

Effects of Culling on Bison Demographics in Wind Cave National Park, South Dakota

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ABSTRACT: We used a stochastic Leslie matrix model parameterized with demographic data from Wind Cave National Park to evaluate effects of four culling strategies on population growth rates and age and sex structure of bison (*Bison bison* Linnaeus). The four culling scenarios we modeled included removal of: (1) yearlings only; (2) calf/cow combination; (3) a herd-wide proportional cull (i.e., individuals taken in proportion to their availability); and (4) calves only. We also allowed either one, two, or three years to elapse between culls to mimic current management activities, and chose culling values for each scenario that would maintain a stable population (i.e., $\lambda \approx 1.00$). In the absence of culling, our model projected a growth rate of 16% per year ($\lambda = 1.16$) (SD = 0.02) for the Wind Cave bison population. The modeled population was characterized by a unimodal age structure for bulls and cows and a 1:1 bull:cow ratio. Removal of 75% of the yearlings or 75% of the calves every year was needed to maintain abundance at current size. These culling strategies altered the age distribution from baseline conditions, resulting in nearly equal proportions of age classes 2–15. When yearling culling or calf removal was skipped one year or two consecutive years, the yearling or calf removal option resulted in positive population growth even in the presence of a 90% cull. Because these strategies nearly removed entire cohorts, corresponding gaps were introduced in the age structure. About 40% of calves and 20% of cows needed to be removed under the annual calf/cow cull to stabilize population growth, producing a unimodal age structure of cows. However, the proportion of bulls in the 2–16 age classes increased, and the proportion of males was nearly equal across the middle age classes. The proportional cull, regardless of time between culling operations, resulted in the most symmetric age structure for males and females. To achieve $\lambda \approx 1.00$ under a proportional cull strategy, 16% of all animals would need to be removed annually, 33% every other year, or 50% once every three years. Sensitivity and elasticity analysis indicated that adult females (5–13 years old) were the most important group of bison affecting λ . These modeled effects, along with factors such as logistical constraints, costs, efficacy, viewing opportunities for tourists, genetics, behavior, and agency policies should be considered when managers choose among culling strategies. When considering historical predation and harvest by Native Americans, we hypothesize that the calf/cow combination cull would have most closely approximated natural bison demographics after the widespread availability of horses (*Equus* spp.) in the year 1735. Before 1735, we hypothesize that the proportional cull would most closely represent historic conditions, although even this option might not reproduce the variability inherent in historical bison dynamics. We discuss the possibility and management implications of variable culling that might more closely mimic historical influences on bison populations on the Northern Great Plains.

Index terms: age structure, bison, culling, demographics, Great Plains, matrix model, National Parks, population structure

INTRODUCTION

National Park Service policies call for parks to conserve native flora and fauna, maintain natural conditions, and retain natural processes (National Park Service 2006). However, most National Park units are too small to support natural conditions and allow natural processes, such as disturbances, to operate without human intervention or at the large spatial scales that formerly characterized many of these processes. Therefore, active management is needed to maintain species assemblages and to mimic natural conditions. This need is well established in National Park Service policies, operations, and culture and has been generally accepted for decades. For example, the Leopold Report (Leopold et al. 1963) endorsed culling of overabundant animals when necessary to protect park resources, while at the same time stating

somewhat paradoxically that “naturalness should prevail” in park management and that each park should be an “illusion of primitive America.” Soukup et al. (1999) stated essentially the same when they argued that National Park Service policies implied that parks should maintain or restore ecosystem integrity and manage for ecosystem processes.

Bison (*Bison bison* Linnaeus) occupy three National Park units in the Midwest Region – Badlands National Park, Theodore Roosevelt National Park, and Wind Cave National Park (WICA). However, although all parks support relatively large areas of native grasslands, all three parks are too small to encompass the range of natural conditions and processes under which bison evolved. None of the parks supports wolves (*Canis lupus* Linnaeus) or grizzly bears (*Ursus arctos horribilis* Linnaeus),

the most significant native predators of bison. Park fences confine the formerly nomadic bison herds. To prevent herds from exceeding management objectives for abundance, managers routinely cull excess individuals. During culls, managers must decide which age and sex classes should be removed and in what proportion. In the past, the age and sex structure of animals removed in Midwestern National Parks included: (1) yearlings only; (2) a combination of cows and calves; (3) herd-wide proportional cull (i.e., individuals taken in proportion to their availability); and (4) calves only. However, managers lack information about the comparative effects of these strategies on bison demographics.

To compare these culling options, we used a stochastic Leslie matrix population model to simulate herd demography and culling. We evaluated the effects of the four culling strategies used in these parks on population growth rates and age and sex structure of bison populations. We used demographic data for the bison herd at WICA to parameterize the model. We determined culling rates that would be necessary to maintain a stable population ($\lambda = 1.00$) and examined the demographic structures produced by various culling options.

STUDY AREA

Wind Cave National Park was established in 1903 and significantly expanded in 1912 through the addition of the Wind Cave National Game Preserve. Bison, Rocky Mountain elk (*Cervus elaphus nelson* Linnaeus), and pronghorn (*Antilocapra americana* Ord) were shipped to the Preserve early in the twentieth century to reestablish populations (Bauman 1998). The park now encompasses 11,451 ha and the perimeter is fenced to prohibit bison movements across the boundary. The vegetation of WICA is a mixture of woodlands, shrublands, and mixed-grass prairie vegetation. The park is managed to create an environment that resembles conditions prior to European settlement. Many of the wildlife components of the mixed-grass prairie ecosystem occur at the park, including large ungulates such as bison, elk, and deer (*Odocoileus virginianus* Zimmermann and *O. hemionus* Rafinesque). Bison are culled annually and elk are culled periodically to reduce grazing pressure. At the time of the study, the culling of surplus bison in WICA consisted of removing yearling animals at a 50:50 sex ratio (i.e., yearling cull).

METHODS

Bison Population Model

We used a stochastic age- and sex-structured Leslie matrix model to evaluate culling strategies (Leslie 1945; Caswell 2001). A Leslie matrix model of this type requires three components. First, the model has a vector, denoted as \underline{n}_t , that contains the number of females and males in each age class of age x at the beginning of the model run. In this case, let the vector:

$$\underline{n}_t = \begin{bmatrix} n_{1F} \\ n_{2F} \\ \vdots \\ n_{kF} \\ n_{1M} \\ n_{2M} \\ \vdots \\ n_{kM} \end{bmatrix}$$

denote the number of females (n_{iF}) and males (n_{iM}) in the bison population at time t (Skalski et al. 2005). We assigned initial conditions (i.e., age structure and initial vector of abundance) using data for herd composition subsequent to the 2004 roundup, which is a typical population structure for WICA. Our initial vector of female abundance included: 50 female calves, 14 yearling females, 31 females aged 2-4 years, 65 females aged 5-13 years, and 22 females aged > 13 years. Our initial vector of male abundance included: 50 male calves, 15 yearling males, 34 males aged 2-4 years, 68 males aged 5-13 years, and 23 males aged > 13 years.

Second, a projection matrix (i.e., the Leslie matrix [Leslie 1945], \mathbf{M}) provides the age-specific demographic rates, including the net number of female offspring recruited per female of age i (i.e., F_{iF}), the net number of male offspring recruited per female of age i (i.e., F_{iM}), the probability of a female aged i surviving to age $i+1$ (i.e., S_{iF}), and the probability of a male aged i surviving to age $i+1$ (i.e., S_{iM}). The projection matrix for the two-sex model is written as (Leslie 1945):

$$\mathbf{M} = \begin{bmatrix} F_{0F} & F_{1F} & \dots & F_{kF} & 0 & \dots & 0 \\ S_{0F} & S_{1F} & & & \vdots & \ddots & \vdots \\ & & \ddots & & & & \\ & & & S_{k-1F} & 0 & 0 & \dots & 0 \\ F_{0M} & F_{1M} & \dots & F_{kM} & 0 & \dots & 0 \\ 0 & \dots & & 0 & S_{0M} & & \\ & & & & & S_{1M} & \\ \vdots & & & \vdots & & & \ddots & \\ 0 & \dots & & 0 & & & & S_{k-1M} & 0 \end{bmatrix}$$

The population at time $t = 0$ can be projected to time $t = 1$ by a series of coupled linear equations. For our bison model, input parameters included age and sex-specific annual survival rates for

ages 1 to 23, summer (birth to autumn) and over-winter survival rates for calves, and age-specific fecundity rates (average number of calves born per female) for ages 2 to 24. Age 24 was the maximum age allowed, and the survival rate of age 24 animals was set to 0. We started each year with the post-cull population, predicted the pre-cull population one year later, subtracted the cull (if any), and then repeated the process. Each model year started at an autumn cull, and ended with a census the following autumn immediately before the next cull.

We used data collected during WICA's annual autumn bison roundup to help parameterize probability distributions for survival and fecundity. We used data collected each year from 1966-2003, excluding 1973, 1976, 1990, and 2002 when no data were collected. At each capture, animals were sexed and tagged with ear tags; implant tags were also given to some animals starting in 1982, and by 1994 all animals received ear tags, implant tags, and (in most years) hip tags. For each year, we put animals into age classes (0.5 to 23.5). We pooled data from all years in order to determine average survival estimates for each age class. For each age class and sex, we calculated the minimum number known alive, which is the number of unique individuals captured when they were age i , plus the number not captured at i but that were known to be alive because they were captured at a later age. For the minimum number alive at age i , we then calculated the number of animals culled, the number not culled that were never captured again, and the number not culled that were captured in a subsequent year. The naive survival estimate was computed as: (number not culled, captured again)/(not culled, captured again + not culled, not captured again). Although this calculation has some negative bias because of imperfect trap success (some animals not captured in later years and assumed dead were likely alive but not captured), inspection of capture histories and discussion with park biologists indicate that most age classes had high capture probabilities. We used a similar approach to define fecundity for WICA cows, using proportions of individuals that were lactating at the time of the roundup. We assumed lactating animals had calved, individuals < 4 years old did not breed, and only one offspring was produced per cow (Berger and Cunningham 1994). We also assumed a 50:50 sex ratio of calves at birth.

The third component of our model was a harvest matrix to permit population projections in the presence of removals (Caswell 2001). When a fixed proportion of each sex/age class is removed each year, the form of the modified Leslie matrix equation can be written as (Skalski et al. 2005): $\underline{n}_{t+1} = \mathbf{H}\mathbf{M}\underline{n}_t$ where \mathbf{H} = a diagonal matrix of dimension $2(k+1) \times 2(k+1)$. The harvest matrix is of the form (Skalski et al. 2005):

$$\mathbf{H} = \begin{bmatrix} h_{0F} & 0 & \dots & & & & & & & 0 \\ 0 & h_{1F} & 0 & \dots & & & & & & 0 \\ 0 & & \ddots & & & & & & & \vdots \\ \vdots & & & h_{kF} & & & & & & \\ & & & & h_{0M} & & & & & \\ & & & & & h_{1M} & & & & \\ & & & & & & \ddots & & & 0 \\ 0 & \dots & & & & & & 0 & h_{kM} & \end{bmatrix},$$

where h_{kF} and h_{kM} were the probability of females and males surviving the cull (Skalski et al. 2005).

Our Leslie matrix model describes population growth without resource limitation (i.e., density-independent population growth). Although it is possible to include density dependence in Leslie matrix models (Caswell 2001; Skalski et al. 2005), density-dependent effects on bison vital rates appear to be weak or absent for the moderate population densities maintained by park managers (Berger and Cunningham 1994).

We included parameter stochasticity to account for variability in vital rates (Figure 1). For each demographic parameter, we used mean estimates from the analysis of WICA roundup data. We set the beta distribution mean to our naive pooled estimates, and graphically examined different beta distributions to select values that would produce a plausible variance and shape for the beta distribution. For each simulation at each time step, we generated random survival and fecundity values from these beta distributions. Our intention was not to base simulations on a formal survival estimate and statistical estimates of empirical variability. Rather, we examined data as a guide for producing realistic distributions with conservative estimates of variability (i.e., erring on the side of incorporating more uncertainty than existed for this single data set).

Modeling Scenarios

We modeled culling strategies currently used by Midwestern National Parks to manage bison herds. The four scenarios we modeled included: (1) yearlings only; (2) calf/cow combination where two calves were culled for each cow; (3) a herd-wide proportional cull; and (4) a calves only cull. To mimic current management activities for each culling option, we allowed either one, two, or three years to elapse before another cull of the same type. We did not specify a population size objective or specific numbers of removals, but rather assumed that park managers would want to maintain current abundance (i.e., assumed goal was $\lambda = 1.00$). For each age/sex class, we specified a culling threshold: when an age class was below this threshold, no culling of that age/sex group occurred that year to ensure that over time a minimum of 10 individuals remained in each age class up to age nine, and five individuals remained in each of the older age classes.

For the yearling cull and calf cull simulations, we removed 90%, 75%, and 50% of all yearlings or calves (male and female) every year. We simulated two additional yearling and calf cull options: a 90% cull every other year and a 90% cull once every three years.

For both the calf/cow combination cull and the proportional cull, we used removal proportions chosen by exploration to produce $\lambda = 1$. For the annual calf/cow simulation cull, we removed 40% of all calves (males and females) and 20% of all adult cows between the ages of 3-15 years. For the every-other-year cull,

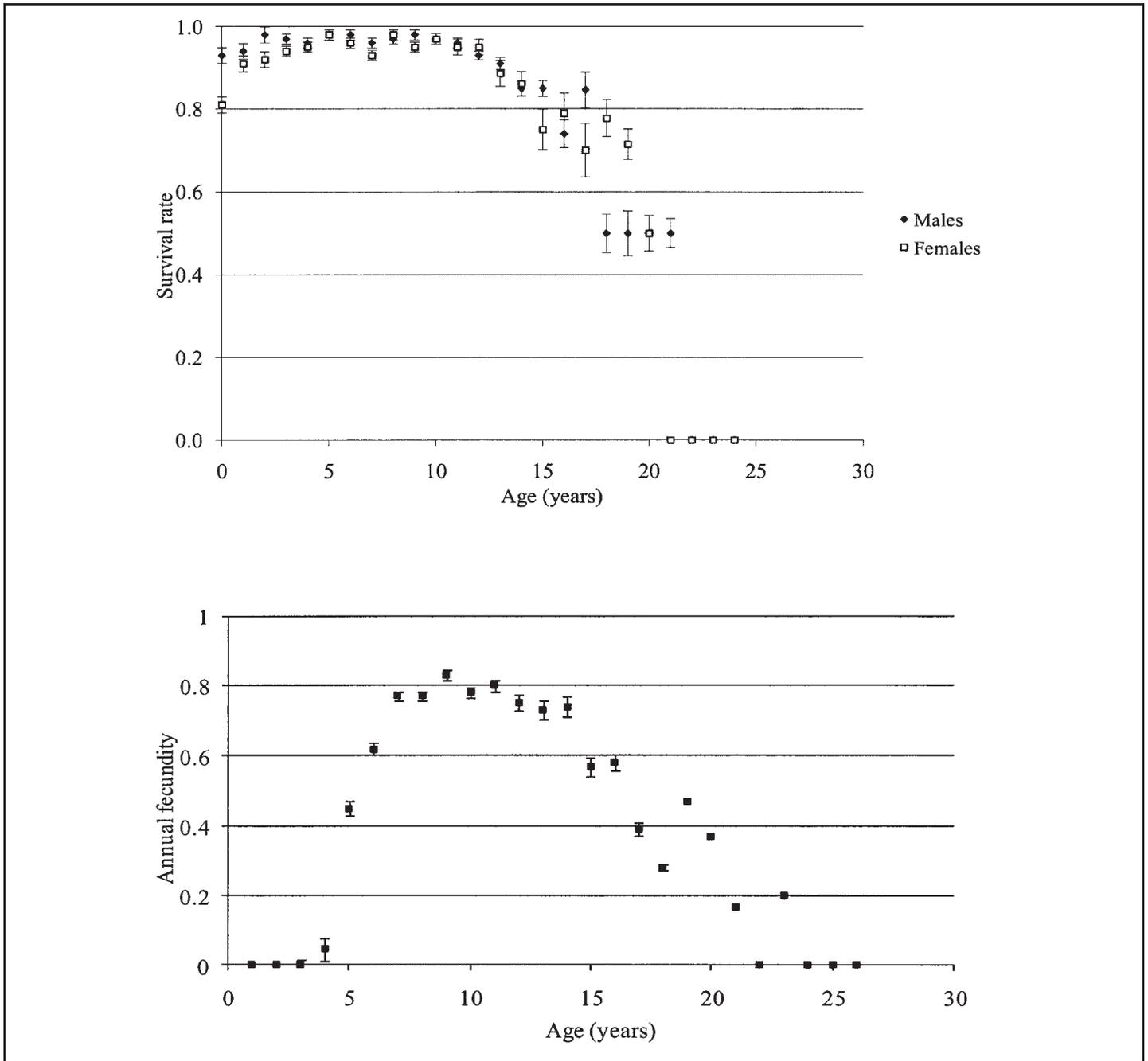


Figure 1. Initial estimates used in demographic model for bison at Wind Cave National Park, including male and female survival rate (top), and annual fecundity (bottom). Error bars = 1 SD.

we removed 75% of all calves and 37.5% of adult cows between 3-15 years old. In contrast, for the proportional cull, we removed 16% of all individuals for the annual culling strategy, 33% for every other year culling, and 50% reduction across all age categories once every three years. We assumed a 25-year planning horizon for our models and summarized results from 100 runs of the stochastic model. Although

population simulations frequently use thousands of replications for each model scenario, variability in the outcome among 100 runs was low, and more simulations were not needed to capture the general effects of each culling option. Similarly, we examined a short period (25 y) because managers were most interested in the immediate effects of culling, given the current demographic structure, rather than

long-term equilibrium dynamics.

Sensitivity and Elasticity Analysis

To determine the relative importance of different ages and genders in influencing λ , we conducted a sensitivity and elasticity analysis, following the steps outlined by Caswell (2001) and Skalski et al. (2005). To assess the sensitivity of λ to a change

in the value of the demographic parameter a_{ij} in the Leslie matrix, we used (Caswell 2001):

$$s_{ij} = \frac{v_i w_j}{\sum \mathbf{v}' \mathbf{w}}$$

where v_i and w_j relate to the i th and j th elements in the reproductive vector \mathbf{v} (i.e., the right eigenvector of the Leslie matrix at the stable age distribution) and stable age vector \mathbf{w} respectively. Elasticity (e_{ij}) is the proportional change in λ for a proportional change in a matrix element, calculated as (Skalski et al. 2005):

$$e_{ij} = \frac{\left(\frac{a_{ij}}{\partial a_{ij}} \right)}{\left(\frac{\lambda}{\partial \lambda} \right)} = \frac{a_{ij} s_{ij}}{\lambda}$$

RESULTS

Survival rate estimates and annual fecundity are presented in Figure 1. Survival estimates were typical of other large mammal populations, with relatively high calf survival (> 80% annually), high survival between years 1 and 14, and a gradual decline in annual survival starting after age 14. Annual fecundity was highest among animals aged 7-14 years (Figure 1).

Assuming no removals and no density dependence, our modeled WICA bison population increased exponentially with a mean $\lambda = 1.16$ (SD = 0.02, Figure 2). Population growth for these simulations was characterized by a unimodal age structure (i.e., calves most abundant, with each successive age class declining in abundance) and a 1:1 bull:cow ratio (Figure 2).

The yearling cull and the calf-only cull simulations produced similar results. Culling 90% of yearlings or 90% of calves every year was not a viable strategy, with an average $\lambda = 0.93$ (SD = 0.03, Figure 3) over the 25-year period. The proportion of animals age 2-5 years was reduced by half when compared with current conditions (Figures 4 and 5). Culling 75% of calves or of yearlings every year produced a stable population (average $\lambda = 1.00$, SD =

0.02). With these strategies, all ages were nearly equally represented in both male and female segments of the population until age 15 (Figures 4 and 5). Culling 50% of calves or of yearlings every year resulted in an average annual population growth of $\lambda = 1.08$ (SD = 0.02) (Figure 3) and resulted in nearly double the proportion of males and females 2-5 years old in contrast to the 75% reduction simulation (Figures 4 and 5). When yearling culling or calf removal was skipped a year or two consecutive years, nearly entire cohorts were removed with subsequent gaps in the age distribution (Figures 4 and 5). When culling of yearlings or calves skipped one or two years, even culling 90% in other years did not reduce population growth (Figure 3). For example, culling 90% of yearlings every other year resulted in an average $\lambda = 1.10$ (SD = 0.02).

Because we chose culling levels that ensured $\lambda \approx 1$ (i.e., 40% of all calves and 20% of all adult cows between the ages of 3-15 years for annual cull), the simulated population growth was nearly stable for the calf/cow removal simulation ($\lambda = 0.99$, SD = 0.02) (Figure 3). The annual calf/cow cull resulted in a unimodal age structure of cows and bulls. However, the total proportion of males 2-16 years old increased over other simulations and remained relatively constant in these age categories (Figure 5). This option produced double the proportion of 6-11 year old males in contrast to females and triple the proportion of males age 12-16 years (Figures 4 and 5). In contrast, culling cows and calves every other year at a level that ensured $\lambda \approx 1$ produced a nearly equal sex ratio (Figure 5); however, gaps in the age distribution formed (Figure 5).

As expected from the structure of our model and general principles, the proportional cull, regardless of time between culling operations, altered baseline conditions the least (Figures 4 and 5). With proportional culling, it was necessary to cull 16% of the population each year to maintain $\lambda \approx 1$ (Figure 3). When culling was reduced to once every two or three years (33% and 50%, respectively), the age structure remained similar to the annual cull (Figures 4 and 5).

Results of our sensitivity and elasticity analysis demonstrated that adult females were most important to population growth. For example, 13-year old females have the highest elasticity value of 0.24, which means that a 1% increase in adult survival will cause a 0.24% increase in λ . Adult females between 5-13 years old contributed two times that of females > 13 years to offspring production (i.e., standardized reproductive value of 1.5 and 0.7, respectively). Other parameters have much less influence. For example, fecundity values had elasticity values ≤ 0.11 . These results indicate that culling adult females will have the largest influence on controlling population size.

DISCUSSION

We evaluated short-term effects of culling on simulated populations with initial age and sex structure matching the current WICA herd structure. Effects of these culling options on herds at Badlands and Theodore Roosevelt National Parks may be slightly different due to minor differences among parks in initial herd age and sex structure, and vital rates. However, other simulations produced the same general patterns and conclusions for these other herds (Millsbaugh et al. 2005). Our reporting of results focused on average trends rather than examining uncommon scenarios (e.g., several years of greatly reduced reproduction) that might have been evident with longer-term simulations and more replications. This focus is appropriate given the management context of our work. Short-term, average effects of different culling options were relevant to managers who must choose culling strategies to implement during the next few decades. In contrast to managers attempting to maintain threatened populations of elusive species, WICA can assess population status annually and alter bison management prescriptions if culling or natural events (e.g., prolonged drought) produces trends that do not match population objectives.

We focused on differences among culling strategies in their demographic effects, particularly their effectiveness at maintain-

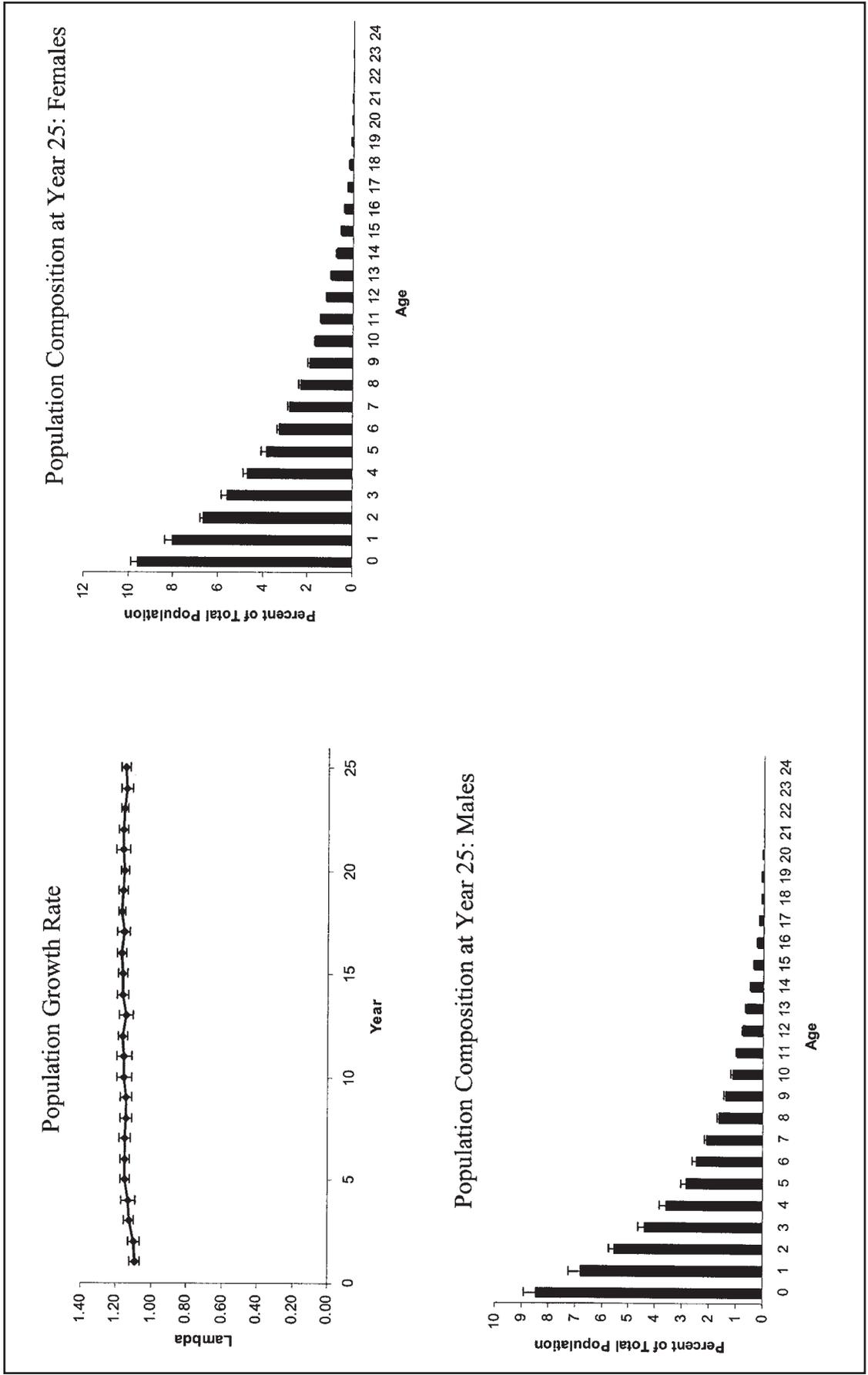


Figure 2. Projected demographic characteristics of bison at Wind Cave National Park in the absence of culling. From upper left to right: population growth rate (λ), population composition of females at year 25 in the simulation, and population composition of males at year 25 in the simulation.

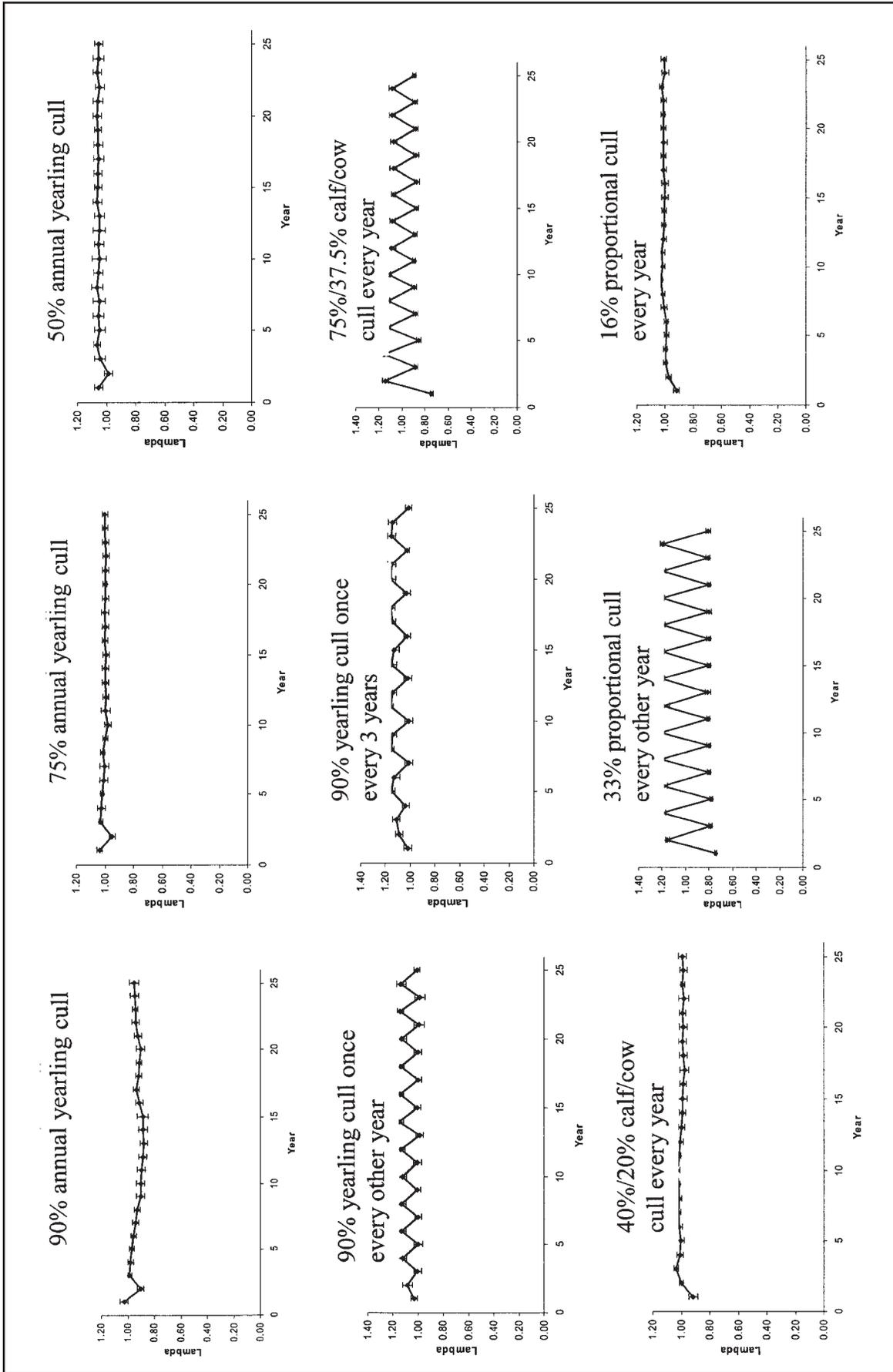


Figure 3. Effects of culling on population growth rates (λ) of bison at Wind Cave National Park for variations of 4 culling strategies. From upper left to right: 90% annual yearling cull; 75% annual yearling cull; 50% annual yearling cull; 90% yearling cull every other year; 90% yearling cull every three years; 75%/37.5% calf/cow combination cull every year; 40%/20% calf/cow combination cull every year; 33% proportional cull every other year; and 16% proportional cull every year.

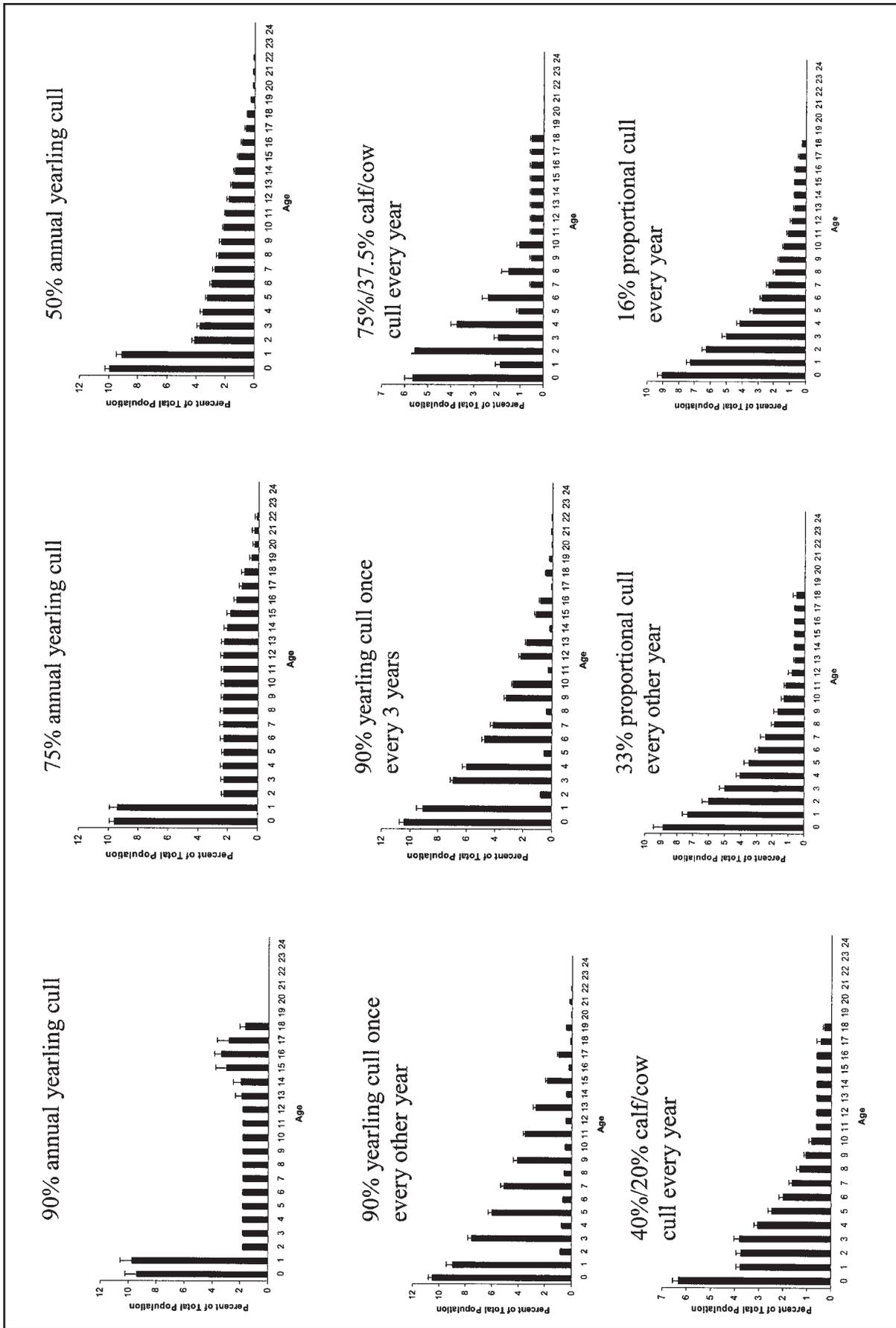


Figure 4. Effects of culling on age structure of female bison at Wind Cave National Park. From upper left to right: 90% annual yearling cull; 75% annual yearling cull; 50% annual yearling cull; 90% yearling cull every other year; 90% yearling cull once every three years; 75%/37.5% calf/cow combination cull every year; 40%/20% calf/cow combination cull every year; 33% proportional cull every other year; and 16% proportional cull every year.

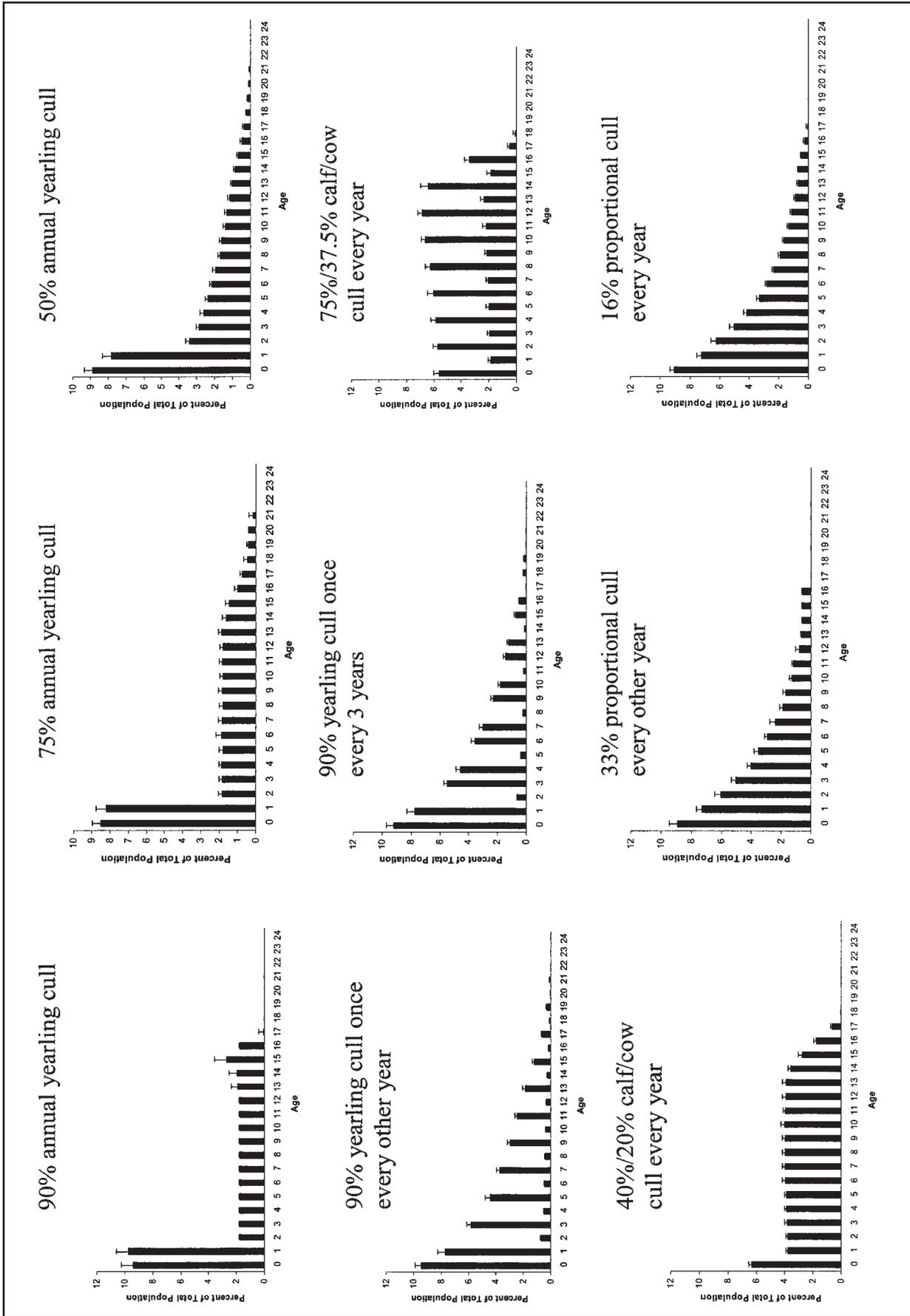


Figure 5. Effects of culling on age structure of male bison at Wind Cave National Park. From upper left to right: 90% annual yearling cull; 75% annual yearling cull; 50% annual yearling cull; 90% yearling cull every other year; 90% yearling cull once every three years; 75%/37.5% calf/cow combination cull every year; 40%/20% calf/cow combination cull every year; 33% proportional cull every other year; and 16% proportional cull every year.

ing stable populations and their effects on population structure. Except for the proportional cull, each strategy modified the current age structure, and strategies varied in their ability to produce a stable population. However, managers must also consider how these strategies differ in logistics, costs, efficacy, effects on viewing opportunities, and other management objectives (e.g., similarity with pre-settlement population structure). The proportional cull can be efficient when compared to other methods, and it maintains the current population structure. However, removal and transportation of 16% of all bison each year may be difficult (e.g., due to difficulties and danger in rounding up older bulls). If only cows and calves are removed, about 40% of the calves and 20% of the females would need to be culled each year to stabilize population growth. The calf/cow cull would offer the highest proportion of males in the population, an important factor if managers wish to increase the number of large bulls for viewing by park visitors. However, additional males could influence breeding dynamics by increasing competition for mates among males, potentially increasing stress levels and injuries.

Logistically, calves are easiest to load and transport; skipping years between culls is cost-effective. However, even at high rates of removal (90%), a biannual calf cull did not prevent population growth. Similar results for the yearling-only cull indicate the need to remove adults in addition to calves or yearlings to maintain or reduce abundance. Moreover, to maintain population levels, intermittent culling requires removal of nearly an entire cohort during culling years. Thus, culling yearling and calves every two or three years produced the largest gaps in age structures of any culling strategies we simulated. Managers should consider and investigate the genetic, behavioral, and demographic consequences of removing entire cohorts from the population.

To be consistent with National Park Service policy, all of these factors (i.e., ecological, genetic, social considerations, park legislation) must be balanced against the National Park Service objective to maintain prevailing natural conditions.

Historically, bison in the northern Great Plains were preyed on by wolves, mountain lions (*Felis concolor* Linnaeus), and grizzly bears. Based on early accounts (Ludlow 1875; Bailey 1926; Young and Goldman 1944; Licht 1997), wolves probably were the predominant predator in the region. Most evidence suggests that bison calves would have been more vulnerable than adults to predation; however, old adult bison are taken by wolves in other areas (e.g., at Wood Buffalo National Park in Canada) (Fuller 1966). Native Americans also harvested bison, but their effects on bison age and sex structure were largely influenced by the availability of horses (*Equus* spp.) (Flores 1991). The prevalence of horses by about the year 1735 allowed for selective harvesting of bison. Native Americans preferred cows 2-5 years of age for their superior meat and thin hide, which allowed for easier hide preparation (Flores 1991). Prior to that time, bison harvest by Native Americans would have been less selective and been more closely proportional to their availability (Frison 1970; Flores 1991). Thus, we suspect that either the calf/cow combination cull or the proportional cull would most closely mimic pre-settlement conditions (Millspaugh et al. 2005). However, demographic effects of harvest likely changed before and after the widespread availability of horses. Moreover, the arrival of the horse coincided with increased contact between Native Americans and Europeans, initializing the onslaught of numerous deadly plagues, including smallpox, which decimated tribes in the Dakotas. Thus, while the horse allowed more selective culling of bison, there were simply less Native Americans alive in the Dakotas to take part in the harvest. Defining "natural" conditions depends on the time period used as a management benchmark.

Managers often consider population stability a desired goal for populations of large mammals. This goal could be met with consistent culling that maintains a stable population. In contrast, to mimic prevailing dynamics and grazing-induced heterogeneity typical of pre-settlement periods, variable culling that produces significant population fluctuations across years (e.g., such as the high intensity cull every three

years) may be preferable (Fuhlendorf and Engle 2001). However, such prescriptions are difficult to implement and culling would need to select animals carefully to prevent loss of genetic diversity during low population years. Selection of high vs. low culling years would need to consider year-specific prescribed burning patterns and precipitation because landscape-level bison movements likely were strongly affected by these and other factors. This produces a complex management environment. However, the Northern Great Plains was a highly dynamic and heterogeneous system. For example, bison densities likely changed rapidly due to normal large-scale movements. Restoring historic conditions and process may require active management for this spatial and temporal variability. However, before attempting to meet this objective, managers should give more thorough consideration to the scale and magnitude of this historic variation and careful consideration of whether culling could help provide an adequate replication of such population fluctuations. The choice among culling strategies depends on the weight managers place on maintaining a semblance of pre-settlement conditions vs. logistical issues, costs, and other priorities for the park herd.

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