

Effects of Population Control Strategies on Retention of Genetic Diversity in National Park Service Bison (*Bison bison*) Herds

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Abstract

We simulated the dynamics of bison herds inhabiting National Park Service (NPS) units to evaluate the consequences of management actions on retention of genetic diversity. We used an individual-based model to evaluate the effects of management strategies on the retention of genetic heterozygosity (H_0), retention of alleles, and on herd sex and age structure. To identify general recommendations that could be applied across conditions typical of captive bison herds, we estimated vital rates of herds occupying harsh, average, or good ranges, and we used these vital rates to drive simulations with herd size targets of 200 to 2000 animals. Simulations were initialized with data from observations of microsatellite allele frequencies obtained from NPS bison herds (Halbert 2003). We examined the effects of removal of bison that were young, old, or a random selection of ages, and removals that contained a high proportion of cow-calf groups (24% or 50% of animals removed). We also evaluated the effects of using contraceptives applied to young, old, or a random selection of breeding-age cows. Over the 200-year period of the simulations, herd size accounted for more variation in retention of H_0 and loss of alleles than any other factor. Based on Monte Carlo analysis of 500 replicate simulations, bison herds with more than 400 animals generally met the objective of achieving a 90% probability of retaining 90% of the herd's H_0 for 200 years. Differences in generation time accounted for about 75% of the variation in retention of H_0 in herds of 200-800 bison. When allelic diversity was used as the key criterion for evaluating management alternatives, a population size of about 1000 animals was needed to achieve a 90% probability of retaining 90% of alleles. Under simulated conditions, the choice of population control strategies can have large impact on retention of genetic variation when population sizes are small, but population control strategies have far less influence as population sizes increase. Population control strategies that increase generation time, such as removal or contraception of young animals, most effectively retain genetic variation. Population control strategies had huge effects on the age and sex composition of bison herds.

Introduction

Human activities have profoundly influenced the Earth's natural resources. Foremost among man's effects has been the fragmentation of historically large and contiguous habitats, and the associated transformation of large and extensive populations into a number of smaller, isolated populations. Long-term management of small populations presents special problems associated with random population processes that can lead to skewed sex ratios, genetic drift, founder effects, loss of genetic variation, and expression of deleterious alleles. Populations with fewer than 500 breeding individuals are thought to be especially susceptible to harmful consequences of inbreeding depression and other effects that can be directly traced to the genetic composition of the populations (Frankham 1995; Keller and Waller 2002).

Biologists are concerned about the genetic health of bison (*Bison bison*) herds because all North American herds were founded by few individuals and they have generally been maintained at small population sizes (Boyd 2003). National Park Service (NPS) bison herds were established from groups of about 20 to 50 bison (Halbert 2003:16) and NPS herds have largely been managed to maintain a size of fewer than 1000 animals. The small size and isolation of bison herds has led to concerns about their long-term genetic health. Expressions of inbreeding depression are now well documented in many wild vertebrate populations (Keller and Waller 2002), and considerable attention has been directed towards identifying general guidelines for

the genetic management of small, isolated, and/or intensively managed populations. Key questions focus on the minimum effective population size needed to avoid loss of genetic variation and inbreeding depression, population control strategies to minimize harmful genetic consequences, and on the rates of animal movements between isolated populations needed to achieve an adequate rate of gene flow. General recommendations to managers were based on landmark studies by Wright (1931, 1969) that led to the “one-migrant-per-generation” rule. Further studies suggested that populations with a genetically effective population size (N_e) of 50 to 500 were secure (Meffe and Carroll 1995:171), where N_e is the size of an ideal population composed of randomly breeding individuals (See Hartl and Clark [1997:289] or similar for a more complete, technical definition of N_e).

While the one-migrant-per-generation and minimum size rules have been widely publicized and adopted, these rules remain controversial and difficult to implement. A realistic evaluation of the one-migrant-per-generation rule requires an understanding of the many assumptions on which the rule is based, and it is widely acknowledged that many of these assumptions are unrealistic (Frankham 1995; Mills and Allendorf 1996; Vucetich and Waite 2001; Wang 2004). Most theoretical analyses in population genetics require estimation of N_e , but N_e is notoriously difficult to estimate in real populations because it is strongly affected by variation in population attributes such as sex ratio, age-specific breeding success, and fluctuations in population size (Harris and Allendorf 1989; Shull and Tipton 1987). Since all real populations exhibit variation in these factors, accurate estimation of N_e is usually intractable (Harris and Allendorf 1989). For bison, N_e/N has most commonly been estimated to be between 0.2 and 0.35 (Shull and Tipton 1987; Berger 1996; Wilson and Zittlau 2004), although Shull and Tipton (1987) estimated that N_e/N could be as low as 0.09 in managed herds. Uncertainty in our understanding of mating behaviors of bison, variation in age structure, and other complications result in high degree of uncertainty in estimates of N_e/N . For large ungulates, especially those that exhibit a dominance hierarchy (i.e., high variation in individual breeding success), large uncertainty in estimates of N_e reduces the usefulness of N_e for designing and evaluating realistic management alternatives, such as the one-migrant-per-generation or minimum size rules.

The plains bison (*Bison bison*) is an exemplar species for examining genetic conservation of a charismatic large mammal. Wild bison once roamed vast areas of North America in huge herds and the total population is estimated to have consisted of millions of individuals. These huge populations were decimated by hunters, and by the late 1800s bison were restricted to a few herds with a total of fewer than 1,000 animals (Hornaday 1913; Seaton 1937). This population reduction represents a genetic bottleneck of epic proportions. The subsequent “recovery” of the species is reasonably well documented. Recent analyses of the genetic composition of bison herds have shown that some individuals in most herds contain genetic material that can be unambiguously attributed to hybridization with domestic cattle (Halbert 2003). Bison herds thought to be free of cattle genes are mostly small, and the long-term genetic health of these herds is a serious management concern. Management of captive bison herds is further complicated because some bison herds are infected with *Brucella abortus*, a bacteria that is the causative agent for brucellosis. Recent studies revealed that low levels of inbreeding – levels previously thought to be insignificant – were very highly correlated with susceptibility to bacterial disease in sea lions (*Zalophus californianus*) (Acevedo-Whitehouse *et al.* 2003). These results suggest that the effects of genetic depression in wild populations may be much more widespread than previously thought. Bison are hosts to a wide variety of diseases (Williams and

Barker 2001), and transfers of bison between herds have been restricted by regulations designed to inhibit the spread of disease.

Our objectives were to identify options for managing the bison populations inhabiting National Park units and to evaluate the relative consequences of management actions on retention of genetic diversity. We focused our evaluations on population attributes and management strategies that might influence decisions on management in the near future. In addition, we wanted to identify recommendations that applied generally to bison herds and other managed herds of large mammals. To achieve these goals, we constructed an individual-based population model that simulated the dynamics of bison herds and their responses to management actions. We developed sets of model parameters that represented herds in habitats that were harsh, average, or good, and we evaluated interactions between management strategies and herd characteristics.

Methods

Our model operated on an annual time step and explicitly represented breeding, recruitment, removals, contraceptive treatments, natural mortality, and aging. The sex, age, breeding status, number of matings, and genetic composition of each individual were explicitly represented in the model.

Demographic processes and parameter estimation

Our model simulated the demographic processes of birth and death by comparing age and sex-specific probabilities of mating, birth, and death to a random number drawn from a uniform 0 -1 distribution. Breeding was simulated by first determining which cows would breed and then selecting a bull for mating. Age-specific breeding rates of bulls (Figure 1) were estimated from Berger and Cunningham (1994: 189) and Wilson et al. (2002). Data on breeding rates by bulls are extremely limited and we thus developed parameter estimates from available literature and interviews with bison herd managers. We then tested additional, hypothetical breeding rates to examine the sensitivity of model results to changes in this vaguely defined function. For all parameter sets we evaluated, calculations of simulated lifetime breeding rates showed that almost all prime-aged bulls breed, though individuals varied in the number of offspring they sired. In a specific breeding event, the likelihood that a particular bull mated with a cow was determined by the number of breeding-age bulls in the population and the age-specific probability of mating of each male. Data on other factors that may influence lifetime breeding success of bison bulls, such as size, social status, mating group size, etc., are poorly documented and were not included in the model.

For each breeding pair of bison, Mendelian inheritance of selectively neutral alleles was simulated by selecting one allele from each parent at each of the loci simulated. The model was initialized with 3-10 alleles at each of 51 autosomal loci, based on frequencies reported by Halbert (2003). Initial gene frequencies ranged from 0.001 to 1.0 (e.g., from an allele in only one individual to an allele carried by all herd members) based on data from bison herds in National Parks.

Vital rates of bison were estimated from population surveys conducted by NPS biologists and from observed growth rates of bison herds (Meagher 1973; Berger and Cunningham 1994;

Kirkpatrick *et al.* 1996). Although data were not suitable for highly detailed analyses, vital rates clearly differed among herds and we estimated three sets of vital rates that characterized herds in harsh, average, and good habitats, with corresponding rates of fecundity and survival (Figure 1). Vital rates for the harsh, average, and good habitats roughly correspond to observations from the central Yellowstone (YELL) bison herd, Badlands (BADL), and Grand Teton (GRTE) National Parks, respectively. Survival rates at GRTE and BADL appear to be high compared to wild populations, presumably due to supplemental feed (GRTE) and relatively mild winters. Except for YELL and GRTE bison, all bison herds under the jurisdiction of the Department of Interior are subjected to intensive management programs that maintain herd sizes thought to be well below the long-term carrying capacity of the occupied range. In these populations, very high survival and breeding rates indicated that density dependence was of little importance. In YELL, bison respond to increased density mainly by increasing the area used in winter (Taper *et al.* 2000). Because there was considerable uncertainty in estimates of bison vital rates, we conducted a sensitivity analysis to evaluate the potential influence of variation in vital rates on simulation results. When vital rates and management treatments varied within realistic limits, the only significant difference we noted was in the number of animals that needed to be treated to limit population size.

Model treatments

Simulations were conducted to evaluate management strategies that focused on the fundamental decisions that managers confront when developing a strategy to control size of bison populations. Treatments were based on target population size (how many animals?), the type of intervention used to attain the population size target (removal or apply contraceptives?), and which animals to treat (how many males and females, and of what age?).

Removal or contraceptive treatments were simulated by applying rules based on current population size, post-treatment population objective, sex and age of animals to be treated, and the minimum number of animals in each sex/age class that were to remain unaffected by the treatment. To determine the annual control treatment, the population was first compared to size thresholds used to categorize the population as small, normal, or large. If the population size was less than or equal to the lower threshold, it was categorized as small. If the population size was greater than the lower threshold and less than or equal to the higher threshold, it was categorized as normal. If greater than the upper threshold it was considered large.

Removal treatments were categorized as young, old, or random for the age of animals emphasized in the treatment. Some random treatments selected bison randomly with regard to sex or age until the population objective was reached, and some random treatments controlled for sex ratio and selection was completely random only for age. For old animal treatments, the oldest animals in the population were selected first, whereas young treatments first removed the youngest animals first. For both treatments, a minimum of 10 animals (or those left after natural mortality) were left in each yearly age class up to 9 years, and 5 animals in each age class up to 20 years.

The proportion of cows treated with contraceptives varied in response to vital rates of the population. For each contraception treatment, the level of contraception was initially calibrated to achieve a relatively stable population size. The baseline rate of contraceptive treatment of cows was 60% for YELL and 80% for other populations. For all treatments, the application rate

of contraceptives was increased or decreased 15% when population size was less than or greater than the target, respectively. Contraceptive treatments were administered every year and treated cows remained infertile for one year. As with removals, cows were selected for contraceptive treatments based on age, using rules that selected breeding-age cows randomly, or that selected the oldest or youngest cows first.

Cow-calf removal treatments selectively removed cows with their calves. Halbert (2003) estimated that 24% of the bison harvested from YELL were cow-calf pairs, while Shaw and Carter (cited in Shull and Tipton 1987) estimated that roundup procedures for captive populations resulted in capture of about 50% of cows with their calves. Our reference treatments used these rates – 24% cow-calf pairs for YELL and 50% for other herds – and we conducted sensitivity analyses by varying the proportion of cow-calf pairs removed (Appendix 1). The procedure used for reference simulations of cow-calf removals (reported below) was to first calculate the number of animals to be removed, then remove the target proportion of cow-calf pairs from the population. After removal of cow-calf pairs, other animals were selected for removal by following rules for the random removal treatment.

Evaluation of model output

Studies of bison and other species have established a well-accepted relationship between genetic heterozygosity (H_0) and various components of inbreeding depression (Reed and Frankham 2003; for bison: Halbert *et al. in press*). Following Hartl and Clark (1997) we calculated H_0 as

$$H_0 = \frac{\sum_{n=1}^N \frac{\text{heterozygotes at locus}_n}{\text{number of individuals}}}{N}$$

where N is the number of loci. Previous studies clearly showed that H_0 can be an insensitive indicator of many changes in genetic resources (Allendorf 1986; Gross 2000), and in particular, many rare alleles can be lost with little change in H_0 . We therefore evaluated retention of alleles in response to simulation treatments.

There are currently no quantitative NPS or US Fish and Wildlife Service management objectives for conserving genetic diversity. Gross (2000) used a goal to achieve a 90% probability of maintaining 90% of the selectively neutral genetic variation for 200 years, following recommendations by Soule *et al.* (1986). This goal is consistent with U.S. Bureau of Land Management operational guidelines for wild horse management (Coates-Markle 2000) and we used it as the default evaluation criterion.

Generation time (T), an important variable determining the rate of loss of genetic diversity, can be estimated by a variety of methods. We followed Carey (1993: 86) and estimated generation time as

$$T = \frac{\sum_{x=0}^{\omega} x l_x m_x}{\sum_{x=0}^{\omega} l_x m_x}$$

where x is age (years), ω is the last possible age, l_x is survival from birth to age x , and m_x is the average number of offspring produced by a female in the interval x to $x + 1$.

Initial conditions and simulation procedures

We used data from Halbert (2003) for initial allele frequencies at the 51 autosomal loci simulated in these model experiments. Halbert (2003: 38) reported two to 11 microsatellite alleles per locus, with a total of 350 alleles. Two loci were fixed at THRO-North and one at GRTE, and initial H_0 in National Park bison herds varied from 0.517 – 0.654 (Halbert 2003: 40). We created initial populations that matched population size targets (200-2000 individuals). Observed heterozygosities in these initial populations were mostly within 1% of the values reported by Halbert and all were within 2%.

Scenarios were evaluated from the results of 500 (main treatments) or 100 (some sensitivity analyses) Monte Carlo replicates, each lasting 200 years. Each replicate simulation was conducted with a unique set of random variates and the distribution of results was estimated from model outputs. Eight population size objectives were examined: 200, 300, 400, 500, 600, 700, 1000, and 2000 bison. These population objective treatments were crossed with population control treatments (removal or contraceptive) and with age-specific treatments.

Results

In general, results from the six parks varied in a consistent manner and the small differences between parks appeared to be related to the number and frequency distribution of alleles and (more importantly) differences in vital rates. To simplify the presentation of results, we generally report results of simulations using inputs estimated from bison in YELL and Theodore Roosevelt National Park, North Unit (hereafter THRO). Of all National Park bison herds (Halbert 2003: 40), the YELL herd had the highest proportion of all alleles, the second highest H_0 , and the most severe environmental conditions. THRO North had the lowest proportion of all alleles, the lowest H_0 , and relatively benign environmental conditions. These herds are thus most likely to exhibit the extremes in simulation results.

Treatments and demographic effects

Sets of parameters for vital rates resulted in average annual growth rates (λ) of 1.14, 1.22, and 1.22 for the poor, average, and good habitats, respectively. These growth rates are similar to those reported for the representative parks (YELL, GRTE, and BADL).

Removal and contraception treatments had dramatic and different effects on the age structure of herds (Figure 2). Removal of old animals resulted in populations that consisted almost entirely of animals less than 8 years old, while removal of younger animals resulted in populations with an unusually high proportion of older animals. Contraception treatments led to herds with an extremely even age structure. Target population size had no effect on demographic structure, and herd age structure was only slightly different between the simulations using the three sets of vital rates.

An important consequence of variation in age structure for populations managed by removals was a change in generation time (Figure 3). With a shift to older animals, a greater proportion of young were born to old cows, resulting in an increase in generation time. Generation time of

females ranged from less than 5 years when old animals were removed or treated with contraceptives, to a maximum of 12.7 years when contraceptives were applied only to young animals and virtually all breeding was by very mature, older cows. For contraceptive treatments, age of reproduction was determined by infertility treatment, and age of reproduction was a function of the age structure of the population. Changes in generation time for contraceptive treatments followed logically from treatments – a shift in breeding to younger animals by administering contraceptives to older animals led to a decrease in generation time, and generation time increased when contraceptives were administered to younger animals.

The proportion of the population that had to be removed or treated with contraceptives to achieve a target population size varied between treatments, but not with target population size. For contraceptive treatments, 60-65% of all cows were treated each year in average and good populations, and 40-45% of cows from YELL. In contrast, population control based on removals selecting for cow-calf groups required removal of only 7% to 14% of the population each year (for YELL with 50% cow-calf pairs in harvest, and THRO with 10% cow-calf pairs in harvest, respectively). Removal of animals of random age, old, or young animals required removal of an average of 16%, 13%, or 13% of animals, respectively, except for removal of young animals with a target size of 200. In this case, about 25% of animals were removed each year, apparently due to compromises necessary to maintain a small population while leaving an adequate number of animals in each age class. Differences in the proportion of the population that needed to be “treated” were clearly related to changes in sex and age structure of the population, and to the expected reproductive contribution (reproductive value) of animals removed. Treatments that shifted the sex ratio towards males or that increased the proportion of young (non-breeding) cows led to lower average population growth rates, thereby reducing the need for active population management.

Changes in genetic variation

There were large differences in retention of observed heterozygosity (H_0) between simulated herds with different population sizes and between management treatments (Table 1, Figure 4). Over the range of population sizes and treatments simulated, the effects of population size on retention of genetic variation were large relative to all treatments except contraception of young cows. In general, a minimum population size of about 400 was needed to meet the objective of retaining 90% of selectively neutral variation with a 90% probability for 200 years (Table 1, Figures 4, 5). However, it is important to recognize that these results are based on simulations that precisely implemented management treatments. Under typical field conditions, implementation of treatments will surely be less precise than simulations, and it would be prudent to accommodate the inevitable variation.

Allelic diversity was more sensitive to management treatments than was average H_0 (Figures 6, 7). On average, a high proportion of alleles with an initial frequency of less than 0.05 were lost when herd target sizes were less than 400. In Figure 7, coefficients of variation (CV) were large; after year 100 of simulations CVs exceeded 100% for some treatments. The high uncertainty in simulation results emphasizes the need to use a precautionary approach because our predictive ability is limited. The much greater sensitivity of allelic variation, compared to H_0 , is clearly evident by comparing Figures 6 and 7 (note different scales of vertical axes).

When target population size was held constant, differences in generation time accounted for about 75% of the variation in retained H_0 for populations of 200-800 bison for the 200 year period (Figure 8). Remaining variation in loss of genetic diversity is probably due to modification of herd sex and age composition, variation in population growth rates related to specific management strategies, and to stochastic events.

Discussion

Measuring changes in genetic variation

A typical conflict for wildlife managers is a need to maximize population size to avoid loss of genetic variation, and a need to maintain small population sizes to conserve forage or other habitat-related resources. Our simulations show that the choice of a specific population control strategy can have a major influence on the rate of loss of genetic variation in small bison populations, but as population size approaches 1000 animals the effects of population management strategy on genetic variation are small.

Table 1. Proportion of observed heterozygosity (H_0) remaining after 200 years for populations with target sizes of 200-2000, with populations controlled by different population management strategies. Values in table are mean H_0 after 200 years and 10% lower observation interval (in parentheses). Results (1A) using gene frequencies and vital rates characteristic of Yellowstone National Park (YELL) bison, and (1B) using gene frequencies and vital rates characteristic of Theodore Roosevelt National Park (THRO), North Unit. Bold values indicate those scenarios that did not achieve at least a 90% probability of retaining 90% of H_0 .

Table 1A. YELL

Target size	Remove cow-calf				Contracept		
	Remove random	(0.24)	Remove old	Remove young	random	Contracept old	Contracept young
200	0.89 (.86)	0.90 (.86)	0.88 (.84)	0.90 (.87)	0.91 (.88)	0.87 (.84)	0.93 (.90)
300	0.92 (.89)	0.93 (.90)	0.92 (.89)	0.93 (.91)	0.93 (.91)	0.91 (.88)	0.95 (.93)
400	0.94 (.91)	0.94 (.92)	0.94 (.92)	0.94 (.92)	0.94 (.92)	0.93 (.90)	0.96 (.94)
500	0.95 (.92)	0.95 (.93)	0.95 (.93)	0.95 (.93)	0.95 (.93)	0.94 (.92)	0.97 (.95)
600	0.95 (.93)	0.96 (.94)	0.96 (.94)	0.96 (.94)	0.96 (.94)	0.95 (.93)	0.97 (.95)
700	0.96 (.94)	0.96 (.94)	0.96 (.94)	0.96 (.95)	0.96 (.94)	0.95 (.93)	0.97 (.95)
1000	0.97 (.95)	0.97 (.96)	0.97 (.95)	0.97 (.96)	0.97 (.95)	0.96 (.94)	0.98 (.96)
2000	0.98 (.97)	0.98 (.97)	0.98 (.97)	0.98 (.97)	0.98 (.96)	0.97 (.96)	0.98 (.97)

Table 1B. THRO, North Unit

Target size	Remove cow-calf				Contracept		
	Remove random	(0.50)	Remove old	Remove young	random	Contracept old	Contracept young
200	0.86 (0.80)	0.89 (0.85)	0.88 (0.84)	0.90 (0.86)	0.91 (0.88)	0.87 (0.83)	0.95 (0.92)
300	0.91 (0.87)	0.92 (0.89)	0.92 (0.89)	0.92 (0.89)	0.94 (0.91)	0.92 (0.88)	0.96 (0.94)
400	0.93 (0.90)	0.94 (0.91)	0.94 (0.91)	0.94 (0.91)	0.96 (0.93)	0.94 (0.91)	0.97 (0.95)
500	0.94 (0.91)	0.95 (0.93)	0.95 (0.93)	0.95 (0.93)	0.96 (0.94)	0.95 (0.92)	0.98 (0.96)
600	0.95 (0.93)	0.96 (0.94)	0.96 (0.93)	0.96 (0.94)	0.97 (0.95)	0.96 (0.93)	0.98 (0.96)
700	0.96 (0.94)	0.97 (0.94)	0.96 (0.94)	0.97 (0.95)	0.97 (0.95)	0.96 (0.94)	0.99 (0.97)
1000	0.97 (0.95)	0.98 (0.96)	0.98 (0.96)	0.98 (0.96)	0.98 (0.96)	0.98 (0.96)	0.99 (0.98)
2000	0.99 (0.97)	0.99 (0.97)	0.99 (0.97)	0.99 (0.98)	0.99 (0.98)	0.99 (0.98)	1.00 (0.99)

An important insight from these simulations is the identification of different recommendations that result from evaluations of H_0 versus retention of individual alleles. Most previous studies emphasized H_0 , which is most simply defined as the proportion of individuals heterozygous at a locus. H_0 readily lends itself to theoretical analysis of the effects of bottlenecks or small populations sizes on genetic variation. However, under certain conditions, H_0 can be insensitive to the number of alleles at a locus. Allendorf (1986) provided an example to illustrate this point: Consider two populations. The first population (Pop1) has two alleles at equal frequency (0.5) at a particular locus. A second population (Pop2) has seven alleles, one allele with a frequency of 0.7 and the other six alleles with a frequency of 0.05. Our intuitive evaluation is that Pop2 has greater H_0 , but this is wrong. For Pop1, $H_0 = 0.500$, whereas $H_0 = 0.495$ for Pop2. While this exact situation will be rare in nature, it illustrates the potential problem of relying on H_0 to evaluate changes in genetic variation. Halbert (2003) reported an average of 4.4 alleles (maximum = 10 alleles) at each locus for the six NPS bison herds. Across all NPS bison herds, 84% of all loci have at least four alleles and H_0 is thus likely to be a relatively insensitive indicator of loss of genetic variation.

If retention of H_0 is the primary aim of management, our simulations suggest that a population objective of about 400 animals is likely to achieve a goal of retaining 90% of currently existing H_0 (Table 1). However, a much larger population objective – on the order of 1000 bison (Figure 8) – is required to achieve a reasonable assurance of retaining 90% of currently existing alleles. In evolutionary terms, H_0 is an index to the overall degree of genetic variance at a locus and it would be expected to reflect the magnitude of short-term responses to artificial or natural selection (James 1971). High allelic diversity will virtually always be correlated with the occurrence of many alleles that have a low frequency in the population. These rare alleles are unlikely to contribute substantially to short-term population responses to selection, but they can be a very important limit to the response to selection over many generations (James 1971; Allendorf 1986). Allelic diversity is thus considered important to the long-term survival of a species, especially where there may be substantial environmental changes, range expansions, or (re)introduction into new sites.

Considerations of the relative merit of management objectives that focus on H_0 or allelic diversity are clearly pertinent to management of NPS bison herds. Halbert (2003) noted that bison in these herds may have retained much of their pre-bottleneck genetic variation, and the genetic composition of NPS bison herds is characterized by the occurrence of many rare alleles (Figure 10).

Nonrandom cow-calf pair removals, as modeled here, are a likely consequence of routine bison removal programs because bison calves generally remain with their mothers throughout the first year of life (Berger and Cunningham 1994). Our results indicate that the short-term genetic effects of cow-calf pair removals is probably minimal compared to other treatments, but we did not explicitly model non-random removal of extended matrilineal groups.

Bison have been reported to naturally assemble into matriarchal groups including several generations of related females and calves (Seton 1937; Haines 1995). In YELL, where culling is primarily through opportunistic selection of bison groups as they exit park boundaries, Halbert (2003) estimated that 24% of the removals were cow-calf pairs, about 50% more cow-calf pairs than we estimated would be removed through a random selection of bison ($p < 0.05$). The extent

of matrilineal group removal from YELL cannot be accurately determined given current limitations in bison sampling as they exit the park. The genetic consequences of non-random removal of matrilineal groups (3 or more generations) was not explicitly considered in this study and it merits further study, although results from simulations with very high levels of cow-calf removals suggest that the effects of matrilineal removals in YELL may be small. While the effect of removal of matrilineal groups from YELL has been most actively discussed, this may be a more important issue in parks where a significant proportion of the herd was traditionally harvested at the same location year after year.

The genetic subpopulation structure of the YELL bison population complicates accurate simulation modeling and the interpretation of the existing simulations. Meagher (1973) reported geographically distinct bison herds within YELL, but as the number of bison in YELL increased some of the herds merged (Taper et al. 2000). Recent radiotelemetry data indicated little interchange of bison between the northern and central herds (Edward Olexa, personal communication) and historical sightings indicated high densities of bison in several distinct areas of activity (Taper et al. 2000). Recent work revealed genetically distinguishable subpopulations in YELL (Halbert 2003) and cluster analysis of this data (Pritchard et al. 2000) revealed at least 2, and most likely 3, genetically distinguishable subpopulations among those YELL bison sampled (Halbert 2003). Furthermore, statistically significant genetic differentiation between bison collected in different locals (West Yellowstone vs. Gardiner) were observed for between 65 and 78% of the markers analyzed, a result also indicative of subpopulation structure (Halbert 2003). Subpopulation structure serves to reduce N_e from that estimated by the overall population size, and the rate of interchange will need to be considered in the long-term genetic management of YELL bison.

At present, data from YELL are inadequate to accurately estimate rates of genetic interchange between herds, particularly as the total number of bison in YELL varies from 2500 to more than 4000. However, it appears that animal movements between herds are relatively rare (E. Olexa, personal communication), and thus model results should be interpreted as representing a single herd unit (e.g., the northern range herd unit or West Yellowstone). A more complex simulation analysis will be necessary to fully assess the long-term genetic consequences of subpopulation structure and interchange, and non-random removal of matrilineal groups.

Managing populations and genetic variation

We evaluated a relatively small subset of potential strategies that could be used to control the size of bison herds. Currently, removal (of live or dead animals) is the only available alternative, although there is widespread support for use of contraceptives. Development of contraceptives for bison appears promising (Miller *et al.* in press) and contraceptives may eventually provide a useful management tool. We simulated very simple scenarios that relied on exclusive use of removal or contraception, but it seems likely that many Parks will combine these management tools. Combined use of contraceptives and removals could help mitigate changes in sex or age structure of herds. The combined use of removals and contraceptives was evaluated for wild horses (Gross 2000) and it has been favorably received by horse managers.

When fully developed, contraceptives offer advantages for controlling bison populations, but they may also increase risks. Application of contraceptives would presumably result in a smaller number of cows in estrus at any one time, thus one or a few bulls may be more able to dominate

breeding. Our understanding of breeding behavior in bison limits our ability to forecast the effects of management options. There are no data for evaluating breeding behavior with the use of contraceptives, and potential changes in breeding behaviors were not accounted for in simulations. The magnitude of effect that they could have on loss of genetic diversity is unknown. Any application of contraceptives should be accompanied by studies that evaluate both the effectiveness of contraceptives to control population size, and changes in behavior and breeding success of individual males. Ideally, genetic markers would be used to determine parentage.

An obvious strategy for maintaining or enhancing genetic diversity of NPS bison herds is to move animals between herd units, thereby supplementing the gene pool and managing herds as an extended metapopulation. Wright (1931) postulated the simple “one-migrant-per-generation” rule, showing that (in theory) a low rate of migration was sufficient to prevent inbreeding depression, regardless of population size. More recent analyses have clearly shown that more information is required to estimate a migration (or transfer) rate needed to meet explicit goals for retaining genetic variation. For example, small or fluctuating population sizes can greatly increase the number of migrants necessary to avoid an increase in inbreeding coefficient, as does a small ratio of N_e to census population size (N) (Vucetich and Waite 2000, 2001). Wang (2004) considered a wide range of population characteristics, including N_e/N , variation in population size, and skewed sex ratios. Based on these considerations, transfer of about 10 individuals of either sex per generation should be adequate to maintain an acceptable level of similarity in subpopulations. However, Wang (2004) noted that a more accurate estimation requires an understanding of the factors that lead to a small N_e/N .

Simulation modeling could be used to estimate the number of migrants needed to maintain genetic variation across a number of bison herds. However, the implementation of a credible simulation approach requires clear identification of a limited number of realistic management scenarios and clear definition of evaluation criteria. For NPS bison herds, this is currently a difficult challenge due to hybridization of bison with cattle (Halbert 2003), occurrence of infectious diseases, and the enormous number of permutations defined by the animals moved (sex, age, number), frequency of movement, source, and target herds. Allendorf (1994) and Halbert *et al.* (*in press b*) conducted very simple simulation experiments to examine the potential benefits of transferring animals into small populations. Allendorf (1994) forecast a considerable reduction in the rate of loss of genetic heterozygosity by introducing two individuals every generation into a small grizzly bear population. Halbert *et al.* (*in press b*) simulated introduction of bison from YELL into the highly inbred Texas bison herd. A one-time introduction of 3-9 bison from YELL would dramatically enhance heterozygosity and increase allelic diversity in that inbred herd. These results demonstrate the case-specific nature of simulation analyses of animal transfers, and they emphasize the need to clearly identify a limited set of realistic scenarios for analysis.

This study emphasized the ability of managers to alter rates of loss of genetic diversity through selection of population control treatments whose effects are mediated primarily by altering generation time. Other alternative strategies may also be available to retain genetic diversity. Frankham *et al.* (2002: 441) reviewed the potential use of reproductive technologies such as artificial insemination, cryopreservation, cloning, and genome resource banks for preserving genetic material. Robison *et al.* (1998) examined the potential application of reproductive

technologies to conservation of genetic material from brucellosis-infected bison herds, and provided preliminary data demonstrating the practicality of this strategy. Technologies investigated by Robison et al. (1998) might permit transfer of genetic material between bison herds, circumventing some problems related to disease and breeding success. Similarly, Derr and Halbert (personal communication) suggested the use of cryopreservation of bison tissues. For example, eggs or sperm might be frozen for an extended period and then reintroduced into the same herd or a different herd. Presumably, the increase in generation time would be proportional to the time between sample collection and reintroduction and the number of transfers.

Interpreting model results

Any interpretation of simulation model results must consider the quality of the data used to drive the model, the assumptions on which the model is founded, and the sensitivity of model results to uncertainty in model inputs and assumptions. Sensitivity analyses showed that our model results were relatively insensitive to realistic variation in vital rates, initial population structure, and initial genetic composition of herds. In this model, sensitivity analysis showed that a potentially realistic variation in male breeding success could significantly affect results, primarily in populations with fewer than about 600 animals. We identified complicated interactions between variation in male breeding success, population control strategy, and target population size. In general, greater levels of variation in male breeding success affected treatments that removed old animals to a greater extent than those that removed young. There are extremely few reliable data available to estimate variation in lifetime breeding success of bison, or for that matter, any other large ungulate (Wilson et al. 2002; McEligott and Hayden 2000; Roed et al. 2002; Coltman et al. 1999). The reliability of simulation model predictions for some treatments could be significantly increased by incorporating data on paternity analysis based on genetic samples from herds of interest. At present, there are no data from bison herds that can be used to estimate how herd size, sex ratio, habitat characteristics (e.g., open vs closed), age structure, or other factors influence variation in male success. The absence of this information constrains our ability to realistically forecast the effect of population control measures on retention of genetic diversity.

Comparisons of results from simulations initialized with genetic data from different NPS bison herds exhibited small differences in retention of H_0 (Appendix 1). We suggest that model results be interpreted conservatively. The model used in this study has explicit random variation and no two sets of 500 runs will be exactly the same. Stochastic models better reflect the variation seen when observing actual populations, but they also complicate evaluation of results.

Summary and recommendations

Because there are inherent uncertainties in model assumptions, input data, and our ability to properly interpret model results, the most appropriate use of these results is to support general recommendations on management of NPS bison units. Management actions can be simulated with a much higher degree of precision than they can be implemented under field conditions. Given these caveats, there are several clear conclusions:

1. For small bison herds (say, fewer than 500 animals), removal or contraception of young animals can significantly enhance retention of genetic variation. Other treatments that significantly increase generation time will yield similar results.

2. Bison herds with fewer than about 400 animals are unlikely to meet a long-term goal of achieving a 90% probability of retaining 90% of genetic heterozygosity for 200 years.
3. A moderate bison population size - about 1000 animals – is necessary to meet a long-term goal of achieving a 90% probability of retaining 90% of allelic diversity for 200 years.
4. Goals described in 2 & 3 can be achieved with much smaller herd sizes if animals can be moved between herds. Development and evaluation of a set of realistic management strategies that involves transferring animals between herds requires knowledge of individual herd characteristics, including genetic composition and disease status, and a clear statement of management objectives. A similar result might be obtained by other treatments not identified or evaluated by this study (e.g., preserving and reintroducing sperm or eggs).
5. In particular, the absence of reliable data on and understanding of variation in male lifetime reproductive success is a constraint to developing more specific management recommendations.

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References

- Acevedo-Whitehouse, K., F. Gulland, D. Greig, and W. Amos. 2003. Disease susceptibility in California sea lions. *Nature* 422:35.
- Allendorf, F. W. 1986. Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology* 5:181-190.
- Allendorf, F. W. 1994. Genetically effective sizes of grizzly bear populations. Pages 155-156 in: G. K. Meffe and C. R. Carroll, eds. *Principles of Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Berger, J. 1996. Scenarios involving genetics and population size of bison in Jackson Hole. Report to National Park Service.
- Berger, J. and C. Cunningham. 1994. *Bison: Mating and conservation in small populations*. Columbia University Press, New York.
- Boyd, D. 2003. Conservation of North American bison: status and recommendations. Master's Degree Thesis, University of Calgary, Calgary, Canada. 222 pages.
- Briskie, J. V. and M. Mackintosh. 2004. Hatching failure increases with severity of population bottlenecks in birds. *Proceedings of the National Academy of Sciences of the United States of America* 101:558-561.
- Carey, J. R. 1993. *Applied demography for biologists*. Oxford University Press, New York.
- Coates-Markle, L. 2000. Summary recommendations - BLM wild horse and burro population viability forum. *Resource Notes* 35:1-4.
- Coltman, D. W. and J. Slate. 2003. Microsatellite measures of inbreeding: a meta-analysis.

- Evolution 57:971-983.
- Coltman, D. W., J. Smith, D. Bancroft, J. Pilkington, A. MacColl, T. Clutton-Brock, and J. Pemberton. 1999. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *American Naturalist* 154:730-746.
- Couvet, D. 2002. Deleterious effects of restricted gene flow in fragmented populations. *Conservation Biology* 16:369-376.
- Dobson, A. and M. Meagher. 1996. The population dynamics of Brucellosis in the Yellowstone National Park. *Ecology* 77:1026-1036.
- Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. *Journal of Wildlife Management* 49:997-1012.
- Frankham, R. 1995. Conservation genetics. *Annual Review of Genetics* 29:305-327.
- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. *Introduction to Conservation Genetics*. Cambridge University Press, New York.
- Gross, J. E. 2000. A dynamic simulation model for evaluating the effects of removal and contraception on genetic variation and demography of Pryor Mountain wild horses. *Biological Conservation* 96:319-330.
- Haines, F. 1995. *The buffalo: the story of American bison and their hunters from prehistoric times to the present*. University of Oklahoma Press, Norman.
- Halbert, N. D. 2003. The utilization of genetic markers to resolve modern management issues in historic bison populations: implications for species conservation. Ph.D. Dissertation, Texas A&M University, College Station.
- Halbert, N. D., W. A. Grant, and J. N. Derr. *In press a*. Genetic and demographic consequences of importing animals into a small population: a simulation model of the Texas state bison herd (U. S. A.). *Ecological Modelling*.
- Halbert, N. D., T. Raudsepp, B. P. Chowdhary, and J. N. Derr. *In press b*. Conservation genetic analysis of the Texas state bison herd. *Journal of Mammalogy*.
- Harris, R. B. and F. W. Allendorf. 1989. Genetically effective population size of large mammals: an assessment of estimators. *Conservation Biology* 3:181-191.
- Hartl, D. L. and A. G. Clark. 1997. *Principles of population genetics*. Sinauer Associates, Sunderland, Massachusetts.
- Hoelzel, A. R., J. Halley, S. J. Obrien, C. Campagna, T. Arnbom, B. Leboeuf, K. Ralls, and G. A. Dover. 1993. Elephant seal genetic-variation and the use of simulation models to investigate historical population bottlenecks. *Journal of Heredity* 84:443-449.
- Hornaday, W. T. 1889. The extermination of the American bison, with a sketch of its discovery and life history. Report to the U.S. National Museum, 1886-1887. Part 2: 367-548.
- Hornaday, W. T. 1913. *Our Vanishing Wildlife: Its Extermination and Preservation*. New York Zoological Society, New York.
- James, J. W. 1971. The founder effect and response to artificial selection. *Genetical Research* 12:249-266.
- Keller, L. F. and D. M. Waller. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17:230-241.
- Kirkpatrick, J. F., J. C. McCarty, D. F. Gundermuth, S. E. Shideler, and B. L. Lasley. 1996. An assessment of the reproductive biology of Yellowstone bison (*Bison bison*) subpopulations using noncapture methods. *Canadian Journal of Zoology* 74:8-14.
- Lacy, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology*

1:143-158.

- Lande, R. 1995. Breeding plans for small populations based on the dynamics of quantitative genetic variance. Pages 318-340 in: J. D. Ballou, M. Gilpin, and T. J. Foose, eds. *Population Management for Survival and Recovery*. Columbia University Press, New York.
- Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. Pages 471-501 in: J. C. Avise and J. L. Hamrick, eds. *Conservation Genetics: Case Histories from Nature*. Chapman and Hall, New York.
- McEligott, A. G. and T. J. Hayden. 2000. Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). *Behavioral Ecology and Sociobiology* 48:203-210.
- Meagher, M. 1986. *Bison bison*. *Mammalian Species* 266:1-8.
- Meagher, M. M. 1973. The bison of Yellowstone National Park. National Park Service Scientific Monograph Series 1:1-161.
- Meffe, G. K. and C. R. Carroll. 1994. *Principles of Conservation Biology*. Sinauer Associates, Inc., Sunderland, MA.
- Miller, L. A., J. C. Rhyan, and M. Drew. 2005. Contraception of bison by GnRH vaccine: a possible means of decreasing transmission of brucellosis in bison. *Journal of Wildlife Diseases* In press.
- Mills, L. S. and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. *Conservation Biology* 10:1509-1518.
- Nunney, L. and K. A. Campbell. 1993. Assessing minimum viable population size: demography meets population genetics. *TREE* 8:234-239.
- Peterson, M. J., W. E. Grant, and D. S. Davis. 1991. Bison-brucellosis management: simulation of alternative strategies. *Journal of Wildlife Management* 55:205-213.
- Peterson, M. J., W. E. Grant, and D. S. Davis. 1991. Simulation of host-parasite interactions within a resource management framework: impact of brucellosis on bison population dynamics. *Ecological Modelling* 54:299-320.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.
- Reed, D. H. and R. Frankham. 2003. Correlation between fitness and genetic diversity. *Conservation Biology* 17:230-237.
- Reynolds, H. W., R. D. Glaholt, and A. W. L. Hawley. 1982. Bison. Pages 972-1007 in J. A. Chapman and Feldhamer, G. A. *Wild Mammals of North America*. John Hopkins University Press, Baltimore.
- Robison, C. D., D. S. Davis, J. W. Templeton, M. Westusin, W. B. Foxworth, M. J. Gilsdorf, and L. G. Adams. 1998. Conservation of germ plasm from bison infected with *Brucella abortus*. *Journal of Wildlife Diseases* 34:582-589.
- Roed, K. H., O. Holand, M. E. Smith, H. Gjostein, J. Kumpula, and M. Nieminen. 2002. Reproductive success in reindeer males in a herd with varying sex ratio. *Molecular Ecology* 11:1239-1243.
- Ryman, N., R. Vaccus, C. Reuterwall, and M. H. Smith. 1981. Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. *Oikos* 36:257-266.
- Seton, E. T. 1937. *Lives of game animals*. Literary Guild of America, New York.
- Shull, A. M. and A. R. Tipton. 1987. Effective population size of bison on the Wichita Mountains Wildlife Refuge. *Conservation Biology* 1:35-41.
- Soule, M. E., M. Gilpin, W. Conway, and T. Foose. 1986. The millennium ark: how long a

- voyage, how many staterooms, and how many passengers? *Zoo Biology* 5:101-114.
- Starfield, A. M., H. A. Rowley, H. Quadling, and T. J. Foose. 1995. Genetic risk analysis of a small wild lion population. Pages 155-179 in: J. D. Ballou, M. Gilpin, and T. J. Foose, eds. *Population Management for Survival and Recovery*. Columbia University Press, New York.
- Taper, M. L., M. Meagher, and C. L. Jerde. 2000. The phenology of space: spatial aspects of bison density dependence in Yellowstone National Park. Final report to United States Geological Service, Biological Resources Division, Bozeman, Montana. 1-114.
- Vucetich, J. A. and T. A. Waite. 2000. Is one migrant per generation sufficient for the genetic management of fluctuating populations? *Animal Conservation* 3:261-266.
- Vucetich, J. A. and T. A. Waie. 2001. Migration and inbreeding: the importance of recipient population size for genetic management. *Conservation Genetics* 2:167-171.
- Vucetich, J. A., T. A. Waite, and L. Nunney. 1997. Fluctuating population size and the ratio of effective to census population size. *Evolution* 51:2017-2021.
- Wang, J. 2004. Application of the one-migrant-per-generation rule to conservation and management. *Conservation Biology* 18:332-343.
- Williams, E. S. and I. K. Barker. 2001. *Infectious diseases of wild mammals*. Iowa State University Press, Ames.
- Wilson, G. A., W. Olson, and C. Strobeck. 2002. Reproductive success in wood bison (*Bison bison athabasca*) established using molecular techniques. *Canadian Journal of Zoology* 80:1537-1548.
- Wilson, G. A. and C. Strobeck. 1999. Genetic variation within and relatedness among wood and plains bison populations. *Genome* 42:483-496.
- Wilson, G. A. and K. Zittlau. 2004. Management strategies for minimizing the loss of genetic diversity in wood and plains bison populations at Elk Island National Park. Unpublished report, 41 pages.
- Woodworth, L. M., M. E. Montgomery, D. A. Briscoe, and R. Frankham. 2002. Rapid genetic deterioration in captive populations: causes and conservation implications. *Conservation Genetics* 3:277-288.
- Wright, S. J. 1931. Evolution in Mendelian populations. *Genetics* 16:97-159.
- Wright, S. J. 1969. *Evolution and the genetics of populations*. Volume 2. The theory of gene frequencies. University of Chicago Press, Chicago, Illinois.

Appendix 1. Sensitivity analyses: effects of sex ratio and proportion of cow-calf pairs in removals on retention of genetic diversity

In addition to the population control treatments described in the main body of the report, we conducted sensitivity analyses to examine interactions between herd sex ratio, population control treatment, and the relative strength of effect of vital rates and allelic composition of herds on retention of genetic diversity. These sensitivity analyses were designed to address three questions:

1. How does removal of cow-calf pairs influence herd sex ratio when ‘non cow-calf’ removals are random with regard to sex and age?
2. What effect does herd sex ratio have on retention of genetic diversity when animals are randomly removed or when cow-calf pairs are selectively removed?
3. What are the effects of variation in the genetic composition and vital rates of NPS herds on retention of genetic diversity?

The first question relates to the effect of removing a prescribed proportion of cow-calf pairs. Because equal numbers of male and female calves are born, the sex ratio of cow-calf pairs will be female-biased (i.e., all cow-calf pairs include the cow, and on average $\frac{1}{2}$ of the calves will be female). Thus the average sex ratio of this proportion of the removals will be three females for every male ($0.5 + 0.5 \times 0.5$). Sex-ratio biases due to harvesting will increase with increases in the proportion cow-calf pairs harvested, while efforts to harvest nearly the same number of males and females will obviously compensate for this effect. In general, males had slightly higher mortality rates than females, and difference in mortality thus contributed to unequal numbers of males and females.

The second question follows from a desire to understand potential interactions between effects due to biased sex ratio and those attributable to population control strategy. Stated in a different way, are differences in the rate of loss of genetic diversity due to direct effects of the treatment under investigation (i.e., harvesting strategy), or are they due to the indirect effect of changes in sex ratio that result from a treatment effect? We explored this question by explicitly controlling sex ratio in those treatments where the proportion of each sex could diverge from nearly equal numbers of males and females.

Cow-calf removals, sex ratio, and H_0

We conducted simulations using parameters from THRO (used here to represent THRO North Unit) and YELL and we varied the proportion of the harvest consisting of pre-selected cow-calf pairs from 0% to 50% of all animals removed. The composition and number of animals harvested was determined by the following process. First, the number of animals to be removed was determined by comparing the current herd size to the objective herd size. Next, the target proportion of cow-calf pairs was removed. For treatments where only the proportion of cow-calf pairs was controlled, the remaining animals to be removed were selected randomly with regard to sex and age. For treatments where both sex ratio and the proportion of cow-calf pairs removed were controlled, cow-calf pairs were removed first and an attempt was then made to remove animals of each sex in the quantity needed to achieve the desired sex ratio, subject to the constraint that no additional animals were removed once the target population size was achieved. Thus the criterion for target size was given a higher priority than that for sex ratio. Selection of animals to be removed was independent of age.

The proportion of males in simulated bison herds increased with the proportion cow-calf pairs removed (Table 1.1). Cow-calf removals had a more pronounced effect on sex ratio in THRO than in YELL because bison in THRO exhibited a greater growth rate, which therefore required removal of a larger proportion of the population to maintain population size. Sex-biased removals had a direct effect on sex ratio of the herd. Age-specific survival rates of males (resulting from both natural and harvest-related mortality) were positively related to the proportion of cow-calf pairs harvested, and this shifted the age structure of, especially, the male component of herds to older-aged bull (Figures 1.1, 1.2). With the increased proportion of older bulls, the average age of mating bulls increased, which was reflected by changes in generation time. Both age structure and generation time of cows was also influenced by the degree of selection for cow-calf pairs, but in a direction opposite to that of bulls (Table 1.1, Figure 1.1). Population growth rates increase with the proportion of reproductively active females in the herd, thus the proportion of the population harvested when removals were comprised of 10-50% cow-calf pairs ranged from 0.10 to 0.07 for YELL and 0.14 to 0.09 for THRO.

The proportion cow-calf pairs harvested had a small effect on retention of H_0 over a 200 year period, especially when compared to effects of population target size (Figure 1.3).

Table 1.1. Average sex ratio (proportion males; std in parentheses) and generation time (yrs; std in parentheses) of cows and bulls from simulations of THRO and YELL where the proportion of cow-calf pairs harvested (cow-calf pairs) varied from 0 (i.e., random removal) to 0.50. After the targeted proportion of cow-calf pairs was removed, additional animals were removed by harvest of a random selection of animals (i.e., no selection by sex or age). Standard deviations were calculated from overall means of each level of cow-calf removal.

Cow-calf pairs	Theodore Roosevelt			Yellowstone		
	Proportion males	Generation time (yr) cows	Generation time (yr) bulls	Proportion males	Generation time (yr) cows	Generation time (yr) bulls
0.00	0.43 (0.008)	6.67 (0.002)	7.06 (0.093)	0.41 (0.001)	7.02 (0.005)	8.31 (0.013)
0.10	0.54 (0.008)	6.62 (0.009)	7.66 (0.092)	0.45 (0.003)	7.00 (0.003)	8.47 (0.023)
0.20	0.60 (0.004)	6.56 (0.007)	7.98 (0.064)	0.48 (0.003)	6.97 (0.004)	8.61 (0.020)
0.30	0.63 (0.004)	6.52 (0.008)	8.17 (0.052)	0.50 (0.003)	6.95 (0.003)	8.70 (0.018)
0.40	0.65 (0.003)	6.47 (0.006)	8.31 (0.047)	0.52 (0.003)	6.93 (0.006)	8.78 (0.017)
0.50	0.67 (0.002)	6.43 (0.004)	8.42 (0.040)	0.53 (0.002)	6.91 (0.002)	8.84 (0.011)

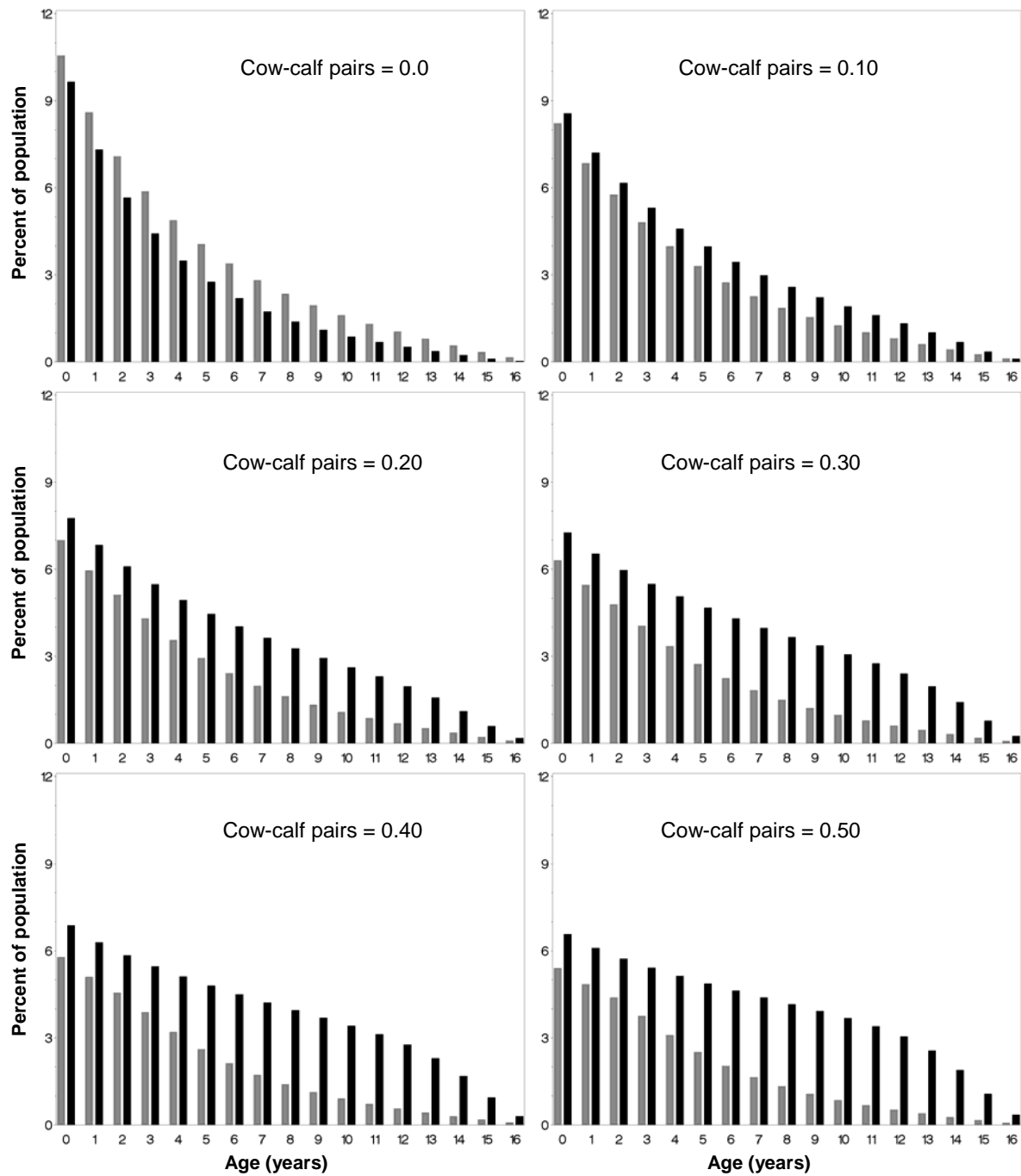


Figure 1.1. Age structure of simulated bison herds where cow-calf pairs constituted 0 to 50% of animals removed (other bison removed randomly with respect to sex and age). Based on vital rate parameters for THRO. Gray bars are females, black bars are males. Age structure did not vary with population size.

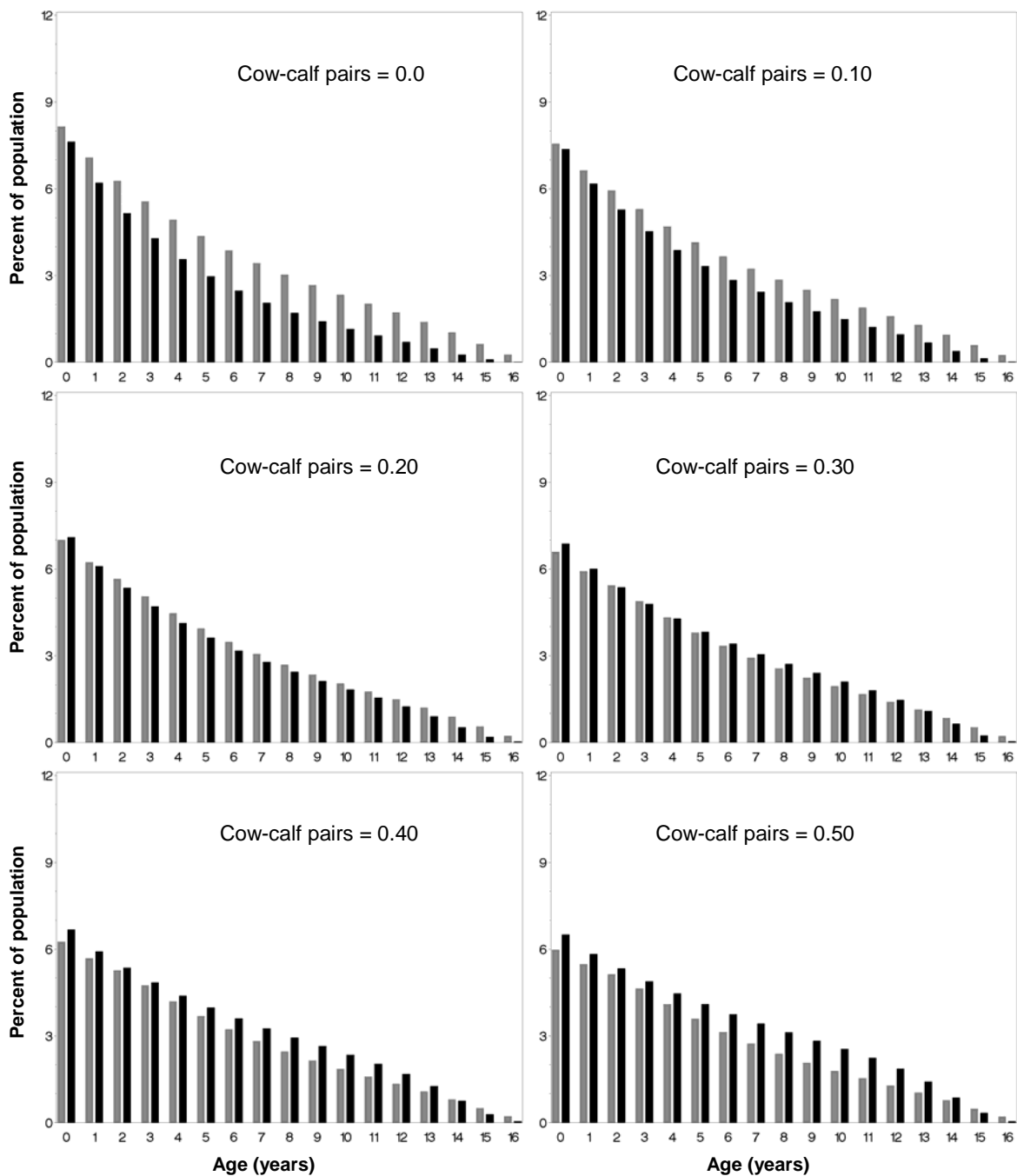


Figure 1.2. Age structure of simulated bison herds where cow-calf pairs constituted 0 to 50% of animals removed (other bison removed randomly with respect to sex and age). Based on vital rate parameters for YELL. Gray bars are females, black bars are males. Age structure did not vary with population size.

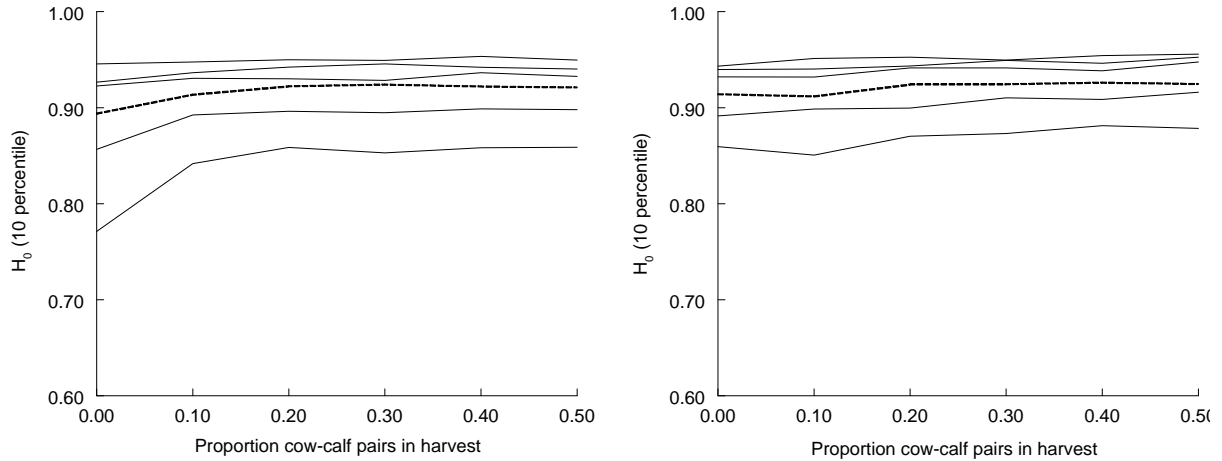


Figure 1.3. Lower 10 percentile of retained heterozygosity at year 200 as a function of the proportion of cow-calf pairs selected for harvest in THRO (left plot) or YELL (right plot). Lines, from bottom to top, are results for population target sizes of 200, 300, 400 (dashed), 500, 600, and 700.

Effects of sex ratio - cow-calf removals

We evaluated the effects of controlling sex ratio in cow-calf treatments from 100 simulations for each parameter set with target population sizes of 200, 300, 400, 500, 600 and 700. Because target population size had a higher priority than sex ratio, target sex ratios were not always achieved in simulations with a target proportion of males greater than 0.60 (Table 1.2). Herds with a low proportion of males (< 0.50) retained less H_0 than herds with a higher proportion of males (Figure 1.6). This effect was more pronounced for THRO than YELL.

Effects of sex ratio – random removals

In simulations conducted for this project, random removals represented a ‘null model’ for treatment effects. Random removal treatments did not control or bound changes in age structure or sex ratio, and these population-level attributes thus varied a result of vital rates and the

Table 1.2. Target and average (std) achieved sex ratios for random and cow-calf removal treatments using YELL and THRO vital rates. Averages calculated from years 20-200, across population targets of 200, 300, 400, 500, 600, and 700. There were no differences in achieved sex ratios between removal strategies.

Target	THRO	YELL
0.2	0.20 (0.000)	0.18 (0.000)
0.3	0.30 (0.000)	0.28 (0.000)
0.4	0.40 (0.000)	0.39 (0.000)
0.5	0.50 (0.000)	0.49 (0.000)
0.6	0.59 (0.000)	0.58 (0.002)
0.7	0.69 (0.001)	0.60 (0.001)
0.8	0.74 (0.003)	0.60 (0.001)

sampling error inherent to processes in small populations (demographic stochasticity). However, herd managers may set an objective for a prescribed herd sex ratio and we thus conducted simulation experiments to examine the likely consequences of managing for both a prescribed herd size and sex ratio. We conducted a limited set of simulations where target sex ratios were to achieve herds composed of 20% to 80% males and sex ratio was held constant. Cows and bulls of random ages were selected for harvest.

Treatments that resulted in highly biased herd sex ratios had profound effects on the age structure of the herd, especially when there were few males (Figure 1.4, 1.5). Retention of H_0 was much lower in strongly female-biased herds (Figure 1.6). Two obvious factors that contributed to this result were (1) very high growth rates that required annual removal of a relatively large proportion of the herd to maintain the target size, and (2) the very small proportion of breeding-age males in these herds.

Loss of H_0 was much greater when sex ratios were female biased, while a strong male bias in sex ratio had relatively little effect (Figure 1.6). Effects of a strong male bias were greater for simulations of THRO than for YELL, which reflected the influence on male age structure in these herds and the resulting greater numbers of breeding-age males (Figure 1.4, 1.5). The very small proportion of breeding-age males in some cow-calf removal treatments were accompanied by very high variation in individual male breeding success, especially in THRO (Figure 1.7). Trends in retention of H_0 were also related to changes in generation time of males, but the effects of changes in variation in individual breeding success clearly had a much strong influence on H_0 (Table 1.3).

Table 1.3. Average generation time (years) of cow and bull bison from simulations where removal treatment (cow-calf removals, random removals) and the target proportion of males ('Target males') in the population varied. Maximum achieved proportion of males varied by treatment and park, and the maximum for YELL and THRO were about 0.60 and 0.73, respectively. Values are means (std) across populations of 200, 300, 400, 500, 600, and 700. There was very little variation in generation time between population sizes.

Target males	YELL Cow-calf removal (0.24)		YELL Random removals		THRO Cow-calf removal (0.50)		THRO Random removals	
	Cows	Bulls	Cows	Bulls	Cows	Bulls	Cows	Bulls
0.2	6.9 (0.01)	6.6 (0.05)	7.0 (0.00)	4.8 (0.01)	6.3 (0.00)	5.6 (0.03)	6.7 (0.02)	6.4 (0.07)
0.3	6.9 (0.00)	7.3 (0.02)	7.0 (0.00)	5.5 (0.01)	6.3 (0.01)	6.1 (0.01)	6.7 (0.01)	6.9 (0.04)
0.4	7.0 (0.00)	7.7 (0.01)	7.0 (0.01)	6.0 (0.01)	6.4 (0.00)	6.6 (0.01)	6.7 (0.01)	7.4 (0.02)
0.5	7.0 (0.01)	8.1 (0.01)	7.0 (0.01)	6.5 (0.01)	6.4 (0.00)	7.0 (0.00)	6.7 (0.01)	7.7 (0.01)
0.6	7.0 (0.01)	8.3 (0.01)	7.0 (0.01)	6.8 (0.01)	6.4 (0.00)	7.4 (0.00)	6.7 (0.01)	8.0 (0.01)
0.7*	7.0 (0.01)	8.5 (0.31)	7.0 (0.01)	6.9 (0.01)	6.5 (0.00)	7.7 (0.00)	6.7 (0.01)	8.3 (0.01)
0.8*	7.0 (0.01)	8.6 (0.29)	7.0 (0.01)	7.0 (0.01)	6.5 (0.01)	7.8 (0.00)	6.7 (0.01)	8.4 (0.01)

* These targets were not always achieved – see Table 1.2.

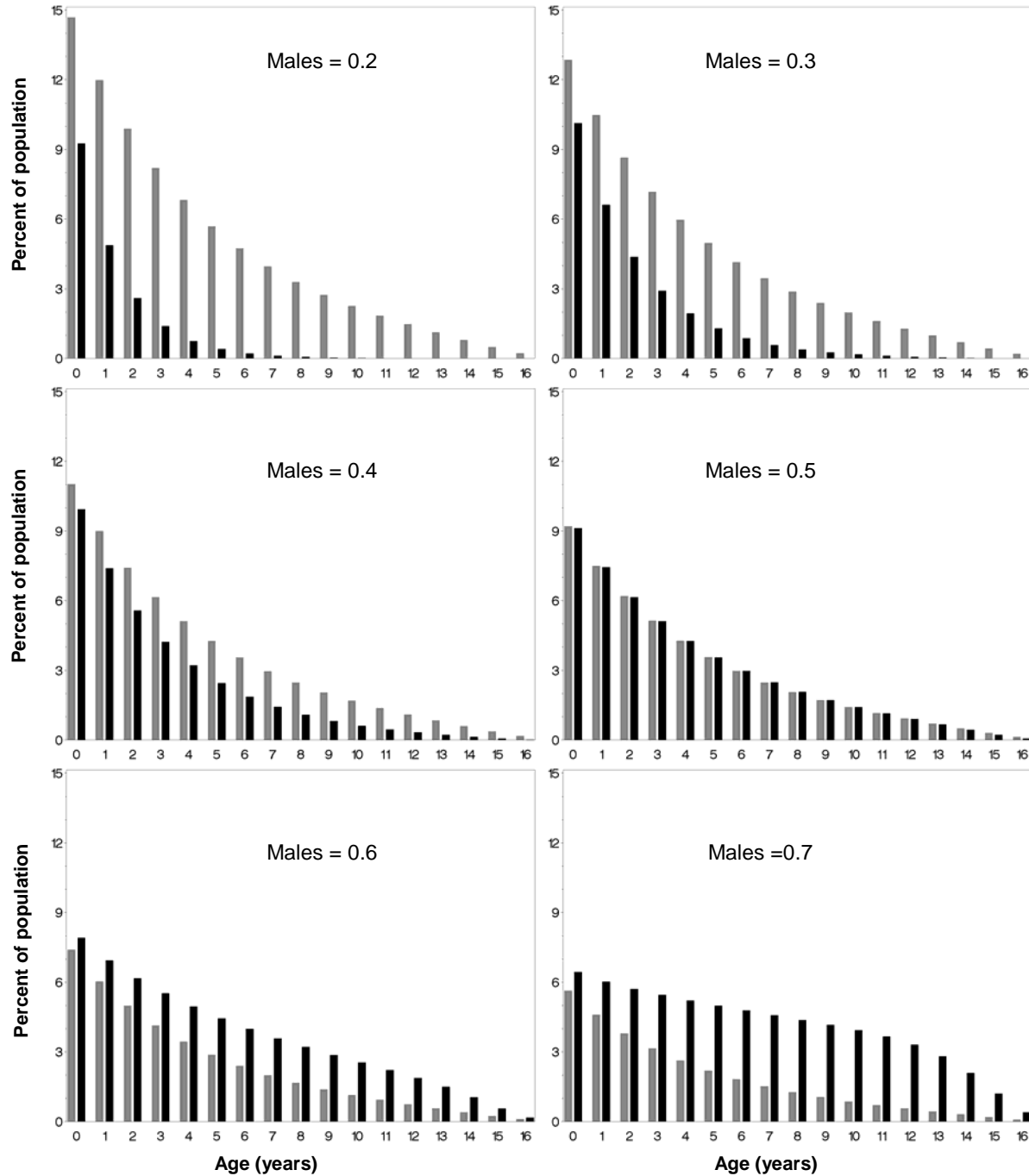


Figure 1.4. Age structure of simulated bison herds subjected to random-age removals where sex ratio was controlled, and the target proportion of males in the population varied from 0.2 to 0.7. Based on vital rate parameters for THRO. Gray bars are females, black bars are males. Age structure did not vary with population size.

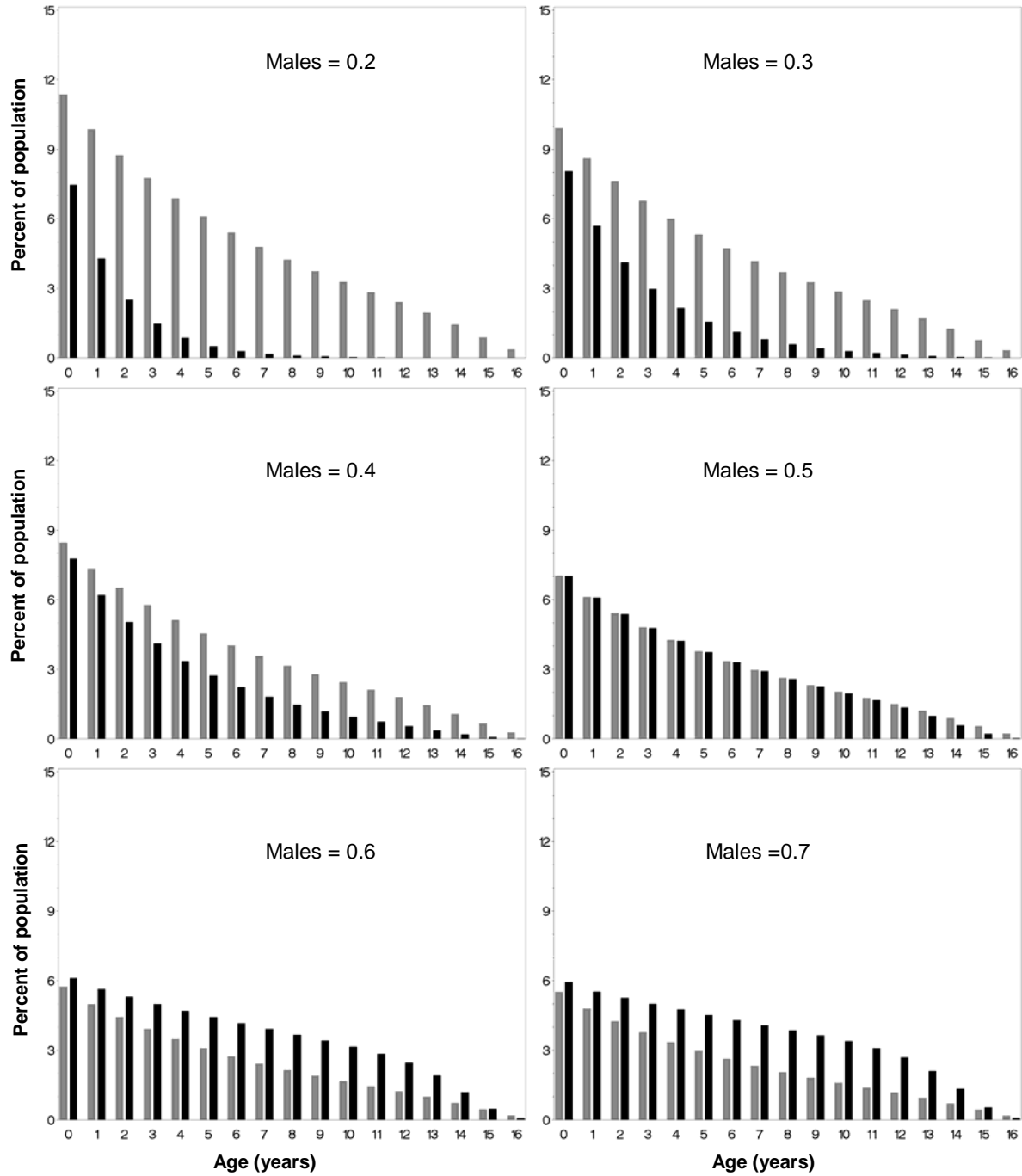


Figure 1.5. Age structure of simulated bison herds subjected to random-age removals where sex ratio was controlled, and the target proportion of males in the population varied from 0.2 to 0.7. Based on vital rate parameters for YELL. Gray bars are females, black bars are males. Age structure did not vary with population size.

Relative effects of vital rates and genetic constitution

We examined the relative effects of high (THRO) and low (YELL) reproductive and survival rates for bison and of high (YELL) and low (THRO) levels of extant genetic diversity by crossing model inputs for these factors and comparing retention of H_0 . To do so, we initialized the model with populations that used vital rates from one population and genetic data from the other. We simulated random age removals using all four combinations of parameter sets (YELL-YELL, YELL-THRO, THRO-THRO, THRO-YELL) with target proportions of males of 0.20 to 0.80. Simulations were conducted as described above.

Differences in genetic composition of YELL and THRO had a small but consistent effect on retention of H_0 (Figure 1.8). Simulated populations initialized with genetic data from YELL consistently lost slightly more H_0 than those initialized data from THRO, reflecting the greater number of rare alleles in YELL and initial greater H_0 . The effects of genetic composition were more pronounced for simulations using vital rates from THRO than YELL, which is consistent with higher growth rates of THRO (and thus a decreased generation time, higher reproductive variance, and harvest of a larger proportion of the population). However, the effects of differences in genetic composition were small compared to other factors, especially population size.

Vital rates had a strong influence when sex ratios were highly female-biased, but relatively little effect when herd sex ratios were near unity (Figure 1.9). Similarly, the effects of vital rates were more pronounced in small populations. When there was an effect, higher survival and reproductive rates led to more rapid losses of H_0 , but population size had a greater effect than vital rates.

These results clearly show that decisions on management of population size can have a profound effect on genetic diversity in small populations. As population size increases, the consequences of a biased sex ratio, harvest strategy, and variance in individual reproductive success are much reduced, and for very large bison herds (say, > 1500), management decisions are unlikely to significantly affect retention of genetic variation.

Our simulations assumed that individual bison in herds mixed randomly and that herds were relatively homogeneous. Population substructures can result in reduced rates of genetic recombination and in non-random harvest of animals. Results in this report are thus more appropriately applied, for example, to the YELL northern range herd or the YELL central herd, rather than to the entire YELL bison population. Similarly, spatial structuring in a park like BADL may lead to highly non-random removals, thereby increasing the loss of genetic diversity relative to these simulations.

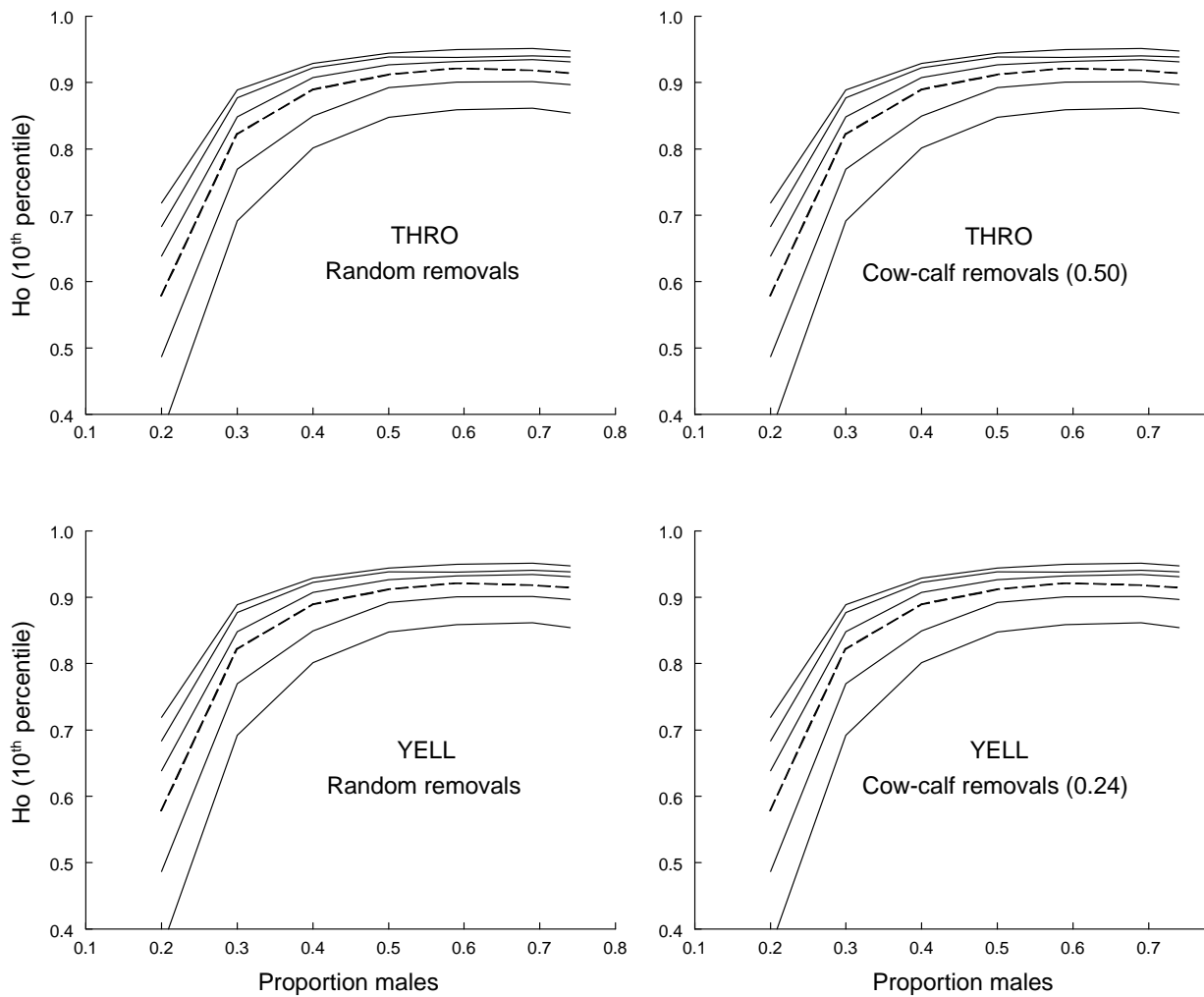


Figure 1.6. Observed heterozygosity (H_o ; lower 10 percentile) at year 200 for simulations using vital rates and genetic data (Halbert 2003) from YELL and THRO. See text for treatments; cow-calf removal rates were 50% and 24% for THRO and YELL, respectively. Lines, from bottom to top, show results for population sizes of 200, 300, 400 (dashed line), 500, 600, and 700.

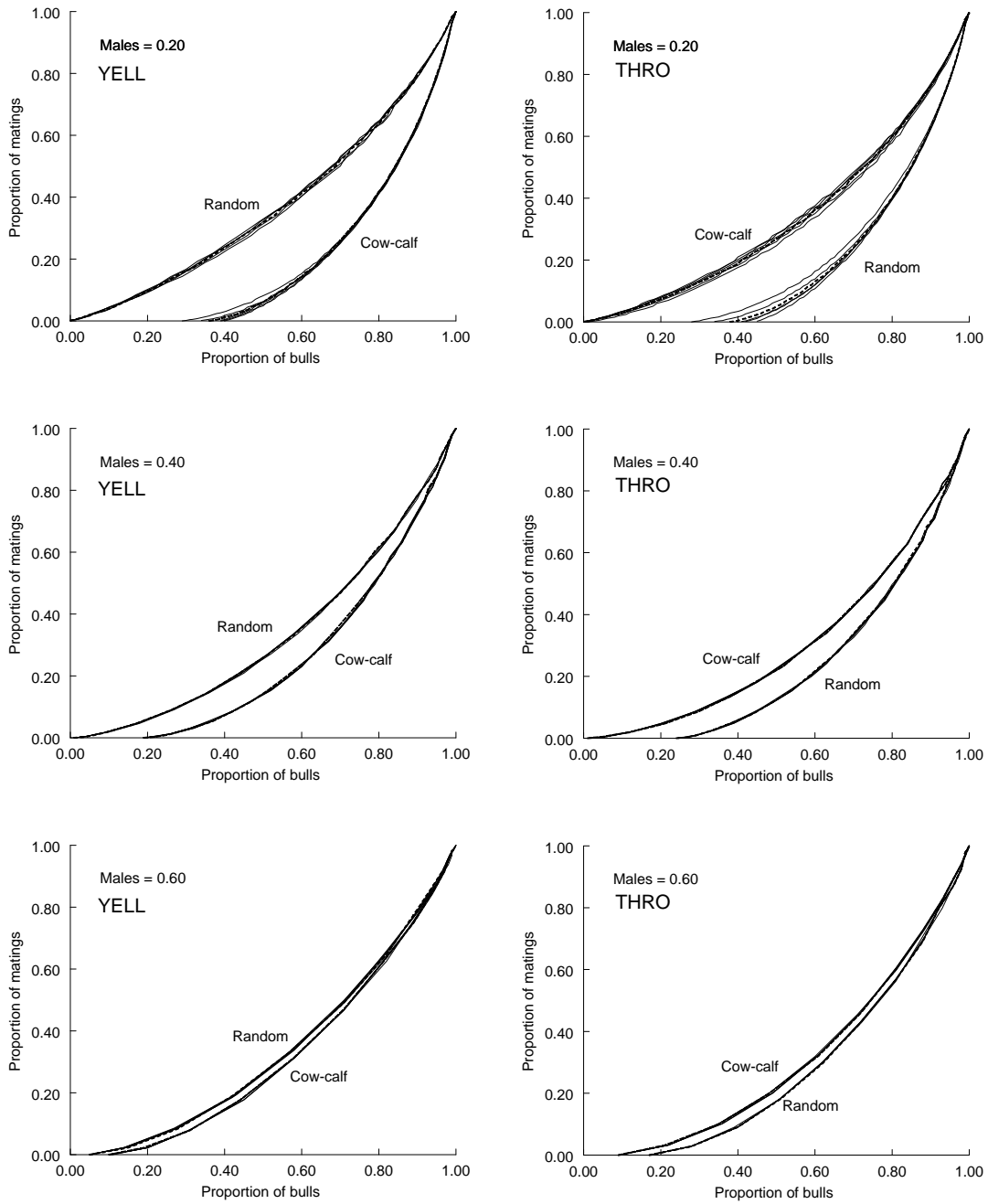


Figure 1.7. Cumulative distribution of individual male breeding success for random removals (Random) and removal of cow-calf pairs (Cow-calf) for YELL (left column) and THRO (right column). Note contrasting effects of treatments for on variation in breeding success. Lines are for population sizes of 200, 300, 400 (dashed line), 500, 600, and 700.

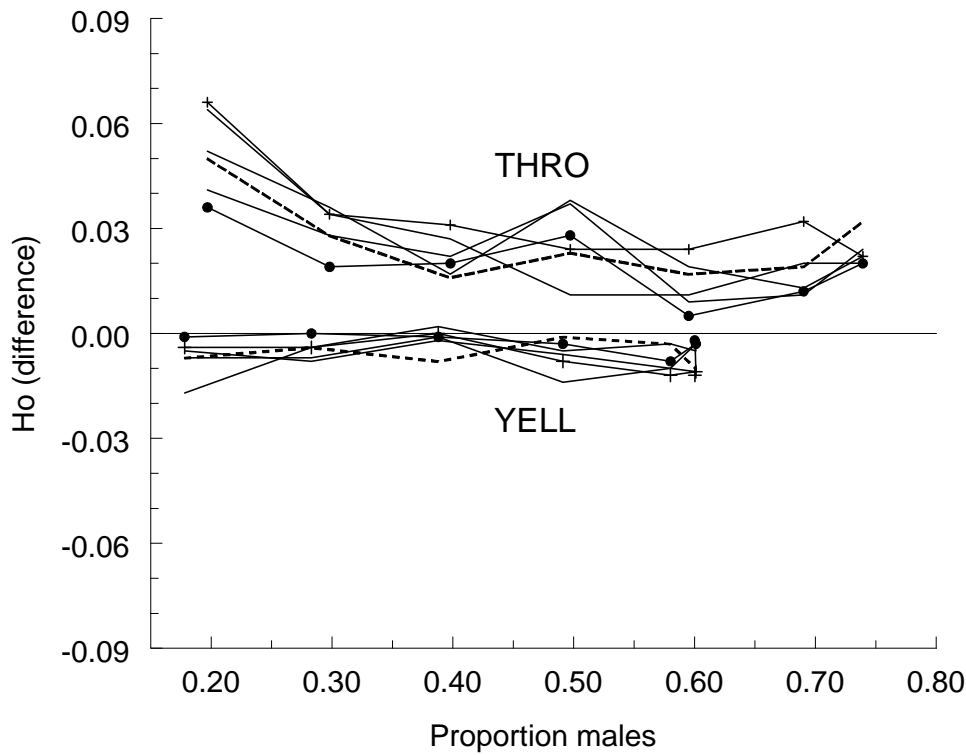


Figure 1.8. Plot showing the small effect of genetic constitution on retention of H_o . Vertical axis is the difference in H_o (lower 10 percentile) at year 200 for simulations of cow-calf removals using vital rates and genetic data (Halbert 2003) from YELL and THRO. Top set of lines (THRO) are results from simulations that used THRO vital rates and bottom set of lines (YELL) used YELL vital rates. Top lines were obtained by subtracting results from simulations initialized with YELL genetic data from those using the THRO genome. Bottom lines were obtained by subtracting results from simulations using THRO genetic data from those using the YELL genome. See text for treatments; cow-calf removal rates were 50% and 24% for THRO and YELL, respectively. Lines are results for population sizes of 200 (line with +), 300, 400 (dashed line), 500, 600, and 700 (line with filled circle).

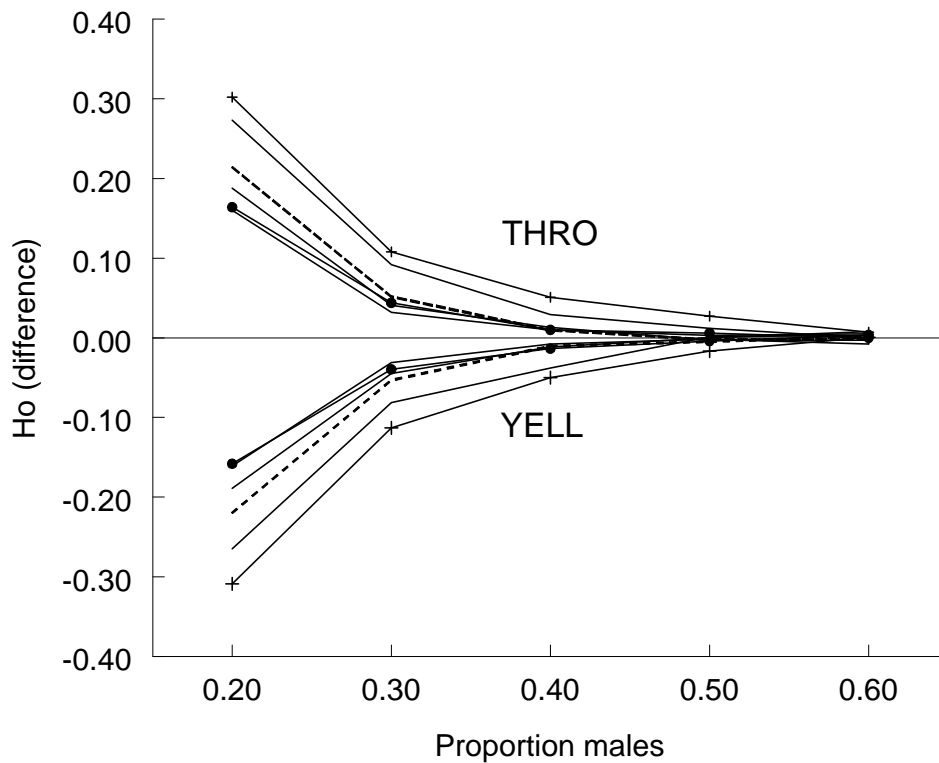


Figure 1.9. Plot showing effects of differences in vital rates on H_o for a relatively diverse herd (YELL) and a relatively homogeneous herd (THRO). The vertical axis is the difference in observed heterozygosity (H_o ; lower 10% percentile) at year 200 for simulations of cow-calf removals, with controlled sex ratio, using vital rates and genetic data (Halbert 2003) from YELL and THRO. Top set of lines (THRO) are results from simulations that used THRO genetic composition and bottom set of lines (YELL) used genetic data from YELL. Results displayed in the upper set of lines are differences obtained by subtracting results from simulations that used THRO vital rates from those using YELL vital rates; bottom lines were obtained by subtracting results from simulations using YELL vital rates from those using THRO vital rates. Cow-calf removal rates were 50% and 24% for THRO and YELL, respectively. Lines are results for population sizes of 200 (line with +), 300, 400 (dashed line), 500, 600, and 700 (line with filled circle). Results reported only for simulations where average sex ratios were approximately equal across treatments (20% to 60% males; Table 1.2).