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RH: Population substructure in Yellowstone bison • Wallen et al.

History, genetic analyses, and observations converge to describe population substructure in Yellowstone bison

OR:

Genetic analyses, radio tracking, and history converge to reveal female philopatry and population substructure in Yellowstone bison

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ABSTRACT Population substructure and gene flow influence the rate of loss of genetic diversity and adaptation to environmental change. Yellowstone bison are an important genetic resource for restoration of the species (*Bison bison*) because they exhibit high diversity and are one of only three remaining populations havingno evidence of hybridization with cattle. We used fecal DNA collected during the breeding season in 2005-2008 to evaluate genetic diversity and substructure between discrete breeding groups. Mitochondrial DNA analyses revealed two haplotypes, with high genetic differentiation between northern and central herds (F_{ST} = 0.40; P<0.001). Nuclear (n) DNA microsatellite analyses revealed very low differentiation between

the central and northern breeding herds (F_{ST} = 0.02 in 2006 and 0.01 in 2008; P >0.05 in both years). The higher mtDNA differentiation suggests strong female philopatry and male-mediated gene flow. Radio-marked adult females also provided evidence of philopatry, but migration between breeding groups was substantial during 2007-2011. Eleven of 108 marked females switched breeding ranges while 4 moved back and forth between the two breeding ranges in different years indicating little fidelity to a particular breeding group. The low nDNA differentiation and substantial movements by radioed females suggest the two breeding groups can be managed as one management unit, unless the conservation of matrilines or mtDNA lineages is deemed important.]We recommend long-term monitoring of nDNA and mitochondrial markers to track genomic diversity and population substructure in the face of culling and accelerating environmental change..

KEY WORDS bison, conservation, genetic diversity, gene flow, subdivision, population fragmentation, connectivity, philopatry, telemetry, management, Yellowstone.

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Maintaining genetic diversity is necessary for wildlife species to avoid inbreeding depression and adapt to changing environments (Frankham 1996, Allendorf and Luikart 2007). The rate of adaptation in response to environmental variation such as climate change, disease challanges, and anthropogenic influences is generally correlated with the amount of genetic diversity among individuals in a population (Mills 2007). Harvesting wildlife populations may increase the rate of loss of genetic diversity and result in reduced evolutionary potential (Allendorf et al. 2008). Conversely, harvesting may not result in a significant loss of genetic diversity if movements occur among subpopulations, population abundance is high, and harvests are small and random (Allendorf et al. 2008).

Maintenance of genetic diversity in bison is important because their history (including near extinction) and current status (few remaining non-hybridized populations) make them vulnerable to negative effects associated with lost variation (Hedrick 2009?). During the 19th century, tens of millions of plains bison (*Bison bison*) ranged across North America from the Arctic Circle to Mexico and from Oregon to New Jersey (Hall and Kelson 1959, Dary 1974, Isenberg 2000). Bison are an essential component of native grassland system ecology and North American tribal cultures (McHugh 1972). However, >95% of contemporary bison are managed like livestock on private ranches and conservation preserves. About 5% are managed as wildlife, but only 2% (including the bison of Yellowstone) are managed as free-ranging populations subject to many natural evolutionary processes (Freese et al. 2007, Hedrick 2009, Gates et al. 2010).

Yellowstone bison occupy the headwaters of the Yellowstone and Madison River watersheds (USDI and USDA 2000, Plumb et al. 2009). Their distribution is constrained by a court-mediated agreement to a conservation area that includes Yellowstone National Park and limited public lands outside the park in Montana (Figure 1). Bison that migrate to lower elevations (often outside the park) during winter gain access to food resources that are more readily available due to lower snow depths (Bjornlie and Garrott 2001, Gates et al. 2005). However, the Yellowstone bison population has been chronically exposed to the disease brucellosis (*Brucella abortus*) and management operations to prevent co-mingling of bison with cattle outside the park disproportionately remove migratory individuals (Plumb et al. 2009).

Yellowstone bison are a valuable conservation population because they represent the only population to continuously occupy portions of their current distribution, are one of only a few bison populations that interact with the full suite of native ungulates and predators in a harsh wilderness environment, and have shown no evidence of hybridization with cattle (Meagher 1973, Halbert and Derr 2007, Plumb et al. 2009). The population dwindled to 25-50 individuals during 1850-1902. Subsequently, the population was restored through husbandry, protection, and translocation and, today, more than 3,500 bison in two breeding herds (central, northern) are an integral part of the Yellowstone ecosystem (Gates et al. 2005, White et al. 2011a).

The conservation and management of Yellowstone bison is controversial because they are chronically infected with brucellosis (*Brucella abortus*) and management actions to limit the risk of transmission to cattle outside Yellowstone National Park in Montana have resulted in the killing of >6,000 bison since 1985 (Keiter 1997, Cheville et al. 1998, Bienen and Tabor 2006, White et al. 2011a). While conservation constituencies argue for greater tolerance of Yellowstone bison in Montana, agricultural interests argue for constraining their distribution within the boundary of the park until brucellosis is eliminated (Plumb et al. 2009). There is also litigation regarding whether the Yellowstone bison population has significant genetic substructure that warrants separate management for different breeding herds (Figure 1; Animal Welfare Institute 2008, Western Watershed Institute et al. vs. Salazar et al. 2010).

Yellowstone bison have high genetic variation relative to other North American bison populations (Wilson and Strobeck 1999, Halbert and Derr 2008) and currently are subdivided into two breeding herds during the rut. The northern herd congregates in the Lamar Valley and on nearby plateaus for the breeding season during July 15 through August 15 (Figure 1). During the remainder of the year, these bison use habitats in the Yellowstone River drainage, which extends 80 kilometers between the upper Lamar and the Paradise Valley north of Gardiner, Montana. The central herd occupies the central plateau of Yellowstone National Park, extending from the Pelican and Hayden valleys in the east to the lower elevation and thermally influenced Firehole Valley and Madison headwaters area in the west. Bison from the central herd congregate in the Hayden Valley for breeding. Most of these bison move between the Madison, Firehole, Hayden, and Pelican valleys during the rest of the year. However, some bison travel to the northern portion of the park and mix with the northern herd before returning to the Hayden Valley for the subsequent breeding season (Geremia et al. 2011).

Halbert et al. (2012) reported evidence of population substructure in Yellowstone bison from DNA collected opportunistically when bison were culled on winter ranges outside the boundaries of Yellowstone National Park in Montana during 1999 through 2003. They surmised this substructure was a result of genetic drift evolving naturally over eight bison generations (1936 to 2000). However, their samples were collected on winter ranges rather than on the breeding ranges where reproduction occurs. No capture facilities are located within the geographic range

of the breeding groups and chemical immobilization for sample collection is risky when groups of bison are congregated in large numbers during the breeding season. Thus, a non-invasive sampling approach is necessary to evaluate genetic differences among the breeding groups.

Our objectives were to (1) develop a non-invasive fecal DNA sampling approach for wild bison, (2) quantify maternal (mtDNA) and nDNA genetic population substructure between Yellowstone bison breeding groups, and (3) compare genetic and observational data (via radio-marked individuals) to estimate gene flow between subpopulations.

METHODS

Sample collection and DNA preparation

We collected 59 fecal samples from bison in the central breeding herd during July 2005 and 152 fecal samples from bison in both the central and northern breeding herds during August and September in 2006 and 2008. Samples (~4 grams) were collected within 30 minutes of defecation, mixed with 20 ml of 95% ethanol, and stored in coolers for up to 8 hours before being stored at -20º C for up to 1 year prior to DNA extraction. Each sample was assigned a relative age class determined through field observations of bison horn length and width, body size, and body condition. We sampled different sexes and ages, but limited our sampling to less than 20% of individuals within each observed grouping of bison and moved among congregations within each breeding range to avoid re-sampling individuals.

We extracted DNA in a laboratory designated only for non-invasive studies and located in a separate building from where PCR was conducted. We used the QIAamp© Stool Mini Kit (QIAGEN) according to manufacturer's protocol with the following modifications. We thoroughly mixed fecal material from each sample to ensure homogeneous distribution of cellular material. We transferred ~1.5 ml of fecal suspension into 2 ml microtubes which were centrifuged at 16,100 relative centrifugal force for 5 minutes. As much ethanol as possible was drawn off, leaving behind approximately 200 µl of feces, which was then used in the QIAamp© Stool Mini Kit extraction protocol until the final step, which was repeated to harvest as much DNA as possible (Gardipee 2007).

Mitochondrial DNA

Previous mtDNA sequencing studies revealed eight unique haplotypes from samples collected across the species distribution of *Bison bison* (Ward et al. 1999, Vogel et al. 2007). We used primers BISCR-16348F 5'-CTACAGTCTCACCGTCAACCC-3' and BISCR-16990R 5'-GATGAGATGGCCCTGAAGAA-3' (Shapiro et al. 2004, Vogel et al. 2007) to amplify a 470 bp segment of the bison mtDNA control region. PCR was carried out in 25 µl volumes containing 8.95 µl sterile HPLC H_2O, 2.5 µl Invitrogen©10X PCR buffer, 1 µl dNTP's, 0.5 µl of each primer, 2.5 µl BSA (2 ng/µl), 1.25 µl MgCl (50 mM), 0.3 µl Invitrogen© Platinum *Taq* Polymerase (5 units/µl), and 7.5 µl of the DNA extract. Amplification was performed in an MJ Research PTC-200 Peltier Thermal Cycler using the following touchdown protocol: 94 C for 5 min, followed by one cycle of 94 C for 30 s, 60 C for 30 s, and 72 C for 30 s. For the subsequent 10 cycles, all conditions remained the same except that the annealing temperature decreased by 0.5 degrees per cycle. This was followed by 25 cycles of 94 C for 30 s, 55 C for 30 s, and 72 C for 30 s. The profile concluded with a single extension of 72 C for 5 min.

Prior to sequencing, we purified PCR products using QIAquick© purification columns according to manufacturers' instructions with 1 exception; the final elution was carried out with 20 µl of Buffer EB instead of the recommended 30-50 µl to compensate for potential low

quantity template DNA. Negative extraction and PCR controls were used to monitor for possible contamination. No evidence of contamination was detected. We analyzed 70 samples with restriction enzyme analysis of PCR products using *Ssp1*, which cuts haplotype 8 into two fragments (372 bp and 98 bp), but does not cut haplotype 6. Restriction digests were conducted following manufacturer's instructions (Invitrogen). Digested products were run out on 2% agarose gels for two hours, stained with ethidium bromide solution, and visualized using a Hitachi FMBIOII scanner. The combined results of sequencing and RFLP analysis were used to determine the frequency of haplotypes among bison sampled on different breeding ranges.

Microsatellite DNA

Waples and Gaggiotti (2006) suggest that genetic structure may be detected even when migration rates are high if an adequate number of highly variable markers are used (e.g. 10-20 microsatellite loci). We chose 17 loci, which represent a subset of the 54 informative markers previously used by Halbert (2003), because of their short fragment length ($\leq$200 base pairs), high variability among Yellowstone bison, and amplification success from fecal DNA samples.

We amplified the 17 microsatellite loci within five different multiplex PCR profiles. Fragment analysis was carried out on an ABI 3130*xl* using the GS-600 LIZ size standard and GeneMapper v3.7 software was used to size fragments and identify alleles for each locus. Peaks less than 50 relative fluorescent units were not scored. Genotypes were independently scored by two individuals for all electropherograms for each locus. Each sample was repeat genotyped a minimum of four to eight times for all loci. Consensus genotypes for each sample were determined per locus using the following criteria; a heterozygote genotype had to be observed at least twice, and a homozygote was observed at least three times among replicate PCR's.

Genetic data analysis

Amplification success was calculated by the proportion of PCR amplifications that resulted in a clearly scoreable genotype. Allelic dropout rate was inferred when a homozygous genotype was scored for a locus that produced at least two independent heterozygote genotypings. Allelic dropout rate was computed for each locus as the proportion of all independent genotypings among individuals (PCR replicates) with a dropout. False alleles were inferred when a distinct third allele was observed within a PCR compared to other replicate PCR's for each sample.

GenAlEx 6.3 (Peakall and Smouse 2006) was used to estimate allele frequencies, number of alleles, observed heterozygosity, expected heterozygosity, F-statistics, and number of emigrants between breeding herds. Dispersal (or emigration) is defined as movement from one spatial unit to another, without return (at least in the short term; Stenseth and Lidicker 1992). We used ARLEQUIN v.3.1 (Excoffier et al. 2005) and GENEPOP v. 1.2 (Raymond and Rousset 1995, Rousset 2008) to estimate F_{ST} between Yellowstone bison in the central and northern breeding herds, test for Hardy-Weinberg proportions and gametic disequilibrium. Allelic richness, a measure of allelic diversity that accounts for sample size, was estimated using FSTAT (Goudet 2002). We used the Wilcoxon signed ranks test and the sign test in SPSS v. 16.0 to test for significant differences in allelic richness between our results (loci) and Halbert (2003). Population assignment tests were conducted using GenAlEx 6.3 (Peakall and Smouse 2006) and Arlequin v.3.1 (Excoffier et al. 2005). GenAlEx uses the frequency-based assignment test based on methods from Paetkau et al. (1995 and 2004). The expected genotype frequency at each locus is calculated for each sample, assuming random mating within each population, multiplied across loci and log-transformed to give a log likelihood value (Peakall and Smouse 2006). For each

sample, a log likelihood value is calculated for each population, using the allele frequencies of the respective population. Arlequin determines the log-likelihood of each individual multi-locus genotype in each population sample, while assuming that the individual originated from that population (Excoffier et al. 2005). The allele frequencies estimated in each sample from the original composition of the samples are used for computing the likelihood. All loci are assumed to be independent, such that the global individual likelihood is obtained as the product of the likelihood at each locus (Excoffier et al. 2005).

Radio collared studies of female bison

During 2002-2010, 108 adult female bison were fit with telemetry collars as a part of ongoing monitoring actions to track population demographic and disease prevalence rates (Bruggeman et al. 2007, Geremia et al. 2009). Bison were chemically immobilized following standard capture procedures and released (Kreeger et al. 2002, Gannon et al. 2007). We captured and collared bison primarily during October-December of each year, but a limited number of bison were fitted with collars during January-May (Wallen and Blanton 2007, White et al. 2011b). Bison were generally relocated monthly, but at least once every three months using telemetry homing techniques (White and Garrott 1990).

RESULTS

Mitochondrial DNA

The mtDNA analyses revealed two haplotypes among the 151 bison tested during 2005 and 2006. These haplotypes differed by four nucleotide sites and matched published haplotypes 6 and 8 (Ward et al. 1999, Gardipee 2007). Haplotype 6 was the most common, while haplotype 8 was found in only 34 bison, most of which were from the northern breeding herd (Table 1). Haplotype frequencies in the central breeding herd appeared stable and the temporal F_{ST} (within the central herd) was not significantly different from zero between 2005 and 2006. Therefore, we pooled both years of samples from the central herd for comparisons of F_{ST} with the northern herd (Table 1). Strong and highly significant genetic differentiation was evident between the northern and central breeding herds due to the high frequency of haplotype 8 in the northern breeding herd ($F_{ST} = 0.402$, $P < 0.001$).

Microsatellite DNA

Amplification success was high (range = 0.93-1.00 among loci) and averaged 0.95 for samples collected in 2006 and 0.99 for 2008 samples (Appendix A). Allelic dropout was the main source of genotyping error, while few false alleles were observed. The average allelic dropout for 2006 samples (0.11) was higher than observed in 2008 samples (0.04). The error rate for false alleles ranged from 0.00-0.02 for each year. Fifty-three individual fecal DNA samples with high genotyping error rates were excluded from further analysis to minimize potential genotyping errors in the data set. Report probability of identity here (briefly); “The probability of identity (PID) among samples was less than 1 in 1,000,000 thus very little chance incorrectly identifying individuals”.>

All 17 loci were polymorphic within each breeding herd (range = 2-6 alleles per locus). No pair of loci showed significant gametic disequilibrium ($P < 0.01$). Deviation from Hardy-Weinberg expectations was observed in a single locus (BMS 911) in both years and breeding areas (Appendix B). BMS911 occurs on the X chromosome and thus we dropped it from some

analyses. Three private alleles were observed in bison from the northern herd, and no private alleles were observed in the central herd (Appendix C)

The two breeding herds show similar genetic diversity (Table 2). Mean and range of heterozygosity among loci for the central and northern herds was $\bar{x}$ = 0.659 (range = 0.574 to 0.789) and $\bar{x}$ = 0.659 (range = 0.523 to 0.772) respectively (Appendix B). There was no significant difference in the expected heterozygosity between years for the central herd (P= 0.07) or the northern herd (P=0.62). Heterozygosity for all samples combined across all years was 0.638.

We documented relatively low levels of population subdivision in our nuclear microsatellite data. Our F_{ST} was 0.012 in 2008and 0.022 in 2006 using all 17 markers. We identified four loci with relatively high inbreeding coefficient (F_{IS}) (Appendix B). Removal of these four loci (and X-linked MBS911) individually from estimates of F_{ST} reduced our genetic differentiation results by less than one percent (Table 3). These data suggest a statistically significant but very low genetic (nDNA) differentiation (P <0.01 in all estimates)the two breeding groups. Analysis of microsatellite loci revealed much lower population subdivision between bison sampled from the central and northern breeding herds than the mtDNA revealed.

Population assignment tests provided evidence that the two breeding groups are genetically distinguishable and that emigration is apparent. There was 89 percent agreement in population assignment between the two programs. Arlequin assigned samples to the range of collection more often than GenAlEx. By combining all samples into the respective locations they were collected, regardless of year collected, a total of 80 bison (81 %) assigned to one of the two breeding groups with greater than or equal to 70 percent probability of assignment. The remaining 19 bison failed to assign to a single sub-population resulting in a conclusion of mixed origin. Twenty two percent of bison sampled on the northern range (11 of 51) assigned to the central range (with xx% certainty) while only four percent of bison sampled on the central range (2 of 48) assigned to the northern range (Table 4).

Observations of radio-marked female bison

During 2002-2011, 108 radio-collared females were monitored to track which ranges they occupied during the breeding season and where they migrated during winter. Since 2007, 11 of these bison dispersed from the central breeding herd to the northern breeding herd, while four bison dispersed from the northern herd to the central herd. Of the 15 dispersing females, four moved back and forth between breeding ranges among years. Thirteen of the dispersing bison produced calves on their new range (e.g., northern) that were conceived on the range they left (e.g., central), while 25 calves were produced by these dispersing bison through mating and calving on their new range. Ninety-three percent of these migrants successfully reared at least one calf with the breeding herd to which they dispersed (i.e., representing effective gene flow). One female produced four calves, while two females produced three calves. Eleven of these emigrants were still alive in 2012.

DISCUSSION

Influence of historic management practices

The history of restoring Yellowstone bison to a wild, free-roaming population is complex and likely influences contemporary genetic population structure. After Congress passed the Lacy Act in 1896 to provide the Army with legal measures to protect the remaining two dozen wild bison in the central portion of Yellowstone National Park, a long and intensive restoration

program was initiated. The introduction of 21 bison from two populations of unrelated breeding descent in Montana and Texas brought together divergent genetic stock at the turn of the 20th century in northern Yellowstone (Cahalane 1944). Also, several individuals were gathered from the endemic herd in the Pelican Valley of central Yellowstone and introduced into the northern herd during the early population growth period. After 12 years of restoration efforts and many males escaping from the introduced herd, it was thought that the two groups began to mingle and interbreed (Cahalane 1944).

Until the mid-1960s, park management practices limited natural restoration of a wild bison population exhibiting their ecological role in the system (Meagher 1973). Through 1938, park staff annually rounded up the northern herd at the Lamar Buffalo Ranch to cull and feed the bison during winter. In 1936, 71 bison from the northern herd were re-located to vacant ranges in the Firehole and Hayden valleys of central Yellowstone (Cahalane 1944). Subsequently, the northern herd was gradually released from traditional animal husbandry practices and allowed to evolve some natural patterns of distribution and abundance by 1952 (Meagher 1973). However, periodic culling of bison in the Lamar, Firehole, and Pelican valleys was conducted to manage population abundance and eliminate brucellosis reactors until 1967 (Meagher 1973). In 1968, a policy shift towards the preservation of ecosystem processes and the natural regulation of ungulates released the bison population from artificial culling, and the restoration of grizzly bears and wolves in the system provided opportunity for Yellowstone bison to further restore themselves as a wild free-roaming population subject to the evolutionary processes of competition, predation, weather, and social interaction (Cole 1971). Total population abundance increased to approximately 5,000 bison in 2005 and has fluctuated between 2,000 and 5,000 for the past 30 years (Plumb et al. 2009). Thus, the population subdivision and genetic differentiation exhibited by Yellowstone bison was likely initially created in large part by an active restoration program and intensive management of the population.

Genetic evidence of population subdivision

Our mtDNA results suggest genetic differences (that they hypothesized existed) between the central and northern breeding herds of Yellowstone bison are most likely due to female philopatry. Philopatric behavior by females from many species of wildlife is common. Waterfowl including trumpeter swans (*Cygnus buccinators*), Canada geese (*Branta canadensis*), wood ducks (*Aix sponsa)*, common eider (*Somateria mollissima*), canvasbacks (*Aythyava lisineria*), mallards (*Anasplaty rhynchos*), and harlequin ducks (*Histrionicus histrionicus*) tend to migrate back to the natal breeding grounds of the female (Hepp et al. 1987, Anderson et al. 1992). Mammals, including ungulates, also exhibit a high degree of female philopatry especially among reindeer (*Rangifer tarandus*), moose (*Alces alces*), pronghorn (*Antilocapra americana*), and bighorn (*Ovis canadensis*) (Ryman et al. 1980, Côté et al. 2002, Coltman et al. 2003, White et al. 2007). With strong female philopatry, excess heterozygosity can occur within lineages without substantial changes in population heterozygosity. The proportion of genetic variance among lineages will depend on the lineage size and the number of male breeders per lineage (Chesser 1991). Lastly, if females grow up to be philopatric mothers, this strategy should be more successful if the males disperse to avoid inbreeding with their mothers and other philopatric female relatives. Wolff (1994) noted no evidence that juvenile dispersal resulted from resource competition or parental aggression. In contrast, he observed that juvenile dispersal appeared to be voluntary and associated with the presence of the opposite-sex parent in the natal area. Consequently, our results support that these ecological processes (female

philopatry and male dispersal) occur in Yellowstone bison and benefit the population by protecting genetic diversity and limiting the potential for breeding among related individuals.

Halbert et al. (2012) suggested that genetic differences between the central and northern herds was due to the combined effects of maintained population substructure, genetic drift, and effective population size, and that non-random culling of the population could lead to reduced genetic diversity and distinctiveness among the two groups. While genetic drift affects the genetic diversity observed among the two breeding groups, intensive management practices also affected the differentiation currently observed through the deliberate establishment of a second bison breeding group (northern herd) from animals that were translocated from other herds in Montana and Texas with different genetic lineages. The introduced herd on the northern range was eventually influenced by interbreeding with the wild herd when they both began breeding in the high elevations (Mirror Plateau) between the Lamar Valley and the Pelican Valley and likely began a process of reduction in differentiation.

The population substructure was further artificially modified when the park re-located a subset of the northern herd to central Yellowstone in the 1930s. Bison that wintered in the Pelican and Hayden valleys began intermingling by the 1950s (Gates et al. 2005), which most likely influenced the genetic diversity of the central herd. Today, bison breeding activities are concentrated in the Hayden (central) and Lamar (northern) valleys, with migration to lower elevation ranges as winter progresses (Geremia et al. 2011). In addition, the two groups have overlapping winter range use in the Yellowstone River valley downstream from the northern herd summer range. Thus, the relatively low differentiation (F_{ST} =0.0321) reported by Halbert et al. (2012) and in our study, has declined slightly in one generation, and represents small differences in allele frequencies.

Halbert et al. (2012) assume that in 1936 $F_{ST} = 0$, and consequently their analyses project a constantly increasing level of differentiation over time. The history of intensive management makes it difficult to imagine how F_{ST} could have been zero in 1936 when the 71 transplanted bison from the northern range were introduced on to the central range. We believe that differentiation between the endemic population and the introduced herd was likely high initially and that restoration efforts and management practices lead to a continual decrease. The current population structure of Yellowstone bison is likely a result of the differential influence the endemic gene pool provided to the introduced gene pool through genetic drift on two separate breeding areas combined with natural selection processes on the separate ranges, and continued intensive management on the park boundary winter ranges to prevent dispersal from the conservation area.

Observations of bison movement behaviors

Few movement studies have been conducted to describe the differences in migratory movements among bison genders. However, it has been observed that adult bull bison move about the system more widely and will pioneer new habitats prior to female led groups occupying these same locations (Meagher 1989, Taper et al. 2000, Gates et al. 2005). This kind of dispersal behavior allows adult males the opportunity to find suitable unrelated mates and facilitates access to new resources when population densities limit the acquisition of food. This behavior has been reported for other ungulates such as white-tailed deer (*Odocoileus virginianus*) and moose (Ryman et al. 1980, Nelson and Mech 1984) and in other bison subspecies (Larter et al. 2000). Taper et al. (2000) described how wide-ranging movements by males led to range expansion by Yellowstone bison when individuals began using habitats along

the west boundary of the park in the 1990s. This type of exploratory behavior can lead to more regular migration and ultimately emigration if individuals decide that resources are more available in new areas. Movements by radio-collared females revealed that, on average, 28 percent of females from the central herd migrated to northern Yellowstone during winter (Geremia et al. 2011). Several of these individuals began simply by migrating to the north during winter and eventually stayed after a number of years exhibiting migratory tendencies. Our low microsatellite F_{ST} values suggest high gene flow between the two breeding herds has occurred and is likely facilitated by males moving between herds. However, our observations of radio-marked female bison exhibit clear evidence that in the most recent generation female groups are emigrating between the ranges in substantial numbers and contributing to changes in allele frequencies such that differentiation between the breeding groups is likely decreasing (White and Wallen 2012). Fuller et al. (2009) suggested that a significant amount of emigration has likely occurred between the two breeding ranges since 1981. Demographic studies revealed that the northern herd grew in abundance during 1981-2000 while sustaining a rate of culling that equaled the growth rate of the group. With emigration between the two breeding groups clearly evident in the population, a low genetic differentiation value should be expected and our microsatellite analysis supports this process.

Yellowstone bison benefit from population subdivision

Population subdivision with moderate dispersal rates among subpopulations can minimize the rate of loss of genetic diversity and the probability of extinction (Allendorf and Luikart 2007). Subdivision within a population provides a mechanism to more efficiently retain genetic diversity than a population with a single group of randomly breeding individuals (Lacy 1987, Wilson and Zittlau 2004). Thus, the probability that the same alleles will become fixed in all subpopulations is low. Genetic diversity is often correlated with individual fitness and population performance (Newman and Pilson 1997). Understanding patterns of gene flow and dispersal can facilitate the development of effective conservation programs (Reed and Frankham 2003, Estes-Zumpf et al. 2010).

The concept of populations is central to the ecology and conservation of species and numerous definitions can be found in the literature (Waples and Gaggiotti 2006). Most populations are not uniform, but have genetic diversity related to the spatial substructure of the population (Manel et al. 2003). A population with an intermediate level of subdivision in which individuals have a reasonable probability of genetic migration among all subpopulations is likely the best opportunity for conserving genetic diversity and minimizing the probability of extinction. This type of scenario provides for local adaptation where a progression toward panmixia would not be expected.

Brucellosis risk management actions resulted in the removal of nearly 3,700 Yellowstone bison from the population during 2001-2009 (Government Accountability Office 2008, White et al. 2011). The culling of wildlife populations can lead to three types of genetic change: alteration of population subdivision; loss of genetic diversity; and selective genetic changes (Allendorf et al. 2008). Our results characterize the level of population subdivision in Yellowstone bison and genetic diversity indices for the two breeding herds. Our estimates of allelic diversity and heterozygosity are similar to those computed approximately one generation ago from pooled data of 500 bison sampled on winter ranges beyond the boundary of Yellowstone National Park (Halbert et al. 2012; Figure 2, Appendices D and E).

The National Park Service conservation mandate for wildlife populations includes allowing them to exert their natural function and role on ecosystem processes (National Park Service 2006). Yellowstone bison provide disturbance that enhances and sustains native plant communities through wallowing, seed dispersal, grazing, nitrogen deposition, and rubbing on trees. Yellowstone bison are also a food resource for predators, scavengers, and decomposers. Bison survival is dependent upon locating forage, water, and refugia in a diverse landscape with extreme climatic conditions (Barmore 2003, Garrott et al. 2009). Thus, allowing Yellowstone bison to migrate freely is an important evolutionary process and a long-term monitoring effort will provide information to evaluate fluctuations in genetic diversity (including population substructure).

MANAGEMENT IMPLICATIONS

The identification of management units is fundamental to the conservation of wildlife populations and represents crucial baseline information for interpreting long-term monitoring results that characterize management effects (Palsbøll et al. 2006). Our results support that Yellowstone bison can be characterized as a single population (management unit) with genetically similar, yet distinguishable, breeding groups on the northern and central ranges. When harvesting, managing, or conserving wildlife populations, evolutionarily enlightened management occurs when both the ecological and evolutionary consequences of management decisions are considered (Ashley et al. 2003). Our assignment test analyses provide evidence of emigration among the two breeding groups. In addition, our observations of dispersal by radio-collared, adult females during 2006-2011 (10 percent) is similar to the Wright's (1969) general estimator of genetic migrants (or emigration to the non-geneticists). Each radio-collared female bison likely represents more than one individual dispersing because their gregarious nature generally keeps them in groups of 25 or more as they move about the ecosystem (McHugh 1972, Berger and Cunningham1994). Thus, there are likely enough genetic migrants to protect against inbreeding processes within the population. Given our results , we recommend managers implement measures to (1) facilitate population sex ratios that do not deviate more than 10% from equal proportions, and (2) preserve subpopulation distribution during the breeding season that protects near equal proportions, or at least greater than 1,500 bison on the northern and central ranges. Additionally, the park should monitor genetic diversity, inbreeding potential, and probability of genetic migrants in the Yellowstone bison population at least once every one to two generations.

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Figure 1. Current and historic areas of the National Park used during breeding season by Yellowstone bison and the intensive management zones at the boundary of the park where bison migrate to during some winters. The IBMP management area indicates zones where bison are tolerated in Montana during winter under certain constraints pursuant to the Interagency Bison Management Plan (USDI and USDA 2000).

684 **Figure 2.** Allelic richness (Ar) comparisons for samples collected from Yellowstone bison
685 during 1997-2002 and 2006-2008. Different ladders were used in each laboratory, which may
686 have resulted in a 1-4 base pair shift in allele calls. Therefore, there may be some imprecision in
687 these comparisons because of the difference in allele calls between the two laboratories.
688
689

690 **Table 1.** The number of Yellowstone bison sampled during 2005-2006 and the frequency of
691 haplotype 6 in the mitochondrial DNA results.
692

	Sample Size			Proportion of Haplotype 6 (%)	
Breeding Group	**2005**	**2006**	**Total**	**2005**	**2006**
Central Range	**59**	**35**	**94**	**89.8**	**100**
Northern Range	**0**	**57**	**57**	**NA**	**50.8**
Total Samples	**59**	**92**	**151**	**-**	**-**

693
694

695 **Table 2.** Genetic diversity comparisons across population segments and across years. Data
696 reported for Halbert (2003) represent only the 17 loci that we used in our study and reported in
697 her Appendix B. Data reported for Halbert et al. (2012) represents her diversity indices for
698 genetic clusters she reported following assignment tests. Na = Average number of different
699 alleles per microsatellite loci, Ho= Observed Heterozygosity, Ha= Expected Heterozygosity
700

Study	Year of collection	Number loci sampled	Number of separate bison sampled	Na	Ho	He
Northern Range						
This Study	**2006**	**17**	**23**	**4.529**	**0.611**	**0.642**
This Study	**2008**	**17**	**28**	**4.529**	**0.623**	**0.655**
Halbert et al. (2012)	**1997-2003**	**54**	**152**	**4.56**	**0.596**	**0.602**
Central Range						
This Study	**2006**	**17**	**21**	**4.176**	**0.597**	**0.607**
This Study	**2008**	**17**	**27**	**4.471**	**0.652**	**0.646**
Halbert et al. (2012)	**1997-2002**	**54**	**453**	**4.63**	**0.621**	**0.623**
Both Ranges Combined (population wide evaluation)						
This Study	**2006-2008**	**17**	**99**	**4.426**	**0.616**	**0.638**
Halbert (2003)	**1997-2003**	**17**	**488**	**5.0**	**0.648**	**0.669**
Halbert et al. (2012)	**1997-2003**	**54**	**661**	**4.71**	**0.616**	**0.626**

701

Table 3. Summary of analyses to define a fixation index based on 17 microsatellite markers evaluated on DNA extracted from fecal samples collected on the breeding grounds of the Yellowstone bison.

Loci Used For F_{ST} Estimates	F_{ST} Estimate For 2006 Data	F_{ST} Estimate For 2008 Data
All 17 microsatellite markers	**0.022**	**0.012**
Without BMS911 included (n = 16)	**0.015**	**0.005**
Without BMS 410 included (n = 16)	**0.015**	**0.008**
Without BMS 2258 included (n = 16)	**0.015**	**0.008**
Without TGLA 122 included (n = 16)	**0.014**	**0.007**

709 **Table 4.** Population assignment of 99 Yellowstone bison where all assignments were of greater
710 than or equal to 70 percent probability of assignment to a particular range.

Samples Collected From	Population assignment	
	Central Range	**Northern Range**
Central Range	**28/48 (58 %)**	**2/48 (4%)**
Northern Range	**11/51 (22%)**	**39/51 (76%)**

711