built a model scenario that represents our best understanding of current dynamics and management of AP's bison herds. In this scenario, the herds at Sun Prairie and White Rock are maintained at the current carrying capacities, bison roundups and exports occur biennially for each herd, hunters harvest 30 animals annually, and there are no imports of bison from other conservation herds.

In the *Baseline* model, extinction risk for both herds is zero, and both grow to their carrying capacities where they remain at an equilibrium size maintained by exports and annual hunter harvests (Fig. 9).

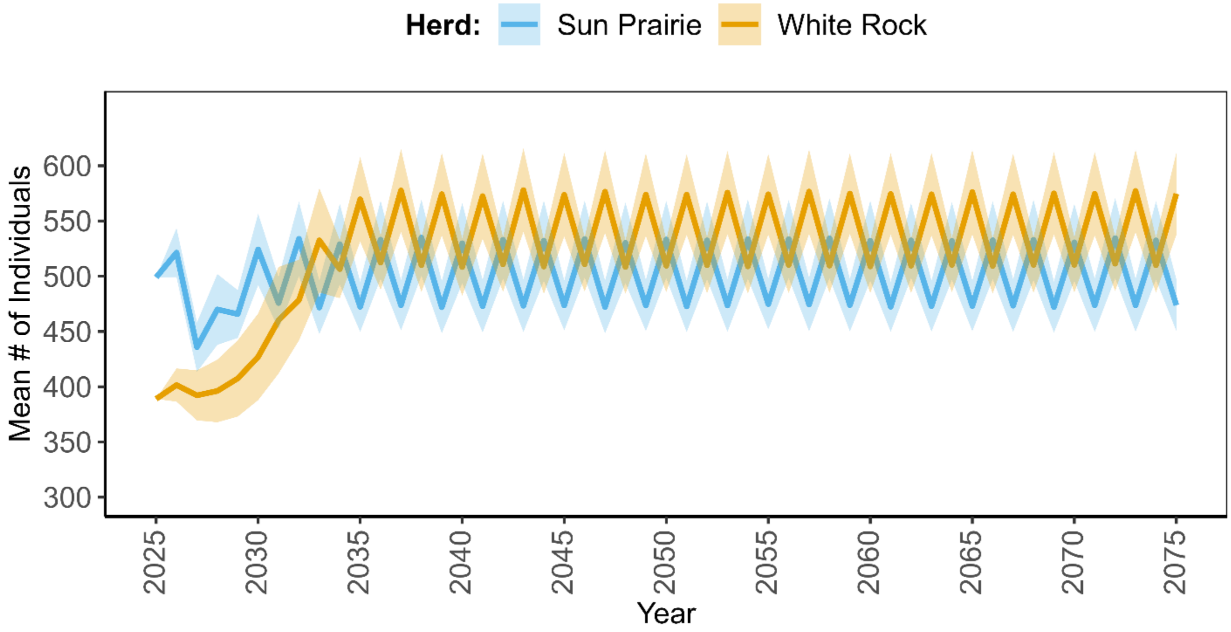

Figure 9. Mean number of bison per year (±SD) in the White Rock and Sun Priaire herds. Census counts were recorded in each model year after calving ended, but before hunter harvest or exports.

Following a large export of animals out of the Sun Prairie herd in year one (mean = 96.7±24), the herd then grows to equilibrium by 2030. At equilibrium, the herd oscillates annually between 472 (±24) bison the fall after a roundup and 535 (±34) the fall of a roundup, and maintains that size for the remainder of the simulation. Once the Sun Prairie herd reaches equilibrium, it averages between ~104 births per year following a roundup and ~118 births in a roundup year (Fig. 10). At equilibrium, ~110 animals are exported from the Sun Prairie herd in roundup years.

Reproduction and growth in the White Rock herd, which begins the simulation with 131 PZP contracepted cows, is slow in the initial four model years. The impact of PZP is evident in the estimated proportion of adult females producing calves in the White Rock herd: during the first four model years only 29–37% produced a calf annually, compared to 54–59% in the Sun Prairie herd. After model year 10, more than 60% of White Rock cows produced calves. Once the PZP treated cows age out of the population, and younger cows reach reproductive maturity, the population reached its equilibrium size of around 600 animals by model year 10 on average. At equilibrium, the herd oscillates annually between 476 (±27) individuals the fall after a roundup and 578 (±38) the fall of a roundup. At equilibrium, the White Rock herd averaged ~110 births the year after a roundup and ~125 in a roundup year, with ~120 animals exported in roundup years.

By model year 50, both populations have an estimated mean gene diversity of 0.227, which represents a loss of ~2.6% of each population's initial gene diversity.

Growth Scenario

PVA team members wanted to simulate the growth of AP's herds to a total of ~5,000 individuals. To do this, we created a model scenario in which the carrying capacities for Sun Prairie and White Rock herds incrementally increase (Table 3), and a new herd is created with a carrying capacity of 2,000 animals, creating a combined population that approaches ~5,000 animals. This scenario maintains the existing system of annual hunter harvests and biennial exports, with no new genetic imports. We also created an alternate new herd that can grow to a total of 1,000 animals, instead of 2,000.

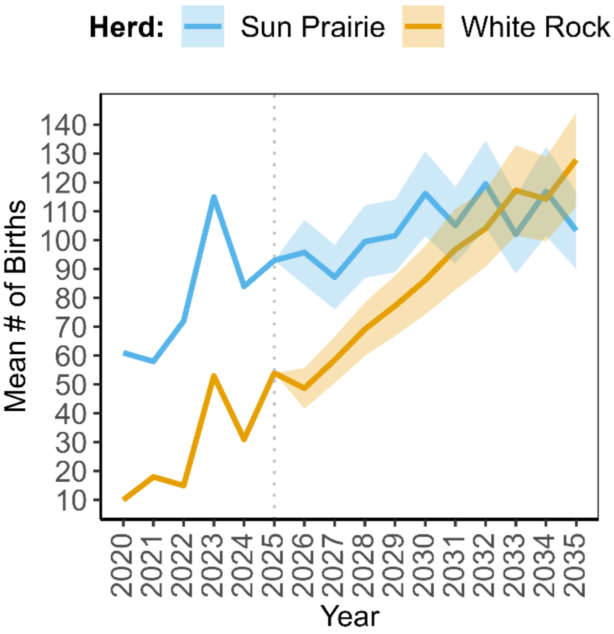

Figure 10. The observed number of births per year from AP calf counts (2020 to 2024) at Sun Prairie and White Rock and the mean projected number of births per year (±SD) in those herds from the *Baseline* model scenario across the first 10 model years. The dotted gray line shows where data from observed calf counts ends and model projections begin.

Both the 1,000 and 2,000 animal herds are created in model year 10, when 150 bison are translocated from existing AP herds. Annual hunter harvests begin with a quota of 30 animals per year once these herds exceed 400 animals. For the larger herd, this quota increases to 100 animals annually when the herd grows beyond 1,000 animals.

Table 3. Carrying capacity for the White Rock and Sun Prairie herds by model year in the *Growth Scenario*.

Sun Prairie		White Rock	
Carrying Capacity	**Model Year**	**Carrying Capacity**	**Model Year**
556	1-8	600	1-4
1000	9-11	800	5-9
1500	12-50	1100	10-50

With the carrying capacities set in the model, the maximum number of bison allowed in this scenario is 4,600. The three herds combined approach that total in model year 34 on average, when the "2,000" population, which started with 150 animals in model year 10, grows to its carrying capacity and exports begin (Fig. 11). At equilibrium, the "2,000" population fluctuates between 1,702 (±69) and 1,938 (±110) animals, with an average of between 401 (±112) and 418 (±111) animals exported from the population each roundup year.

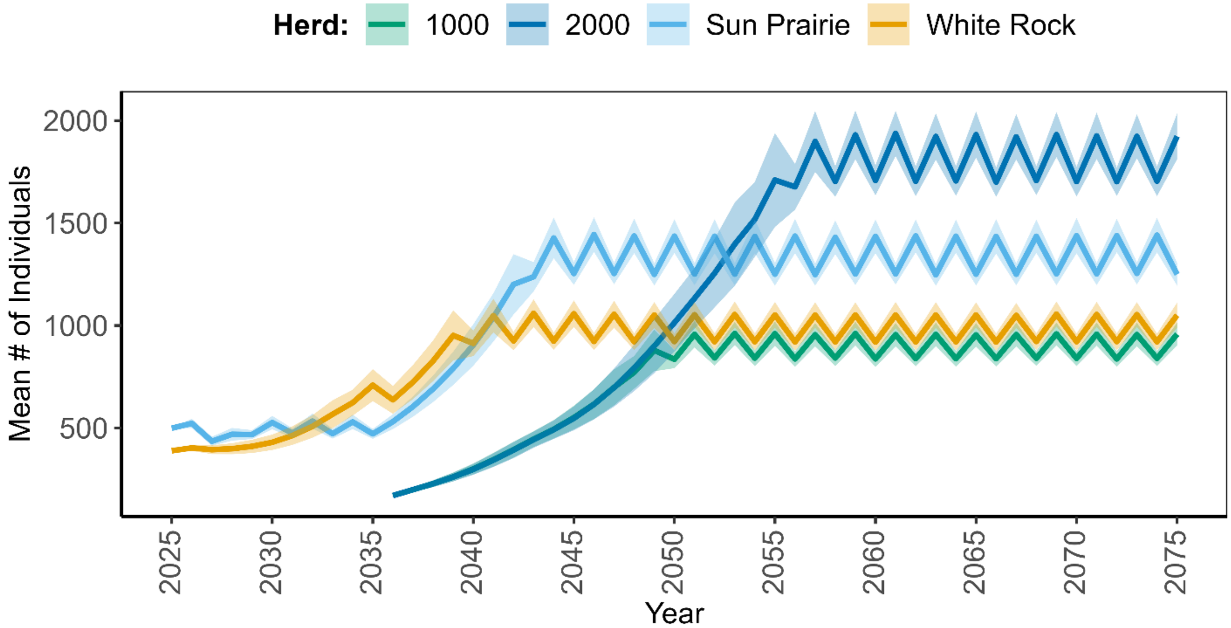

Figure 11. Mean number of bison per year (±SD) in the White Rock and Sun Prairie herds, as well as two herds with carrying capacities set at 1,000 and 2,000 bison. Census counts were taken each model year after calving ended, but before hunter harvest or exports.

Growth in the White Rock and Sun Prairie herds is staggered due to the incremental increases in each herd's carrying capacity, but the Sun Prairie and White Rock herds reach their equilibrium sizes on average in model years 19 and 16, respectively. At equilibrium, between 337 (±83) and 350 (±86) are exported biennially from the Sun Prairie herd and 239 (±62) to 250 (±69) animals from White Rock. If roundups were conducted for the Sun Prairie and "2,000" herd in the same year, when herds have grown to their maximum size, over 700 animals would be exported from AP that year under the current management system. A population that begins with 150 bison in model year 10, but can only grow to 1,000 animals, reaches its equilibrium size at year 26 on average. At equilibrium, between 216 (±59) and 222 (±58) animals are exported from the population in roundup years.

In model year 50, mean gene diversity in the Sun Prairie herd is 0.2298, 0.2292 in White Rock, 0.229 in the "2,000" herd, and 0.2283 in the "1,000" herd. At the two extremes, this means that the Sun Prairie herd lost 1.47% and the "1,000" herd lost 2% of its initial gene diversity on average. Generally, the larger a population, the more gene diversity it retains. However, in this case the "2,000" herd retained less gene diversity than both the smaller Sun Prairie and White Rock herds. This is likely due to the relatively small founding base of the "2,000" herd, all of which came White Rock where individuals already shared some level of relatedness.

Classified as Wildlife

PVA team members wanted to explore the structure and growth of bison populations without management actions. To explore these aspects of bison demography, we created a model scenario in which a bison herd with the size and age structure of Sun Prairie, is allowed to grow for two bison generations (16 years) without hunter harvests, exports, or a carrying capacity.

Starting from its initial size of 499 bison, the *Classified as Wildlife* population reaches an average size of 4885 (±638) individuals in model year 16 (Fig. 12). Across 16 model years, the population averaged 0.142 (±0.46) annual growth and, in the final year of the simulation, the population produced an average of 961 (±161) births.

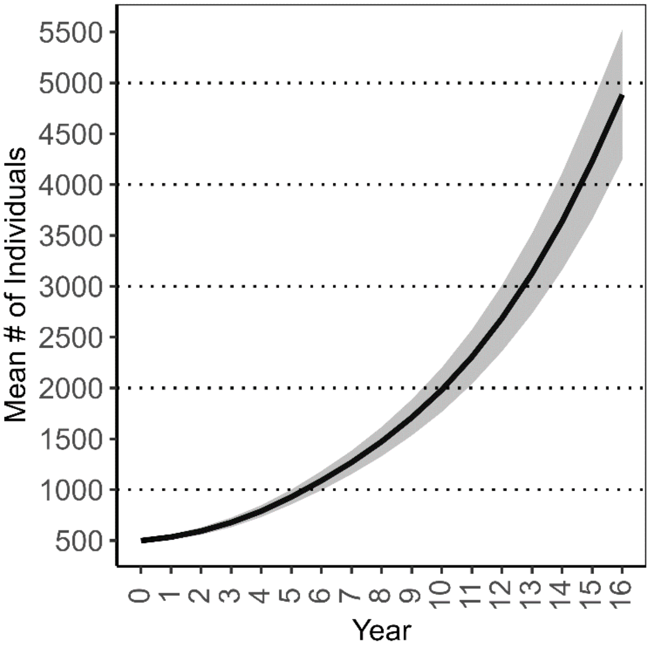

Figure 12. Mean number of bison per year (±SD) in a herd free of management activities across 16 model years. Dotted black lines occur at intervals of 1,000.

We compared the age and sex structure of the *Classified as Wildlife* population to that of the Sun Prairie herd in the *Baseline* scenario, which experiences hunter harvest and export management (Fig. 13). Both populations have a female sex bias, but it was weaker in the *Classified as Wildlife* herd (one male to every 1.15 females) than in the *Baseline* herd (one male to every 1.51 females). The largest differences occurred in the “dominant” and “mature” age classes: on average the unmanaged herd had fewer mature (−1.9%) and dominant females (−2.8%) but more mature (+3.6%) and dominant males (+2.3%) compared to the *Baseline* herd.

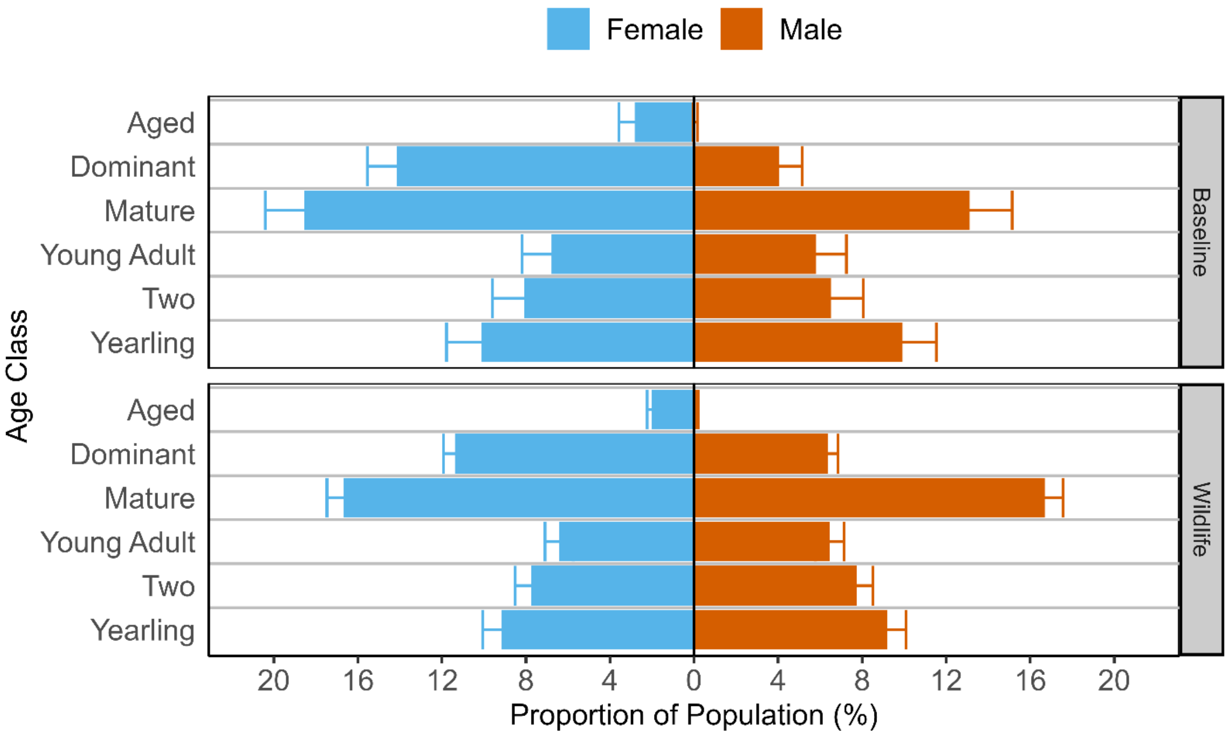

Figure 13. Mean proportion of individuals in each age and sex class (±SD) at model year 50 in the *Baseline* scenario (top) and for a herd free of management activities (*Wildlife*; bottom).

Harvest Scenarios

To assess how bison management influences the age and sex structure of a population, we created a range of scenarios in which 30 animals are harvested annually, but the age and sex composition of those removed varied (Table 4). We compared the resulting structures to those of the population in the *Classified as Wildlife* scenario (i.e., a population free of harvest or management) to identify which harvest strategy best maintains a "natural" age and sex structure.

Table 4. The number of males and females of each age class harvested annually in five scenarios, the mean (±SD) number of births per year in the last year of the simulation, and the resulting ratio of the mean number of male to female bison at model year 50.

	Wildlife		**Baseline**		**No Adult Males**		**Female Heavy**		**Adult Female Heavy**	
Age Harvested	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
Calf	0	0	5	4	12	4	4	5	5	4
Yearling	0	0	9	3	9	3	3	9	3	3
Two	0	0	0	1	0	1	1	0	0	1
Adult	0	0	7	1	0	1	1	7	7	7
Mean Births/Year (Year 50; ±SD)	961.1 (±160.8)		104.3 (±13.4)		106.6 (±13.3)		83.3 (±11.1)		93.4 (±12.2)	
Ratio M:F (Year 50)	1: 1.15		1: 1.51		1: 1.6		1: 0.9		1: 1.19	

Among the three alternate harvest scenarios, harvesting a larger proportion of adult females produced an average sex ratio of one male to 1.19 females at model year 50, which most closely approximated the ratio observed in unmanaged herds (one male to 1.15 females). When the proportion of females harvested increases, the number of calves produced annually decreases (Table 4), and the population's growth rate declines. In the *Female Heavy* harvest scenario, there were ~20 fewer births in model year 50 compared to the *Baseline* scenario.

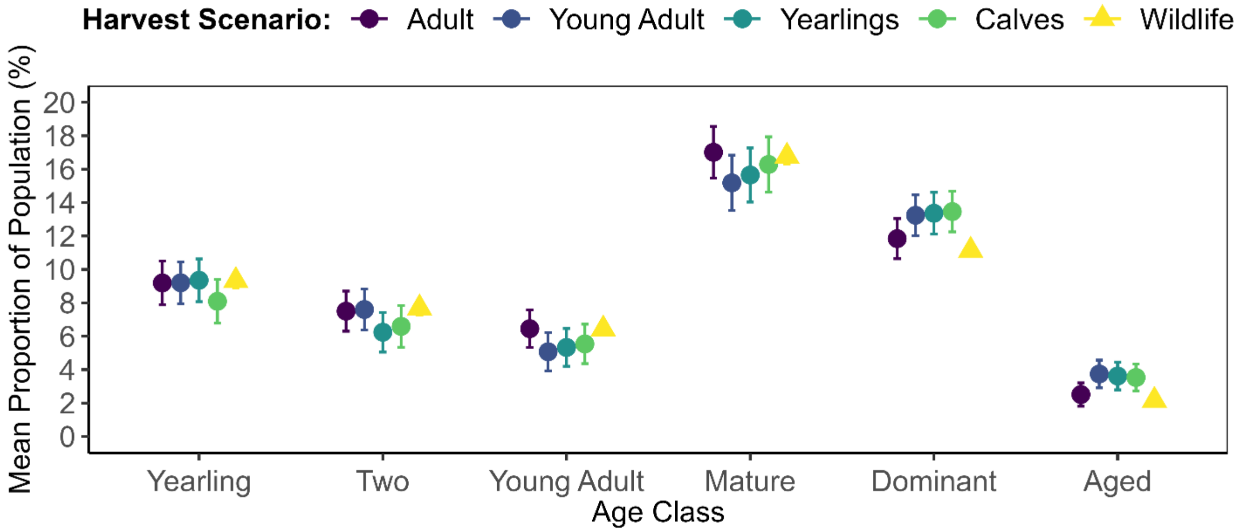

Figure 14. Mean proportion of females in each age class (±SD) at model year 50 under scenarios where different age classes of females (adults, young adults, yearlings and calves) were harvested at higher rates than in the *Baseline* model. The yellow triangles represent the proportion of females in each age class in a population free of management actions (*Wildlife*).

To further explore the impacts of female harvest, we created three alternate scenarios where harvests targeted a larger proportion of young adult females, female yearlings, or calves (Appendix I, Table 1). While a harvest strategy aimed at removing more adult female bison still best approximated the age and sex structure of an unmanaged population (Fig. 14), all increased female harvest scenarios produced male-to-female sex ratios in line with our projections for an unmanaged bison herd, and the differences between scenarios were minimal.

No Access to BLM Grazing Leases

AP bison units are comprised of a combination of properties owned by AP and adjoining public land managed by the BLM where AP holds the grazing rights. It is possible that the BLM could revoke the grazing permit for properties that AP leases, and AP would have to remove bison from those areas. If that were to happen to the White Rock and Sun Prairie herds, AP has a goal of not reducing their total herd size by more than five percent. AP would have to maintain their herd at this smaller size until grazing rights are restored.

We created a model scenario to simulate the loss of grazing rights on BLM holdings at Sun Prairie and White Rock for the full model duration. The model is initialized at a total metapopulation size of 888 bison, so a five percent loss in total herd size would leave a population of 844 animals. If both the White Rock and Sun Prairie herds were maintained at the same population size after the initial reduction, each herd would be managed to a maximum carrying capacity of 422 animals (844/2=422). To achieve this in the model, the Sun Prairie herd was reduced from its current size (initial N = 499) at the first biennial roundup to meet the new carrying capacity of 422 animals, while the White Rock herd (initial N = 389) would grow to the new target size.

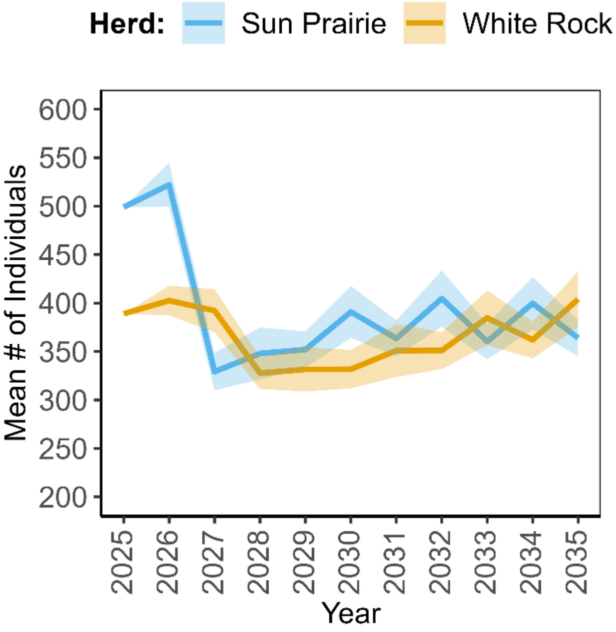

Figure 15. Mean number of bison per year (±SD) in the White Rock and Sun Priaire herds across the first 10 model years. Census counts were taken each model year after calving ended, but before hunter harvest or exports.

In this scenario the Sun Prairie herd experienced a reduction in size in the first model year when 193±25 individuals were exported from the population (Fig. 15). The Sun Prairie herd then grows to its equilibrium size by model year five. Due to the biennial roundup schedule, the first export from White Rock occurs in model year two when the population was already nearing its reduced carrying capacity. At this point 63 (±23) individuals are exported, and the herd reaches its equilibrium around model year eight. Once each herd reaches equilibrium, ~75 animals are exported in roundup years.

At 50 model years, the Sun Prairie herd averages 0.2246 and the White Rock herd averages 0.2244 gene diversity, meaning each herd lost approximately 3.5% of its initial gene diversity.

Import Scenarios

One of AP's management goals is to incorporate the five remaining bison lineages into its herd. To achieve this, bison from unrepresented lineages must be imported, reproduce, and leave enough descendants for their genetics to persist. AP managers wanted to know which combination of age, sex, and number of imported bison would maximize the long-term retention of their genetics in the herd.

Historically, genetic imports have involved no more than 30 bison. To evaluate retention under different conditions, we modeled the impact of importing cohorts ranging from five to 30 individuals in model year one, varying by age class (calves to adults) and sex into the Sun Prairie herd.

If the goal is to ensure that descendants of an import cohort remain in the population while importing the fewest individuals, managers should preferentially choose to import adult females (Fig. 16A). According to our projections, there is an 87% chance that descendants of an initial import of five adult females will remain in the population at 50 model years. The next best class to import is female yearlings, followed by adult males. However, no matter which age and sex class is imported, if 30 individuals are imported there is a greater than 95% chance that descendants of those imports will remain at 50 model years (see Appendix I, Fig. 4 for the average number of descendants from each import).

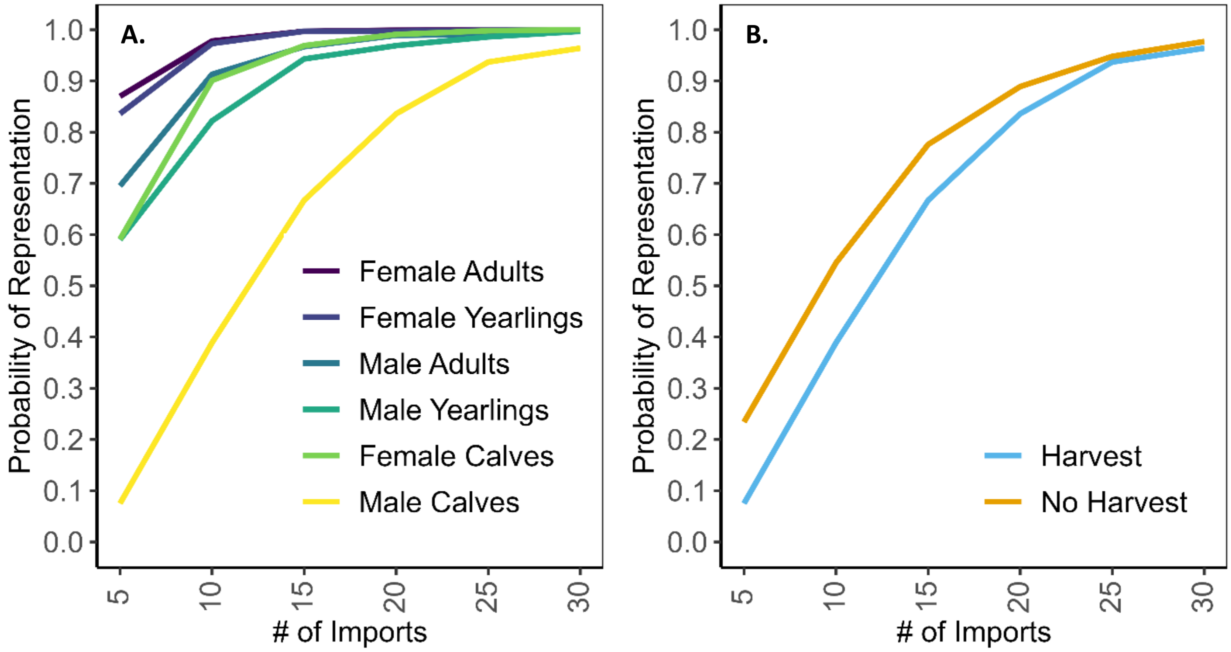

Figure 16. The probability of representation (i.e., the probability that at least one descendant remains in model year 50) from an initial import in model year one of cohorts ranging from five to 30 individuals, varying by age class (calves to adults) and sex into the Sun Prairie herd. A.) shows a comparison of all import cohort scenarios under Baseline mangaement conditions, and B.) compares the probability of represenation for importing cohorts of males calves under Baseline annual hunter harvest conditions (blue) and without hunter harvest (orange).

Importing male calves produces the lowest odds of retention, with five male calves providing only a 7.5% chance of having descendants in the population at 50 years. One potential explanation is that male calves make up a relatively large proportion of annual hunter harvests in our model. To test this, we created a scenario where male calves are no longer harvested, and compared the probability of their descendants remaining in the population at 50 years (Fig. 16B). Without male calf harvest, the odds of descendant persistence do increase, but still remain far below those achieved through imports of other sex and age classes. The low odds of representation associated with importing male calves are likely due to the cumulative impacts of hunter harvest, the delayed age of reproduction for males, and the high mortality rates of males in the peak reproductive age classes.

We also explored the impact on gene diversity of importing cohorts of different sizes (Fig. 17). If importing adult females, a cohort of 10 or more individuals increases the amount of gene diversity in the population at year 50 beyond its initial level.

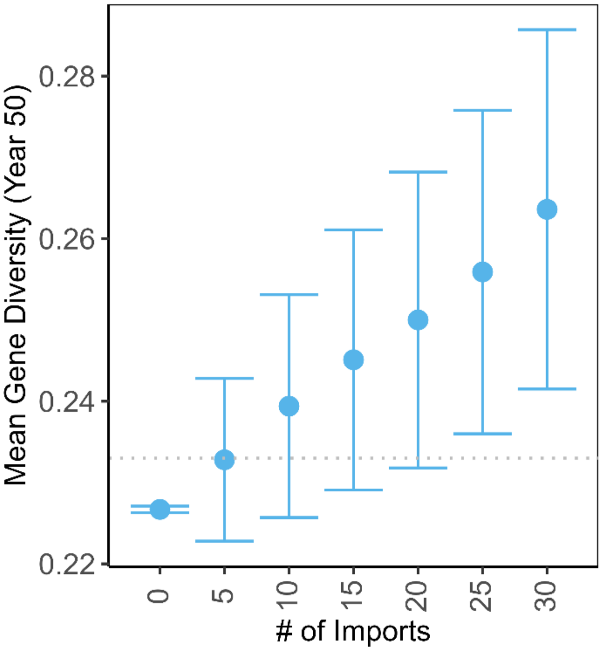

Figure 17. Mean gene diversity (±SD) at model year 50 in scenarios where cohorts of adult female base varying in size from five to 30 individuals were imported into the Sun Prairie herd in model year one. The dotted line represents the initial gene diversity for the AP herds as estimated by Zimmerman et al. (2026).

Mycoplasma Outbreak

Mycoplasma bovis is a bacterial pathogen of domestic cattle that is now a major pathogen in bison herds in North America. Observed fatality rates for individual bison presenting clinical signs of *M. bovis* infection range from 50 to 100% (Bras et al., 2017), and while herd-level mortality is generally low, with a median of 6% reported in a study of production bison herds (Martin et al., 2024), some herds have experienced a 32-45% loss during an outbreak (Martin et al., 2024). Outbreaks can and do reoccur within a herd, with a median of six years between outbreaks recorded in production herds (Martin et al., 2024).

We created a set of model scenarios to explore the potential impacts of a severe *M. bovis* outbreak on AP herds. In the model, these outbreaks occur an average of two times over 50 model years, and cause 32-45% mortality in an outbreak year. These outbreaks affect the White Rock and Sun Prairie herds independently.

In scenarios where an average of two *M. bovis* outbreaks occur in 50 years, herds are smaller than in the *Baseline* scenario (Fig. 18), produce fewer calves, and export fewer animals during roundup years on average. For instance, the White Rock herd is on average ~25–40 animals smaller at equilibrium and produces ~20 fewer animals during roundups compared to the *Baseline* scenario. Mean gene diversity at model year 50 for the Sun Prairie and White Rock herds is 0.2264, representing a loss of around 2.8% of initial gene diversity.

In the *Mycoplasma* scenario, the White Rock herd has a probability of extinction of 0.01 (*see* Appendix I, Fig. 5 for a visualization of extinction at White Rock), while the Sun Prairie herd is near zero (0.002). The White Rock herd is likely more susceptible to extinction due to its smaller initial size and lower reproductive rates in the initial years driven by the large proportion of PZP contracepted cows in the population. To explore steps AP could take to prevent extinction, we created a scenario where hunter harvests are paused for two years following an outbreak to offset the combined impacts of disease and harvest. If annual hunter harvests are paused the year of and the year after an outbreak occurs, the probability of extinction drops to near zero for the White Rock herd and zero for the Sun Prairie herd.

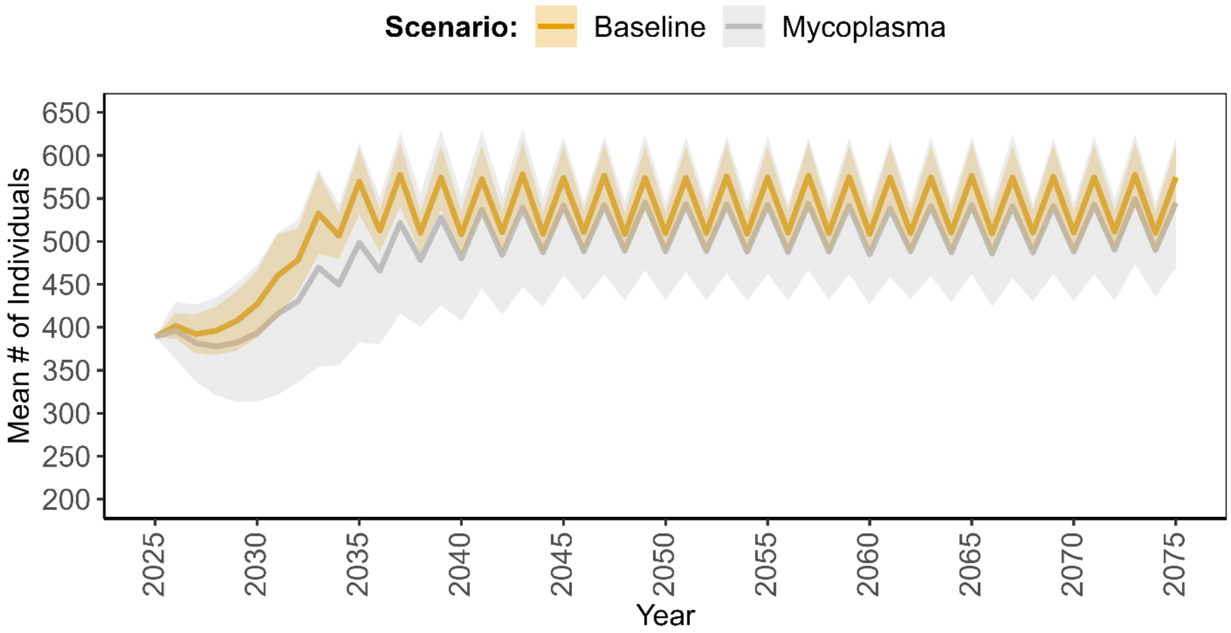

Figure 18. Mean number of bison per year (±SD) in a White Rock herd that experiences an average of two *M. bovis* outbreaks in 50 years (*Mycoplasma*) and in the *Baseline* scenario. Census counts were taken each model year after calving ended, but before hunter harvest or exports.

Small Population

We created a model scenario to explore the behavior of a small population of bison (carrying capacity = 50 animals) under AP's current bison management system. This population was founded by an import of 20 bison (six males and 14 females) from the Sun Prairie herd in model year one.

On average this population reaches its carrying capacity and equilibrium at model year six (Fig. 19). From that point forward, between 12 (±7) and 15 (±7) animals are exported during biennial roundups, and the population averages between seven and 10 births per year.

Without imports from other herds, mean gene diversity declined to 0.1798 over 50 model years, representing a loss of 21% from the initial gene diversity in the Sun Prairie herd. To examine strategies for maintaining gene diversity in this small population, we created two alternate

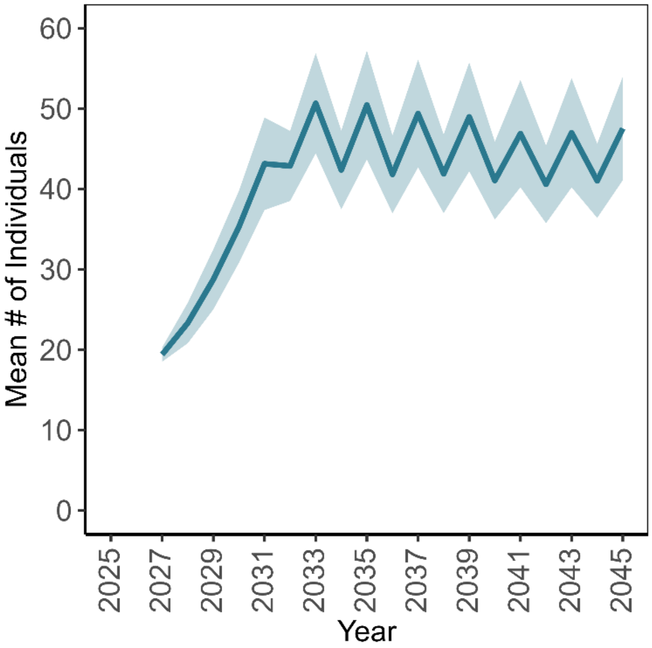

Figure 19. Mean number of bison per year (±SD) in a herd with a carrying capacity of 50 individuals across the first 20 model years. Census counts were taken each model year after calving ended, but before hunter harvest or exports.

scenarios in which groups of five female yearlings from the Sun Prairie herd were imported into the small population at five-year or 10-year intervals. Populations receiving imports every five years had a mean gene diversity of 0.2017 (11% loss) at 50 model years and the population with imports every 10 years had a mean gene diversity of 0.1932 (15% loss).

Roundup Every Three Years

AP staff wanted to explore what management of a larger population might look like when roundups and exports occur every three years, instead of biennially. In theory this would mean that while roundups occur less frequently, more bison would be exported following each roundup event. For this scenario, we initiated the model with the Sun Prairie herd, but managed the herd to a maximum size of 700 with round-ups and exports occurring every three years.

On average this population reaches its carrying capacity and equilibrium at model year five (Fig. 20). From that point forward, between 178 (±50) and 192 (±51) animals are exported every three years. At equilibrium the average population size varies between a high of around 623 (±50) to 634 (±51) animals during the fall of a roundup year and a low of 413 (±12) to 415 (±11) animals the spring after a roundup. Across 50 model years, an average of 2951 (±180) total bison are exported in this model scenario compared to around 2637 (±148) in the *Baseline* scenario where the population is managed to a lower size and exports occur every two years.

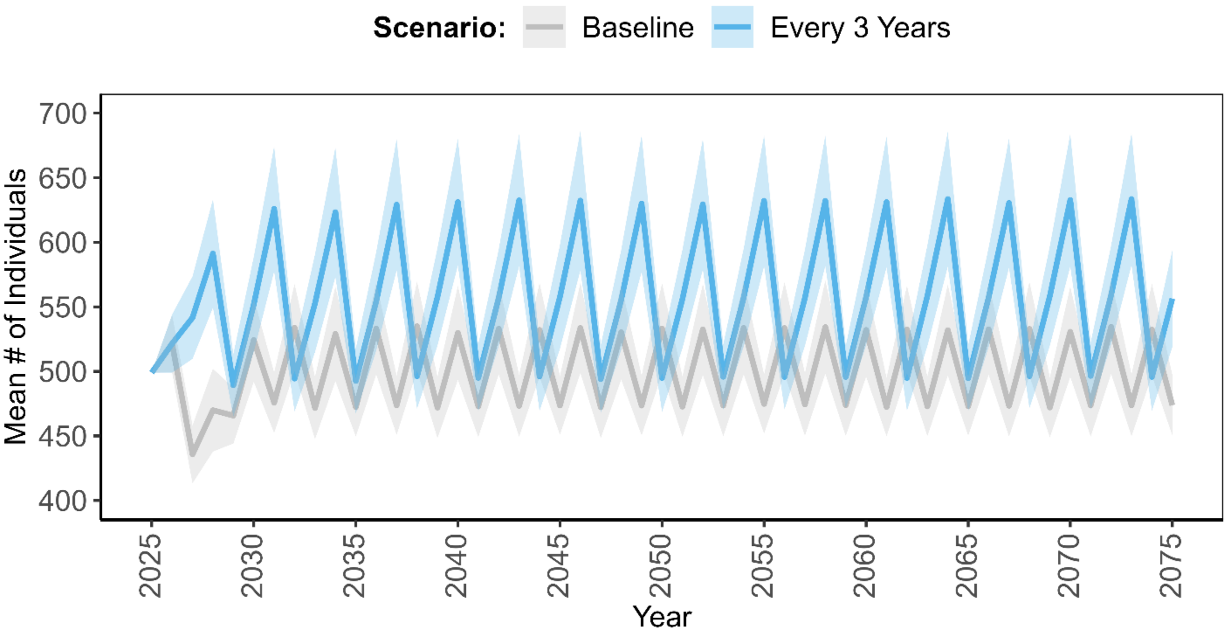

Figure 20. Mean number of bison per year (±SD) in the Sun Priaire herd in a scenario where roundups occur every three years ("Every 3 Years") and every two years ("Baseline"). Note the carrying capactiy in the "Every 3 Year" scenario is higher than in the "Baseline" scenario. Census counts were taken each model year after calving ended, but before hunter harvest or exports. Exports occur every three years in this model scenario.

At model year 50, the Sun Prairie herd averages 0.2274 gene diversity, meaning the herd lost approximately 2.4% of its initial gene diversity.

Discussion

American bison are adaptable, hardy, and their populations are capable of rapid and sustained growth (Brodie, 2008). This means that at the densities that bison are maintained at within fenced conservation herds today, the limits on population growth are not usually biological, but regulatory, logistical, or financial. Even for bison that range across the Yellowstone/Teton landscape, where they contend with a full suite of native large carnivores, diseases like brucellosis, and deep winter snow, population managers still have to take significant steps to manage the herd to its target size (Geremia et al., 2014). Overall, in order to model the dynamics of bison herds at AP, we had to model both bison population dynamics and human management of those populations.

Model Uncertainty

Since we developed this model with bison managers at AP, it effectively simulates the AP export and harvest driven management system. However, our model validation showed that the observed historical growth rate of the Sun Prairie bison herd was generally higher than the model's growth rate. This means that, at least at historical herd sizes and bison densities, our model under-predicted the number of bison on the ground. This is an important reminder that PVA should not be viewed as an exact predictor of the future, but instead a tool for comparing the relative impacts of changes to herd management on population growth and persistence.

This is especially relevant when interpreting results for scenarios in which AP herds grow beyond their current size. The current model does not incorporate density-dependent limits on population growth, in part because AP herds are managed below the expected ecological carrying capacity, and no empirical estimates of a bison-specific carrying capacity on AP properties exist. However, as herds grow, carrying capacity and density-dependent demographic effects will become important considerations, as these impacts have been observed in other bison populations (Brodie, 2008; Koons et al., 2015). Moreover, although bison can mitigate some density-dependent effects by moving long distances in search of food (Plumb et al., 2009), this strategy could be limited for fenced herds (Koons et al., 2015).

At the time of writing, large carnivores do not influence bison mortality at AP, and the calf and yearling mortality rates used in this model were from other fenced herds without predation. In 2023, the first grizzly bear (*Ursus arctos*) was recorded on AP, marking the return of this species to the Missouri Breaks landscape, and gray wolves (*Canis lupus*), present throughout much of western Montana, are expected to recolonize areas within AP. Both species prey on bison (Jung et al., 2023; Varley & Gunther, 2002), although bison kills by grizzlies are rare (Varley & Gunther, 2002) and wolves preferentially choose other ungulate prey when available (White & Garrott, 2005). However, mortality rates for calf and yearling bison in YNP, where there are both grizzlies and wolves, are significantly higher (Traylor-Holzer, 2016; Appendix I, *Yellowstone National Park Mortality Rates*) than those used in this model. Even if predators do not cause significant mortality for AP herds in the future, their presence alone can change the behavior and movement of bison (Laundré et al., 2001).

With potential changes on the horizon, AP could benefit from a standardized data-collection framework that supports estimation of survival rates across all age classes. Most adult bison on AP are individually identifiable through ear tags, so the foundation is already in place for estimating adult survival using mark–recapture or known-fate methods. The major information gap is calf and yearling survival. Bison are tagged during biennial roundups, and depending on when a calf is born relative to the roundup schedule, individuals may be approaching two years old before they enter AP's bison database. AP staff do estimate calf numbers during the annual fall aerial census, but these counts include only calves that have already survived the vulnerable early-life stages. Given that calf survival is variable in bison (Brodie, 2008) and a key driver of population growth (Traylor-Holzer, 2016), improving early-life data collection would improve our understanding of population dynamics at AP. Collecting this information now would also allow managers to assess the impacts of predation and increased population size in the future.

Genetics

Of the criteria for success for AP's bison herds, only the goal that the herds should have all five unique bison lineages represented directly addresses genetics. When bison were at their nadir in North America, the species existed only in five private ranch herds (i.e., five lineages) and a small group of wild individuals in YNP (Hedrick, 2009). Descendants of these five herds therefore represent all of the remaining genetic diversity of the species, including herds from both the northern and southern reaches of their historical range. The goal of incorporating bison from all five unique lineages is based on the desire to maximize the adaptive potential of AP herds; for example, if Northeastern Montana becomes hotter and drier in the future, genetics from southern-plains–adapted bison may help AP herds continue to thrive. Our model shows that importing 30 individuals of any sex or age class from an unrepresented lineage yields a >95% probability that their descendants will be represented in the population in 50 years. Fewer individuals could be imported and achieve a similar result if any sex or age class other than male calves is imported.

Over the course of the PVA workshop, we also discussed the genetic management goals of maintaining 90% founder gene diversity for 200 years (Soulé et al., 1986) and maintaining an effective population size (N_e) of greater than 100 individuals (Frankham et al., 2014). These goals focus on avoiding the impacts of inbreeding depression in the short term, rather than increasing adaptive potential. In the *Baseline* model, the Sun Prairie and White Rock herds are close to meeting both goals due to their large size and high growth rates. Research has shown that the AP herds are genetically diverse and have low levels of inbreeding compared to other conservation herds (Zimmerman et al., 2026). This finding, combined with our projections of gene diversity loss, means that without importing bison, the White Rock and Sun Prairie herds are in a good position to avoid inbreeding depression, at least for the model duration.

However, another of AP's criteria for success is that their herds grow to a combined size of 5,000 individuals. According to conversations with the PVA team, this goal is in part rooted in achieving an N_e of 500 (5,000 bison * N_e/N of 0.1 = N_e of 500), which was the previous benchmark for maintaining evolutionary potential of a population over the long term (Franklin, 1980) and has since been updated to the "100/1000" rule recommending an N_e of 1,000 (Frankham et al., 2014). Using the N_e/N ratio suggested by Frankham et al. (2014) of 0.1 to 0.14, a bison herd would need between 7,143 and 10,000 individuals to achieve an N_e of 1,000. In our *Growth* scenario, which reflects the most likely path to ~5,000 bison given favorable regulatory conditions, the maximum population size achievable was 4,600 bison. Maintaining the long-term evolutionary potential of the AP herds will therefore require periodic importation of bison.

Our model did not explore the implications of periodically importing bison into the AP herd, but we can draw from the findings of the DOI bison model (Hartway et al., 2020) which focused on maintaining genetic diversity in bison herds through translocations. Hartway et al. (2020) recommends that herds import two to three bison every five to 10 years. Larger herds (>500 bison) require translocations less frequently than smaller herds, a finding supported by the projected loss of gene diversity in the *Small Population* scenario (Fig. 21). The source of translocations is one of the most important considerations. Hartway et al. (2020)

found that importing bison from the least genetically related herds, and varying the source for translocations, resulted in the greatest increases in genetic diversity. Additionally, it is recommended that a mix of males and females be imported to retain sex-specific genetic diversity (Frankham et al., 2017). Identifying the least-related herd for imports is outside of the scope of this analysis, but both the DOI Bison Metapopulation Management Working Group and the Association of Zoos and Aquariums Bison SAFE program have the expertise and resources to help.

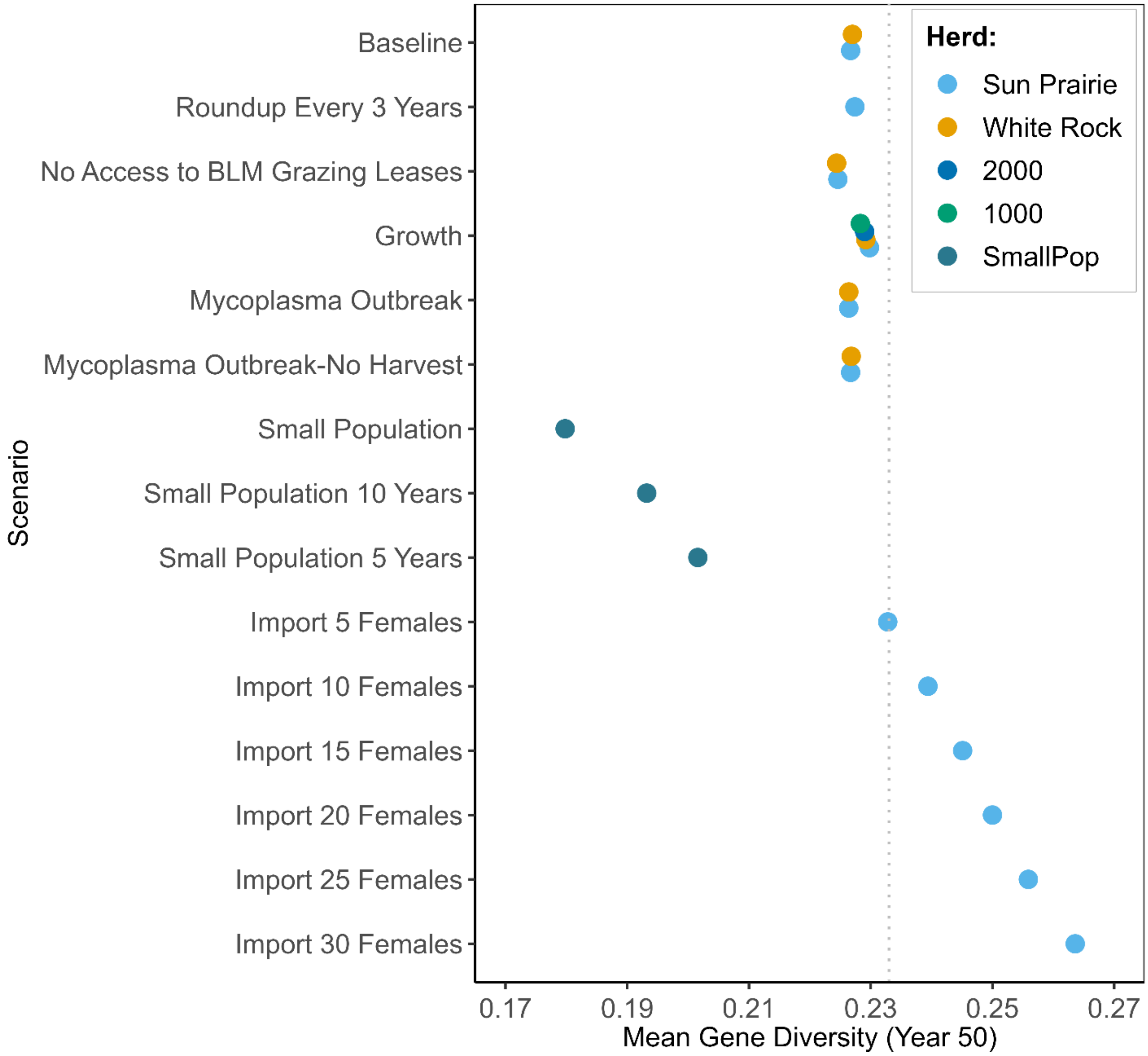

Figure 21. Mean gene diversity in each herd in model year 50 for all scenarios. The dotted line represents the initial gene diversity for the AP herds as estimated by Zimmerman et al. (2026).

Finally, in our *Growth* scenario, new herds exhibited relatively low genetic diversity despite their large projected sizes (see “1000” and “2000” herds; Fig. 21). This resulted from our assumption that all White Rock animals, which served as the sole founders, are related. The reality is more complex: White Rock bison originate from EINP or YNP, and thus share some degree of kinship due to the small founder sizes and long-term interbreeding of those source herds. However, EINP and YNP bison are not related to each other. Hartway et al. (2020) recommends establishing new herds with at least 15 founders (i.e., 15 bison that are not directly related to each other), and augmenting the population with additional bison in subsequent years to increase gene diversity. If AP starts a new herd from a small founder base, we recommend identifying a founding group of bison that represents each of the unique lineages already found at AP, and minimizing the number of direct relatives (e.g., siblings, parents, cousins) in the group.

Herd Management

The robust growth rates of the AP herds mean that continuing exports and hunter harvests are required to maintain populations within the designated carrying capacities.

With the current restrictions on the growth of AP's herds, biennial roundups are the most important tool for maintaining herds at their target size. They also require substantial AP resources, from building, moving, and dismantling the roundup pens, to herding, processing, and exporting the bison. As AP herds grow, and new herds are created, these demands increase (Fig. 22 and Appendix I, Fig. 6). Our model highlights a few important points for planning future roundups. First, the model does not preferentially select specific sex or age classes for export. This is an important consideration since our *Harvest* scenarios show that small changes in the sex and age of animals removed from the population can have large impacts on the sex and age structure. If specific sexes and ages are preferentially chosen for export, managers may want to change the sex and ages of animals removed through hunter harvest to achieve the target sex ratio. Second, the frequency of roundups and exports is important to consider. The Sun Prairie herd in our *Roundup Every Three Years* scenario has a higher carrying capacity and more individuals are exported at each roundup event, but since roundups occur less frequently, the total number of bison exported is only marginally greater than in the *Baseline* model where roundups occur every two years (Fig. 22). Lastly, for future planning, it is important to consider the combined total number of exports for all herds under management. For instance, in the *Growth* scenario if the White Rock, Sun Prairie, and the "2,000" herd all grow as projected to their target sizes, managing those herds would require exporting an average of ~15,000 bison across 50 years.

Although hunter harvest removes far fewer animals than biennial exports, it still has an outsized influence on AP herd growth and structure. Our *Harvest* scenarios show that even small shifts in the age or sex composition of the 30 animals taken each year can markedly affect population structure and growth. For example, increasing the annual harvest of adult females from one to seven shifted the sex ratio toward that of an unmanaged herd (*see* the *Wildlife* scenario) and reduced births by ~10 per year compared to *Baseline*, lowering population growth.

Within all but the *Growth* scenarios, the number of animals harvested by hunters remains the same each year no matter the size of the population. This inflexibility means that hunter harvests remove a small proportion of the herd when a population is large, but a much larger proportion when a population is small. This can have serious implications. Our *Mycoplasma* scenarios showed that when the population is at its lowest size following an outbreak, hunter harvests increase the probability of "extinction" for the White Rock herd from zero (with no harvest) to one in one hundred. If managers want to increase growth rates in the population, harvesting fewer females or pausing harvests entirely could be effective management options.

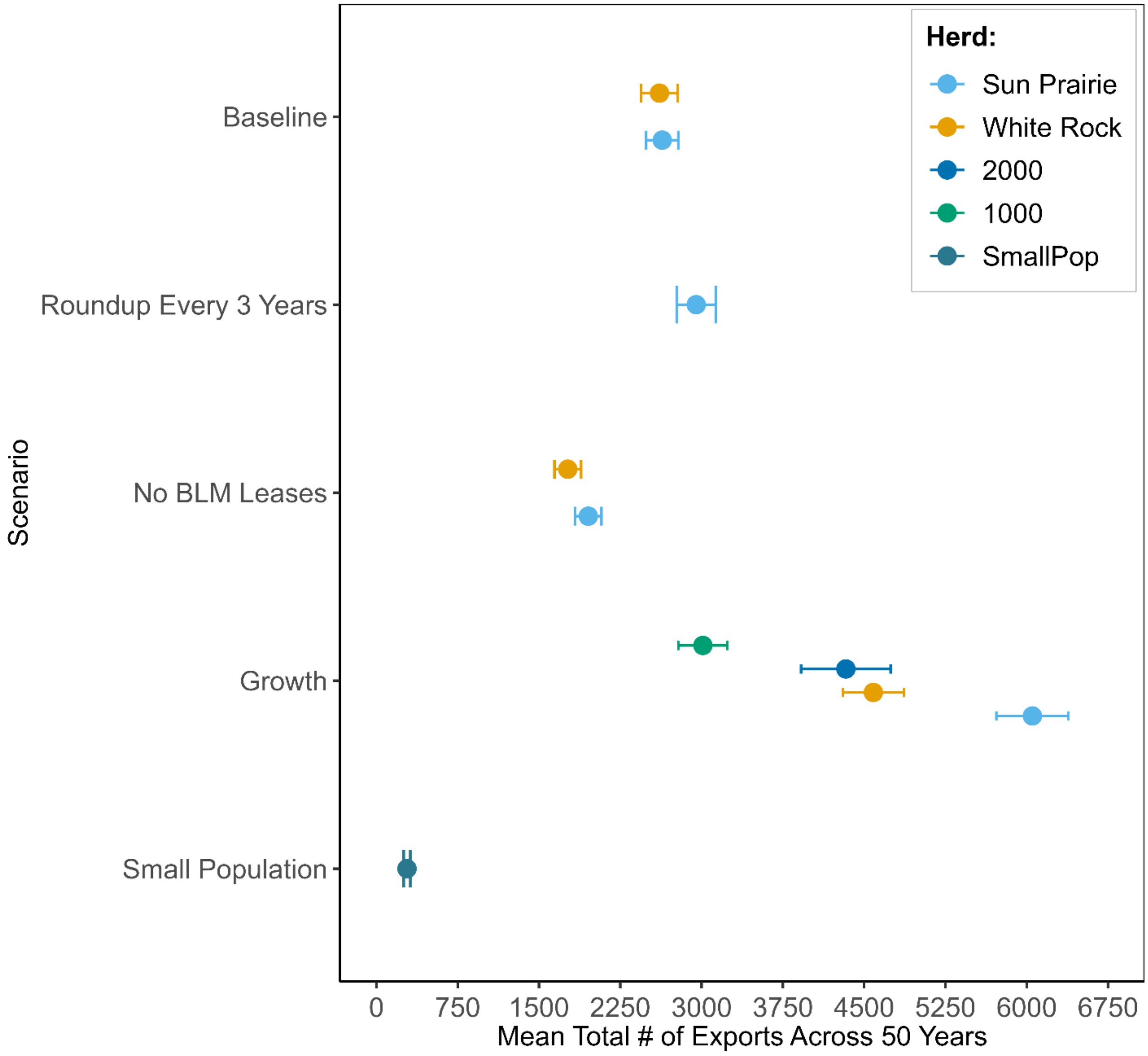

Figure 22. The mean total number of bison exported (±SD) from each herd in each scenario across 50 model years.

Conclusion

Our model shows that AP bison populations are capable of rapid growth and are resilient to the impacts of emerging threats such as *M. bovis*. However, realizing long-term conservation goals including maintaining genetically healthy, demographically stable, and ecologically resilient herds will require proactive planning in the face of potential change. If AP bison herds can expand onto new properties and herds continue to grow, managers will need to account for density-dependent dynamics, potential recolonization by large carnivores, and the demographic consequences of both hunter harvest and roundup exports. At the same time, maintaining genetic diversity at levels consistent to ensure long-term evolutionary potential will require periodic translocations from other conservation herds. Developing standardized data-collection protocols, planning for roundups with larger herds, and coordinating genetic management across herds will allow AP to achieve their goal of restoring large, ecologically functional bison herds to the Northern Great Plains.

Acknowledgements

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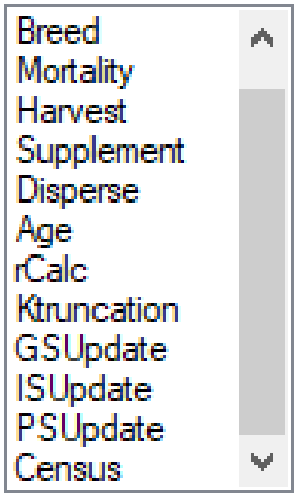
Appendix I. Supporting Materials



Breed
Mortality
Harvest
Supplement
Disperse
Age
rCalc
Ktruncation
GSUpdate
ISUpdate
PSUpdate
Census

Figure 1. The annual order of operations within our Vortex model.

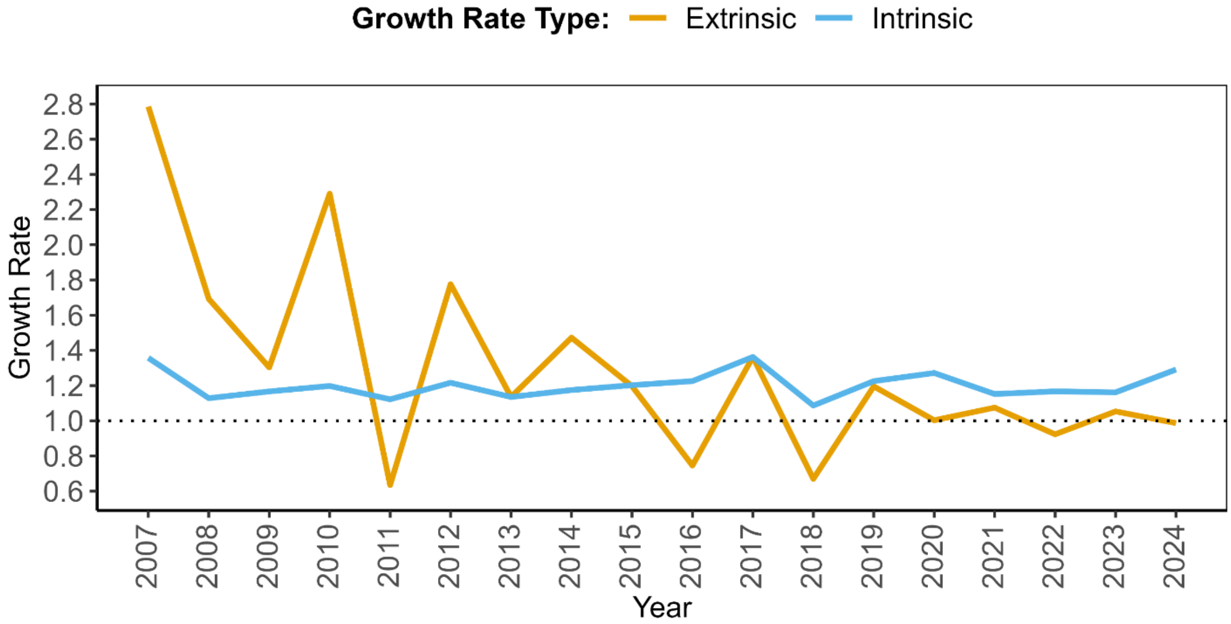


Figure 2. Annual extrinsic and intrinsic growth rates calculated for the Sun Prairie herd from AP data (2007-2024). A growth rate greater than one indicates that a population is growing, and below one indicates a population is shrinking. The extrinsic growth rate represents the overall population growth that results from both internal demographic processes (births and natural mortality) and external influences such as imports, exports, and hunter harvests. The intrinsic growth rate controls for external factors, and is solely the product of births and natural mortality within the population.

Harvest Scenarios

Table 1. The number of males and females of each age class harvested annually in five female heavy harvest scenarios and the resulting ratio of the mean number of male to female bison at model year 50.

	Wildlife		**Calves**		**Yearlings**		**Young Adult**		**Adult**	
Age Harvested	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
Calf	0	0	5	10	5	4	5	4	5	4
Yearling	0	0	3	3	3	9	3	3	3	3
Two	0	0	0	1	0	1	0	7	0	1
Adult	0	0	7	1	7	1	7	1	7	7
Mean Births/Year (Year 50; ±SD)	961 (±160)		96 (±12)		95 (±12)		93 (±12)		93 (±12)	
Ratio M:F (Year 50)	1: 1.15		1: 1.14		1: 1.16		1: 1.17		1: 1.19	

Yellowstone National Park Mortality Rates Scenario:

The calf and yearling mortality rates used in our model were from other fenced herds free of predation. During the second PVA workshop, participants discussed what the age and sex structure of bison herds would look like when the herds experience predation. To explore this question, we built a model scenario using the age and sex specific mortality rates used by Traylor-Holzer (2016) to model the bison herd at YNP which co-occur with a full suite of native predators. This scenario did not include exports or hunter harvests, and we ran the scenario for 16 years to facilitate comparison with the *Wildlife* scenario.

Table 2. Age and sex specific mortality rates for bison at YNP from Traylor-Holzer (2016)

Age Class	Female	Male
0	35	38.5
1	20	22
2	3	10
3	3	10
4	3	5
5	3	5
6	3	3.3
7	3	3.3
8	3	3.3
9	3	3.3
10	18	3.3
11	18	3.3
12	18	3.3
13	18	40
14-19	25	40
20	100	100

The YNP mortality rates do not include the effects of managed removals or culling of bison. Mortality rates for calf and subadult bison are significantly higher at YNP than those used in our model (Table 2), although we cannot disentangle the impact of predation on these rates compared to other factors at YNP.

Growth in a population experiencing YNP mortality rates (mean stoch-r = 0.624) is much lower than in our *Wildlife* scenario (mean stoch-r = 0.142), and the population achieves a final size of 1192 (±188) bison compared to 4885 (±638) in the *Wildlife* scenario. For reference, bison managers in YNP ended an annual culling program in 1966, and in the winter of 1968 the park supported an estimated 418 bison. By the winter of 1994, the population had increased to approximately 4,100 individuals (White et al., 2022). Assuming a constant growth rate over this 26-year period, the YNP population grew at an average annual rate of 8.8%. Similarly, following a large cull in 1997, an estimated 2,170 bison remained in the park in 1998. By 2005, the population had increased to approximately 5,015 individuals (White et al., 2022), corresponding to an average annual growth rate of about 12%. This indicates that observed growth in the YNP bison population has at times exceeded, and in some cases substantially exceeded, the average growth rate (6.2%) in our simulation under estimated YNP mortality rates.

The sex ratio in the YNP population is more female biased than in the *Wildlife* scenario with 1.2 females to every male compared to 1.15 females to every male. With higher calf and subadult mortality rates, the YNP population also has a higher proportion of mature and dominant bison, and a lower proportion of younger bison compared to the *Wildlife* scenario (Fig. 3).

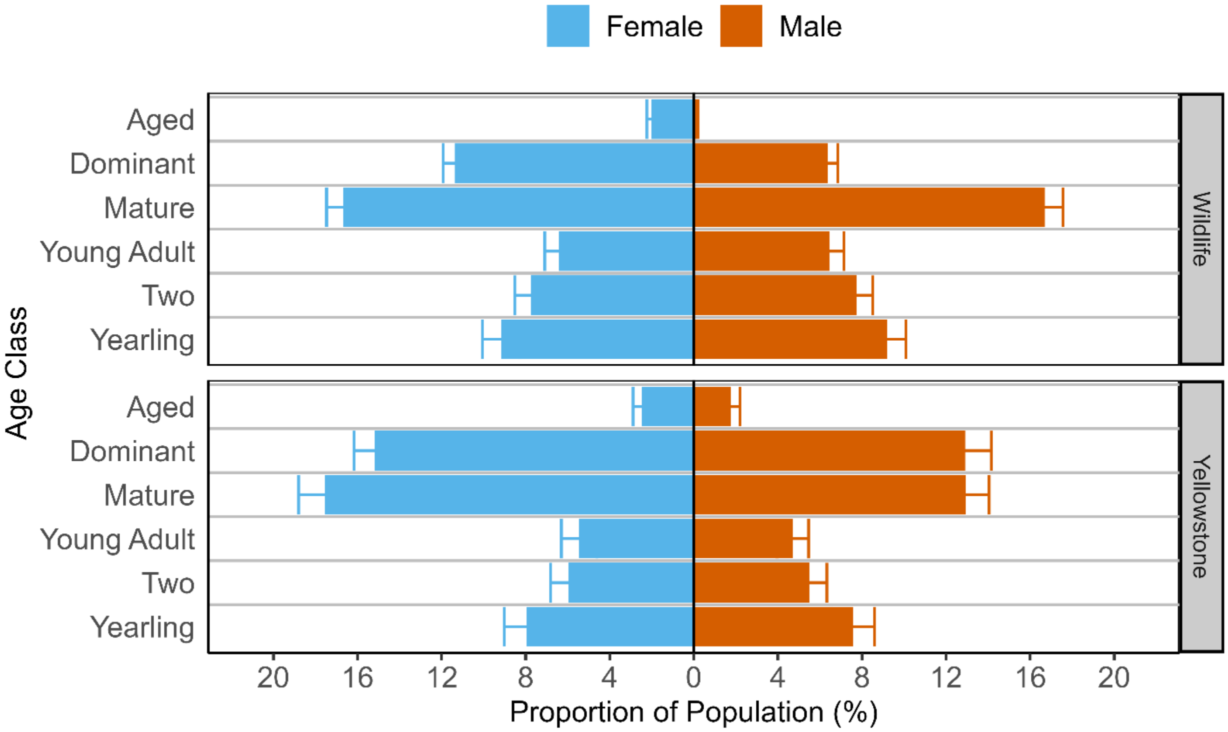


Figure 3. Mean proportion of individuals in each age and sex class (±SD) at model year 50 in the *Wildlife* scenario (top) and for a herd experiencing YNP mortality rates (*Yellowstone*; bottom).

Import Scenarios:

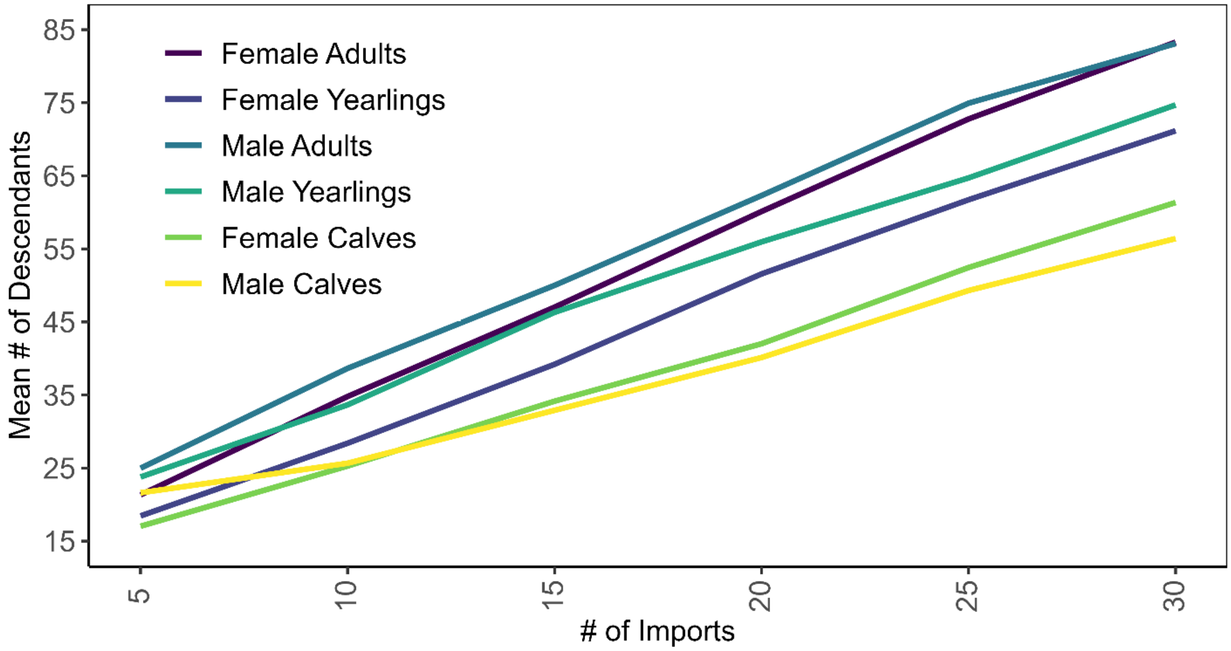


Figure 4. The mean number of descendants in the population at model year 50 following an initial import in model year one of cohorts ranging from five to 30 individuals, varying by age class (calves to adults) and sex into the Sun Prairie herd.

Mycoplasma Outbreak Scenario:

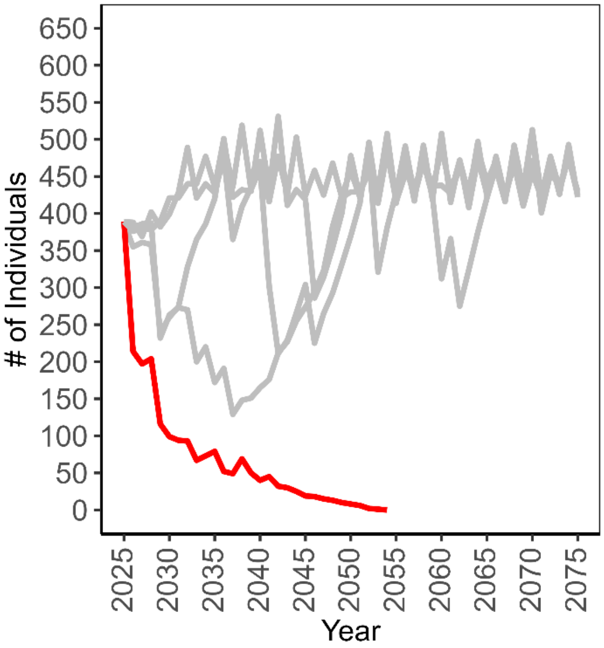


Figure 5. Projected number of bison per year in the White Rock herd that experiences an average of two *M. bovis* outbreaks in 50 years. Each line represents an individual model run; gray lines show runs where the population was extant at model year 50, while the red line shows a run where the population went extinct. We ran the model for 1,000 iterations, but this plot only shows five model runs for visual clarity. Census counts were taken each model year after calving ended, but before hunter harvest or exports.

Herd Management:

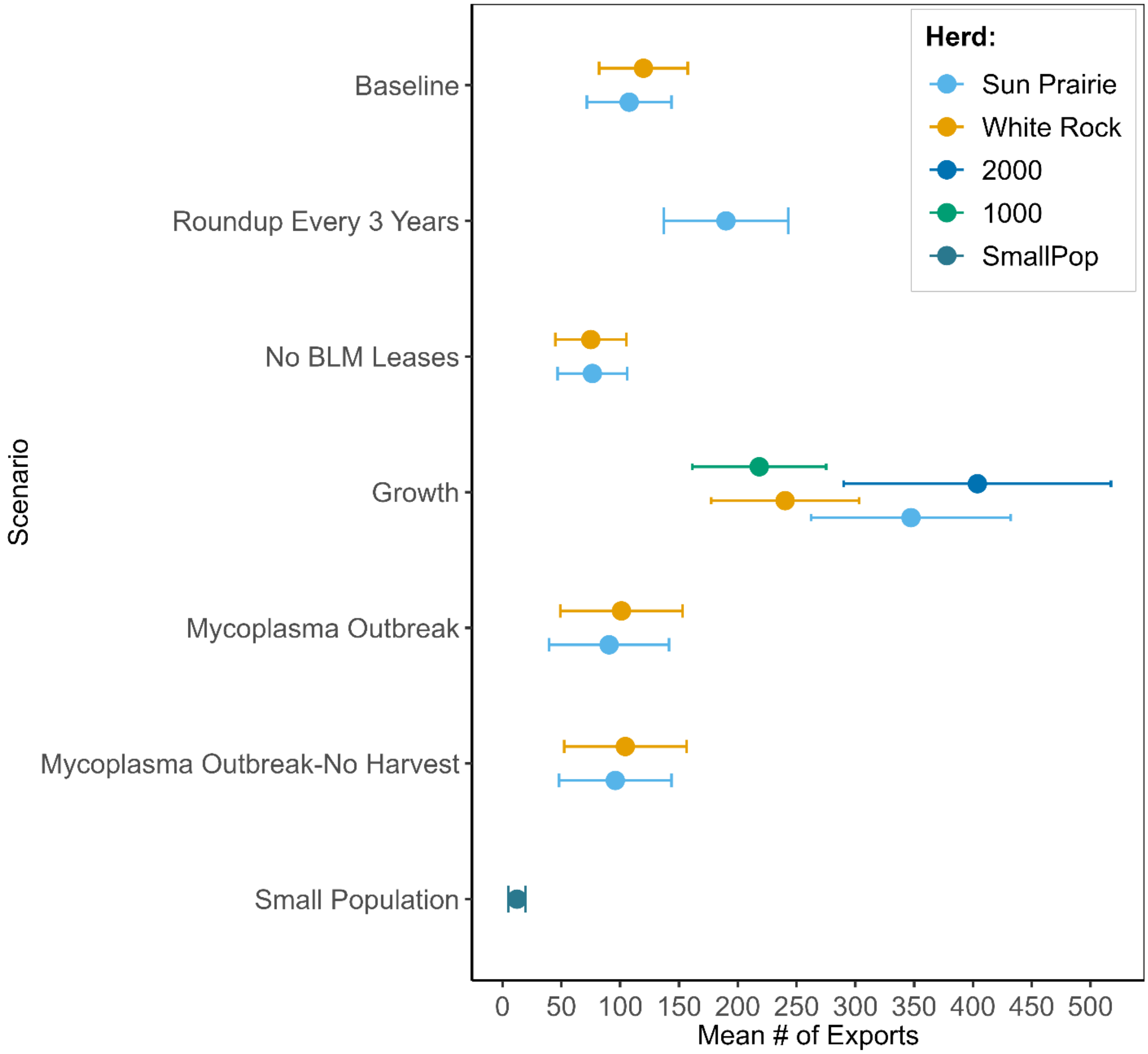


Figure 6. Mean number of exports (±SD) from each herd in model year 49 or 50, depending on which year the last biennial roundup/export events occured, for all model scenarios.

Appendix II. Model Outputs

Table 1. The projected stoch-r, gene diversity (GD), and number of births per year as well as the standard deviation around those outputs from each model scenario in the last year of the simulation across 1000 iterations.

Scenario	Herd	Years of Simulation	stoch-r	SD (r)	GD	SD (GD)	Births/Year*	SD (Births/Year)
Baseline	Sun Prairie	50	-0.002	0.128	0.227	0.000	104.625	14.135
Baseline	WhiteRock	50	0.002	0.122	0.227	0.000	126.506	15.901
Growth	1000	50	0.039	0.130	0.229	0.000	421.602	47.356
Growth	2000	50	0.056	0.115	0.228	0.000	200.000	23.594
Growth	SunPrairie	50	0.018	0.140	0.230	0.000	255.716	29.691
Growth	WhiteRock	50	0.014	0.131	0.229	0.000	218.183	25.444
Mycoplasma Outbreak	SunPrairie	50	-0.003	0.142	0.226	0.001	101.273	14.790
Mycoplasma Outbreak	WhiteRock	50	0.001	0.138	0.226	0.001	121.007	19.214
No Access to BLM Grazing Leases	SunPrairie	50	-0.008	0.138	0.225	0.001	83.828	11.462
No Access to BLM Grazing Leases	WhiteRock	50	-0.005	0.118	0.224	0.001	92.432	12.562
Roundup Every Three Years	SunPrairie	50	0.001	0.174	0.227	0.000	121.628	15.723
Small Population	SmallPop	50	0.012	0.185	0.180	0.007	9.429	2.764
Classified as Wildlife	SunPrairie	16	0.142	0.046	0.232	0.000	961.108	160.797
YNP Mortality Rates	SunPrairie	16	0.057	0.0494	0.232	0.000	293.71	54.136
Harvest-Adult Females	SunPrairie	16	-0.009	0.112	0.231	0.000	93.449	12.235
Harvest-Female Calves	SunPrairie	16	-0.009	0.117	0.231	0.000	96.270	12.045
Harvest-Female Heavy	SunPrairie	16	-0.012	0.096	0.231	0.000	83.334	11.104
Harvest-Female Yearlings	SunPrairie	16	-0.009	0.113	0.231	0.000	94.757	12.076
Harvest-No Adult Males	SunPrairie	16	-0.007	0.128	0.231	0.000	106.592	13.291
Harvest-Young Adult Females	SunPrairie	16	-0.009	0.110	0.231	0.000	93.194	12.019

*The number of births per year is dependent on whether the population in the last year of the model is at a low size immediately following a roundup, or at a larger size before a roundup occurs.