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Evaluation of Alternative Culling Strategies for Maintenance of Genetic Variaton in Bison (Bison Bison)

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EVALUATION OF ALTERNATIVE CULLING STRATEGIES FOR MAINTENANCE OF GENETIC VARIATON IN BISON *(BISON BISON)*

by

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ABSTRACT
EVALUATION OF ALTERNATIVE CULLING STRATEGIES FOR MAINTENANCE OF GENETIC VARIATON IN BISON *(BISON BISON)*

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Bison (*Bison bison*) once numbered in the millions and roamed across much of the lower 48 states. By the late 1800s, overhunting had reduced the population to around 1,000 individuals. Strong efforts to establish managed herds have resulted in a steady bison population increase. Currently, six herds are maintained by the U.S. Fish and Wildlife Service (FWS) at National Wildlife Refuges (NWRs) and are intensively managed through annual culling to keep herd size at targeted levels. Although various criteria have historically been used to select individuals for culling, the FWS currently employs an allele frequency based strategy that we have generalized as the 'mean allele frequency (MAF)' strategy, with the goal of keeping at least a few individuals that represent each element of genetic variation. Other bison management entities such as the National Park Service often use random culling or slight variations thereof. We have developed an individual-based model to compare the 'MAF' and 'random removal of young' culling strategies to a proposed 'pedigree-based' strategy based on the field of zoo biology to cull individuals based on kinship. The model was parameterized using existing long-term demographic and genetic data from the herd located in the Fort Niobrara NWR, Nebraska. Models were run at 100, 200, and 500 year marks. Variation among iterations

was greatest within the 'random removal of young' culling strategy. This model was outperformed by the 'pedigree-based' and 'MAF' culling strategy across summary statistics (allelic richness, gene diversity, inbreeding, and heterozygosity). A trade off was observed between the 'pedigree-based' strategy and the 'MAF' culling strategies in that the MAF culling strategy performed the best in regards to retaining the highest allelic richness (A) and observed heterozygosity (H_O) and the pedigree-based culling strategy retained the most gene diversity (GD) and maintained the lowest amount of inbreeding ($\bar{F}$). The models will aid in the long-term management of bison and provides a useful tool for other intensively managed mammal species.

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"The last word in ignorance is the man who says of an animal or plant, "What good is it?" If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering."

— Aldo Leopold, *Round River: From the Journals of Aldo Leopold*

Introduction

Wildlife management is an old practice, with Egyptian hunting records dating as far back as 2500 BCE (Leopold 1933, Gilbert and Dodds 2001). Early wildlife management focused mostly on hunting restrictions, limiting the seasons during which hunters could legally take animals. As habitats are increasingly altered and wildlife populations impacted by human activities, more species are being actively managed to assure their persistence (Baker et al. 2011). These increased threats to wildlife populations also are changing the intensity at which we manage wildlife. Many wildlife species are no longer self-sustaining, and require regular, intensive management at the individual or population level to prevent extinction (e.g, strict harvest regulations or moratoria, anti-poaching efforts, predator removal, culling, routine demographic monitoring, individual-based health care or disease management).

One consequence of intensive management is that populations are often managed in small, isolated populations, due to factors such as limited availability of habitat or resources. This, in turn, makes them more susceptible to evolutionary processes, such as genetic drift, that erode genetic variation over time (Wright 1931, Allendorf and Luikart 2007). The rate of genetic drift over time can be quantified through genetic monitoring of wild or captive populations (Briscoe et al. 1992, Ewing et al. 2008), and these data can be used to design management plans that minimize the loss of genetic variation over time. Preserving genetic variation is a main priority for conservation to maintain long-term population viability (McNeely et al. 1990; Lacy 1997) by providing the raw material

for a population to adapt and survive in changing conditions (Allendorf & Luikart 2007; Markert et al. 2010). This correlation between genetic variation and adaptability of a population has been demonstrated in populations exposed to selective pressures such as environmental stress (Frankham et al. 1999), parasite communities (Paterson et al. 1998), as well as artificial selection (Robertson 1960; James 1971). Thus, to foster population persistence in the face of changing conditions and stochastic events, management strategies aim to retain as much genetic variation as possible.

One means by which management may maintain genetic variation is through encouraging gene flow. Gene flow, even in small amounts, can counter the effects of genetic drift to insure the long-term persistence of a population (Mills and Allendorf 1996). For intensively managed populations that are often small and isolated, retaining genetic variation over the long term is a difficult challenge given that genetic drift is strong and the loss of genetic variation cannot be mitigated by gene flow. Current efforts to minimize the loss of genetic variation, therefore, strive to maximize the exchange of genetic information from generation to generation. This may be accomplished by managing such demographic attributes as sex ratios and age structure. Small populations are susceptible to wide fluctuations in sex ratios through demographic events such as an increase in male mortality or all offspring born in a particular year being the same sex (Lande et al. 2003). Populations with skewed sex ratios have been shown to exhibit a greater reduction in genetic variation over time (Gross and Wang 2005), increased inbreeding (Harris et al. 2002, Peek et al. 2002), and more variable population survival (Komers and Curman 2000). In principle, skewing the sex ratio of populations may also

affect mate choice and sexual selection, potentially altering the long-term evolutionary trajectory of populations (Clutton-Brock et al. 1997; Jirotkul 1999; Jiggins et al. 2000). Management actions that balance the sex ratio can buffer the population from the negative effects of skewed sex ratios. For example, if more females are born in a particular year, management may be aimed to keep more males in the population and harvest or cull more females. Managing a population to encourage a balanced sex ratio would limit the loss of genetic variation through drift by maintaining variation in both sexes (Gross and Wang 2005, Allendorf and Luikart 2007) and avoid a reduction in viability due to demographic stochasticity (Shaffer 1981; Brook et al. 1999). Age structure of a population can also impact genetic variation through its influence on the mean generation time. Since alleles are expected to be lost with each generation due to random sampling (i.e., genetic drift), a shorter mean generation time would result in a greater loss of genetic variation in a population over time. Long generation time is one reason why some long-lived species that have gone through severe bottlenecks have retained high levels of genetic variation (Dinerstein and McCracken 1990, Swart et al. 1994, Hailer et al. 2006). Management actions that lengthen generation time, by suppressing young from breeding or removing young from the population, would serve to reduce the rate of loss of genetic variation.

In addition to managing demographic parameters, management actions could be designed to manage genetic variation directly. For example, by either encouraging reproduction of individuals carrying rare alleles or by discouraging reproduction of individuals carrying common alleles. This would attempt to keep all alleles present from the founding

population in future generations and could be helpful to maximize genetic variation, and therefore, evolutionary potential. A simulation of management strategies for Guam Rails showed that a management strategy that maximizes retention of alleles resulted in a higher allelic diversity (Haig et al. 1990). However, the practice of maintaining genetic variation by selecting particular alleles is controversial due to potential deleterious effects they may have (Lacy 2000). Although no deleterious effects may be attributed to neutral markers, there may be potential negative effects of selecting rare neutral alleles in that there may be associations to quantitative traits and may be indirectly impacted through genetic draft, also referred to as hitchhiking (Charlesworth and Guttman 1996; Hey 1999; Otto 2000). An alternative management strategy that has been used in captive populations is one that minimizes the relatedness among individuals as well as the level of inbreeding in the population. This strategy would serve to retain unique variation without specifically choosing particular alleles. Ballou and Lacy (1995) simulated various management strategies and found that a strategy that preferentially bred individuals based on the individual's relatedness to the rest of the population retained more genetic variation and minimized inbreeding in the population compared to the random pairing of individuals. Aside from the potential logistical difficulties in implementing these direct strategies in wild or semi-wild populations, these efforts require genetic data from all individuals in the population and regular, active management on an individual basis. For many large wildlife populations, the genetic data needed to implement such management strategies are likely unavailable. In intensively managed species, in which managing directly for genetic variation could have

the biggest impact, comprehensive genetic data often exist and can be used to design strategies that maximize the retention of genetic variation over the long term.

The American bison (*Bison bison*), the largest extant North American mammal, once numbered in the millions and roamed across much of the lower 48 states. By the late 1800s, overhunting had reduced the population to fewer than 1,000 individuals. The majority of extant herds are descendants of fewer than 100 bison from 5 private herds as well as a remnant population from Yellowstone National Park (Coder 1975). Strong efforts to establish managed herds led to an increase in the number of bison to over 500,000 individuals in North America (NBA 2006). Less than 4% of the contemporary North American bison population is currently maintained in conservation herds, with the rest being maintained in privately owned or commercial herds. These 19,000 bison are contained in 54 conservation herds, where they are managed to maintain the long-term demographic viability of bison in North America (Gates and Aun 2008). More recently, management of bison in several conservation herds has been tailored to maintain genetic variation as well as maintain demographic stability.

Conservation efforts to maintain demographic and genetic viability of bison herds involve intensive management. Conservation herds are generally small and maintained at low population sizes, as space is limited (Boyd 2003). This results in the need to remove or cull individuals from the population every year in order to keep the population size below carrying capacity. Also, little or no gene flow occurs between conservation herds, as bison are hosts to a wide variety of diseases (Williams and Barker 2001) and

regulations have restricted the transfer of individuals in order to inhibit the spread of disease. Furthermore, managed herds were established with very small numbers of individuals, and those founders likely already exhibited reduced genetic variation as a result of the bottleneck of the 1800's. Thus, populations of bison are highly vulnerable to the loss of genetic variation and there exists a need to evaluate alternative culling strategies in order to maximize the retention of genetic variation over the long term as well as reduce the amount of inbreeding. Currently implemented culling strategies vary by herd; some manage for demographic stability (maintaining balanced sex and age ratios) and some incorporate genetic data into the culling selection process.

Population models may be used to evaluate alternative management strategies to aid in conservation decisions. Models can incorporate demographic information to simulate such things as the recovery or viability of a population over time under different management scenarios (e.g. limited harvest (Langvatn and Loison 1999) and increased anti-poaching efforts (Kenney et al. 1995)). They may also be used to predict the probable genetic impact of management actions (Bruford et al. 2010; Tracy et al. 2011; Haig et al. 1990). To monitor changes in the genetic composition of a population over time, individual-based, forward-in-time simulations are commonly used (Hoban et al 2012). For evaluating management strategies where individuals vary in their conservation importance, an individual-based model gives the flexibility to show how the inclusion or exclusion of specific individuals alters the population's genetic variation at various time-steps. By projecting changes far into the future prior to implementation, we can evaluate alternative management strategies prior to putting them into practice on

small, potentially vulnerable populations or on populations of long-lived species in which it would take many decades to observe effects of management actions.

In this study, we provide an assessment of three generalized culling strategies for bison. One strategy involved culling animals only based on indirect demographic information (sex and age), whereas the other two strategies incorporated genetic data when ranking animals for culling prioritization. Our primary goal was to compare the long-term effects of culling strategies on genetic diversity, within an intensively managed bison herd, to determine which strategies appear to provide the clearest advantage for conserving long-term variation. We also examined the accumulation of inbreeding in populations managed under different strategies. To achieve these goals, we built an individual-based model, parameterized in accordance with bison biology, to project levels of genetic variation and inbreeding predicted to persist over time by each of the three bison management strategies.

Methods

Overview of Culling Strategies

Random Removal of Young Culling Strategy

The random removal of young culling strategy involves culling animals randomly within selected sex and age classes. It is a strategy used historically by managers of some bison herds at National Wildlife Refuges (NWRs), and has been supported for herds inhabiting National Park Service (NPS) units (Gross and Wang 2005). This option is also the least

costly both financially and in terms of personnel required to implement. This culling strategy sets out to minimize the loss of genetic diversity due to genetic drift by maintaining balanced sex ratios, to maximize effective population size, and by preferentially culling yearlings to balance age ratios and lengthen generation time. In our random removal of young model, the number of yearlings of each sex to be culled was calculated. Yearlings were then randomly selected for cull one at a time until the number of male and female yearlings to be culled had been reached.

Mean Allele Frequency (MAF) Culling Strategy

In the mean allele frequency (MAF) culling strategy, all alleles found in a population are ranked in priority based on their frequency in the herd. Individual animals are then chosen for retention or culling based on the presence of rare alleles. The rarity of an individual's alleles is summarized as their mean allele frequency (MAF), calculated by averaging the frequency at which an individual's alleles occur in the population. Animals with, on average, more rare alleles are chosen for conservation, whereas those with more common alleles are chosen for culling. In addition to rareness, this strategy also aims to maintain an even sex ratio and preferentially selects yearling animals for culling to maximize generation time. The goal of this strategy is to maximize retention of genetic diversity by conserving as many alleles as possible. This strategy has a distinct advantage in that it does not designate particular alleles as important or 'conservation-worthy', but rather aims to conserve as many alleles as possible at as equal a frequency as possible. In theory, this could produce a population with even higher gene diversity than was present prior to management actions by creating more equal allele frequencies than

existed in the founder population. However, there are potential drawbacks to this culling technique. Most notably, alleles that are rare in a wild, genetically unmanaged population may be rare due to either genetic drift or to natural selection. Thus, because fitness might be impacted by manipulating allele frequencies (Hedrick and Miller 1994), maintaining allele frequency distributions that are representative of wild populations might be beneficial to those that are managed under semi-wild conditions. If alleles are rare due to drift, then the described culling strategy might be effective at maintaining the genetic diversity of populations over the long-term with little or no impact on fitness. If instead alleles are rare because they are of low quality, or associated with quantitative traits that are deleterious, this strategy could lead to reduced fitness in managed populations as the frequencies of deleterious alleles are manipulated. This could be particularly important if large proportions of animals are selected for culling, potentially causing drastic shifts in allele frequencies from generation to generation. However, if a low or moderate level of culling is employed, the genetic benefits of the allele conservation strategy may outweigh the potential costs.

In our MAF strategy model, the number of yearlings of each sex to be culled was calculated. MAF was calculated for each yearling, and individuals were then ranked by their MAF value. Individuals were considered one at a time and culled if their MAF value was highest of all remaining yearlings of that sex. This process was repeated until cull quotas for yearlings of each sex were reached. MAF values were recalculated each year.

Pedigree-Based Culling Strategy

In the pedigree-based strategy, yearlings were chosen for cull based on their degree of relatedness to the rest of the herd. Animals with high levels of relatedness were chosen for culling, and those with low relatedness values were chosen for retention. Similar to the other strategies, this strategy was implemented with a secondary goal of maintaining balanced sex and age ratios.

Pedigree-based strategies are often used to select individuals for breeding in captive population management. The goals of captive breeding programs are very similar to those of wildlife managers; to maintain demographically stable, self-sustaining populations that retain genetic diversity and accumulate limited inbreeding (Foose and Ballou 1988, Hedrick and Miller 1992, Lacy 1994, Ballou and Lacy 1995). As captive population management has evolved, a number of different breeding strategies have been proposed to meet these goals. Some of the most promising breeding strategies for captive population management use kinship, a measure that describes genetic relationships among individuals. The kinship (*f*) of a pair of individuals is the probability that two alleles at a given locus, one randomly drawn from each individual, are identical by descent from a common ancestor (Falconer 1981). An individual's mean kinship (*mk*) is then the average of pairwise *f*s between that individual and all living individuals in the population including itself (Ballou and Lacy 1995). The majority of captive breeding programs use pedigree-based estimates of *f*, rather than molecular estimates, to recommend breeding pairs that minimize a population's kinship. A breeding strategy that minimizes the overall kinship in a population has been shown by both computer

simulations (Ballou and Lacy 1995, Fernandez and Toro 1999, Toro et al. 1999, Ivy and Lacy 2012) and empirical data (Montgomery et al. 1997) to be the best strategy for retaining genetic variation in a population while limiting inbreeding. However, it is unknown whether a similar strategy will be effective for wildlife populations under a culling regimen. In wildlife population management, we are instead interested in removing the animals with high mean kinship rather than recommending only those with the lowest mean kinship for breeding. It is unknown to what degree this logic will influence the suitability of pedigree-based management strategies for culling animals.

In our pedigree-based strategy model, the number of yearlings of each sex to be culled was calculated. Mean kinship was calculated for all yearlings and used to rank individuals such that the yearling with the highest mean kinship was the highest priority for cull. Each individual was culled one at a time until cull quotas for yearlings of each sex were met.

Simulation Overview and Parameters

We have developed an individual-based model to test three general bison management strategies (random removal of young, mean allele frequency, and pedigree-based) (Figure 1). We parameterized the model in accordance with bison biology, using genetic and demographic information from the bison herd managed by the US Fish and Wildlife Service at the Fort Niobrara National Wildlife Refuge (FTN) in north-central Nebraska. This bison herd is intensively managed and monitored annually through roundups. Extensive demographic data, complete genotypes for 54 microsatellite loci, and nearly

complete parentage data for 7 years (2004 to 2010) exist for this herd (Table 1). This population was founded in 1913 with 8 bison (J.W. Gilbert of Friend, Nebraska and Yellowstone National Park) with supplementations occurring in 1935 (Custer State Park), 1937 (Custer State Park), and 1952 (National Bison Range). The herd is currently managed for a target population size of 350 individuals. However, the starting population of the model used 259 genotypes from all 259 known breeders from the 2004 population.

1) We selected the 259 known breeders (100 male, 159 female) in the 2004 FTN bison herd as our initial founding population for our simulations. For this population, we had microsatellite genotypes, sex, and the year of birth for all individuals. For individuals lacking genotype data for a particular locus, the program R was used to fill in the missing alleles by drawing alleles based on their frequency in the population (R Core Team 2014). A kinship matrix containing pairwise kinship values of all individuals in the population was generated for the founding population with the assumption that founders were unrelated.
2) The first step of the model executed was to identify breeding individuals. To reflect the polygynous mating behaviors of bison, the model selects a few dominant males to produce a majority of the offspring. We used the FTN known pedigree to generate M_x values (the number of same-sex offspring produced by an individual at each age class) for all individuals using PM_x (Figure 2; Ballou et al. 2011). From the Mx distribution we derived that breeding generally occurs between the ages of 4 and 16 for males and between 2 and 21 for females.

Calving rates among sexually mature female bison range greatly from herd to herd (Shaw and Carter 1989). Haugen (1974) estimated 78.4% of sexually mature female bison at the Fort Niobrara National Wildlife Refuge produced calves; however, recent reports suggest it has increased to 82% (Borgreen 2010). For simplicity in the model, all females of breeding age were selected for breeding. A proportion of males within breeding age were assigned as breeders based on the proportion of males in a given year that sired offspring from the known FTN pedigree. This ranged in the FTN herd between 27% and 59% of the total number of males within breeding age. Therefore, the mean (40%) was used to characterize the proportion of males within breeding age that would be assigned as breeders. Males assigned as breeders were further categorized as either subordinate or dominate. Dominant males were defined as those that produced 4 or more offspring. The male bison that produced the most offspring and fell into the dominant category were associated with the age at which males sired the offspring. Using the pedigree, we assigned the age criteria for dominant males to be between 8 and 12 (Figure 2). The proportion of dominant males from the FTN pedigree varied between 11% and 21% of total males that sired offspring for a given year. For the model, we used the mean (16%) to assign dominant males from within those males already characterized as breeders. As the number of offspring sired by dominant males varied greatly, between 4 to 10 offspring, the proportion of all offspring sired by the dominant males collectively had a large amount of year-to-year variation (from 29% to 67%). However, for 4 out of the 7 years of pedigree, dominant males sired between 29%-40% of offspring. We used

a conservative estimate of 30% to describe the total number of offspring sired by all dominant males. In the model, this translated to each female within breeding age mating with either a dominant breeding male (30% chance) or a subordinate breeding male (70% chance). The specific dominant or subordinate male was randomly chosen for breeding.

3) Offspring were produced from each mating. Each female produced one offspring that was randomly assigned a sex of male or female and given an age of 0. The genotype of each offspring was generated following Mendelian inheritance by randomly assigning one allele from each parent (sire and dam). In order to track relationships through time, the kinship matrix of all possible pairwise f_s was calculated for each offspring. This was measured as $f_{xy} = 0.5(f_{xs} + f_{xd})$, where subscripts *s* and *d* reference the sire and dam of each individual *y* (Falconer 1981).
4) After offspring were produced, the number of individuals to cull (*C*) was calculated separately for each sex (*s)* to achieve the target population size ($C_s = a - (b + c + d) - (T/2)$). The (*b* + *c* + *d*) component of the equation represented the total number of individuals that were expected to be removed from the population due mortality or the maximum age ceiling where *b* represented the number of individuals that would reach a specified maximum age and be removed from the population at the end of the time step, *c* represented the number of adults of sex *s* expected to be lost to mortality during the time step ("adult" mortality of individuals age 2 or higher calculated as $Q_A \times n_{(A)\ of\ sex\ (s)}$, where Q_A is the mortality rate for adults and $n_{(A)\ of\ sex\ (s)}$ is the number of adults of sex *s*), and *d* represented the number of juveniles of sex (*s*) expected to be lost

to mortality during the time step ("juvenile" mortality of individuals age 0 or 1 calculated as $Q_J \times n_{(J)\ of\ sex\ (s)}$, where Q_J is the mortality rate for juveniles and $n_{(J)\ of\ sex\ (s)}$ is the number of juveniles of sex *s*). The last component of the equation (*T*/2) represents the target population size for each sex, where *T* represented the target population (350 individuals), which was divided by two to insure an equal sex ratio in the population. Both the total number of individuals to be removed due to mortality and the target population size for each sex was subtracted from the total number of individuals of all age classes for each sex (*s*), represented by a. Yearlings were then selected for cull based on the selection criteria for each of the three culling strategies.

5) Once culling was completed, mortality was induced for all age classes. Adult mortality (Q_A) was 3% for females and 5% for males. For juveniles (Q_J), a mortality rate of 5% was induced for both sexes. An age cap at 24 years was enforced for both sexes to ensure a realistic life span (Meagher 1986).
6) All individuals were aged 1 year. Models were run by repeating steps 2-6 for 100, 200, and 500-year time steps. For each culling strategy at each time step, the simulation was repeated for 100 iterations.
7) Summary statistics of genetic variation and inbreeding were evaluated at the end of each iteration. Summary statistics of genetic variation included allelic richness measured as the mean number of alleles per locus (*A*), observed heterozygosity calculated directly for each locus across all individuals and then averaged across loci (Hartl and Clark 1997), and proportional gene diversity (GD; i.e., expected heterozygosity) calculated as $1 - \overline{mk}$ (where $\overline{mk}$ was the average mean kinship in

the population; Ballou and Lacy 1995). An individual's inbreeding coefficient (*F)* was equal to the kinship between the individual's sire and dam; the average of all the individual's inbreeding coefficients (*F)* resulted in the population inbreeding coefficient ($\bar{F}$) (Falconer 1981).

Evaluation of Culling Strategies

Culling strategies were evaluated using the genetic variation and inbreeding measures (A, H_O, GD, and $\bar{F}$) averaged across 100 iterations for each culling strategy at each time step (100, 200, 500 years). The coefficient of variation (CV) was used to characterize the extent of variability of the genetic variation measures across iterations in relation to the mean.

Sensitivity Analysis

We assessed the sensitivity of the model to the input parameters by analyzing the response of the model outputs (genetic diversity and inbreeding measures) to variations in target population size, proportion of males breeding, and mortality.

For the target population size parameter change, the model was run with a target population size of 200, 500, and 1000 individuals. This allowed us to see how the generalized culling strategies compare at an array of realistic population sizes for managed bison herds. However, the number of years culling occurred varied from the original time step length. Because the founding population used for the model included 259 individuals, strategies that allow for larger target population sizes did not cull any

individuals for the first 1-4 years to allow the population to grow (1-2 years when the target population size was 500 and 3-4 years for the 1,000 target population size). Next, we changed the proportion of males breeding in that 100%, 50%, and 5% of males of breeding age (4-16) were chosen for breeding. For this analysis, the dominance parameter of the model was turned off so that all males chosen to breed had an equal probability of actually mating. Lastly we changed mortality of each age and sex class so that it was 50%, 200%, and 300% of its original value.

Results

Founding Population Summary Statistics

The founding population used for the simulations had a mean allelic richness of 5.873, an observed heterozygosity of 0.606, and a gene diversity value of 0.998. Since all founding individuals were assumed to be unrelated, the inbreeding coefficient of the founding population was 0.000 (Table 2).

Evaluation of Model Output

As expected from genetic drift, a reduction in allelic richness and gene diversity was observed for all culling strategies from the founding population; however, the rate at which they were reduced varied based on culling strategy (Table 2). The amount of heterozygosity either increased or decreased from the founding population based on the culling strategy with no overall trend as time step length increased. All strategies observed an increase in inbreeding from the founding population from each time step

with varying rates of accumulation based on culling strategy. After 100 years, differences in genetic diversity and inbreeding measures were observed among the three culling strategies that became more pronounced over time. All strategies succeeded in maintaining an equal sex ratio in the population (Figure 4).

Of the three culling strategies, the random removal of young strategy preserved the fewest alleles, as measured by allelic richness (Table 2). This difference was already evident after the 100-year time step. This strategy also ended with the lowest heterozygosity, lowest gene diversity, and highest inbreeding coefficient across all time steps (Table 2). After 500 years, the random removal of young culling strategy resulted in an average decrease of 34.3% in allelic richness, 7.4% in heterozygosity, 18.7% in gene diversity, and an increase of inbreeding to 0.184 (Table 4, Figure 5).

The MAF culling strategy retained more genetic variation than the random removal of young strategy at all genetic variation measures. Allelic richness decreased by 4.5% and gene diversity decreased by 16.3% over 500 years (Table 4, Figure 5). The MAF strategy resulted in an increase in heterozygosity relative to the founding population; over 500 years heterozygosity increased by 32.3% (Table 4, Figure 5). Inbreeding increased over time in the MAF strategy, rising to 0.160 over 500 years (Table 4, Figure 5)..

The pedigree-based strategy retained the most genetic variation in terms of gene diversity retention (10.2% decrease) and accumulated the least inbreeding (0.099) over 500 years

(Table 2). It performed second to the MAF strategy in retention of allelic richness (decrease of 22.5%) and heterozygosity (increase of 2.5%) (Table 4, Figure 5).

Variation across simulation iterations, measured as CV, varied based on the genetic variation and inbreeding measures. Overall, the random removal of young culling strategy exhibited the greatest amount of variation among iterations for all genetic variation and inbreeding measures for the 500 year time step than was observed in either of the genetically based culling strategies (MAF and pedigree-based) (Figure 3, Table 3). The MAF culling strategy resulted in the lowest amount of variation among iterations at the 500 year time step for the measures of allelic richness and observed heterozygosity. The MAF strategy and the pedigree-based strategy resulted in similar variation values for the inbreeding; however, the pedigree-based strategy had the lowest amount of variation among iterations for gene diversity (Figure 3, Table 3). This indicates that there is less certainty in the outcome of genetic variation and inbreeding when using a random removal of young strategy compared to a culling strategy based on genetic information (MAF and pedigree-based).

Sensitivity Analysis

The three culling strategies proved to be robust to changes in target population size, proportion of males that successfully breed, and mortality for each age and sex class. As the target population size increased above the original value of 350 individuals, allelic richness, heterozygosity, and gene diversity were higher and inbreeding ($\bar{F}$) was lower, but the overall pattern remained the same (Table 5, Figure 6). Generally, more variation

among culling strategies was observed as the proportion of males that successfully bred was reduced (Table 7, Figure 7). Overall, varying the sex- and age-specific mortality values changed the outcome of each culling strategy very little (Table 9, Figure 8).

Discussion

Intensive management of wildlife is expected to impact populations demographically and genetically. For bison, intensive management in small, isolated populations with fixed population sizes and annual removal of surplus animals predicts the erosion of genetic variation over the long term. By evaluating alternative strategies for prioritizing individuals for cull within this intensive management framework, we can determine which culling strategies provide the clearest advantage for conserving long-term variation and limiting accumulation of inbreeding. Our simulations show that in intensively managed bison herds, culling strategies can have a large influence on the rate at which genetic variation is lost. They also show that incorporating genetic data into culling decisions improves the retention of genetic diversity and reduces the accumulation of inbreeding over the long term over strategies based solely on demographic parameters. This is reflected in our individual-based models, where the random removal of young strategy, which considers only demographic information, resulted in a herd with the lowest allelic richness, heterozygosity, and gene diversity, as well as the highest inbreeding of the three culling strategies. When genetic data was incorporated into culling decisions (MAF and pedigree-based strategies) more of the founding genetic variation was retained and the accumulation of inbreeding was impeded. Better retention

of genetic variation through direct genetic management has also been demonstrated when selecting breeders in a captive population (Ballou and Lacy 1995; Ortega-Villaizan and Taniguchi 2011) or selecting founder individuals for reintroductions (Tracy et al. 2011; Haig et al. 1990; Miller et al. 2009; Jamieson 2011). Taken together, these findings indicate that incorporating genetic data into management decisions is an important tool for retaining genetic variation in populations at all stages of management.

Wildlife managers often aim to increase the size of wildlife populations to alleviate problems such as genetic drift (Epps et al. 2005; Dixo et al. 2009) and inbreeding (Soule and Mills 1998). Our sensitivity analysis for target population sizes demonstrated the effect that larger population size has on minimizing the effect of genetic drift; as the target population size grew larger, the differences in the amount of genetic variation retained across different culling strategies diminished. However, for many species such as bison, habitat is limited and wildlife must be maintained in small populations. Our simulations indicate that the genetic differences among culling strategies become more apparent as population size decreases, suggesting that in small populations the choice of culling strategy is a critical component of a successful intensive management strategy. Losses in genetic variation associated with small population size are exacerbated when populations are isolated with little or no gene flow as observed in bison herds managed for conservation. Our data indicate that wildlife management can be tailored to minimize genetic risks to population viability, even when increasing population size or encouraging gene flow from other populations is not a possibility.

In addition to small herd size and a lack of gene flow among managed herds, historical events such as severe bottlenecks and cattle-gene introgression in both conservation and commercial herds threaten the integrity and diversity of the bison species genome (Halbert and Derr 2007; Freese et al 2007; Hedrick 2009). Reduced genetic variation limits the evolutionary potential of populations, but also can have direct and immediate effects on factors such as the response to diseases and new pathogens (O'Brien and Evermann 1988). As some of the remaining conservation herds of bison are infected with brucellosis (Meagher and Myer 1994; Freese et al. 2007), maintaining genetic variation could be essential for the preservation of the species. Furthermore, since the entire bison species went through a severe bottleneck in the late 1800s, and then again as more conservation herds were founded with few individuals, all bison populations can be assumed to have some level of inbreeding. For example, Hedrick (2009) estimated an approximate level of inbreeding of 0.367 (equal to 2 generations of full-sib mating) in the Texas State Bison Herd. Although the direct effects of inbreeding in bison are unclear, even small amounts of inbreeding have been correlated with the susceptibility to bacterial disease in other wildlife populations (Acevedo-Whitehouse et al. 2003). Overall, historical erosion of genetic variation due to severe bottlenecks, multiple founder events, and inbreeding make preservation of remaining genetic variation through effective management strategies even more imperative to the persistence of bison.

Strategies that incorporated genetic information into culling decisions produced the most genetically variable populations. However, there was not a clear best option between the MAF and the pedigree-based strategies. We observed a trade off between the MAF and

pedigree-based strategies. Whereas the MAF strategy preserved the greatest number of alleles and eventually increased the heterozygosity relative to the founding population, it resulted in a population with lower gene diversity and increased inbreeding compared to the pedigree-based strategy. All models also had explicit random variation among iterations, summarized as CV. Observing this variation for each culling strategy did not clarify which of the two genetic based strategies performed best. For example, the MAF strategy had the lowest CV for allelic richness and heterozygosity, whereas the pedigree-based strategy had the lowest CV for gene-diversity and similar values as the MAF for inbreeding ($\bar{F}$)).

Genetic variation measures yield different information regarding the loss of variation due to genetic drift. Using multiple measures has been suggested for monitoring the genetic health of a population, as some measures are more sensitive to changes in populations than others (Allendorf 1986; Luikart et al. 1998). We chose the common measures of allelic richness (A), heterozygosity (H_O), gene diversity (H_e), and inbreeding ($\bar{F}$)). The MAF strategy aimed to maximize the retention of alleles, thus increasing allelic richness and heterozygosity. Heterozygosity is commonly used in monitoring the genetic health of wildlife populations. Some studies, although controversial, suggest that heterozygosity is important in that it influences individual fitness (Reed and Frankham 2003); however, it may not be sensitive to changes in the populations, such as bottlenecks, that tend to yield a loss in genetic diversity (Allendorf 1986, Leberg 2002). Gross and Wang (2005) suggested that observed heterozygosity is likely a relatively insensitive indicator of genetic variation loss in conservation bison herds. Allelic

richness, however, shows how many alleles are lost over a period of time and is a more sensitive measure to the loss of genetic variation due to small population size than heterozygosity (Allendorf 1986). The loss of alleles in small and isolated populations is virtually irreversible for populations that cannot be supplemented with immigration; therefore, maximizing allele retention (and allelic richness) is critical for such populations. However, these measures reflect genetic variation only at the selected subset of loci. Thus, although the MAF strategy resulted in higher amounts of allelic richness and observed heterozygosity at the loci under consideration, the fate of alleles at other loci across the genome is unknown. Hedrick and Miller (1994) simulated breeding strategies that selected rare functional traits in the MHC and observed their effect on the rest of the genome. They urged caution in using this technique as it may have costs to the rest of the genome, including lower overall genetic variation and reduced fitness. Our simulations show that the MAF strategy increased inbreeding more quickly than the pedigree-based strategy, which not only reduces genome-wide variation but also could lead to detrimental fitness effects (Charlesworth and Charlesworth 1999). Although Hedrick and Miller (1994) characterized reductions in genetic variation and fitness associated with selection for variation at a functional locus, similar patterns might be expected when selecting for variation at neutral loci, particularly if the effects of genetic draft are strong (Charlesworth and Guttman 1996; Hey 1999; Otto 2000).

The overall goal of the pedigree-based strategy, in contrast, is to maintain variation at the genomic level by maximizing gene diversity while minimizing the level of inbreeding. These measures are commonly used to assess pedigree-based management strategies in

captive populations (Ballou and Lacy 1995; Ivy and Lacy 2012). Conservation programs aim to minimize inbreeding as high levels of inbreeding may compromise population viability due to deleterious effects on fitness-related traits and lower genome-wide diversity. Gene diversity, or the expected heterozygosity, is directly related to the amount of additive genetic variance for quantitative traits and is a common measure for quantifying evolutionary potential (Falconer and Mackay 1996). It has been shown that breeding strategies that aim to maximize gene diversity also tend to also be efficient in maintaining allelic diversity (Fernández et al. 2004). Although not commonly used in wildlife management, gene diversity may be a useful measure of genetic variation in wildlife populations and for evaluating alternative management. Based on these two measures, the pedigree-based strategy was most effective at maintaining low levels of inbreeding in a population and maintained a higher level of heterozygosity and allelic richness than a random removal of young strategy. This is particularly important in intensively managed wildlife populations, such as bison, where gene flow is either limited or non-existent.

Whereas gene diversity is not commonly used in wildlife management, it is frequently used in captive population management. Since captive population management has incorporated genetic information into management decisions for many species, it may have some applicability when generating alternative strategies for wildlife. Captive management studies have shown that strategies that use mean kinship to breed individuals will result in the retention of genetic variation and reduce the accumulation of inbreeding (Ballou and Lacy 1995; Fernández and Toro 1999; Sonesson and Meuwissen

2001). By using mean kinship to select individuals to breed, the founder contribution to future generations can be maximized, thus maximizing the retention of genetic variation.

Our simulations indicate that mean kinship is also useful for selecting individuals to cull, because it also maximizes the contribution of founder genomes by removing individuals with a high degree of relatedness to the rest of the herd. By targeting measures of genetic variation that reflect genome-wide patterns of variation, the pedigree-based strategy maximizes the amount of genetic variation available to be passed on to the next generation. Further, using a strategy that minimizes inbreeding may be useful for populations in which some level of inbreeding already exists. Current bison herds were founded from small numbers of individuals (100 or fewer) drawn from a pool of perhaps fewer than 1000 individuals (Hedrick 2009). These small founding populations likely exhibited some degree of relatedness. In our model, we assumed that founders were unrelated; however, simulations have shown that breeding strategies based on mean kinship are robust to uncertainty in the pedigree, including when founder relationships are unknown (Rudnick and Lacy 2008).

The application of pedigree-based management strategies is currently limited due to lack of parentage data for wildlife populations. Hedrick (2009) suggested that pedigrees should be established for bison herds to further improve and guide bison management (Hedrick 2009); we add that such data would be helpful for implementing effective culling strategies as well. Unfortunately, all captive and wild populations have some amount of uncertainty present in their parentage, whether pedigrees themselves are

incomplete due to unrecorded parentage or whether the relationships among original population founders were unknown. Rudnick and Lacy (2008) used computer simulations to investigate how the retention of genetic variation and the accumulation of inbreeding in captive populations managed by mean kinship breeding strategies are affected by different levels of uncertainty in the pedigree. In short, the authors did not find a significant reduction in performance of the mean kinship strategy when the relationships among population founders were unknown. For populations with no known pedigree, using molecular data can have limited value for maintaining genetic diversity because high levels of marker polymorphism are needed in order for performance to equate to a strategy using pedigree coancestry (Fernández et al. 2004). In fact, using molecular information of low quality can decrease the genetic diversity in the population as more relationships of individuals are incorrectly assigned. However, several authors have found that molecular data can be useful for resolving unknown relationships within the pedigree (since the original founders; Russello and Amato 2004, Ivy et al. 2009). For example, Ivy et al. (2009) used molecular data to resolve unknown parentage for parma wallabies, and then used the reconstructed pedigree to make breeding recommendations based on a mean kinship strategy. When parentage could not be resolved, the authors used the molecular data to describe the level of relatedness between pairs of individuals. They found that using microsatellite data to resolve unknown parentage (or at least gross levels of relatedness among pairs of individuals) within the pedigree was quite useful for population management, and improved their ability to manage the population using a pedigree-based mean kinship strategy.

The individual-based model developed for this study was designed to be flexible so that it could be utilized to evaluate alternative management strategies for other intensively managed wildlife populations to predict their effects on long-term genetic variation. Parameter values can be easily changed, and mating parameters were designed to easily reflect different mating strategies. For instance, an option allows dominant males to mate for multiple years before selecting new dominant male(s). This parameter may also be switched off so that all males within the set breeding range have the same probability of mating. The sensitivity analysis showed that the culling strategy models were robust to various parameter changes in target population size, proportion of breeding males, as well as change in mortality rates. This was important because it shows that other species with varying mating systems, population sizes, and different mortality rates may still benefit from similar management recommendations based on genetic information.

Our culling model has large applicability in both in-situ as well as ex-situ conservation strategies. Although controversial, we believe these culling recommendations may also be useful for captive population management (Lacy 1995). Maintaining individuals in captive populations uses a lot of resources that could otherwise be allocated to individuals more crucial to conservation goals. Once individuals have bred and are no longer useful for furthering conservation goals, they are deemed "surplus" animals (Lindburg 1991). These animals then occupy space and use resources that could otherwise be allocated to other individuals that could breed or other species of conservation concern. Our simulations show that culling can be used to maintain genetic variation and minimize inbreeding, much like breeding recommendations do in captive

populations. Therefore, culling based on genetic information could be used in captive populations to both maintain evolutionary potential and maximize resources for conservation of other individuals or other species.

Figure 1. Model flow for each simulation. Each culling strategy (random removal of young, MAF, and pedigree-based) was run at three different time steps (100, 200, and 500 years). Simulations for each time step were repeated for 100 iterations.

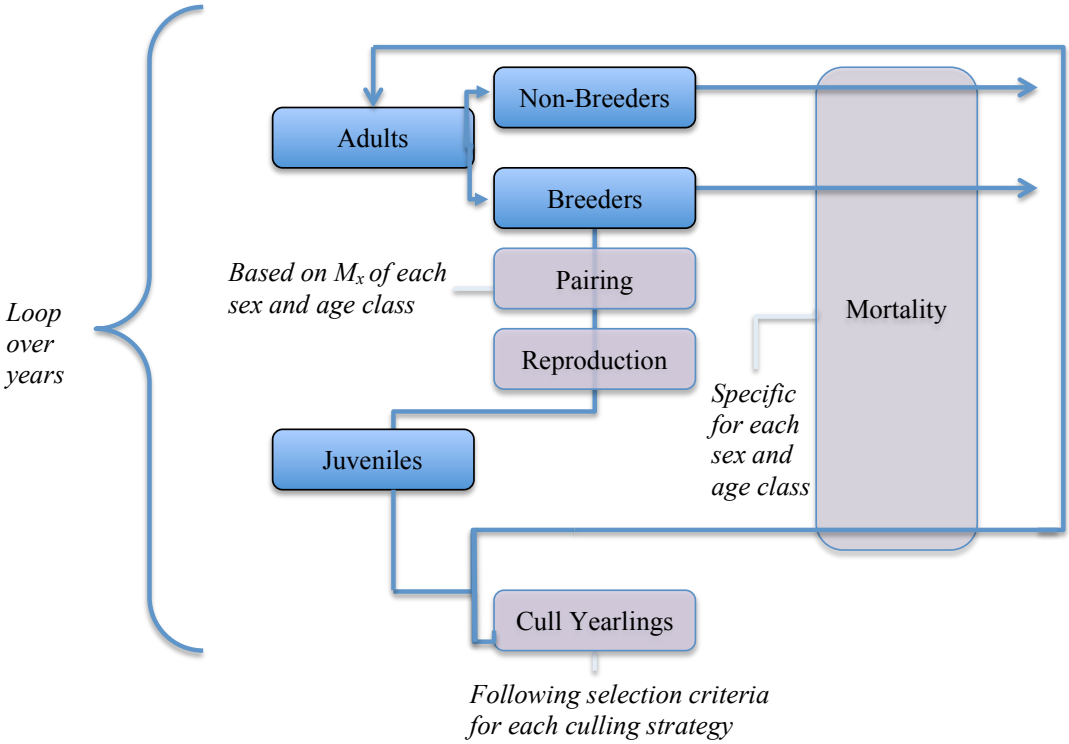

Figure 2. Mx values of males and females from the Fort Niobrara National Wildlife Refuge bison herd generated from known pedigree of 2004 - 2007.

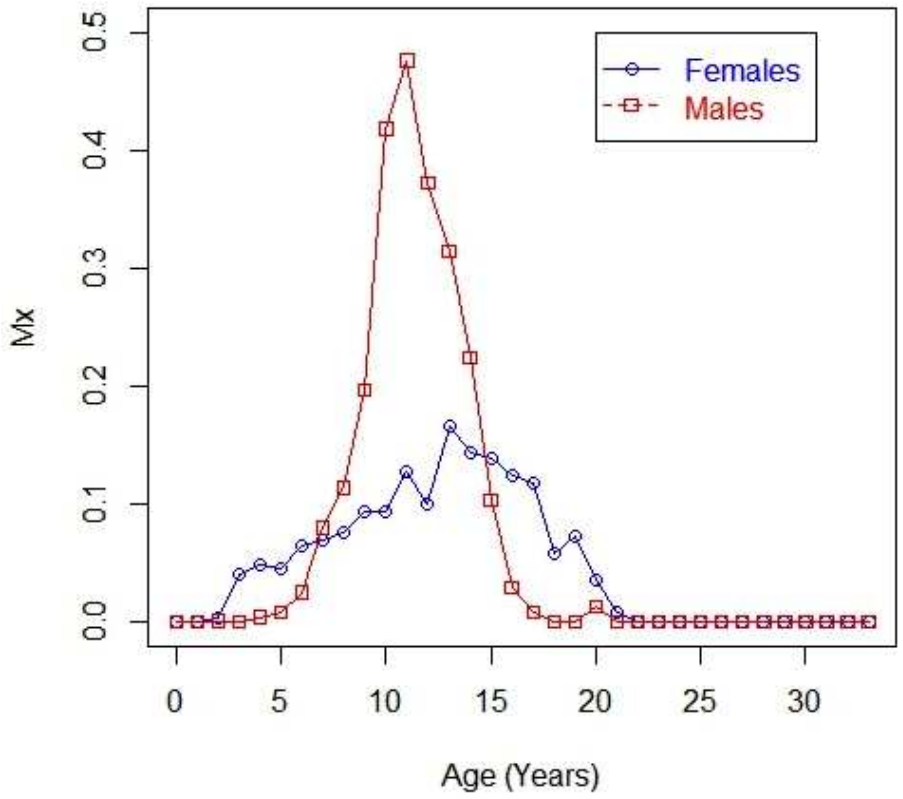

Figure 3. Simulations for each culling strategy over a 500-year time step. Each black line represents one iteration.

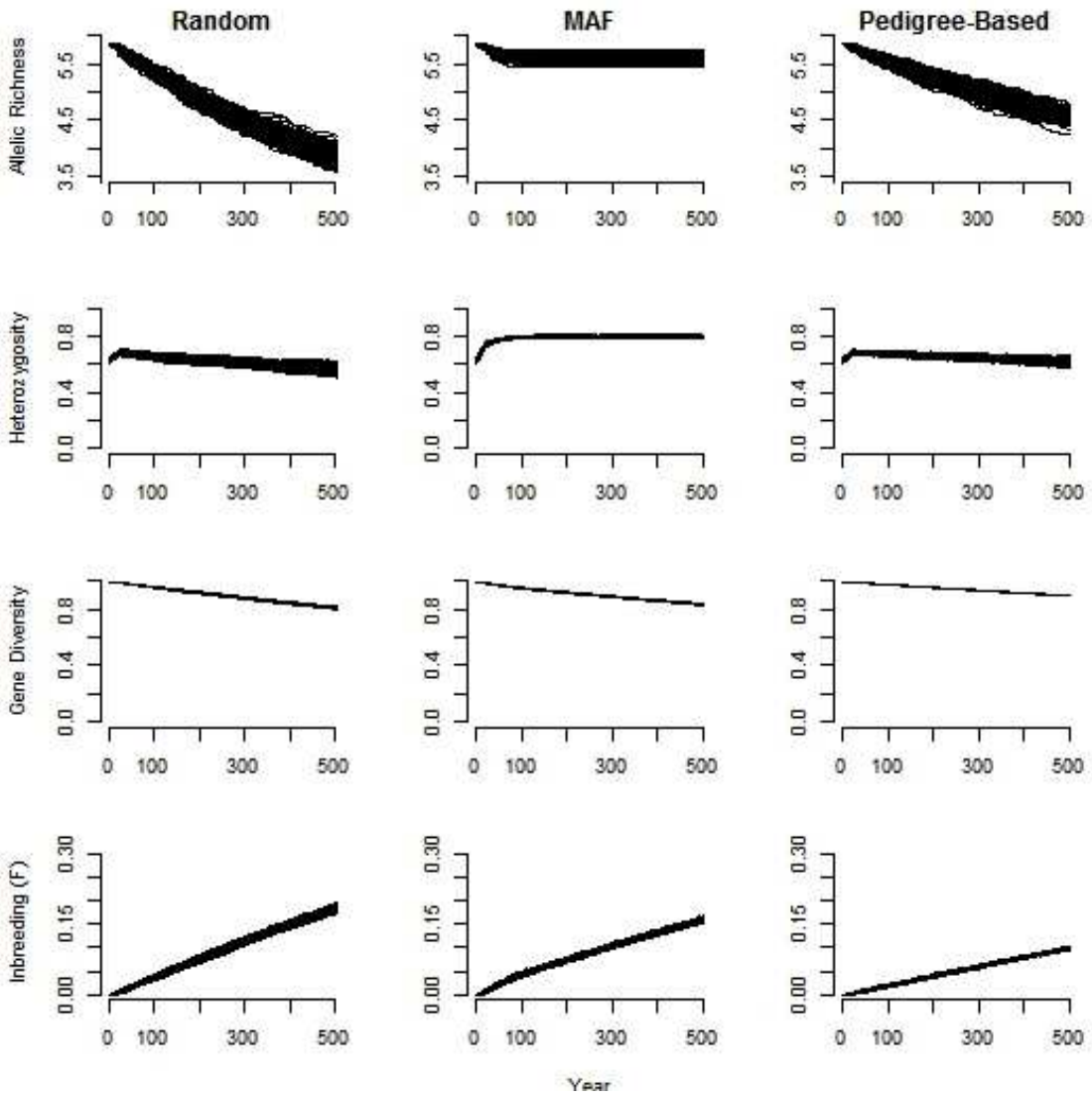

Figure 4. The total number of individuals in the population remains constant around the target population size of 350. The number of each sex remains close to 150 for all time-steps. Each circle represents the population size or the number of each sex at a given year for 100 iterations.

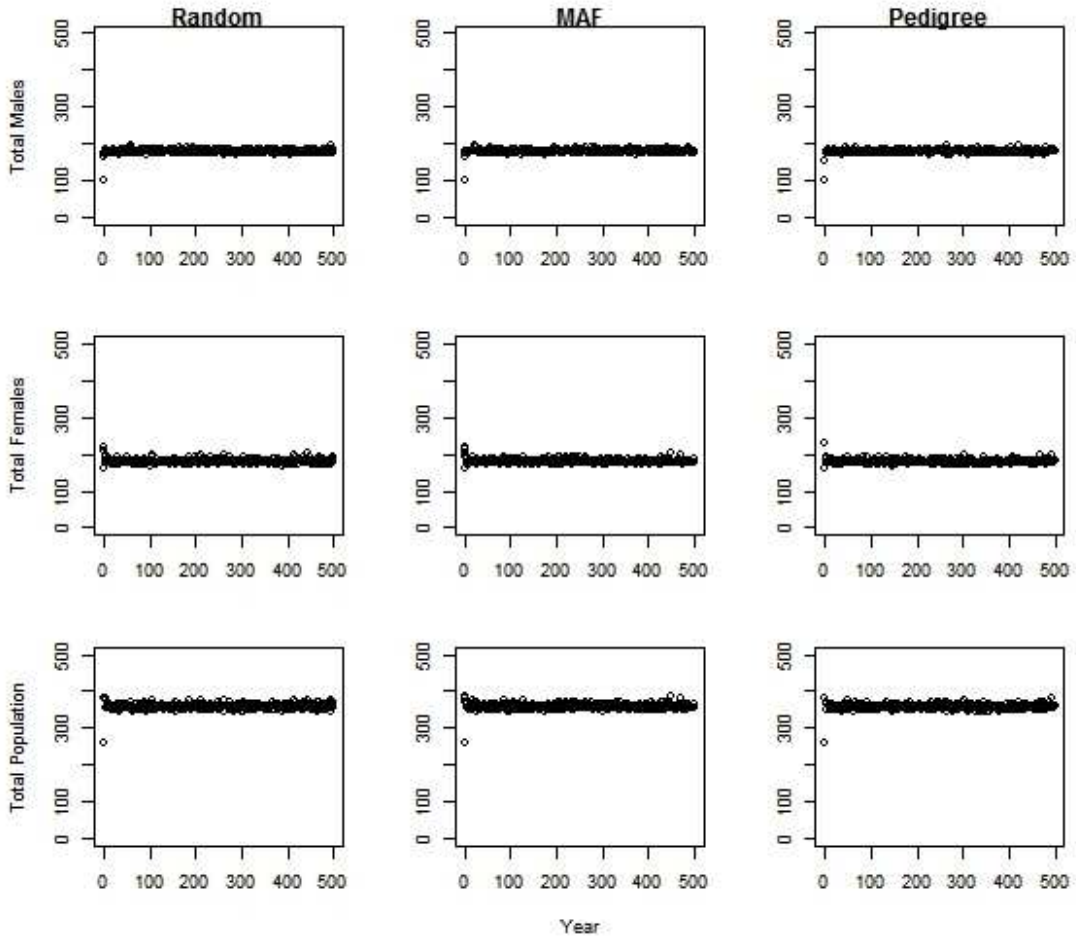

Figure 5. Box plots of genetic variation and inbreeding under each culling strategy after a 500-year time step and averaged over 100 iterations. The dark lines in the boxes represent the median with the box extending to the upper and lower quartiles (25% and 75%). Whiskers extend the range of the genetic variation values with outliers represented with circles (more than 1.5 times larger than the upper and lower quartile). The black dotted lines represent the genetic measure of the founding population.

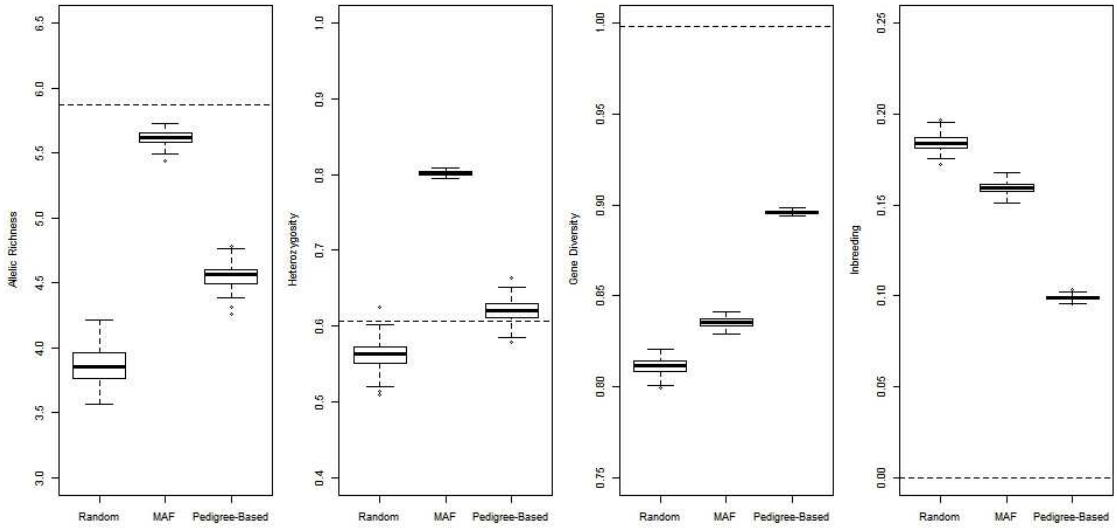

Figure 6. Results from the 500 year time step of the sensitivity analysis reflecting the genetic variation measures under each culling strategy with various target population sizes (200, 500, and 1000). The dark lines in the boxes represent the median with the box extending to the upper and lower quartiles (25% and 75%). Whiskers extend the range of the genetic variation values with outliers represented with circles (more than 1.5 times larger than the upper and lower quartile). The black dotted lines represent the genetic measure of the founding population.

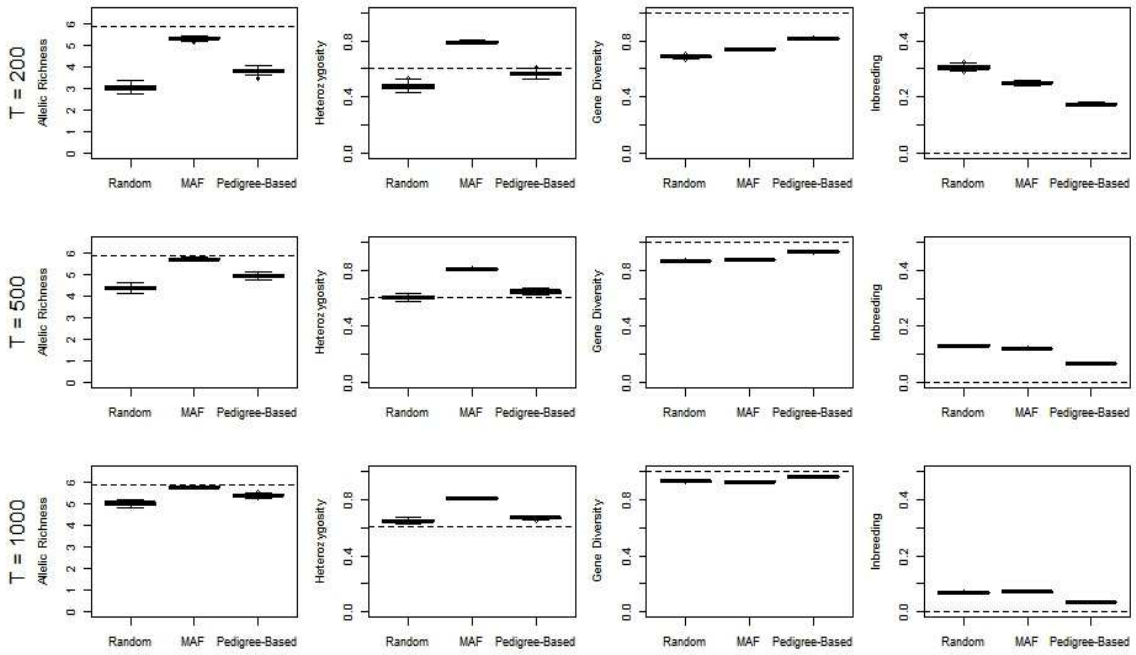

Figure 7. Results from the 500 year time step of the sensitivity analysis reflecting the genetic variation measures under each culling strategy with different proportions of males within breeding age allowed to breed (0.05, 0.50, and 1.00) The dark lines in the boxes represent the median with the box extending to the upper and lower quartiles (25% and 75%). Whiskers extend the range of the genetic variation values with outliers represented with circles (more than 1.5 times larger than the upper and lower quartile). The black dotted lines represent the genetic measure of the founding population.

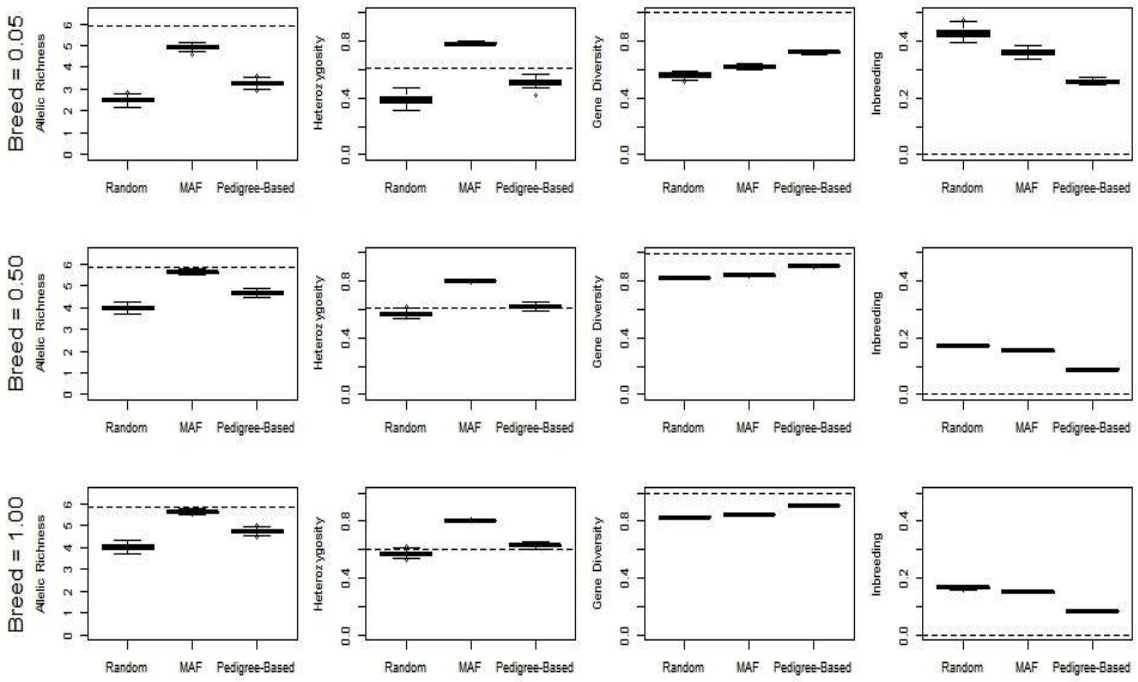

Figure 8. Results from the 500 year time step of the sensitivity analysis reflecting the genetic variation measures under each culling strategy with various rates of mortality measured as proportions of the original sex and age specific mortality rates (0.5, 2.0, and 3.0). The dark lines in the boxes represent the median with the box extending to the upper and lower quartiles (25% and 75%). Whiskers extend the range of the genetic variation values with outliers represented with circles (more than 1.5 times larger than the upper and lower quartile). The black dotted lines represent the genetic measure of the founding population.

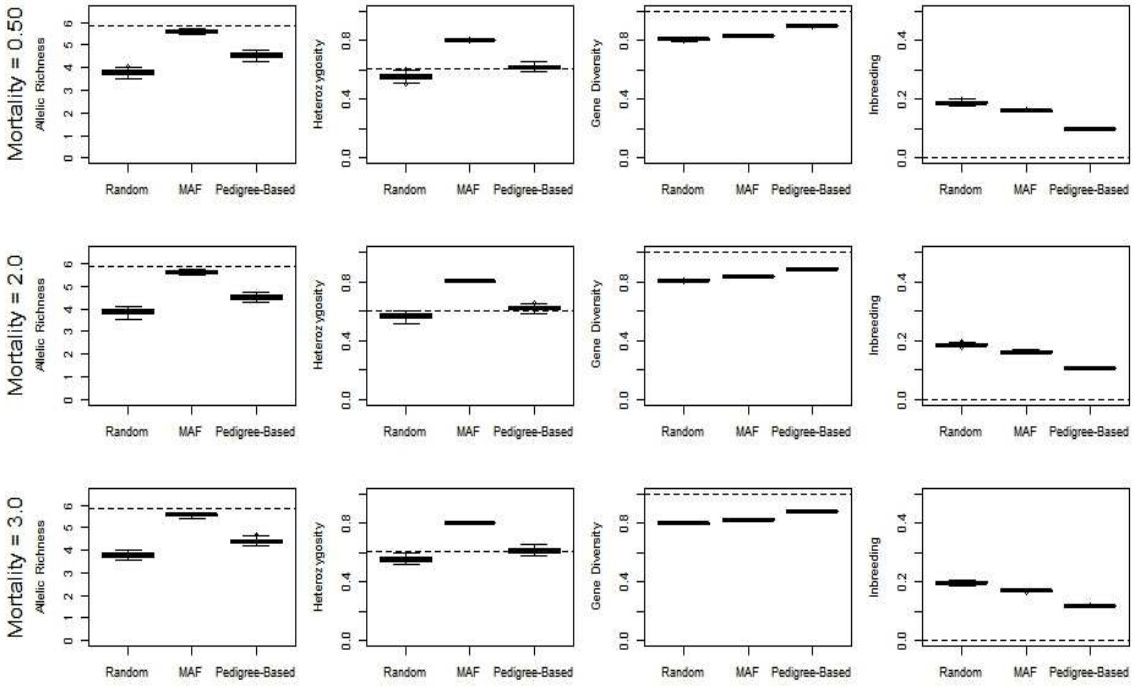

Figure 9. A trade off was observed between the two genetic based culling strategies. The MAF strategy performed best in terms of retention of allelic richness; however, the pedigree-based strategy minimized the greatest amount of inbreeding.

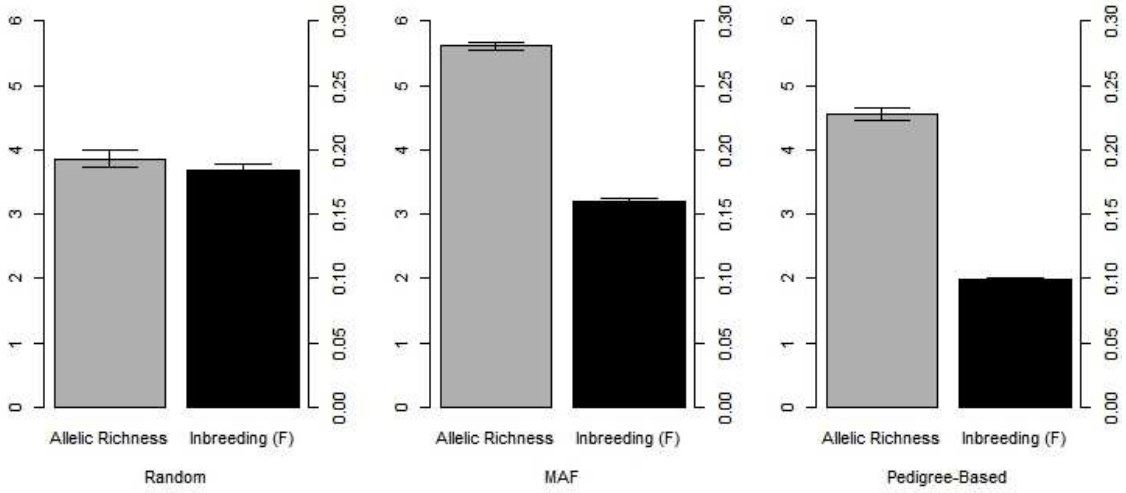

Table 1. Parameters used to simulate the three different culling strategies (Random, MAF, and Pedigree-Based).

Input File Parameters	
Founder Total	259
Microsat Total	55
Loop Parameters	
Target Size (*T*)	350
Number of Years to Run	100, 200, and 500
Iterations	100
Breeding Parameters	
Age Range Males Will Breed	4 - 16
Offspring Produced by Each Breeding Female	1
Proportion of Males that will Breed	0.4
Proportion of Females that will Breed	1
Dominant Male Breeding Parameters	
Proportion of Breeders that are dominant	0.16
Age Range Dominant Males Breed	8 - 12
Proportion of Offspring Produced by Dominant Males	0.3
Number of Years Males are Dominant	1
Mortality Parameters	
Female Adult Mortality (*Q*)	0.03
Male Adult Mortality (*Q*)	0.05
Juvenile Mortality (*Q*)	0.05
Maximum Age (*b*)	24

Table 2. Measures of genetic variation for the founding population and for each culling strategy and time step. Values for simulations are averaged over 100 iterations with standard deviation provided in parentheses.

	Founding Pop.	Random			Mean Allele Frequency			Pedigree Based		
		100 Years	200 Years	500 Years	100 Years	200 Years	500 Years	100 Years	200 Years	500 Years
A	5.873	5.337 (0.063)	4.863 (0.103)	3.857 (0.135)	5.615 (0.056)	5.611 (0.056)	5.611 (0.056)	5.533 (0.058)	5.242 (0.087)	4.550 (0.102)
H_O	0.606	0.662 (0.012)	0.637 (0.013)	0.561 (0.018)	0.797 (0.003)	0.803 (0.004)	0.802 (0.003)	0.677 (0.008)	0.661 (0.010)	0.621 (0.015)
GD	0.998	0.958 (0.002)	0.919 (0.003)	0.811 (0.004)	0.952 (0.002)	0.920 (0.002)	0.835 (0.002)	0.976 (0.000)	0.955 (0.001)	0.896 (0.001)
$\bar{F}$	0.000	0.037 (0.002)	0.076 (0.003)	0.184 (0.005)	0.042 (0.002)	0.074 (0.002)	0.160 (0.003)	0.018 (0.001)	0.039 (0.001)	0.099 (0.002)

Table 3. The coefficient of variation across 100 iterations for each management strategy at each time step (100, 200, and 500 years).

	Random			Mean Allele Frequency			Pedigree Based		
	100 Years	200 Years	500 Years	100 Years	200 Years	500 Years	100 Years	200 Years	500 Years
A	1.2%	2.1%	3.5%	1.0%	1.0%	1.0%	1.0%	1.7%	2.2%
H_O	1.8%	2.0%	3.2%	0.4%	0.5%	0.4%	1.2%	1.5%	2.4%
GD	0.2%	0.3%	0.5%	0.2%	0.2%	0.2%	0.0%	0.1%	0.1%
$\bar{F}$	5.4%	3.9%	2.7%	4.8%	2.7%	1.9%	5.6%	2.6%	2.0%

Table 4. The percent change of each measure of genetic variation under each culling strategy relative to the founding population. Numbers in red reflect a decrease in genetic variation measure.

	Founding Pop.	Random			Mean Allele Frequency			Pedigree Based		
		100 Years	200 Years	500 Years	100 Years	200 Years	500 Years	100 Years	200 Years	500 Years
A	5.873	-9.127	-17.197	-34.327	-4.393	-4.461	-4.461	-5.789	-10.744	-22.527
H_O	0.606	9.241	5.116	-7.426	31.518	32.508	32.343	11.716	9.076	2.475
GD	0.998	-4.008	-7.916	-18.737	-4.609	-7.816	-16.333	-2.204	-4.309	-10.220
$\bar{F}$	0.000	0.037	0.076	0.184	0.042	0.074	0.160	0.018	0.039	0.099

Table 5. Results from the 500 year time step of the sensitivity analysis reflecting the genetic variation measures under each culling strategy with various target population sizes (200, 500, and 1000) and the standard deviation (in parentheses).

	Founding Pop.	Target Population Size								
		200			500			1000		
		Random	MAF	Pedigree	Random	MAF	Pedigree	Random	MAF	Pedigree
A	5.873	3.028 (0.133)	5.304 (0.068)	3.807 (0.127)	4.356 (0.107)	5.701 (0.041)	4.948 (0.084)	5.018 (0.088)	5.779 (0.029)	5.397 (0.060)
H_O	0.606	0.475 (0.021)	0.790 (0.005)	0.565 (0.018)	0.605 (0.014)	0.805 (0.003)	0.647 (0.011)	0.649 (0.011)	0.806 (0.002)	0.671 (0.007)
GD	0.998	0.687 (0.008)	0.742 (0.004)	0.817 (0.003)	0.865 (0.002)	0.876 (0.002)	0.928 (0.001)	0.928 (0.001)	0.927 (0.001)	0.963 (0.000)
$\bar{F}$	0.000	0.306 (0.008)	0.250 (0.005)	0.174 (0.003)	0.131 (0.002)	0.121 (0.002)	0.069 (0.001)	0.070 (0.001)	0.071 (0.001)	0.035 (0.001)

Table 6. The coefficient of variation for each simulation under each culling strategy with various target population sizes at the 500 year time step (200, 500, and 1000).

	Target Population Size								
	200			500			1000		
	Random	MAF	Pedigree	Random	MAF	Pedigree	Random	MAF	Pedigree
A	4.4%	1.3%	3.3%	2.5%	0.7%	1.7%	1.8%	0.5%	1.1%
H_O	4.4%	0.6%	3.2%	2.3%	0.4%	1.7%	1.7%	0.2%	1.0%
GD	1.2%	0.5%	0.4%	0.2%	0.2%	0.1%	0.1%	0.1%	0.0%
$\bar{F}$	2.6%	2.0%	1.7%	1.5%	1.7%	1.4%	1.4%	1.4%	2.9%

Table 7. Results from the 500 year time step of the sensitivity analysis reflecting the genetic variation measures under each culling strategy with different proportions of males within breeding age allowed to breed (0.05, 0.50, and 1.00) and the standard deviation (in parentheses).

	Founding Pop.	Proportion of Males Breeding								
		0.05			0.50			1.00		
		Random	MAF	Pedigree	Random	MAF	Pedigree	Random	MAF	Pedigree
A	5.873	2.519 (0.136)	4.916 (0.091)	3.267 (0.133)	3.946 (0.109)	5.619 (0.049)	4.643 (0.104)	3.996 (0.121)	5.633 (0.049)	4.736 (0.112)
H_O	0.606	0.389 (0.029)	0.782 (0.006)	0.509 (0.023)	0.569 (0.018)	0.803 (0.004)	0.626 (0.015)	0.573 (0.018)	0.803 (0.003)	0.630 (0.012)
GD	0.998	0.561 (0.016)	0.621 (0.010)	0.721 (0.010)	0.823 (0.003)	0.840 (0.002)	0.906 (0.001)	0.830 (0.003)	0.845 (0.002)	0.912 (0.001)
$\bar{F}$	0.000	0.426 (0.017)	0.362 (0.010)	0.258 (0.005)	0.173 (0.003)	0.156 (0.003)	0.090 (0.001)	0.166 (0.003)	0.150 (0.002)	0.084 (0.001)

Table 8. The coefficient of variation for each simulation under each culling strategy with different proportions of males within breeding age allowed to breed (0.05, 0.50, and 1.00) observed at the 500 year time step.

	Proportion of Males Breeding								
	0.05			0.50			1.00		
	Random	MAF	Pedigree	Random	MAF	Pedigree	Random	MAF	Pedigree
A	5.4%	1.9%	4.1%	2.8%	0.9%	2.2%	302.8%	0.9%	2.4%
H_O	7.5%	0.8%	4.5%	3.2%	0.5%	2.4%	314.1%	0.4%	1.9%
GD	2.9%	1.6%	1.4%	0.4%	0.2%	0.1%	36.1%	0.2%	0.1%
$\bar{F}$	4.0%	2.8%	1.9%	1.7%	1.9%	1.1%	180.7%	1.3%	1.2%

Table 9. Results from the 500 year time step of the sensitivity analysis reflecting the genetic variation measures under each culling strategy with various rates of mortality measured as proportions of the original sex and age specific mortality rates (0.5, 2.0, and 3.0) and the standard deviation (in parentheses).

	Founding Pop.	Mortality 0.50			2.00			3.00		
		Random	MAF	Pedigree	Random	MAF	Pedigree	Random	MAF	Pedigree
A	5.873	3.787 (0.114)	5.588 (0.053)	4.543 (0.112)	3.856 (0.121)	5.609 (0.053)	4.510 (0.102)	3.771 (0.106)	5.574 (0.056)	4.401 (0.104)
H_O	0.606	0.555 (0.019)	0.802 (0.004)	0.618 (0.013)	0.563 (0.020)	0.802 (0.003)	0.620 (0.013)	0.555 (0.018)	0.801 (0.003)	0.611 (0.016)
GD	0.998	0.807 (0.005)	0.834 (0.002)	0.896 (0.001)	0.810 (0.004)	0.834 (0.002)	0.889 (0.001)	0.798 (0.004)	0.825 (0.002)	0.876 (0.001)
$\bar{F}$	0.000	0.188 (0.005)	0.161 (0.003)	0.099 (0.002)	0.186 (0.004)	0.162 (0.002)	0.106 (0.001)	0.197 (0.004)	0.171 (0.002)	0.120 (0.001)

Table 10. The coefficient of variation for each simulation under each culling strategy with various rates of mortality measured as proportions of the original sex and age specific mortality rates (0.5, 2.0, and 3.0) observed at the 500 year time step.

	Mortality								
	0.50			2.00			3.00		
	Random	MAF	Pedigree	Random	MAF	Pedigree	Random	MAF	Pedigree
A	3.0%	0.9%	2.5%	3.1%	0.9%	2.3%	2.8%	1.0%	2.4%
H_O	3.4%	0.5%	2.1%	3.6%	0.4%	2.1%	3.2%	0.4%	2.6%
GD	0.6%	0.2%	0.1%	0.5%	0.2%	0.1%	0.5%	0.2%	0.1%
$\bar{F}$	2.7%	1.9%	2.0%	2.2%	1.2%	0.9%	2.0%	1.2%	0.8%

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