

Genetic and demographic consequences of importing animals into a small population: a simulation model of the Texas State Bison Herd (USA)

Natalie D. Halbert^a, William E. Grant^b, James N. Derr^{a,*}

^a Department of Veterinary Pathobiology, Texas A&M University, College Station, TX 77843, USA

^b Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA

Received 25 June 2003; received in revised form 17 February 2004; accepted 26 February 2004

Abstract

The extant 40 bison (*Bison bison*) constituting the Texas State Bison Herd (TSBH; USA) are directly and exclusively descended from a bison herd assembled by Charles Goodnight in the 1880s, representing a historically and genetically valuable resource. The population currently suffers from low genetic variation, low heterozygosity, high calf mortality, and low natality rates compared with other closed bison populations. Population viability analysis using the VORTEX program previously indicated a 99% chance of population extinction within the next 41 years [J. Mamm. 85 (2004) in press]. We developed a stochastic simulation model to evaluate the genetic and demographic consequences of various management scenarios for the TSBH using genotypic data from 51 microsatellite loci and demographic information recorded over a 6-year period. Our results reveal that without the introduction of new genetic variation, approximately 37% of the representative microsatellite loci will become fixed as the TSBH continues to lose genetic variation at a staggering rate of 30–40% within the next 50 years. Furthermore, if the current trends in natality and mortality rates continue, our model indicates the TSBH faces a 99% chance of extinction in the next 51 years. With the importation of unrelated male bison into the TSBH, and under the assumption of increased fitness, the probability of population survival in the next 100 years increases to 100%, and the population will reach the approximate carrying capacity of 200 bison in 15–16 years. Furthermore, our model predicts increases in genetic diversity and heterozygosity of 24.7–48.4% and 17.5–36.5%, respectively, in the next 100 years following the addition of new genetic variation. We conclude that the importation of bison into the TSBH is necessary to prevent extinction and ensure long-term population survival.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Individual-based model; Genetic diversity; Bison; Population dynamics; Population viability

1. Introduction

The American bison species (*Bison bison*) suffered a severe population bottleneck during the late 1800s

* Corresponding author. Tel.: +1 979 862 4775;

fax: +1 979 845 9972.

E-mail address: jderr@cvm.tamu.edu (J.N. Derr).

(Coder, 1975; Dary, 1989). Charles Goodnight was one of a few private ranchers who worked to save this species from near extinction (Coder, 1975). With 5 wild-caught calves, Goodnight began his herd in the mid-1880s (Coder, 1975). Records indicate that this herd had increased to 13 bison by 1887, 125 bison by 1910, and 200–250 bison during the 1920s (Coder, 1975; Haley, 1949). After changing ownership several times following Goodnight's death in 1929, the herd presumably remained small, though accurate census records are not available. In 1997, the remaining herd of 36 bison were donated to Texas Parks and Wildlife and moved to Caprock Canyons State Park in the Texas (USA) panhandle (Texas State Bison Herd: TSBH; Swepston, 2001).

There are likely few bison populations worldwide managed as closely as the TSBH. The herd receives supplemental feed, yearly vaccinations, and is monitored almost daily by state biologists. The bison are not afflicted with any known ungulate disease (Danny Swepston, personal communication). Nevertheless, the TSBH is suffering from low natality and high mortality rates compared to other captive bison herds. From 1997 to 2002, the natality rate (number of calves/adult female/year) averaged 39.2% (Swepston, 2001; Table 1). In comparison, Berger and Cunningham (1994) reported approximately 60% natality at Badlands National Park over a 5-year study period and Meagher (1973) estimated a natality rate of 52% at Yellowstone National Park. TSBH mortality rates from 1997 to 2002 averaged 53.9% for yearlings, which is significantly higher than the 4.2% calf mortality rate previously reported, while the average 5.5% mortality rate for bison older than 1 year is only slightly higher than the 3.2–4.2% previously reported (Berger and Cunningham, 1994). Consequently, the census population size has only increased from 36 to 40 bison over the past 6 years, and the average age of the population has risen by 2.64 years (Table 1; Swepston, 2001). In 2001, all 40 extant bison from the TSBH were sampled for genetic testing, including parentage analysis, estimation of genetic variation, and karyotyping. The results of these analyses indicate that the TSBH contains very little genetic variation and low heterozygosity for the loci sampled compared with other closed bison populations (Halbert et al., 2004).

Many types of models have been used to assess population viability and develop conservation management

plans for an array of species, including plants (e.g. Giho and Seno, 1997; Schenk, 1996), fish (e.g. Bartholow, 1996; McKenna, 2000), and mammals (e.g. Jerina et al., 2003; Maudet et al., 2002). However, relatively few population viability models directly account for the effects of genetic pressures, such as variation, inbreeding, and heterozygosity (Jetschke, 1992). For instance, the widely-used population viability analysis program VORTEX (Lacy, 1993) assigns random, unique alleles to each individual and uses the infinite alleles model to track changes in diversity and inbreeding (Lindenmayer et al., 1995). Given the current TSBH natality and mortality rates and allowing for disease and natural catastrophe as potential stochastic events affecting reproduction and survival, population viability analysis using VORTEX indicates that the TSBH faces a 99% chance of extinction within the next 41 years (Halbert et al., 2004). However, in this analysis actual genotypes could not be associated with individual bison in the TSBH. Here, we present an individual-based stochastic model developed to simulate the effects of current natality and mortality rates on census population size and genetic diversity in the TSBH over the next 100 years. Specifically, our model was designed to simulate the importation of bison males into the TSBH to investigate potential effects of increased fitness and introduction of new allelic variation on long-term census population size, genetic (allelic) diversity, and heterozygosity. Additionally, we utilized our model to examine the effects of various management schemes on these parameters.

2. Model description

The stochastic model simulates changes in census population size, heterozygosity, and genetic diversity based on a 1-year time step using Visual Basic® 6.0 (Microsoft®). The initial conditions of the model include sex, age, and genotype at each of 51 unlinked autosomal microsatellites for the 40 extant bison from the TSBH (as of December 2001; Halbert et al., 2004). Reproductive ages follow that reported in other bison populations (Berger and Cunningham, 1994). In our model, females and males are considered potentially reproductive from 3 to 13 years and from 4 to 14 years of age, respectively. Following observed competition and breeding success among males, when a 7- to 12-year-

Table 1

Average age, census population size, mortality rate, and natality rate estimates based on data from the Texas State Bison Herd over 6 consecutive years and compared with previously published captive bison population data

Year	Average age ^a	Census size ^b	<1 Year mortality ^c	>1 Year mortality ^d	Natality ^e
1997	3.56	36	3/4 (0.750)	5/36 (0.139)	4/21 (0.190)
1998	4.50	32	2/4 (0.500)	3/32 (0.091)	4/17 (0.235)
1999	5.35	31	7/11 (0.636)	2/31 (0.065)	11/15 (0.733)
2000	5.73	33	1/4 (0.250)	1/33 (0.030)	4/17 (0.235)
2001	6.23	35 ^f	3/10 (0.300)	0/35 (0.000)	10/16 (0.625)
2002	6.20	40	4/5 (0.800)	0/40 (0.000)	5/15 (0.333)
TSBH average (small herd)			0.539	0.055	0.392
Captive bison average (large herd) ^g			0.042	0.032–0.042	0.600

^a Exact ages unknown for animals born before 1997, and figured conservatively as either yearlings or adults (3+). This skews the average age of the herd below actual age, but does not change the average increase in age over 6 years.

^b Census size before death and birth for given year.

^c Ratio given as number of deaths/number of calves born up to 1 year in age.

^d Ratio given as number of deaths/number total bison >1 year in age.

^e Ratio given as number of births/number of total adult females ages 3+.

^f 2 Steers donated to Armand Bayou Nature Center (Houston, TX, USA).

^g Derived as conservative estimates from [Berger and Cunningham \(1994\)](#); mortality rate for age classes 0–2 reported as 0.042/year and for ages 3+ as 0.032/year.

old male(s) exists in the simulated population, those younger or older do not mate in a given year ([Berger and Cunningham, 1994](#)). Each time step (year), the age of each bison is advanced and potential breeders recalculated. Females and males are selected and paired randomly from the potential breeding pool. For each locus, an allele from each parent is randomly chosen and assigned to the offspring. The offspring sex ratio is 1:1, as is generally found in closed bison populations ([Berger and Cunningham, 1994](#); [Swepston, 2001](#)). At each time step, genetic diversity is calculated directly as the total number of different alleles existing in the population for the 51 microsatellites. Similarly, heterozygosity is calculated directly for each locus across all individuals (number of heterozygotes/total number of individuals) and then averaged across all loci.

“Small herd demography” natality and mortality rates were calculated from TSBH data from the past 6 years ([Table 1](#)). “Large herd demography” natality and mortality rates were taken as conservative estimates of those calculated by [Berger and Cunningham \(1994\)](#), with the mortality rate for age classes 0–2 years of 4.2% per year and for age classes 3+ years of 3.2% per year ([Table 1](#)). Natality rates are applied to potentially breeding females such that under the small herd demography scenario, for instance, 39.2% of 3- to 13-year-old females are randomly selected to mate and produce offspring. Once bison reach 20 years of age,

the mortality rate is assumed to be 50%, based on the rarity of bison in captive populations observed beyond this age. Furthermore, a mortality rate of 100% is applied to any bison that reach the age of 30 during the simulation. When the census population size is greater than 200 bison, excess calves are randomly culled so as to keep the population from exceeding the approximate carrying capacity at Caprock Canyons State Park ([Danny Swepston, personal communication](#)).

We used our model to evaluate the effects of importing male bison into the TSBH, although clearly one or both sexes could actually be used to achieve this goal. Our choice was based on two criteria. First, we hoped to minimize dilution of the unique bison mitochondrial DNA type found exclusively in the TSBH ([Ward et al., 1999](#); [Ward, 2000](#); population abbreviation JA), with the caveat that Y-chromosome uniqueness in the TSBH compared with other North American bison populations is currently untested. Second, importing a small number of males is more time- and cost-effective than importing the same number of breeding females.

A random number generator was used to select individuals from 142 male Yellowstone National Park bison samples previously collected in our laboratory. Three distinct sets of 3 bison (9 total) were chosen and completely genotyped for the same 51 microsatellite loci utilized for the TSBH ([Halbert et al., 2004](#)). All males are imported in the model as 7 year-olds (breed-

ers). Breeding may occur either randomly with replacement, with one male mating all potential females in a given year with replacement the following year, or with 3 imported males breeding all potential females during the year of importation followed by random mating of all potentially breeding males (native and imported) in all subsequent years. Migration occurs with either 3 males imported into the population in year 1 or with 9 males total imported at a rate of 3 males every 5 years (importation in years 1, 6, and 11). In general, we assumed that fitness, as reflected by birth and death rates, would most likely increase following the importation and subsequent mating of new bison into the TSBH (Lewontin and Birch, 1966; Spielman and Frankham, 1992; see Section 5). Unless otherwise noted, 20 replicates were used in each evaluation and averages were taken for each year across all replicates for the parameters of interest.

3. Model evaluation

3.1. Choice of particular males for importation

To examine the sensitivity of the model to the choice of particular imported bison, we simulated the introduction of the 3 groups of 3 bison from Yellowstone National Park separately. In each case, the 3 bison were imported into the population in year 1 and allowed to mate all potentially breeding females preferentially, with random mating of all males (native and imported) in every subsequent year. No further assumptions were made regarding the fitness of the imported males versus the original TSBH males, and large herd natality and mortality rates were used (Table 1).

Currently, there are a total of 133 alleles in the TSBH for the 51 nuclear microsatellite loci tested. The introduction of bison from groups 1, 2, and 3 adds 62, 67, and 63 new alleles, respectively. Fig. 1 illustrates differences in the total number of alleles and heterozygosity for the 51 markers in question over 100 years with each of the 3 sets of imported males.

Differences among average values for heterozygosity and number of alleles at 50 and 100 years between the 3 groups were tested using analysis of variance (ANOVA). Average heterozygosity at 50 and 100 years and number of alleles present at 100 years were not significantly different between the 3 groups ($P > 0.05$).

However, the average number of alleles at 50 years between the 3 groups was significantly different ($P < 0.05$). We further tested the differences in number of alleles at 50 years using Tukey's HSD (absolute difference) test, which revealed that the differences between groups 1 and 3 were non-significant ($P > 0.05$) while the other pairwise comparisons showed significant differences ($P < 0.05$). Percent differences between initial and final (100 years) values for total number of alleles are -15.0% (1), -14.3% (2), and -14.5% (3) and for heterozygosity are -12.0% (1), -16.0% (2), and -14.3% (3). Therefore, we conclude that heterozygosity and genetic diversity are not substantially influenced by our choice of one particular group of bison over another for simulated importation into the TSBH. In further analyses involving the importation of only 3 bison into our model, we used group 1, which contributes the least number of new alleles into the TSBH and is therefore likely to provide conservative estimates of predicted changes in heterozygosity and genetic diversity.

3.2. Effects of natality and mortality rates

To examine the sensitivity of population size and genetic variation to changing demographic parameters within our model, we examined the potential effects of natality and mortality rates on population size, genetic diversity, and heterozygosity. Using the averages shown in Table 1 as a guide, we evaluated the effects of natality rates ranging from 40 to 60% and calf mortality rates ranging from 5 to 50% (series A–F; Table 2). Since mortality rates for those bison >1 year of age in the TSBH are similar to previously published reports, large herd mortality rates for age classes >1 year were used in these evaluations (Table 1; Berger and Cunningham, 1994). Each evaluation assumed random mating and no migration.

All of the 120 simulated populations (6 series with 20 simulations each; Table 2) survived to 100 years. Average population size, total number of alleles, and heterozygosity values each year for each series of simulations are depicted in Fig. 2. Although the mean population size trajectory of each series eventually reaches $n = 200$ individuals, the population growth rates are clearly different among the series. The average time for the TSBH to reach carrying capacity is shown in Table 2 as the average year that each simulation reached

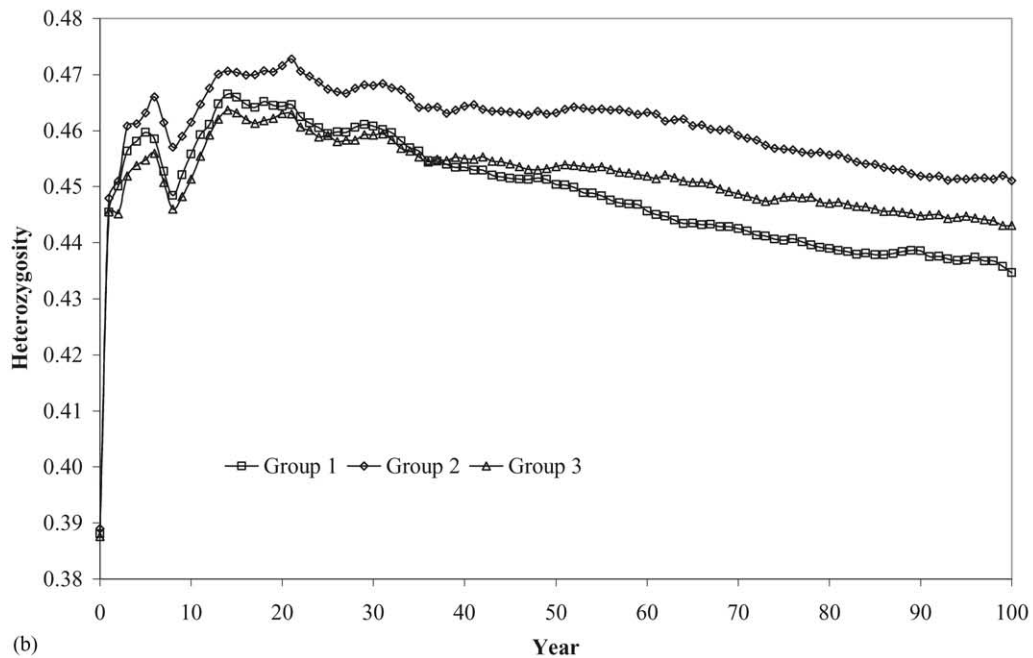
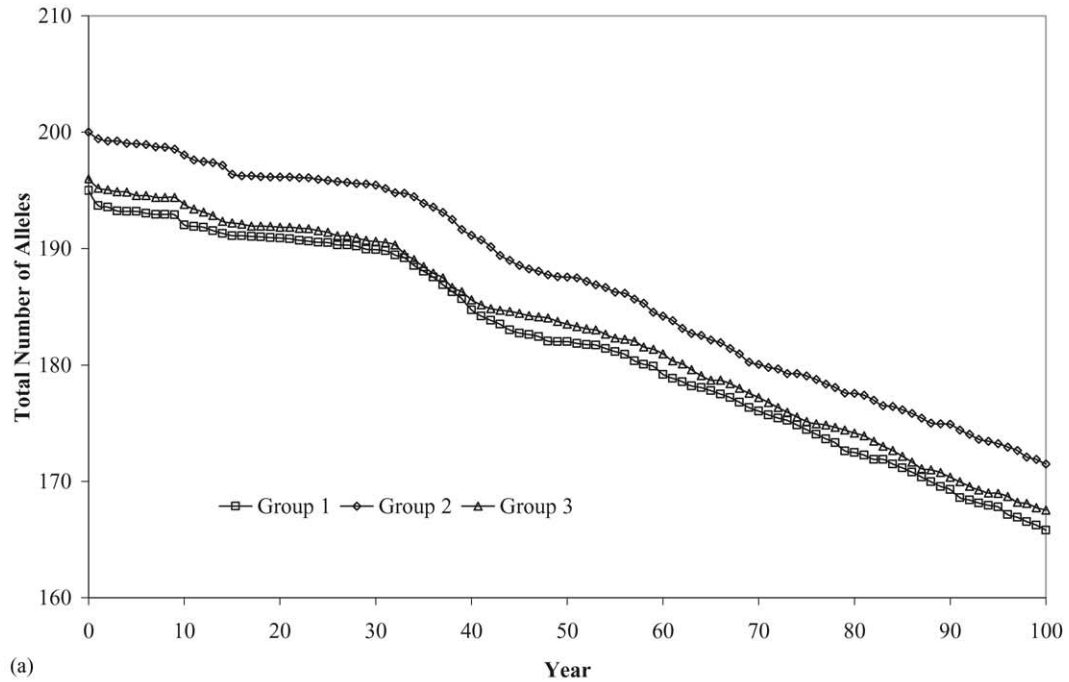


Fig. 1. Evaluation of the effects male choice for importation on the model. Average genetic diversity (total number of alleles) and heterozygosity are compared each year among 3 groups of 3 imported males each, randomly selected from a subset of males from Yellowstone National Park. Averages at 100 years are not significantly different.

Table 2

Description of parameters and summary results for evaluation of the effects of mortality and natality rates on the model

Series	Natality rate	Calf mortality rate	Average year, $n = 200$	Growth rate (bison/year) ^a	Average total number of alleles	Average heterozygosity
A	0.6	0.05	14.8 ± 1.5	10.9	120.0 ± 4.2	34.4 ± 2.2
B	0.5	0.05	18.8 ± 2.9	8.4	120.9 ± 3.0	34.1 ± 2.1
C	0.4	0.05	27.0 ± 5.4	5.7	120.7 ± 3.5	34.2 ± 1.3
D	0.6	0.50	54.6 ± 18.8	1.9	118.1 ± 4.3	33.4 ± 1.3
E	0.6	0.35	27.0 ± 8.6	5.9	119.8 ± 4.2	33.7 ± 1.6
F	0.6	0.20	18.5 ± 2.0	8.5	121.1 ± 4.7	34.2 ± 1.8

Model evaluation conditions include large herd mortality rates for bison >1 year in age, no migration, and random mating. Summary statistics include average time to reach carrying capacity ($n = 200$), growth rate, genetic diversity (total number of alleles), and heterozygosity after 100 years (average ± S.D.).

^a Slope of regression line of average population size up to average year that population reaches $n = 200$ individuals.

$n = 200$. The differences among series in average time to carrying capacity are significant (ANOVA, $P < 0.05$).

The average growth rate of the population for each series was calculated as the slope of the regression line of the average population size for each treatment from year 0 until the average population reached $n = 200$ individuals. Growth rates, average genetic diversity (total number of alleles), and average heterozygosity in year 100 for the various natality and mortality treatments are shown in Table 2. As the natality and mortality rates for series A follow that observed in Badlands National Park by Berger and Cunningham (1994), the finite growth rate is also similar (10.9%/year versus 10.8%/year, respectively).

The results of these analyses indicate that population growth is more sensitive to changes in calf mortality rates than to changes in natality rates. Series C approximates the current natality rate at the TSBH (40%), but includes a dramatically reduced calf mortality rate (5% versus ~50%; Table 1), while series D approximates the calf mortality rate of 50% at the TSBH, but improves the natality rate (60% versus ~40%; Table 1). Fig. 2 clearly shows a difference in the rate of growth and the average time to reach carrying capacity between these two series (5.7 versus 1.9 bison/year and 27.0 versus 54.6 years for series C and D, respectively; Table 2). Furthermore, if only these 2 series are considered, the difference in the average total number of alleles in year 100 is statistically significant (two-tailed t -test, $P < 0.05$; difference in average heterozygosity not significant, $P > 0.05$). As such, it seems that genetic diversity and population growth rates are more sensitive to reductions in calf mortality rates than to increases in natality rates in this population. Similar conclusions

have been made through modeling Sage Grouse populations, where individual survival was found to have a larger impact on population persistence than fecundity (Johnson and Braun, 1999).

4. Model use

We used the model to evaluate 7 different mating and migration scenarios (Table 3). Average population size, genetic diversity, and heterozygosity comparisons are shown in Fig. 3. Under the first scenario mating was assumed random, natality and mortality rates were as calculated from the TSBH records (small herd demography), and no bison were imported into the population. On average, the population went extinct in 47.9 years ± 12.2 S.D. (rate based on extinction of one or both sexes). Of the 20 iterations, none of the populations survived to 100 years. Consequently, the standard deviations for calculations of population size, total number of alleles, and heterozygosity become quite large after 50 years; therefore, we calculated averages for these parameters based on the surviving populations each year only up to 50 years (Fig. 3). Average calculations of census size, genetic diversity (total number of alleles), average heterozygosity, average age, and number of fixed loci from the first scenario are shown in Table 4. This evaluation indicates that within 21 years, 10% of the currently present genetic diversity within the TSBH will be lost, as measured by the change in the total number of alleles present in the population.

The second scenario was similar to the first except that one male was randomly chosen to mate all potentially reproductive females in a given year. This sce-

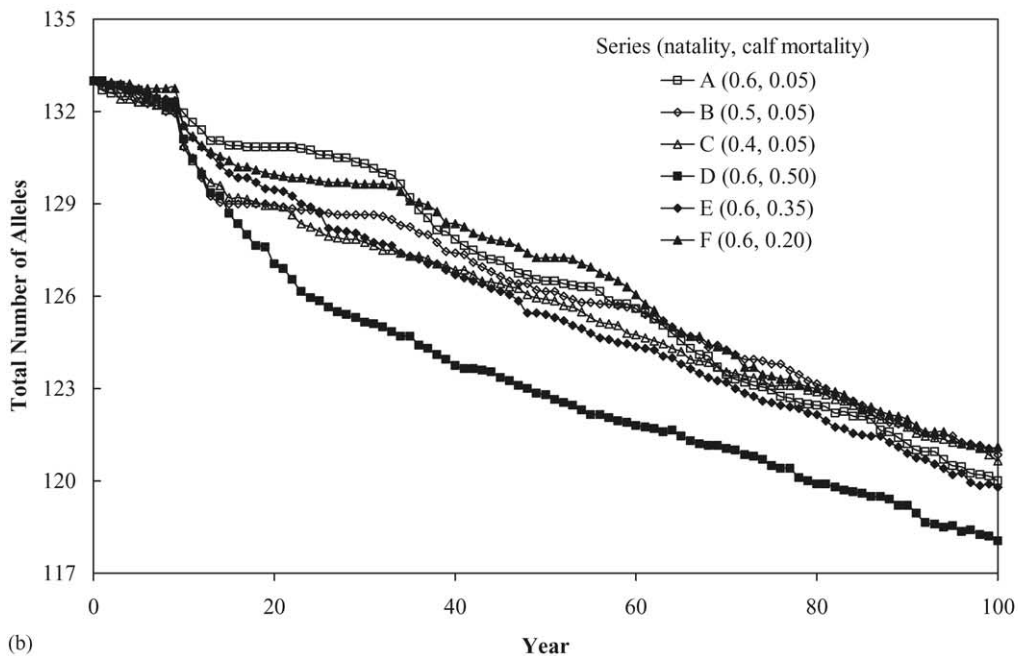
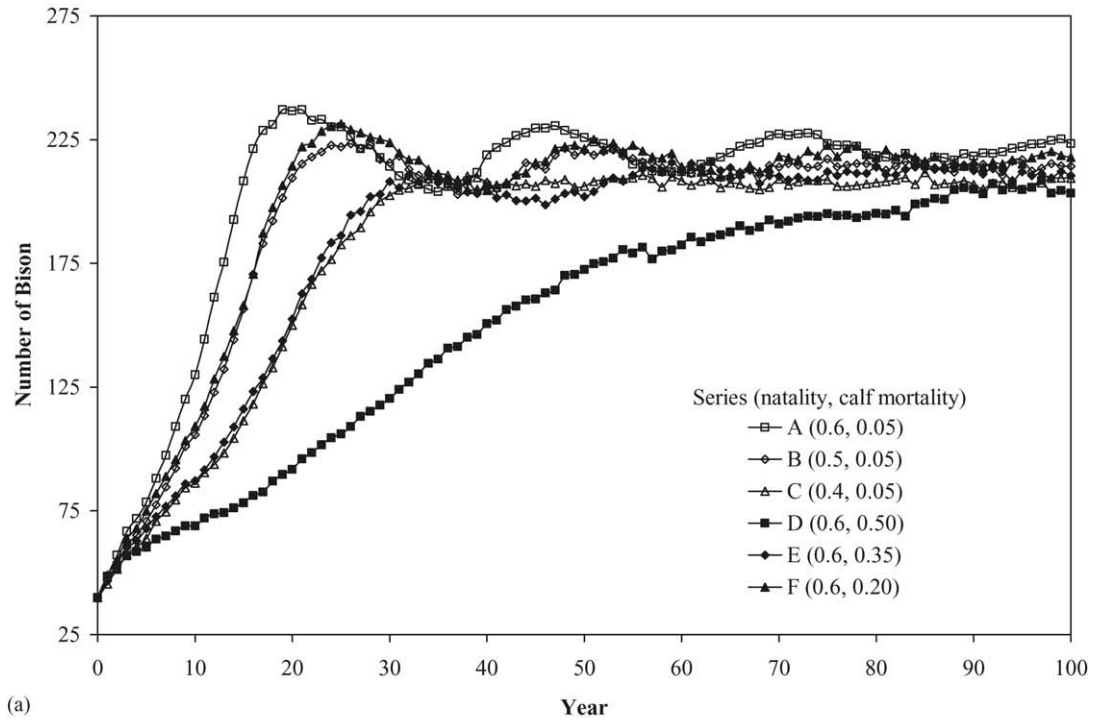


Fig. 2. Evaluation of the effects of mortality and natality rates on the model. Average population size, genetic diversity (total number of alleles), and heterozygosity are compared among the various series of simulations with different natal and calf mortality rates. Model evaluation conditions include large herd mortality rates for bison >1 year in age, no migration, and random mating.

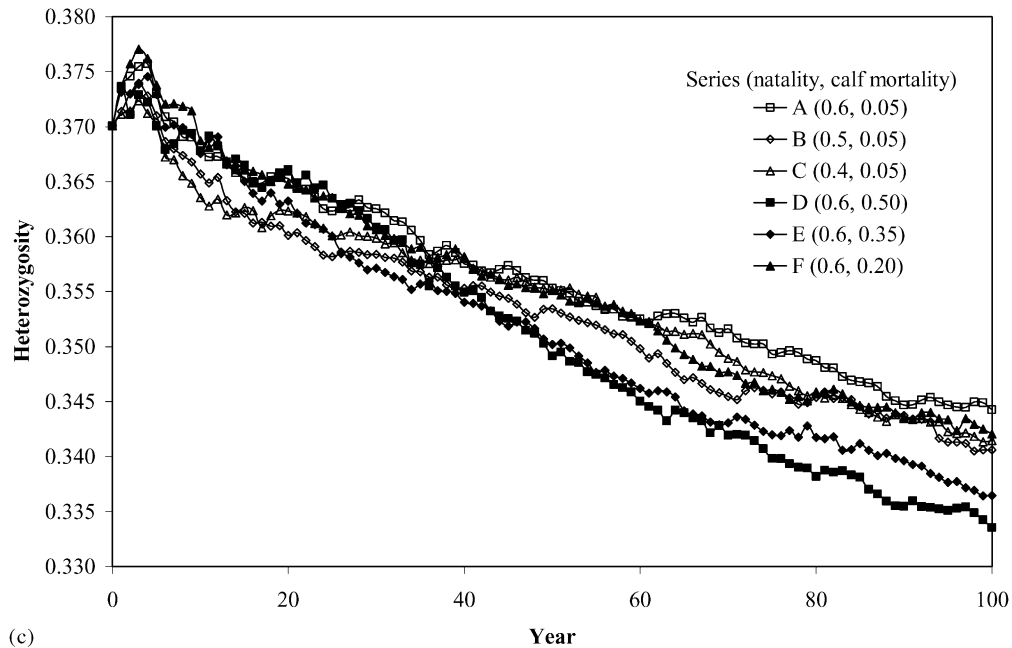


Fig. 2. (Continued).

Table 3

Description of management scenarios evaluated, including description of mating type, birth and death rates, and incidence of importation

Scenario	Description	Mating	Demography	Importation
1	Baseline	Random (7–12-year-old male mate preference)	Small herd	None
2	Single male	One 4–14-year-old male mates all females in give year with replacement	Small herd	None
3	Artificial insemination	Random (7–12-year-old male mate preference)	Large herd natality Small herd mortality	None
4	3 Migrants with random mating	Random (7–12 year-old male mate preference)	Large herd	3 Males in 1st year
5	3 Migrants with preferential mating	Migrants mate all females in year of importation, random mating otherwise	Large herd	3 Males in 1st year
6	9 Migrants with preferential mating	Migrants mate all females in year of importation, random mating otherwise	Large herd	3 Males in years 1, 6, 11
7	9 Migrants with average natality & mortality	Migrants mate all females in year of importation, random mating otherwise	Half fitness ^a	3 Males in years 1, 6, 11

^a 50% natality rate; 29% calf mortality rate; 4.85% mortality rate for age classes 1–2; 4.35% mortality rate for age classes 3+.

Table 4

Summary of population characteristics after 50 years of simulation under scenario 1 (average \pm S.D.)

Year	Census size	Total number of alleles	Average % heterozygosity	Average age	Total number of fixed loci
0	40	133	37.0	6.20	5
10	39.9 \pm 6.7	129.7 \pm 3.0	36.4 \pm 1.1	9.7 \pm 0.9	5.7 \pm 0.7
20	23.9 \pm 8.8	120.5 \pm 4.0	35.7 \pm 2.3	10.1 \pm 1.5	7.9 \pm 1.5
30	14.1 \pm 8.5	107.4 \pm 9.9	34.3 \pm 3.2	11.3 \pm 2.7	11.8 \pm 4.7
40	8.7 \pm 7.1	93.2 \pm 16.3	33.5 \pm 6.1	13.6 \pm 3.9	19.1 \pm 8.7
50	6.0 \pm 4.2	93.2 \pm 12.7	32.9 \pm 4.1	14.0 \pm 3.8	18.9 \pm 7.8

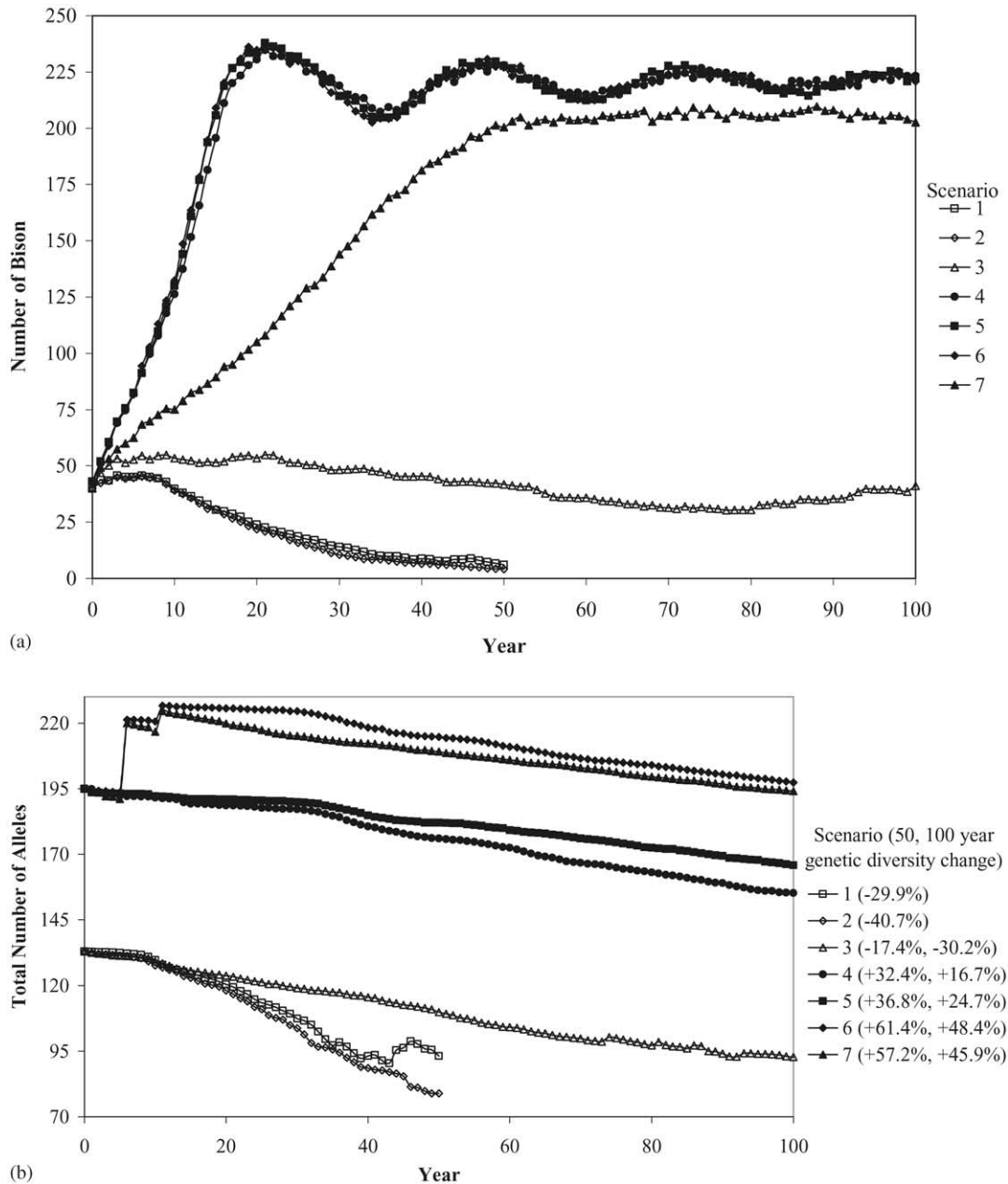


Fig. 3. Comparison of average population size, genetic diversity (total number of alleles), and heterozygosity among 7 management scenarios (Table 3). Averages for scenarios 1 and 2 were only calculated to 50 years, since after this point the majority of simulated populations were extinct (averages taken from only those populations that existed in a given year). Percent difference between initial and final averages for total number of alleles and heterozygosity are given at 50 years and 100 years in the legends. In treatments 6 and 7, 3 breeding-age males were added into the population in years 1, 6, and 11, which is reflected by sharp increases in the respective genetic diversity and heterozygosity curves following importation.

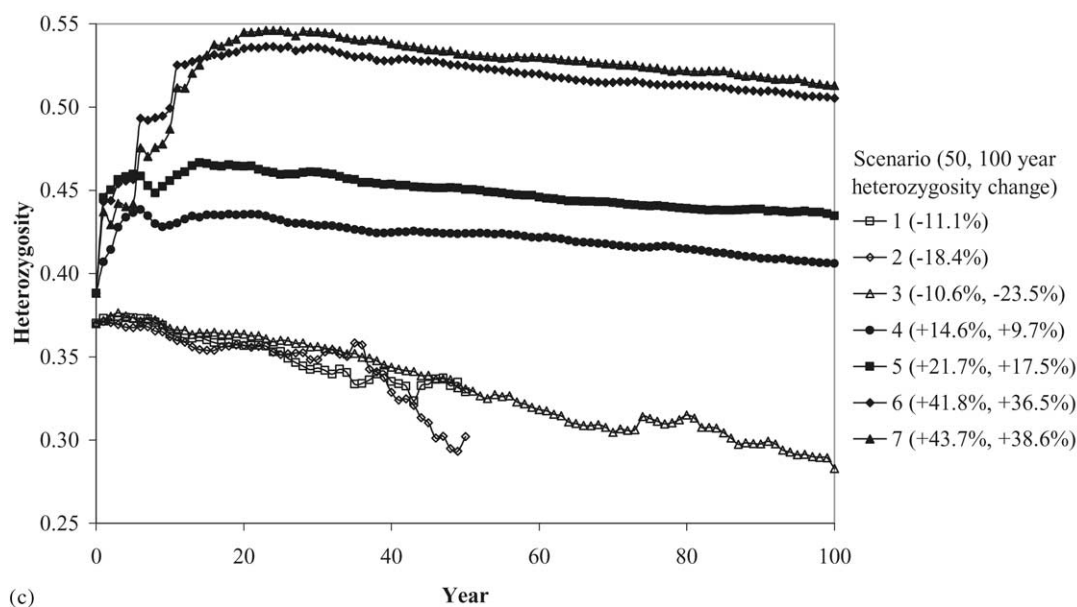


Fig. 3. (Continued).

nario was designed to model the effects of breeding one or a few males preferentially within a population, as is a common practice in private populations and has recently been employed in the TSBH in an effort to improve recruitment rates (Danny Swepston, personal communication). As with scenario 1, all 20 simulations were extinct by year 100. In scenario 2, 10% of the original genetic diversity within the TSBH is lost within 18 years. The average age of the population at 50 years is 14.1 ± 3.1 years, which is comparable to the average of 14.0 ± 3.8 years from scenario 1 (Table 4; averages not significantly different using two-tailed *t*-test, $P = 0.9278$).

The third scenario simulates the effects of artificial insemination within the TSBH using currently present males as well as those “born” in the model as the sources for male gametes. To achieve this effect, we included an increased natality rate of 60% from the baseline conditions, random mating, and no migration. Mortality rates were assumed to remain the same as those currently found in the TSBH. The high incidence of calf mortality despite intense and careful management of this population indicates the calf mortality rates in the TSBH are genetically-influenced and a by-product of low genetic variation (Halbert et al., 2004). In this case, artificial insemination will effectively in-

crease birth rates, but will not substantially improve calf survival rates. Of the original genetic diversity, 10% is lost within 28 years, indicating a slower rate of genetic deterioration compared with scenarios 1 and 2. The average age of the population at 50 years is 8.4 ± 1.5 years, which is significantly lower than that from either of the previous scenarios (two-tailed *t*-test, $P < 0.0001$).

To further investigate extinction rates, population size and birth rates were compared between scenarios 1, 2, and 3 for 100 simulations each. Results for these simulations are shown in Table 5. ANOVA indicates that the averages for time to extinction, year of last birth, and proportion of years with no births are not uniform across the 3 scenarios ($P < 0.001$). Specifically, scenarios 1 and 2 were not different (Tukey’s HSD, $P > 0.01$), while scenario 3 was significantly different from either 1 or 2 ($P < 0.01$). Using the confidence interval for the average time to extinction, there is a 99% chance of population extinction given the conditions of scenarios 1, 2, and 3 in approximately 50.8, 50.5, and 81.3 years, respectively.

The last 4 scenarios simulated the effects of bison importation into the TSBH (Table 3). The fourth scenario included random mating, large herd natality and mortality rates, and 3 migrants in the first year of the

Table 5
Extinction data summarizing results of 100 simulations under scenarios 1, 2, and 3

	Scenario 1	Scenario 2	Scenario 3
Proportion extinct simulations ^a	0.99	1.0	0.26
Time to extinction ^b	47.4 ± 13.3	47.1 ± 13.1	77.2 ± 15.7
Year of last birth ^c	40.0 ± 15.0	39.0 ± 13.1	91.8 ± 15.7
Proportion years with no birth ^d	38.3 ± 9.2%	39.6 ± 8.4%	7.5 ± 11.3%

^a Proportion of simulations in which one or both sexes becomes extinct at or before 100 years.

^b Average time (± S.D.) until one or both sexes becomes extinct, taken only for those simulations that become extinct at or before 100 years.

^c Average (± S.D.) taken for all simulations.

^d Total number of years with no births/total number of years with population size >0 (average ± S.D.).

simulation. Scenario 5 was similar to the fourth except the migrants were allowed to preferentially mate in the year of importation, followed by random mating in all subsequent years. In the sixth scenario, a total of 9 bison were imported into the population at a rate of 3 bison every 5 years with preferential mating in the year of importation (random mating all other years) and assuming large herd natality and mortality rates. Finally, we used the best-case importation scenario of 9 bison total (as in scenario 6), but assumed that fitness would not increase to produce natality and mortality rates as those seen in other captive bison populations (i.e. large herd demography). Instead, we took the average between the small herd and large herd natality and mortality rates for the seventh scenario (Table 3). There is a significant difference in the total number of alleles and heterozygosity in year 100 between these 4 scenarios (ANOVA, $P < 0.0001$). In year 100, significant pairwise differences were found among all scenarios in average heterozygosity and except scenarios 6–7 in total number of alleles (Tukey's HSD; $P < 0.01$). In scenarios 4, 5, and 6, the average time for the population to reach carrying capacity ($n = 200$) is approximately 15–16 years, while that for scenario 7 is 49 years. The

average time to incur a 10% loss of genetic diversity is 49, 69, 71, and 59 years, respectively, while the average age of the population at 50 years is 9.3, 9.5, 9.5, and 8.2 years, respectively.

Table 6 illustrates the proportion of fixed loci present during the simulation on average. Averages are taken only from those simulations with a population size $n > 0$ in a given year. For scenarios 1–3 with no added genetic diversity through importation, the proportion of fixed loci starts at almost 10% and increases steadily thereafter. In the last 4 scenarios, which include bison importation, the proportion of fixed loci starts at around 2% and either increases at a substantially slower rate compared with scenarios not including importation (scenarios 4 and 5), or actually decreases with the importation of additional groups of males (scenarios 6 and 7; Table 6).

5. Discussion

Although the TSBH is genetically distinct from other North American bison populations (Halbert et al., 2004; Ward, 2000), all evidence to date including

Table 6
Average proportion fixed loci out of 51 total loci from 20 simulations, taken only from those simulations with a population size >0 in a given year

Year	Scenario 1 (%)	Scenario 2 (%)	Scenario 3 (%)	Scenario 4 (%)	Scenario 5 (%)	Scenario 6 (%)	Scenario 7 (%)
0	9.8	9.8	9.8	2.0	2.0	2.0	2.0
10	11.2	12.7	11.8	2.1	2.0	0.0	0.0
20	15.4	16.7	14.3	2.4	2.0	0.0	0.0
30	23.1	24.8	16.8	2.5	2.1	0.0	0.0
40	37.5	40.0	18.4	2.7	2.5	0.0	0.0
50	37.1	51.0	22.1	3.1	2.6	0.0	0.0
100	–	–	37.1	5.1	3.2	0.4	0.6

natality and mortality rates, measures of genetic diversity and heterozygosity, and population viability analyses indicate this bison population is in a perilous genetic and demographic situation that will most likely lead to extinction (Halbert et al., 2004). The decision to import unrelated bison into the TSBH should not be made hastily or carelessly, and any potential source of bison for importation into the TSBH should be disease-free, have comparatively high levels of genetic diversity, and should have no history of hybridization with domestic cattle. Our goal was to investigate the effects of increased genetic diversity due to importation into the TSBH regardless of the actual source; the logistics and feasibility of actually importing bison from Yellowstone National Park into the TSBH were not considered. A direct historic link does exist between the TSBH and Yellowstone National Park, as Charles Goodnight donated 3 bison bulls to help establish the Yellowstone population in 1902 (Corder, 1975). Although the Yellowstone bison population currently suffers from brucellosis, the population has high levels of genetic diversity compared with other closed bison populations, including the TSBH (Halbert et al., 2004; Schnabel et al., 2000; Wilson and Strobeck, 1999). Furthermore, the Yellowstone bison population has no history of hybridization with domestic cattle, and domestic cattle mitochondrial DNA has not been detected in Yellowstone bison (Ward et al., 1999; Ward, 2000). Yellowstone bison have previously been used as founding stock for several private herds such that even if obtaining bison directly from Yellowstone National Park is not realistic, other sources exist that should exhibit similar levels of genetic diversity and be free of disease. Additionally, several other US federal bison populations are free of disease and regularly cull excess bison, therefore providing an additional potential source for the TSBH.

Without the addition of novel genetic variation into the TSBH, our model reveals that the population is likely to become extinct. The management practice of breeding a single male to all females in a given year (scenario 2) compared with random mating (scenario 1) has probable genetic consequences of reduced heterozygosity and overall diversity, although the probability of population survival is equivalent (Fig. 3, Table 5). Furthermore, the average proportion of fixed loci is notably higher after 50 years in scenario 2 versus 1. Although bison natural mating practices

include polygamy (Berger and Cunningham, 1994), unnatural exacerbation of this mating regime seems imprudent given the small size of this population and already low genetic variation. Indeed, the least cost- and time-intensive change in the current management strategy that will at least slow the degradation of genetic diversity in the TSBH would be to employ a more random mating scheme. However, neither of these scenarios is recommended for the long-term management of this population, as the extinction rates predicted by our model are prohibitive. The rate of extinction under the third scenario, designed to simulate artificial insemination, is slower than that from scenarios 1 and 2. Nevertheless, we do not believe artificial insemination is a plausible management alternative for the TSBH due to the necessarily high investment of resources and diminishing returns of low population survivability and long-term genetic erosion (Fig. 3, Table 6).

Immigration is commonly recommended to alleviate inbreeding depression and improve population fitness in small closed populations. Furthermore, immigration into small populations is likely to increase the probability of population persistence, as indicated by African wild dog population modeling (Vucetich and Creel, 1999). The number of migrants necessary to counter the effects of drift is commonly taken to be one migrant per generation (OMPG) based on theoretical and experimental evidence (Franklin, 1980; Spielman and Frankham, 1992; Spieth, 1974). However, OMPG is sufficient only for minimizing loss of polymorphism and heterozygosity within subpopulations while allowing for divergence in allele frequencies among subpopulations. OMPG is not sufficient in cases involving small populations, where individual viability will likely decrease and deleterious mutations will increase, collectively leading to an increased probability of extinction (Couvett, 2002). Mills and Allendorf (1996) also argue that OMPG is inadequate and suggest a minimum of 1 and maximum of 10 migrants per generation (to prevent erosion of local adaptations and outbreeding depression) in cases involving inbreeding depression, when effective population size is much less than total population size, when migrants are likely to be at a disadvantage in terms of survival and breeding success, when the receiving population has been isolated for many generations, and/or when demographic or environmental variation indicates high danger of extinction without aggressive supplementations. Notably,

the TSBH meets each of these criteria (Halbert et al., 2004).

The minimum number of immigrants necessary to substantially improve the probability of long-term survival of the TSBH is unknown, so we modeled the effects of both a single importation event of 3 bison (scenarios 4 and 5) and an importation event approximately once per generation for the next 3 generations (scenarios 6 and 7). With importation our model clearly shows increases in population size, a slower rate of genetic deterioration, improvements in heterozygosity, and a substantially slower rate of fixation of neutral loci (Fig. 3, Table 6). According to our results, the best breeding strategy following importation would be to selectively breed the newly imported bison to allow for the largest and fastest possible genetic contribution to the breeding pool (scenario 5).

The introduction of new variation into small, closed populations tends to increase fitness and adaptive response (Lewontin and Birch, 1966; Spielman and Frankham, 1992). However, the level of improvement in fitness and probability of population persistence is difficult to measure and likely different for every species and individual populations. In our model, we assumed that the introduction of new bison in scenarios 4–6 would lead to increased fitness such that natality and mortality rates would mimic those observed in larger captive bison populations (Tables 1 and 3; Berger and Cunningham, 1994). Following the report by Spielman and Frankham (1992) that reproductive fitness increases in isolated, small, inbred *Drosophila melanogaster* populations with OMPG to approximately half that of the original populations, we investigated the effects of importing 9 bison into the TSBH while increasing natality and decreasing mortality to halfway between the current TSBH and large herd rates (scenario 7, Table 3). Although the differences in natality and mortality rates clearly change the population growth rate, the expected levels of genetic diversity and heterozygosity after 100 years are not statistically different from the same treatment using the large herd natality and mortality rates (scenario 6, Fig. 3). Therefore, we conclude that even with moderate changes in fitness coupled with immigration of bison into the TSBH, the likely fate if this population is substantially improved.

Few individual-based genetic models for population management have been developed to date. In most, individual genotypes are estimated from

allelic frequencies and changes in average population heterozygosity are calculated as a function of effective population size (e.g. Gross, 2000). We were fortunate to have sampled and genotyped each bison in the TSBH, which allowed our individual-based model to initially include complete genotypes for each extant bison, followed by random allele sorting to form the genotype of each newly-created individual in the model and direct calculation of population heterozygosity at each time step. As such, our model has the advantage of being a better predictor of future demographic and genetic population trends in the TSBH. Furthermore, this model should be easily modified for use in other closed bison populations where it is possible to genotype most extant individuals. Due to the simplistic design of our model, mitigating factors that might influence our calculations of genetic diversity and population size such as catastrophic loss due to weather or disease, selection, and linkage could be easily incorporated. In this case, however, catastrophic loss was not included in the model due to insufficient frequency and severity data on natural catastrophes affecting bison. Selection and linkage were not considered due to the presumed near-neutrality of these microsatellites and previous chromosome mapping data in domestic cattle indicating synteny of more than 40cM for any marker pair used in the model (Halbert et al., 2004).

Our model has shown that without the introduction of new genetic variation, the TSBH will likely continue to suffer both genetically and demographically. Furthermore, without intervention this population faces a 99% chance of extinction in the next 51 years. We believe sufficient evidence exists concerning the current status and probable fate of the TSBH to justify and necessitate importing unrelated bison into this population. The likely long-term advantages of importing new bison into this historically valuable resource include increased genetic variation, improved population fitness, decreased levels of inbreeding, increased adaptive response (Lewontin and Birch, 1966; Soulé, 1980), and perhaps most significantly, a substantially higher probability of population survival.

Acknowledgements

Funding was provided by grants from Texas Parks and Wildlife (90339) and the National Park Service (00CRAG0036). We thank Danny Swepston and Texas

Parks & Wildlife for generously providing information about and access to the Texas State Bison Herd and Dr. Peter Gogan for the provision of Yellowstone National Park samples. We are also grateful to Dr. Michael Longnecker for advice on statistical analysis and Christopher Seabury for insightful discussion and reviews of early manuscripts.

References

- Bartholow, J.M., 1996. Sensitivity of a salmon population model to alternative formulations and initial conditions. *Ecol. Modell.* 88, 215–226.
- Berger, J., Cunningham, C., 1994. *Bison: Mating and Conservation in Small Populations*. Columbia University Press, New York, p. 330.
- Coder, G.D., 1975. Ph.D. dissertation. The National Movement to Preserve the American Buffalo in the United States and Canada Between 1880 and 1920. The Ohio State University, Columbus, p. 348.
- Couvet, D., 2002. Deleterious effects of restricted gene flow in fragmented populations. *Conserv. Biol.* 16, 369–376.
- Dary, D.A., 1989. *The Buffalo Book: The Full Saga of the American Animal*. Swallow Press, Chicago, p. 384.
- Franklin, I.R., 1980. Evolutionary change in small populations. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, pp. 135–149.
- Giho, H., Seno, H., 1997. Transition matrix modelling on disturbance-controlled persistence of plant populations. *Ecol. Modell.* 94, 207–219.
- Gross, J.E., 2000. A dynamic simulation model for evaluating effects of removal and contraception on genetic variation and demography of Pryor Mountain wild horses. *Biol. Conserv.* 96, 319–330.
- Halbert, N.R., Raudsepp, T., Chowdhary, B.P., Derr, J.N., 2004. Conservation genetic analysis of the Texas State Bison Herd. *J. Mamm.* 85, in press.
- Haley, J.E., 1949. *Charles Goodnight: Cowman and Plainsman*. University of Oklahoma Press, Norman, p. 485.
- Jerina, K., Debeljak, M., Džeroski, S., Kobler, A., Adamič, M., 2003. Modeling the brown bear population in Slovenia: a tool in the conservation management of a threatened species. *Ecol. Modell.* 170, 453–469.
- Jetschke, G., 1992. Stochastic population models and their relevance for the conservation of species. *Ecol. Modell.* 63, 71–89.
- Johnson, K.H., Braun, C.E., 1999. Viability and conservation of an exploited sage grouse population. *Conserv. Biol.* 13, 77–84.
- Lacy, R.C., 1993. VORTEX: a computer simulation model for population viability analysis. *Wildl. Res.* 20, 45–65.
- Lewontin, R.C., Birch, L.C., 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20, 315–336.
- Lindenmayer, D.B., Burgman, M.A., Akçakaya, H.R., Lacy, R.C., Possingham, H.P., 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife metapopulations. *Ecol. Modell.* 82, 161–174.
- Maudet, C., Miller, C., Bassano, B., Breitenmoser-Würsten, C., Gauthier, D., Obexer-Ruff, G., Michallet, J., Taberlet, P., Luikart, G., 2002. Microsatellite DNA and recent statistical methods in wildlife conservation management: applications in Alpine ibex [*Capra ibex (ibex)*]. *Mol. Ecol.* 11, 421–436.
- McKenna Jr., J.E., 2000. FITPOP, a heuristic simulation model of population dynamics and genetics with special reference to fisheries. *Ecol. Modell.* 127, 81–95.
- Meagher, M.M., 1973. *The Bison of Yellowstone National Park*. National Park Service, Washington DC, p. 161.
- Mills, L.S., Allendorf, F.W., 1996. The one-migrant-per-generation rule in conservation and management. *Conserv. Biol.* 10, 1509–1518.
- Schenk, H.J., 1996. Modeling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. *Ecol. Modell.* 92, 1–32.
- Schnabel, R.D., Ward, T.J., Derr, J.N., 2000. Validation of 15 microsatellites for parentage testing in North American bison, *Bison bison* and domestic cattle. *Anim. Genet.* 31, 360–366.
- Soulé, M.E., 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, pp. 151–169.
- Spielman, D., Frankham, R., 1992. Modeling problems in conservation genetics using captive *Drosophila* populations: improvement of reproductive fitness due to immigration of one individual into small partially inbred populations. *Zoo Biol.* 11, 343–351.
- Spieth, P.T., 1974. Gene flow and genetic differentiation. *Genetics* 78, 961–965.
- Swepton, D.A., 2001. Texas State Bison Herd, second annual report. Texas Parks & Wildlife, Austin, p. 8.
- Vucetich, J.A., Creel, S., 1999. Ecological interactions, social organization, and extinction risk in African wild dogs. *Conserv. Biol.* 13, 1172–1182.
- Ward, T.J., 2000. Ph.D. dissertation. An Evaluation of the Outcome of Interspecific hybridization Events Coincident With a Dramatic Demographic Decline in North American Bison. Texas A&M University, College Station, p. 116.
- Ward, T.J., Bielawski, J.P., Davis, S.K., Templeton, J.W., Derr, J.N., 1999. Identification of domestic cattle hybrids in wild cattle and bison species: a general approach using mtDNA markers and the parametric bootstrap. *Anim. Conserv.* 2, 51–57.
- Wilson, G.A., Strobeck, C.M., 1999. Genetic variation within and relatedness among wood and plains bison populations. *Genome* 42, 483–496.