Genetic variation and differentiation in parent-descendant cattle and bison populations[1,2,3]

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ABSTRACT: Genetic variation and differentiation at 32 microsatellite loci was quantified for parent-descendant cattle populations and parent-descendant bison (*Bison bison*) populations. We compared heterozygosity (*Ho*) and allelic richness (*AR*) for 587 cattle of four breeds and three lines derived from them, and 188 bison in three pairs of parent-descendant populations. *Ho* and *AR* were less in the Line 1 Hereford inbred cattle population than in the parent Hereford breed. *Ho* and *AR* were intermediate in a composite population (CGC, derived from crossing Red Angus, Charolais, and Tarentaise) compared to the three parent breeds. Crossbreeding of Line 1 with CGC resulted in an F_1 generation with increased *Ho* and *AR* relative to Line 1 and CGC, followed by decreased *Ho* and *AR* in 2 backcross generations to Line1. Three transplanted wild bison populations had smaller *Ho* and *AR* than their respective parent populations. These data demonstrate that genetic variation reduced from founder effects or inbreeding can be restored with crossbreeding and gene flow.

Key words: cattle, bison, genetic variation, heterozygosity

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INTRODUCTION

Quantification of genetic variation and its effect on fitness is integral to cattle research and breeding programs. Genetic issues relevant to bison (*Bison bison*) management are like those with cattle, including loss of genetic variation and inbreeding in small populations, adaptation to different environments, migration, and introgression resulting from crossbreeding subspecies and species (Hedrick, 2009; Gates et al., 2010). Research on cattle with known ancestry and controlled breeding allows assessment of the nature and extent of changes in genetic variation resulting from inbreeding, crossbreeding, and selection. Examples include three cattle lines at the USDA Fort Keogh Livestock and Range Research Laboratory in Miles City, Montana. The Line 1 Hereford population has been an inbred line since 1934 (MacNeil, 2009). The composite gene combination (CGC) population was created in 1979 by crossing Red Angus, Charolais, and Tarantaise (Newman et al., 1993). A third descendant line, (Red Face, RF), was established in 2000 by crossing Line 1 Hereford bulls and CGC heifers to produce an F1 generation and two generations of backcrossing Line 1 bulls to RF cows (Grosz and MacNeil, 1999).

Wild bison populations have been established with transplants from parent herds in several areas. Three such populations are in the Henry Mountains of Utah established with stock from Yellowstone

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Table 1. Average and standard error (SE) values of genetic variation[1] in parent-descendant cattle and bison populations

Cattle	Population type		N	*AR*	Na	*Ho*
Hereford	Parental	Mean	25.72	3.84	4.84	0.58
		(SE)	(0.12)	(0.25)	(0.37)	(0.04)
Charolais	Parental	Mean	21.03	4.44	5.75	0.64
		(SE)	(0.11)	(0.24)	(0.33)	(0.04)
Red Angus	Parental	Mean	17.78	4.06	4.78	0.61
		(SE)	(0.07)	(0.22)	(0.28)	(0.04)
Tarentaise	Parental	Mean	8.88	4.19	4.28	0.67
		(SE)	(0.06)	(0.22)	(0.23)	(0.04)
Red Face F1	Descendant	Mean	178.81	3.94	6.25	0.70
		(SE)	(0.09)	(0.18)	(0.48)	(0.03)
Red Face B1	Descendant	Mean	152.47	3.44	5.59	0.57
		(SE)	(0.13)	(0.15)	(0.40)	(0.03)
Red Face B2	Descendant	Mean	70.91	3.14	4.84	0.54
		(SE)	(0.05)	(0.14)	(0.31)	(0.04)
CGC	Descendant	Mean	47.63	4.41	6.47	0.64
		(SE)	(0.42)	(0.25)	(0.49)	(0.03)
LINE 1	Descendant &	Mean	58.41	2.87	3.81	0.46
	Parental	(SE)	(0.14)	(0.15)	(0.26)	(0.03)
Overall Mean		Mean	64.63	4.02	5.18	0.60
		(SE)	(3.40)	(0.18)	(0.13)	(0.01)
Bison	Population type					
Nat. Bison Range	Parental	Mean	23.78	3.42	3.50	0.43
		(SE)	(0.17)	(0.28)	(0.29)	(0.05)
AK plains bison	Descendant	Mean	41.22	3.24	3.56	0.39
		(SE)	(0.36)	(0.26)	(0.30)	(0.04)
Yellowstone NP	Parental	Mean	27.72	3.42	3.56	0.42
		(SE)	(0.16)	(0.28)	(0.30)	(0.05)
Henry Mountains	Descendant	Mean	28.31	2.73	2.81	0.39
		(SE)	(0.33)	(0.21)	(0.22)	(0.04)
Wood Buffalo NP	Parental	Mean	39.03	3.40	3.75	0.42
		(SE)	(0.28)	(0.27)	(0.34)	(0.04)
AK wood bison	Descendant	Mean	24.72	2.84	2.91	0.34
		(SE)	(0.17)	(0.23)	(0.25)	(0.04)
Overall Mean		Mean	30.80	3.80	3.35	0.40
		(SE)	(0.50)	(0.31)	(0.12)	(0.02)

[1]N = Sample size

Na = Average number of alleles/locus

AR = Allelic richness

Ho = Observed heterozygosity

National Park and two bison populations in Alaska, one established with stock from the National Bison Range in Montana and one with stock from Elk Island National Park in Alberta Canada. Such descendant populations are expected to have less genetic variation than the parent population due to founder effect and genetic drift.

In this study we demonstrated livestock breeding practices that can provide guidance for genetic management of bison and other wildlife. Our objective was to quantify and compare changes in genetic variation at the same loci in parent-descendant cattle and bison populations.

MATERIALS AND METHODS

Animals

The cattle used in this project were kept at the USDA Fort Keogh Livestock and Range Research Laboratory in Miles City, Montana. All procedures involving animals used in this research were approved by the Fort Keogh Animal Care and Use Committee (ACUC # 020104-9). The Line 1 Hereford population has been maintained as an inbred line since 1934 after its creation in a project originally designed to achieve heterosis by crossing selected inbred lines (MacNeil, 2009). Research on Line 1 Herefords has contributed

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Table 2. Genetic distances (*Ds*, Nei 1972) in bison and cattle populations

Cattle	Hereford	Charolais	Red Angus	Tarentaise	RF F1	RF B1	RF B2	CGC	LINE1
Hereford									
Charolais	0.209								
Red Angus	0.262	0.205							
Tarentaise	0.273	0.204	0.292						
RF F1	0.087	0.170	0.239	0.235					
RF B1	0.122	0.281	0.369	0.359	0.029				
RF B2	0.140	0.316	0.411	0.405	0.050	0.017			
CGC	0.243	0.139	0.158	0.225	0.200	0.346	0.394		
LINE1	0.205	0.416	0.530	0.506	0.122	0.086	0.090	0.445	
Bison									
	AKPB	NBR	YNP	HM	WBNP	AKWB			
AKPB									
NBR	0.081								
YNP	0.047	0.053							
HM	0.169	0.078	0.116						
WBNP	0.143	0.070	0.092	0.110					
AKWB	0.221	0.135	0.151	0.170	0.061				

to understanding heritability, genetic correlation, maternal genetic effects, heterosis, and genotype x environment interactions in beef cattle. Germplasm from Line 1 Herefords has been used by Hereford breeders across the U.S. and in other countries (Leesburg, 2012). The Line 1 population at Fort Keogh currently has approximately 200 cows. The composite gene combination (CGC) population was created in 1979 with interbreed crosses to produce a final composition of 1/2 Red Angus, 1/4 Charolais, and 1/4 Tarentaise (Newman et al., 1993). The CGC population was developed to produce a line of cattle uniquely suited to the cold and dry environment of the U.S. Northern Great Plains. The CGC population at Fort Keogh currently has approximately 560 cows. A third descendant line, called Red Face (RF), was established in 2000 by crossing Line 1 Hereford bulls and CGC heifers to produce an F_1 generation followed by two generations of backcrossing Line 1 bulls to RF cows (Grosz and MacNeil, 1999; Tshipuliso et al., 2008). The project succeeded in using marker-assisted selection to introgress the S^+ allele at the S-locus (which affects coat color spotting) from CGC into Line 1. This resulted in the RF line without the white face, belly, feet, and tail that are characteristic of Herefords, but with predominantly Line 1 Hereford genetic background. The RF herd had approximately 60 cows when it was dispersed in 2013.

Two bison subspecies are recognized, plains bison (*B. b. bison*) and wood bison (*B. b. athabascae*) based on morphology. However, these designations are equivocal because morphological and molecular genetic data suggest that plains bison and wood bison are not differentiated enough to warrant subspecies status (Cronin et al. (2013) and references therein). Wild plains bison populations were created in the Henry Mountains of Utah (HM) with 23 animals transplanted from Yellowstone National Park (YNP) in the 1940s and in Alaska (AKPB) with 22 animals transplanted from the National Bison Range (NBR) in 1928 (Cronin et al., 2013; Ranglack et al., 2015). The AKPB population currently is about 948 animals in four subpopulations and the HM population is currently approximately 350 animals. A captive wood bison population was established in Alaska (AKWB) in 2003–2008 with 66 animals transplanted from Elk Island National Park Alberta, Canada that originated from the population in Wood Buffalo National Park (WBNP, Polzhein et al., 1996; Wilson and Strobeck, 1999). One hundred thirty Alaska wood bison were released in western Alaska as a wild population in 2015.

Genetic analyses

Genotypes for 32 microsatellite loci were obtained for 587 cattle of four breeds and three lines derived from them (Table 1). Genotypes for the same loci were also obtained for 188 bison in six populations, including three pairs of parent-descendant populations. The microsatellite loci (Supplemental Table S1; see online version of journal to access file) and laboratory methods were described by MacNeil et al. (2007). We excluded two of the 34 loci (BM2613, ILSTS059) used by MacNeil et al. (2007) because no data were obtained in the RF cattle for the BM2613 locus and the ILSTS059 locus did not amplify in bison. The genotype data we used were reported previously for the cattle breeds and bison (MacNeil et al., 2007; Cronin et al., 2013) and for the RF F_1, B_1, and B_2 generations (Tshipuliso et al., 2008). Our analysis included genotypes of cat-

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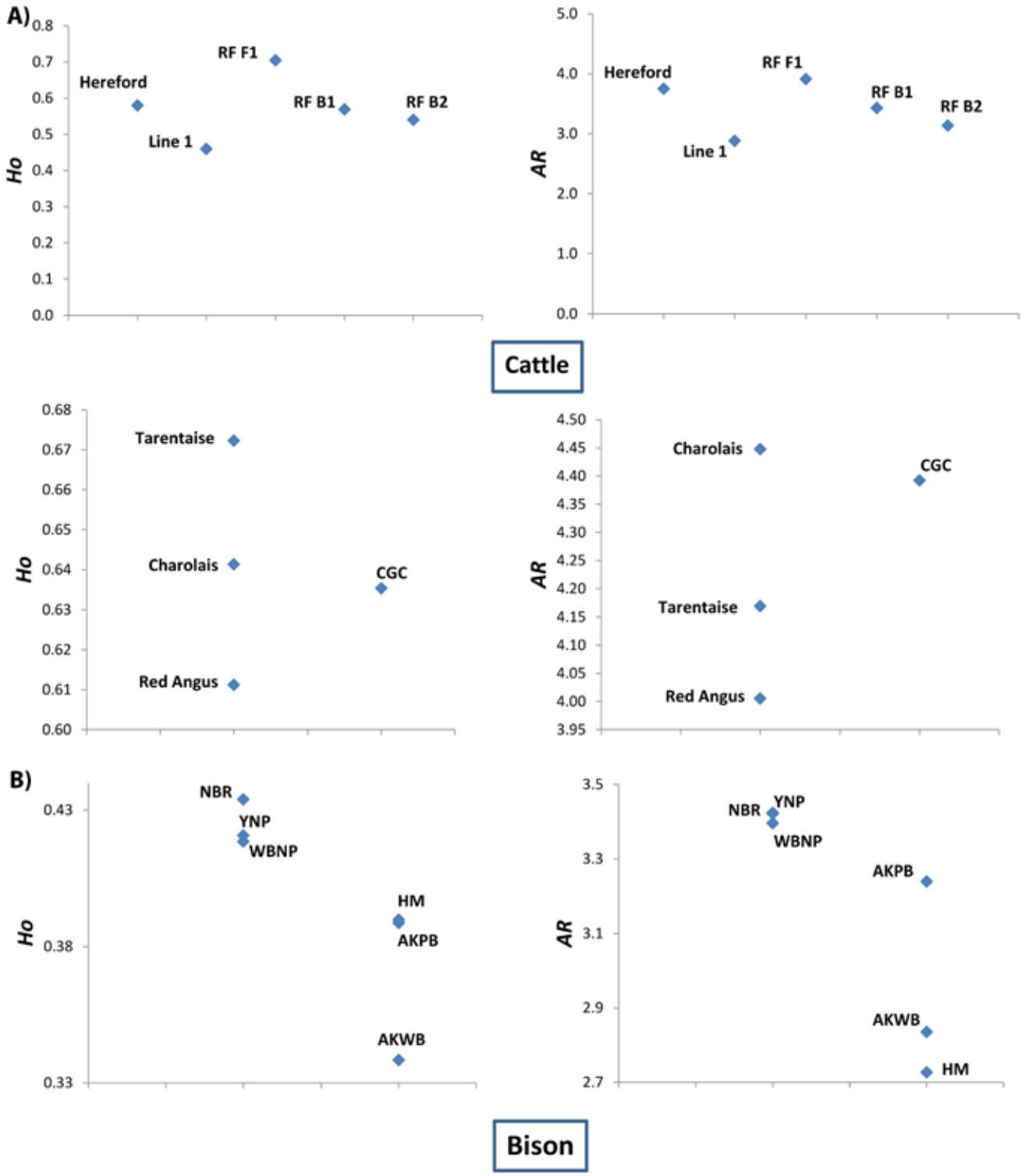

Figure 1. Heterozygosity (Ho) and allelic richness (AR) in (A) cattle and (B) bison populations. Note the different scales on the Y-axes. Abbreviations for cattle populations: Line 1 Herefords (Line 1), Composite Gene Combination (CGC), and Red Face (RF); and abbreviations for bison populations: Yellowstone National Park (YNP), Henry Mountains (HM), National Bison Range (NBR), Alaska plains bison (AKPB), Wood Buffalo National Park (WBNP), and Alaska wood bison (AKWB).

tle representative of Line 1 (born 1988–2003), CGC (born 1989–1995), the RF F_1, RF B_1, and RF B_2 generations (born 2000–2007), and the Red Angus, Charolais, Tarentaise, and Hereford breeds. The bison data we analyzed included parent-descendant populations from Yellowstone National Park (YNP)-Henry Mountains (HM), National Bison Range (NBR)-Alaska plains bison (AKPB), and Wood Buffalo National Park (WBNP)-Alaska wood bison (AKWB).

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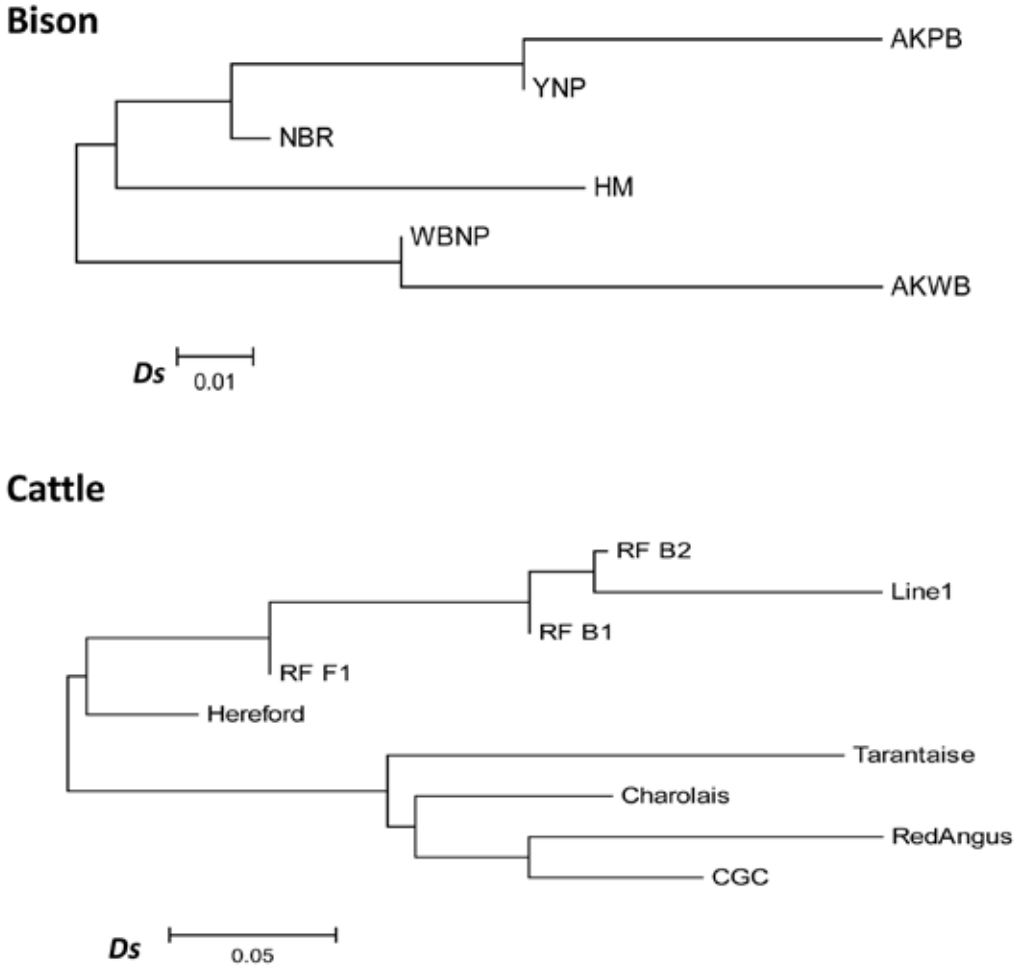

Figure 2. Neighbor-joining (NJ) dendrogram of genetic distances (Ds) between cattle populations and bison populations. Abbreviations for bison populations: Yellowstone National Park (YNP), Henry Mountains (HM), National Bison Range (NBR), Alaska plains bison (AKPB), Wood Buffalo National Park (WBNP), and Alaska wood bison (AKWB).

Observed heterozygosity (*Ho*, number of heterozygotes/number of individuals for each locus, averaged over all loci) and average number of alleles per locus for each population and Nei (1972) genetic distance (*Ds*) between populations were calculated with GenALEx 6.5 (Peakall and Smoose, 2012). Allelic richness (*AR*, the average number of alleles per locus adjusted for sample size, El Mousadik and Petit, 1996) was calculated with FSTAT 2.9.3.2 (Goudet, 1995). Genetic distances were analyzed with MEGA5 (Tamura et al., 2011) to generate a Neighbor-Joining (NJ, Saitou and Nei, 1987) dendrogram. *Ho* and *AR* were compared between pairs of populations with *t* tests of the 32-locus means, and average *Ds* between parent and descendant populations were compared with *Z*-tests of the means with unequal sample sizes, with a significance threshold of $P < 0.05$.

RESULTS AND DISCUSSION

Cattle

Observed heterozygosity (*Ho*) was greater ($P < 0.001$) in the parent Hereford breed than in the descendant Line 1 population (Table 1). *Ho* in the CGC line was intermediate to, but not different ($P > 0.36$) from, those of its parent breeds (Red Angus, Charolais, and Tarentaise). *Ho* was less ($P < 0.0001$) in the inbred Line 1 than in the crossbred CGC. The Line 1 x CGC cross resulted in an RF F_1 generation with *Ho* that was greater ($P < 0.02$) than in either parent population. Following backcrossing of Line 1 with RF, *Ho* decreased but remained greater ($P < 0.0009$) in the RF B_1 and B_2 generations than in Line 1 (Fig. 1A).

Allelic richness (*AR*) values were comparable to those for *Ho* (Table 1, Fig. 1A) and were less ($P < 0.0002$) in Line 1 than in Hereford, CGC, RF F_1, RF B_1, and RF B_2, and were not different ($P > 0.15$) in CGC compared to Charolais or Tarentaise. A differ-

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ence from the pattern for *Ho* was that *AR* was greater ($P < 0.002$) in CGC than in Red Angus.

Genetic distances derived from allele frequencies (*Ds*, Table 2) reflect the cattle population histories, with a greater value ($P < 0.023$) between breeds (average *Ds* = 0.24 between Hereford, Charolais, Tarentaise, Red Angus) than between parent breeds and descendant lines (average *Ds* = 0.18 between Hereford-Line 1; Red Angus-CGC; Charolais-CGC; Tarentaise-CGC). *Ds* between Line 1 and the RF F_1, RF B_1, and RF B_2 generations (average *Ds* = 0.10) was less ($P < 0.0004$) than the *Ds* between CGC and the RF F_1, B_1, and B_2 generations (average *Ds* = 0.31), reflecting the one-time Line 1 x CGC cross to produce the RF F_1 and two backcross generations of RF to Line 1.

The NJ dendrogram derived from *Ds* values reflects the breed ancestry of CGC with the parent Red Angus, Charolais, and Tarentaise breeds in the same cluster (Fig. 2). The other major cluster in the NJ dendrogram reflects the Hereford and Line 1 ancestry, and the decreasing genetic distance (i.e., proximity on the NJ dendrogram) of Line 1 and the RF F_1, B_1, and B_2 generations as shown by Tshipuliso et al. (2008) with Bayesian clustering methods.

Bison

In each of the three pairs of parent-descendant bison populations *Ho* was less in the transplanted descendant population than in the parent population (Table 1, Fig. 1B), although the difference was only significant ($P < 0.016$) between the parent WBNP population and descendant AKWB population. *AR* was also less in the descendant bison populations than in the parent populations, and the difference was significant ($P < 0.002$) between the YNP and HM populations and between the WBNP and AKWB populations.

Ds values of bison were not different ($P = 0.47$) between the parent-descendant populations (average *Ds* = 0.086) and between the parent populations (average *Ds* = 0.071 between YNP, NBR, and WBNP, Table 2). However, the genetic distances reflect the ancestry of the parent-descendant WBNP and AKWB populations that occur in the same cluster in the NJ dendrogram (Fig. 2). The relationships of the other bison herds are not as clear, as the parent-descendant NBR-AKPB populations and the parent-descendant YNP- HM populations do not occur in different clusters in the NJ dendrogram.

Our results demonstrate that crossbreeding (i.e., gene flow) can increase genetic variation after it is reduced during population bottlenecks, founder effects, inbreeding, and genetic drift in small populations. Specifically, one generation of crossbreeding of CGC with the inbred Line 1 cattle resulted in an increase in the number of alleles and heterozygosity in the RF F_1 generation. Two backcross generations resulted in a decrease of variation from the F_1, and also demonstrated the efficacy of marker-assisted introgression of a recessive allele with recovery of a predominantly Line 1 genetic background as indicated by the proximity of the RF B2 generation and Line 1 in Fig. 2 (Grosz and MacNeil, 1999; Tshipuliso et al., 2008).

The example of the RF experiment gives empirical support for management strategies for bison and other wildlife (e.g., Hedrick, 2009; Gates et al., 2010). Bison in the transplanted populations we assessed had less heterozygosity and numbers of alleles compared to the populations of origin. Low genetic variation in a bison population in Texas was associated with negative effects of inbreeding that were overcome by introducing non-related bison stock (Hedrick, 2009). We do not have data regarding fitness and potential inbreeding effects in the bison herds we studied but crossbreeding and gene flow with unrelated stock, as demonstrated with the Line 1, CGC, and RF cattle, can be used to increase genetic variation in bison or other wildlife populations.

LITERATURE CITED

Cronin, M.A., M.D. MacNeil, N. Vu, V.L.R. Leesburg, H.D. Blackburn, and J.N. Derr. 2013. Genetic variation and differentiation of bison (*Bison bison*) subspecies and cattle (*Bos taurus*) breeds and subspecies. J. Hered. 104:500–509. doi:10.1093/jhered/est030

El Mousadik, A., and R.J. Petit. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic of Morocco. Theor. Appl. Genet. 92:832–839. doi:10.1007/BF00221895

Gates, C.C., C.H. Freese, P.J.P. Gogan, and M. Kotzman, editors. 2010. American Bison: Status survey and conservation guidelines. IUCN, Gland, Switzerland.

Goudet, J. 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. J. Hered. 86:485–486.

Grosz, M.D., and M.D. MacNeil. 1999. The "spotted" locus maps to bovine chromosome 6 in a Hereford-cross population. J. Hered. 90:233–236. doi:10.1093/jhered/90.1.233

Hedrick, P.W. 2009. Conservation genetics and North American bison (*Bison bison*). J. Hered. 100:411–420. doi:10.1093/jhered/esp024

Leesburg, V.L.R. 2012. The influence of Line 1 Herefords on the global Hereford population. PhD Dissertation. University of the Free State, South Africa.

MacNeil, M.D. 2009. Invited review: Research contributions from seventy-five years of breeding Line 1 Hereford cattle at Miles City, Montana. J. Anim. Sci. 87:2489–2501. doi:10.2527/jas.2009-1909

MacNeil, M.D., M.A. Cronin, H.D. Blackburn, C.M. Richards, D.R. Lockwood, and L.J. Alexander. 2007. Genetic Relationships between feral cattle from Chirikof Island, Alaska and other breeds. Anim. Genet. 38:193–197. doi:10.1111/j.1365-2052.2007.01559.x

Downloaded from https://academic.oup.com/jas/article-abstract/94/11/4491/4702753 by Texas Tech University Health Sciences Center Library user on 02 January 2019

Nei, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292. doi:10.1086/282771

Newman, S., M.D. MacNeil, W.L. Reynolds, B.W. Knapp, and J.J. Urick. 1993. Fixed effects in the formation of a composite line of beef cattle. 1. Experimental design and reproductive performance. J. Anim. Sci. 71:2026–2032

Peakall, R., and P.E. Smouse. 2012. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research-an update. Bioinformatics First published online July 20, 2012. doi:10.1093/bioinformatics/bts460

Polziehn, R.O., R. Beech, J. Sheraton, and C. Strobeck. 1996. Genetic relationships among North American bison populations. Can. J. Zool. 74:738–749. doi:10.1139/z96-084

Ranglack, D.H., L.K. Dobson, J.T. du Toit, and J.N. Derr. 2015. Genetic Analysis of the Henry Mountains Bison Herd. PLoS One 10(12):E0144239. doi:10.1371/journal.pone.0144239

Saitou, N., and M. Nei. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 4:406–425.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol. Biol. Evol. 28:2731–2739. doi:10.1093/molbev/msr121

Tshipuliso, N.O.M., L.J. Alexander, A. Kotze, K. Ehlers, V.L. Reisenauer Leesburg, and M.D. MacNeil. 2008. Structural assessment of backcrossing using microsatellite markers. S. Afr. J. Anim. Sci. 38:90–292.

Wilson, G.A., and C. Strobeck. 1999. Genetic variation within and relatedness among wood and plains bison populations. Genome 42:483–496. doi:10.1139/g98-147

Downloaded from https://academic.oup.com/jas/article-abstract/94/11/4491/4702753 by Texas Tech University Health Sciences Center Library user on 02 January 2019