

Genetic Variation and Mating Success in Managed American Plains Bison

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Abstract

The American plains bison (*Bison bison*) was pushed to the brink of extinction in the late 1800s but has since rebounded. Less than 5% of animals currently exist in conservation herds that are critical for maintaining genetic variability. Here, we use 25 microsatellite loci to assess genetic diversity and patterns of mating success over a 3-year period in a managed conservation herd at Konza Prairie Biological Station, Kansas (total number of individuals genotyped = 587). Heterozygosity was comparable to and allelic diversity higher than that in 11 other wild and managed herds for which similar estimates are available. Parentage analyses revealed that males within the oldest age classes (5–7 years) sired >90% of calves over the study period, consistent with a polygynous breeding system. Asymmetries in siring success also were observed within age classes, with the same males enjoying high siring success over multiple seasons. Empirical results of paternity will facilitate future modeling and empirical efforts to determine how demographic factors, population size, and variation in siring success interact to determine the retention (or loss) of genetic diversity in natural and managed herds, thus allowing informed recommendations for management practices and conservation efforts of this symbolic North American species.

Key words: bison management, genetic variation, Konza Prairie bison herd, male siring success, parentage analysis, paternity

The American plains bison (*Bison bison*) was a prominent feature of the North American landscape until the late 1800s when populations were decimated by overhunting (Dary 1974; Lott 2002). Historical accounts documenting actual numbers and spatial distributions are variable and biased but suggest that tens of millions of bison possibly roamed throughout North America prior to the arrival of European settlers (Shaw 1995). Bison likely had significant impacts on plant community dynamics from grazing and also provided important sustenance for Native Americans. By the late 1800s, however, the total number of American plains bison was reduced to fewer than 1000 individuals (Dary 1974; Freese et al. 2007). Plains bison were preserved in the late 1800s by private ranchers and the New York Zoological Park when 6 herds were established from fewer than 100 wild-caught individuals (Hedrick 2009). In addition, a small number (down to ~25 animals in 1902 [Meagher 1973]) persisted in what is now Yellowstone National Park. It is from these established and natural herds (and including some bison–cattle hybrids) that all modern day American plains bison derive (Halbert and Derr 2007; Hedrick 2010).

Bison species recovery seemingly can be considered a resounding success because American plains bison have

rebounded from near extinction to >500 000 individuals in just over a century (Freese et al. 2007; Hedrick 2009). The vast majority (>90%) of individuals, however, occur in production herds managed as an agricultural commodity where strong artificial selection is practiced for meat production and herd management traits. Consequently, bison recovery in conservation herds remains a significant challenge and requires careful consideration of population genetic and demographic issues as conservation herds represent only a small fraction of the total population, and the legacy of the bottleneck of this species encountered before recovery remains potentially uncertain (Halbert et al. 2004; Freese et al. 2007; Hedrick 2009).

The number of animals in conservation herds in North America has remained relatively constant at approximately 20 000 individuals since about 1930 (Freese et al. 2007). In 1990, conservation herd sizes for plains bison (Berger and Cunningham 1994) averaged 358 individuals with only 2 herds containing >1000 individuals (Yellowstone National Park and Custer State Park). Among the 34 smaller bison herds compared from the early 1990s, abundances ranged from 5 to 700 individuals, including 8 display herds averaging 18 animals (Berger and Cunningham 1994). Sixty-two conservation

herds are recognized currently, located throughout North America and Mexico (Gates et al. 2010), including a large herd at Tallgrass Prairie Preserve, OK (>2000 animals).

Several recent studies provide important overviews of conservation genetic goals and describe critical benchmarks of bison population genetics based on polymorphic molecular markers (Wilson and Strobeck 1999; Halbert et al. 2004; Halbert et al. 2005; Halbert and Derr 2007; Halbert and Derr 2008a; Hedrick 2009; Gates et al. 2010; Hedrick 2010). These studies have revealed that considerable genetic variation persists within and among populations despite the population bottleneck experienced by this species in the late 1800s. However, exceptions to this general conclusion exist (Halbert et al. 2004). For most conservation herds that have been assayed, genetic variation is greater than that observed for other mammals that experienced population bottlenecks (Gates et al. 2010) and is comparable with other North American ungulates (Wilson and Strobeck 1999; Halbert and Derr 2008a). Polymorphic molecular marker data also can provide accurate assessments of parentage within herds. This information, especially patterns of male siring success, is critical for modeling and empirical efforts aimed at determining minimum population sizes for the long-term maintenance of genetic variation. Unfortunately, however, information on general patterns of parentage and specifically male siring success based on genetic data is lacking for bison conservation herds (Shull and Tipton 1987; Gross et al. 2006).

In this study, we employ polymorphic microsatellite marker data to 1) examine population genetic variation in the Konza Prairie herd of plains bison as a model of a herd that seems typical of many conservation herds with respect to its origin, management, and size and 2) determine patterns of female and male mating success to better understand mating system dynamics and patterns of paternity within the context of herd management practices.

Materials and Methods

Herd History and Attributes

The Konza Prairie Biological Station (near Manhattan, KS; 39°05'N, 96°35'W) is a mesic tallgrass prairie that exhibits a highly variable continental climate consisting of wet springs, hot summers, and dry, cold winters (Knapp et al. 1998). Konza Prairie is a large, protected research site (3487 ha) with long-term, watershed-level burning and bison-grazing experimental treatments (Knapp et al. 1998). Mean annual precipitation is 846 mm, approximately 75% of which occurs in the growing season. The flora is dominated by perennial warm-season tallgrass species (e.g., *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.)); mid- and short grass species can be common on sites with shallow soils. Over 400 forb species have been found on Konza, but grasses contribute about 80% to the total biomass (Knapp et al. 1998; Towne 2002). Bison were introduced to Konza Prairie to facilitate ecological research on fire and grazing interactions with bison conservation a secondary consideration.

The Konza Prairie bison herd is typical of many conservation herds in terms of its initial assembly and subsequent growth. The herd was initiated in 1987 with the introduction of 30 bison to a 450 ha area, with a subsequent introduction of another 32 animals in 1990 (Towne 1999). The herd grew to the current size mostly through natural reproduction with some introductions of animals from other herds. A general genealogy of herd development is shown in Figure 1. In 1992, the area accessible to the bison expanded to 960 ha and included 10 watersheds managed with controlled spring burns at annual, biennial, quadrennial, and 20-year frequencies. A stocking rate of ~6 ha per animal is set to achieve removal of 25% aboveground plant production and is managed by annual culling at the fall roundup. Since 2000, the population has stabilized at approximately 300 individuals after culling. The female to male operational sex ratio averaged 4.7:1 over this period. The calving rate of mature females averages 65%, producing approximately 65–110 new calves annually. Calving typically begins in mid-April, with about 75% of all calves born by 1 June. At roundup, calves are sexed and ear tagged with unique numbers. All calves are subsequently matched with their dams based on observational data of suckling and grooming behavior. During annual fall culling events, most 2-year-old males and females, males older than 7 years, and older females that have not calved in the previous 2 years are removed. Consequently, females in the Konza Prairie can be as old as 20 years, but there are no males older than 7 years. Bison are supplemented with salt and minerals and rarely with hay when adverse weather (e.g., ice storms) prevents access to natural forage.

DNA Sampling and Microsatellite Genotyping

Tail hairs were removed from animals during annual fall roundups in 2007, 2008, and 2009 and placed in envelopes labeled with unique animal IDs corresponding to ear tags. Samples were obtained for the entire herd in 2007 and subsequently for new calves born in 2008 and 2009. DNA was extracted from hair follicles and genotyped at 25 bison-specific microsatellite loci (see [Supplementary Material online](#)) with an ABI 3130xl Genetic Analyzer. These loci are distributed across 21 of 30 *B. bison* chromosomes and represent a subset of loci utilized previously to examine genetic variation in multiple *B. bison* herds (Halbert et al. 2004; Halbert and Derr 2008a). For markers mapping to the same chromosome, 3 pairs (i.e., *BM4440* and *BM2113* on Chr. 2; *RM372* and *BM711* on Chr. 8; *BM47* and *BM1905* on Chr. 23; see [Supplementary Material online](#)) are separated by greater than 50 cM and thus recombine freely. The remaining pair (*BM1225* and *BM4107* on Chr. 20) map 44.4 cM apart. DNA extractions and microsatellite genotyping were outsourced to the DNA Technologies Core Laboratory at Texas A&M University (<http://vetmed.tamu.edu/dnacore>). Relevant molecular protocols can be found in Halbert et al. (2004). Due to a small proportion of failed reactions and/or difficulties in allele calling, the number of successfully scored microsatellite genotypes per individual averaged 24.2 loci and ranged from 18 to 25.

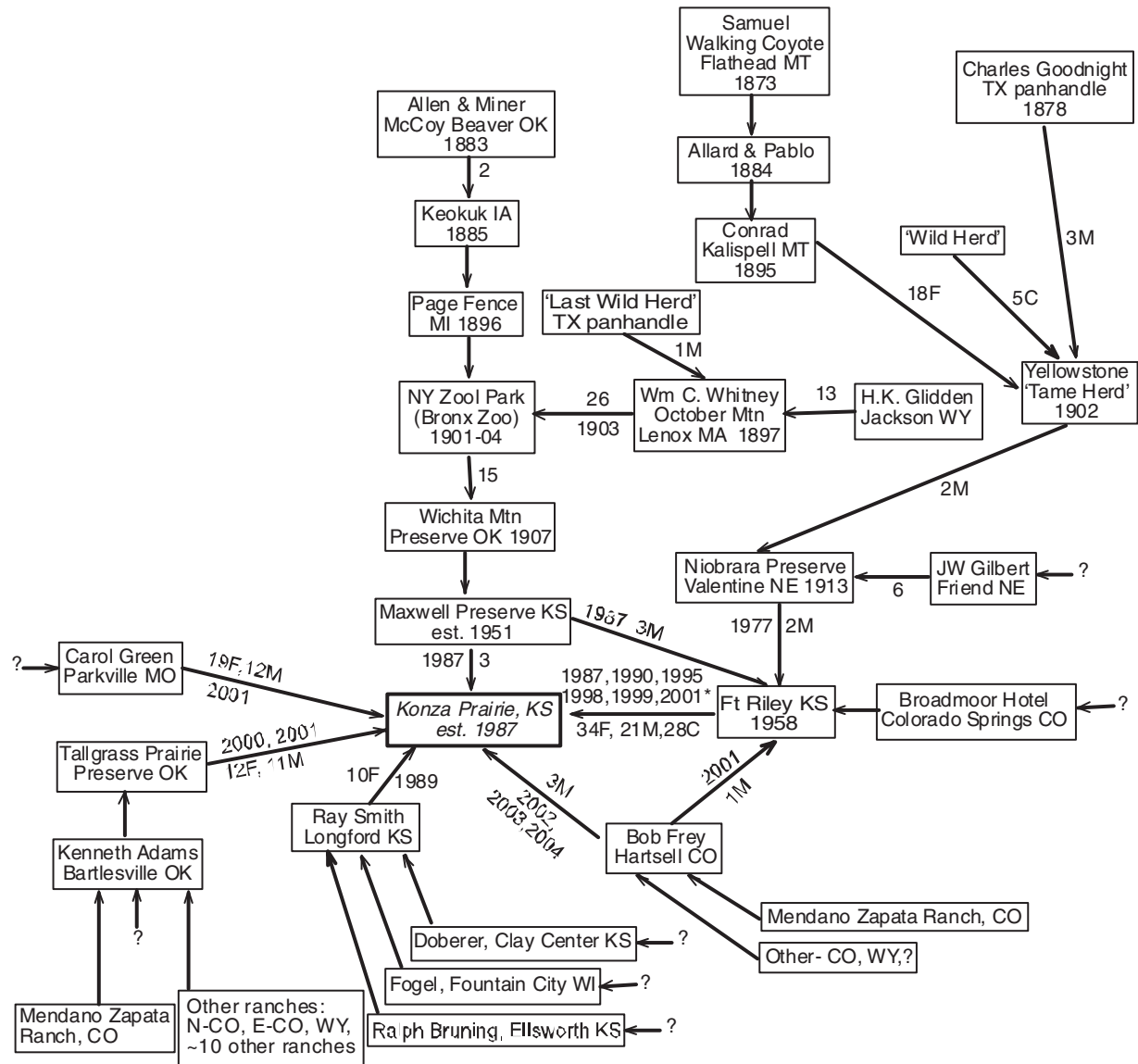


Figure 1. Known genealogy of the bison herd at Konza Prairie Biological Station based on parts of an existing genealogy prepared by Gary Merrill (archived in Konza records—1990) and updated with records from the Konza Biological Station files and discussions with other bison herd managers.

Population Genetic and Parentage Analyses

Observed and expected heterozygosity, allelic richness, and inbreeding coefficient (F_{is}) were determined with the programs FSTAT V 2.9.3 (Goudet 1995) and Microsatellite Toolkit V 3.1.1 (Park 2001). Tests of departure from Hardy–Weinberg equilibrium and tests of pairwise linkage disequilibrium among loci were conducted with CERVUS V. 3.0.3 (Kalinowski et al. 2007) and FSTAT V. 2.9.3 (Goudet 1995), respectively. Significance thresholds for multiple statistical tests were adjusted by the Bonferroni procedure. Estimates of effective population size (N_e) were determined from 1) microsatellite allele frequency data, using the linkage disequilibrium method implemented in NeEstimator

V1.3 (Peel et al. 2004) and outlined in Bartley et al. (1992) and 2) the equation $4 N_m N_f / (N_m + N_f)$, where N_m and N_f are the number of breeding males and females, respectively, as determined from parentage analysis for calves born the following season.

Parentage analysis for calves born from 2007 to 2009 was conducted with the program CERVUS V 3.0.3 (Kalinowski et al. 2007), implementing the *parent pair (sexes known)* analysis option. Default parameters of 95% (strict) and 80% (relaxed) confidence were utilized in all parentage assignments. The proportion of mistyped loci and the likelihood function error rate were both set to 0.01 (default settings) for all analyses. For parentage analyses of calves born in 2008 and 2009, the

proportions of candidate mothers and candidate fathers present in the population were set to 0.95. For parentage analysis of calves born in the 2007, these values were set to 0.95 (proportion of mothers present) and 0.78 (proportion of fathers present). The lower proportion of candidate fathers for the 2007 analysis is on account of several older bulls that were removed from the herd after the 2006 rut but before DNA sampling was initiated in 2007.

Calf and yearling males were identified as the most likely sires in a small number of cases, mostly for parentage analysis of 2007 calves. These assignments were deemed false positives and disallowed on account of 1) mechanical difficulties of matings between these individuals and reproductive females and 2) consideration of the age at which males become capable of sperm production (Woodbury et al. 2007). Possible explanations for these unlikely sire assignments are addressed in the Discussion.

Results

Herd Size and Age Structure

Over the period 2007–2009, the Konza Prairie bison herd was maintained at a population size of 394–430 individuals with annual culls of 93–108 animals (Table 1). Animal age distributions for this period are shown in Figure 2. Marked differences in age structure between females and males are

attributable to different culling practices for the sexes and the designed maintenance of a skewed sex ratio. For example, approximately 44% of culled animals in a given year consist of 1- and 2-year-old males, and males generally are removed from the herd when they are 7 years old.

The population of breeding individuals determined from parentage analysis of calves born the following year (see below) was substantially smaller than the census population and consisted of 101 and 100 individuals in 2007 and 2008, respectively (Table 1). Breeding individuals were female skewed, with f:m ratios of 3.8:1 and 3.6:1 in 2007 and 2008, respectively. Estimates of effective population size based on numbers of breeding individuals (determined from parentage analysis) were 66.5 and 68.6 for 2007 and 2008, respectively. These values are higher than estimates determined from microsatellite allele frequency data ($N_e = 55.4$ and 61.5 for 2007 and 2008, respectively). Confidence intervals (95%) for the latter estimates do not overlap with estimates based on numbers of breeding individuals. Effective population size estimated from microsatellite allele frequency data was highest in 2009 ($N_e = 76.6$).

Population Genetic Analysis

Population genetic parameters based on 25 microsatellite loci were estimated for the period 2007–2009 on both pre and post-cull populations (Table 1). Observed heterozygosity ranged from 0.610 to 0.617, and allelic richness ranged from 5.589

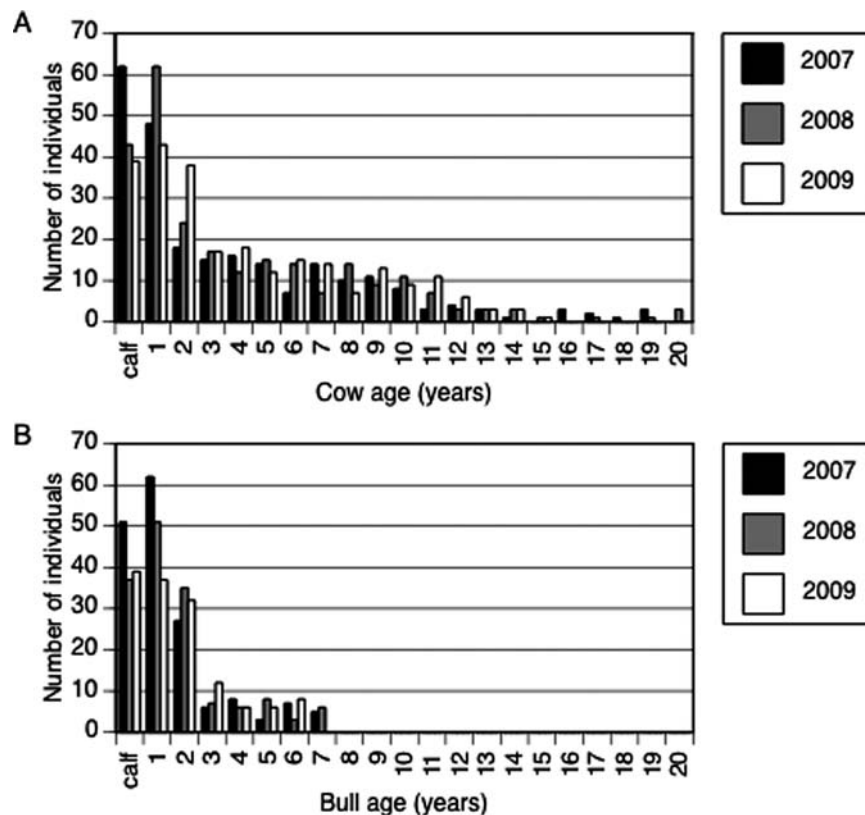


Figure 2. Age distribution data for females (A) and males (B) in the Konza Prairie bison herd from 2007 to 2009.

Table 1 Population genetic parameters for the Konza Prairie bison herd from 2007 to 2009

	<i>N</i>	Breeding individuals	N_e^{\dagger} (95% CI)	N_e^{\ddagger}	H_E	H_O	R_A	F_{is}
2007								
precull	430	80♀, 21♂	55.4 (53.3 – 57.7)	66.5	0.615	0.611	5.65	0.007
postcull	337				0.616	0.613	5.65	0.006
2008								
precull	415	78♀, 22♂	61.5 (59.0 – 64.1)	68.6	0.616	0.612	5.65	0.006
postcull	316				0.617	0.617	5.59	–0.001
2009								
precull	394	na	76.6 (73.3 – 80.0)	na	0.618	0.611	5.813	0.012
postcull	286				0.617	0.610	5.736	0.011

Genetic data are based on 25 polymorphic microsatellite loci. *N*, census population size, includes calves born that year; N_e^{\dagger} , effective population size estimated from microsatellite allele frequency data (see Materials and Methods); N_e^{\ddagger} , effective population size estimated by $4 N_m N_f / (N_m + N_f)$ (see Materials and Methods); H_E , expected heterozygosity of census population; H_O , observed heterozygosity of census population; R_A , mean allelic richness for census population; F_{is} , inbreeding coefficient of census population; na, not applicable.

to 5.813 (Table 1). Culling practices resulted in only minor fluctuations in these parameters during the 2007–2009 period. Significant pairwise linkage disequilibrium among loci was not detected. Multilocus estimates of inbreeding (F_{is}) were near zero for all population samples. Only a single locus (*BM2113*) exhibited significant departure from Hardy–Weinberg equilibrium after Bonferroni correction but only in 2008 and 2009.

Parentage Assignments and Patterns of Mating Success

Using criteria of 95% confidence (strict) and 80% confidence (relaxed) and disallowing calf and yearling sires (see Materials and Methods), the program CERVUS successfully assigned parentage to the majority of calves born during the study period. Of 113 calves born in 2007, female parents were assigned to 104 individuals and male parents assigned to 72 individuals. Assignment rates were higher for 2008 and 2009 calves. Of 80 calves born in 2008, both a cow and sire were assigned to 79 of these individuals. The single 2008 calf for which parentage could not be assigned displayed large amounts of missing genotype data. Of 78 calves born in 2009, cows were successfully assigned to 77 individuals and sires successfully assigned to 75 individuals. The majority of assignments were made with high confidence. For example, approximately 72%, 97%, and 84% of successful parent pair assignments for 2007, 2008, and 2009 analyses, respectively, were made with 95% confidence.

All animals in the Konza herd possess ear tag IDs and extensive observational data exist regarding likely cow–calf pairs, thus allowing comparison of maternal assignments based on genetic and observational data. Cows identified as the most likely mother of a calf based on genetic data consistently matched predictions based on observational data. Of 260 maternal assignments determined by CERVUS for calves born during the study period, 246 (94.6%) were predicted based on observational data. Of the remaining 14 assignments, observational data of cow–calf pairs were not available in 13 cases and in only a single instance was the genetic and observational parentage assignment discordant. It is unclear whether the single discrepancy is due to an error in the observational data set, a false-positive assignment

based on genetic data, or whether this may represent a case of adoption following calf abandonment.

The proportions of calves produced by various age classes of female and male are shown in Figure 3A and B, respectively. Age classes in Figure 3 represent animal ages at the rut preceding the spring calving season in 2007, 2008, and 2009; as such, a cow that was 2 years old at the rut would be 3 years old when her calf was born. Females typically reach reproductive maturity at the rut following their second year and can remain reproductively active throughout their life. The proportion of offspring produced by older females, however, begins to decline at ages 10 or 11, after which age class contributions to new offspring decline sharply (Figure 3A), due in part to declining numbers of older females in the herd (Figure 2A). By contrast, male mating success is heavily skewed toward older animals (Figure 3B). Males aged 5–7 years during the rut typically sire 90%+ of calves in a given year.

Variation in siring success also was found among males within an age class, especially for older males (Figure 4A–C). For calves sired by 7-year-old bulls in 2009, for example, 2 of 6 bulls were responsible for siring 25 of 34 calves (Figure 4C). Additional asymmetries were observed for other age classes and years. Bulls achieving high siring success in a given year typically achieved high siring success in other years, as indicated by selected color coding of histogram bars (individual males) in Figure 4A–C. Among all males in the 5–7 year age class range, only a single individual failed to sire any offspring in 2007 and 2009 (both instances involved 5-year-old bulls), whereas 3 bulls within this age range failed to sire any offspring in 2008 (a single 5-year-old, 6-year-old, and 7-year-old bull). In no case did the same male fail to sire offspring in multiple years.

Discussion

The majority of American plains bison in conservation herds currently are found in populations where the implementation of management and culling practices are routine (Freese et al. 2007). Understanding how these practices impact

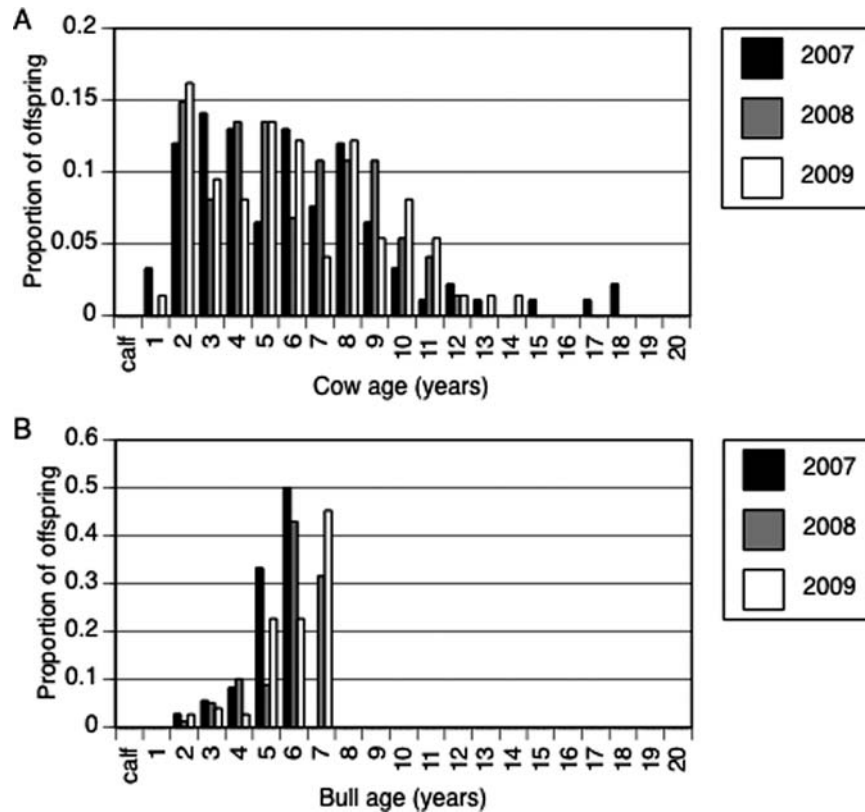


Figure 3. Proportion of offspring produced by different age classes of females (A) and males (B) from 2007 to 2009. In (B), data are not available for the proportion of 2007 offspring sired by 7-year-old bulls because these individuals were culled after the rut in 2006 and before DNA samples were obtained in 2007.

genetic variation and mating success is important for the long-term preservation of genetic variation in this symbolic North American species. We examined the impacts of these factors on the Konza Prairie bison population located on the Konza Prairie Biological Station outside Manhattan, KS. The Konza herd is maintained at roughly 300 individuals (January average) plus about 100 calves produced during late spring with annual culls of approximately 100 animals. This management strategy is employed to provide a consistent natural grazing regime across watersheds burned at various intervals in long-term studies of fire and grazing effects in a tallgrass prairie ecosystem.

An earlier study (Halbert and Derr 2008a) reported genetic variation in 11 other herds representing a cross section of wild and managed populations maintained by the US National Park Service and Fish and Wildlife Service. Observed heterozygosity of the Konza herd ($H_O \sim 0.612$) is intermediate relative to estimates for these 11 other herds (range 0.534–0.653, mean = 0.596), whereas allelic diversity for the Konza herd ($R_A = 5.68$) exceeds values reported for these other herds, (R_A from 3.16 to 4.35). Higher allelic diversity in the Konza herd may reflect historical variation present in the founders and/or variation introduced through breeding success of supplemental animals added after the herd was established in 1987 (Figure 1). It should be noted, however,

that the 25 microsatellite loci utilized in this study represent only a subset of the more than 50 loci utilized in Halbert and Derr (2008a), and thus, it cannot be ruled out that elevated allelic variation in the Konza population is attributable to a nonrandom sample of loci. For comparison more generally, the Konza herd and plains bison exhibit levels of genetic variability somewhat greater than seen for other mammals that experienced genetic bottlenecks (McClenaghan et al. 1990, Bancroft et al. 1995) and similar to levels seen in other North American ungulates (Wilson and Strobeck 1999, Halbert and Derr 2008a).

Levels of heterozygosity and allelic diversity remained similar across years and across culling events within years, indicating that, at least for the short timescale examined herein, management practices are not eroding genetic variability in the Konza bison population. These findings are consistent with a previous report examining the effects of culling practices on genetic diversity in the Badlands National Park bison population over a 4-year period where the scale of population size reductions via culling were comparable (Halbert and Derr 2008b). In only a single herd, the Texas state bison herd, have population genetic, demographic, and sperm-quality analyses suggested considerable inbreeding depression (Halbert et al. 2004). These results are not surprising given the small number of founding individuals for

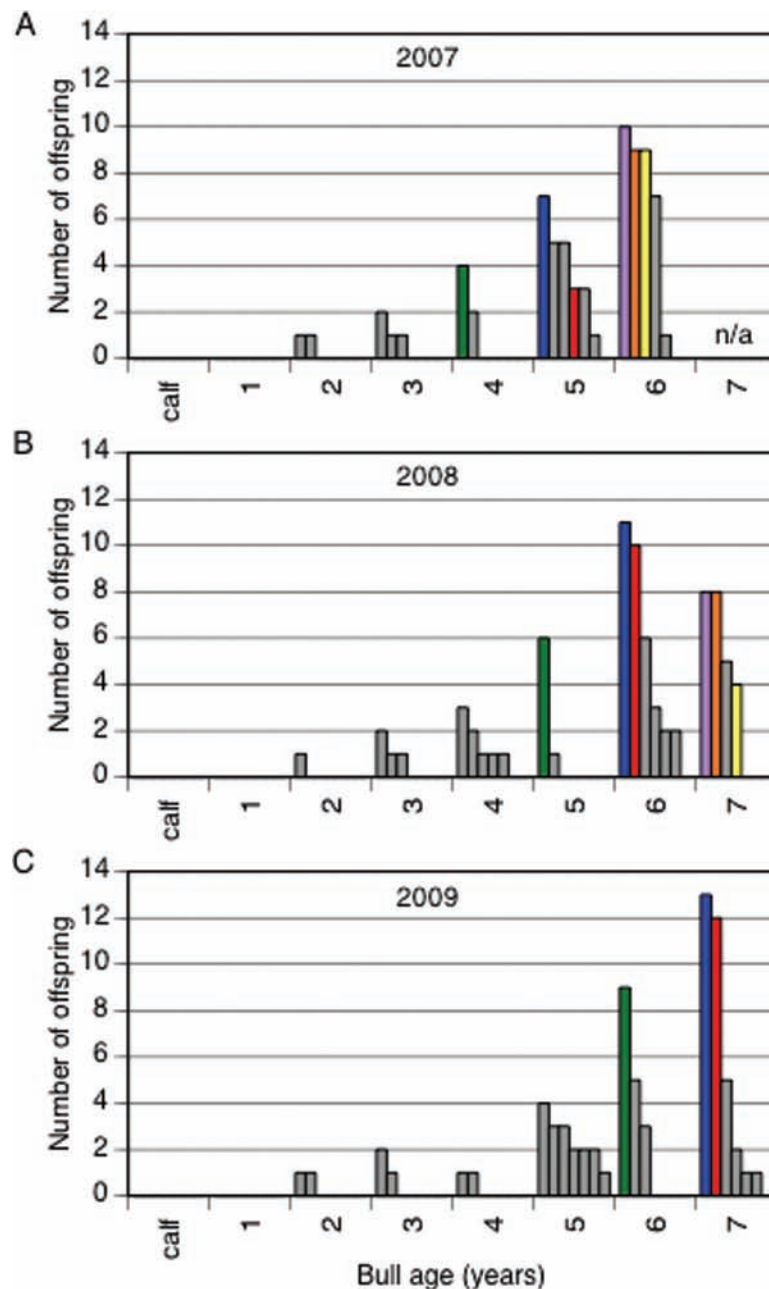


Figure 4. Individual male siring success by age class for calves born in 2007 (A), 2008 (B), and 2009 (C). Colored bars track 6 individual males with the highest siring success over the period 2007–2009. Data are not available for siring success of 7-year-old bulls in 2007.

this herd, its small effective population size and historical isolation (Halbert et al. 2004). The genetic health of Texas state bison herd appears to be improving and inbreeding depression diminishing in response to supplementation with 3 healthy bulls from a different herd (Hedrick 2009).

Effective population size (N_e) estimates varied by year and by estimation procedure (Table 1). Lower N_e values estimated from microsatellite data likely reflect the asymmetries among males in gametic contribution to calf production (Figure 4). N_e estimates determined from genetic marker data

are expected to be sensitive to such asymmetries (Bartley et al. 1992), whereas N_e estimates determined by the equation $4 N_m N_f / (N_m + N_f)$ and unadjusted for such asymmetries are not. Expressed as a fraction of the census population (i.e., $N_e/N = 0.155–0.165$ for N_e based on the number of breeding individuals and $N_e/N = 0.129–0.194$ for N_e based on microsatellite data), these values fall within the range of model estimates based on demographic parameters of a different bison herd under conservation management in Oklahoma (Shull and Tipton 1987) but are lower than estimates of 0.266 to

0.449 provided by [Berger and Cunningham \(1994\)](#) using estimation methods based on observed numbers of breeding individuals for the Badlands South Dakota herd. Differences in N_e/N estimates may reflect differences in population and/or mating dynamics among herds. It also should be noted, however, that with regard to estimates based on numbers of breeding individuals, neither the [Shull and Tipton \(1987\)](#) nor the [Berger and Cunningham \(1994\)](#) N_e/N estimates incorporated male siring success data determined by genetic paternity analysis.

Modeling the minimum population size necessary for preserving genetic diversity is an important component of conservation efforts in plant and animal taxa. An impediment to such efforts in bison conservation has been a lack of detailed knowledge regarding variation in male bison siring success ([Shull and Tipton 1987](#); [Gross et al. 2006](#)). This study represents an important advance by providing detailed information on male siring success over a multiyear period for a managed bison population. Consistent with predictions for a polygynous species, variance in reproductive success was higher for males than for females, and males in older age classes achieved the majority of siring success. These results indicate strong male–male competition where older (and larger) males enjoy a clear advantage. Modest siring success of younger males (ages 2–4 years) also was observed and may be attributable to the skewed sex ratio and inability of larger males to regularly guard all females. Younger bulls have been observed to associate with groups containing cows for longer durations during the rut compared with older bulls ([Berger and Cunningham 1994](#)), thus potentially providing more opportunities for copulations. Observational data of the Konza herd (G.T) also indicate that younger bulls associate with females for periods after the rut and may be responsible for impregnating females that have not already successfully mated.

Although our data demonstrate clearly that older males sire the majority of offspring, considerable variation in siring success also was observed among males within age classes. These patterns of variation persisted from year to year, with the same individual males enjoying high siring success across seasons ([Figure 4A–C](#)). The phenotypic and/or behavioral traits and intrasexual competition dynamics associated with variation in siring success among same-aged males currently are unknown for the Konza herd but may become tractable in behavioral studies coupled with continued DNA sampling and paternity analyses. Although such patterns are a natural outcome of male–male competition, the disproportionate siring success of a small number of males underscores concerns regarding potential losses of genetic diversity in small populations and the importance of maintaining larger bison herds under management practices designed to maximize genetic diversity (IUCN Status Survey and Conservation Guidelines for American Bison [2010], Chapter 4, p. 21).

Paternity analyses of other large mammals reveal similar patterns to those seen here for bison where a small number of males are responsible for most matings ([Coltman et al. 1999](#); [Worthington Wilmer et al. 1999](#); [Rasmussen et al. 2008](#); [Vanpe et al. 2008](#)). Successful paternity typically is age and experience related in mammalian species studied to

date ([Coltman et al. 1999](#); [Rasmussen et al. 2008](#)), and this dynamic mostly applies to the Konza Prairie bison herd. Moreover, knowing paternity is not sufficient to predict population dynamics at the herd level because of the many factors that contribute in age-specific ways ([Clutton-Brock and Coulson 2002](#)), especially in highly managed herds such as those of the Konza Prairie bison.

An unanticipated but interesting finding of this study was higher assignment rates of calf and yearling sires for parentage analysis of 2007 calves (32 instances) relative to 2008 calves (zero instances) and 2009 calves (2 instances). These assignments were disallowed based on both mechanical and potential physiological ([Woodbury et al. 2007](#)) impediments to successful fertilization involving these individuals. Support for these calf and yearling sire assignments in 2007 was lower than that obtained for the remaining sire assignments in the 2007 data. For example, only 7 of 32 (~22%) calf/yearling sire assignments were supported at 95% confidence, whereas 58 of 72 (~81%) of the remaining sire assignments (males aged 2+) were supported at this level. More mismatches (number of loci at which offspring and sire do not have shared alleles) also were detected for offspring–calf/yearling sire pairs (mean = 1.06 ± 0.17) versus offspring–older (age 2+) sire pairs (mean = 0.21 ± 0.07).

The Konza bison herd represents a “closed” population in which all potential parents could be genotyped and included as potential cows/sires in parentage analyses. For parentage analysis of 2007 calves, however, 7-year-old bulls could not be included as candidate sires because they were culled from the herd after the 2006 rut but before DNA sampling began in 2007. Higher assignment rates for calf and yearling sires for the 2007 parentage analysis may be attributable to non-inclusion of multiple true sires with the calf and yearling sire assignments suggested by CERVUS possibly representing the offspring of these individuals. The number of false-positive sire assignments for the 2007 calves would suggest caution in parentage analyses of populations where sampling is likely to be incomplete and the ages of most individuals unknown.

Management Implications

Plains bison conservation herds are relatively small, which challenges managers to maintain appropriate levels of genetic variability in populations. National conservation plans for plains bison ([Gates et al. 2010](#)) address challenges for small herds and include options for managing conservation herds as a metapopulation with the goal of increasing local genetic diversity through targeted exchange of individuals. Most conservation herds, including the one at Konza, were established 20–30 or more years ago before genetic monitoring was practiced widely, and each herd typically grew from small founding populations until a sustainable size appropriate for the site was achieved. In addition, management plans often include protocols aimed for local goals, including culling large bulls at relatively young age (e.g., 7 years for the Konza herd and herds managed by the Nature Conservancy, Midwest Region).

Maintaining genetic diversity appropriate for both local and national goals is a critical challenge, and detailed

information available from molecular techniques provides opportunities to assess levels of genetic variability at multiple levels. Our results for the Konza herd document the population genetics of a representative conservation herd of average size managed in a similar way to many existing conservation herds. Our results indicate that the management plan in place does a reasonable job at maintaining genetic diversity. Three factors probably contributed to this outcome. 1) The founding herd was established with individuals from several unrelated local herds; details are sketchy on this point but the genealogy suggests this is highly likely. 2) Individuals from other herds were introduced periodically during the growth phase of the population, introducing new genetic variation. Moreover, occasional introduction of new genotypes from other herds is important given the relatively small effective population for the Konza herd ($N_e \sim 55\text{--}75$ individuals), a level much smaller than recommended minimum population size for maintaining genetic diversity in a closed herd ($N_e \sim 1000$) (Gates et al. 2010). 3) One consequence of the 7-year culling rule for reproductive bulls is that more individuals are siring offspring over the long term with a positive effect on maintaining genetic diversity. Of course, estimates of genetic variability in this study are based on neutral microsatellite alleles, and we do not have good estimates of selection on critical life-history characteristics (Morrissey et al. 2012) necessary to refine our approach; multivariate genetically based relationships among traits in long-term studies will be required.

Supplementary Material

Supplementary material can be found at <http://www.jhered.oxfordjournals.org/>.

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