

# Cattle ancestry in bison: explanations for higher mtDNA than autosomal ancestry

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## Abstract

Understanding and documenting the process of hybridization and introgression between related species is a major focus of recent evolutionary research using molecular techniques. Many North American bison herds have cattle ancestry introduced by crossbreeding over a century ago. Molecular estimates of this ancestry have shown much higher levels for cattle mtDNA than for autosomal cattle genes. A large part of this difference appears to be the result of partial reproductive isolation between the two species where only bison bull  $\times$  domestic cow crosses are successful, and all the surviving progeny are females. In addition, selection against autosomal cattle genes in bison may have contributed to differential levels of cattle ancestry. The impact of selection against cattle mtDNA and gene flow of bison mtDNA are examined to explain particular combinations of mtDNA and autosomal cattle ancestry. A bottleneck, after the level of cattle ancestry in bison was reduced to a low level, is consistent with the high variance over autosomal loci observed for cattle ancestry, and differential selection among cattle loci in bison does not need to be invoked. Further examination of the cattle genome in bison may shed light on whether these markers, or their associated regions, are indeed neutral.

*Keywords:* bison, cattle, microsatellite loci, mtDNA

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## Introduction

Understanding and documenting the process of hybridization and introgression between related species is a major focus of recent evolutionary research. Using molecular techniques and theoretical approaches in population genetics, the history of hybridization can be reconstructed from contemporary data. In particular, the evolutionary factors and their effects that are consistent with molecular observations can be examined. This approach will be used below to examine cattle ancestry from mtDNA and autosomal markers in North American plains bison (*Bison bison bison*) (hereafter referred to as plains bison or just bison).

Plains bison are thought to have once existed in the ten of millions in western North America (Shaw 1995). In the early 1870s, large numbers of plains bison were

slaughtered, and by the 1880s they were nearly extinct. They were saved from extinction mainly by five ranchers who wanted to improve their cattle by crossbreeding them with bison, that is, to introduce genes resulting in commercially favourable traits into cattle, such as those for meat quality and quantity, hardiness, feed efficiency, and disease resistance (Boyd 1914; Goodnight 1914). Today, although the number of bison has recovered to over 500 000, only around 20 000 plains bison in the United States are in conservation herds (Freese *et al.* 2007). Virtually, all of the nonconservation herds have cattle ancestry and even a number of the conservation herds have cattle ancestry introduced around 120 years ago by these ranchers.

The first molecular genetic assay that found cattle ancestry in contemporary bison was that of Polziehn *et al.* (1995), who found cattle mtDNA in two bison from a sample of 30 in the Custer State Park herd in South Dakota. Since then, a large number of herds have been examined for cattle ancestry using both markers

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for mtDNA and autosomal microsatellite loci. If the reciprocal interspecies crosses, bison bulls  $\times$  domestic cows and domestic bulls  $\times$  bison cows, were equally likely, and various backcrosses were not differentially successful, then the expected cattle ancestry for mtDNA and autosomal markers should be similar.

In general, the level of introgression between species is a function of such factors as the mechanics and success of matings between hybrids, the number of generations of introgression, the frequency of backcrosses, and natural selection for or against introgressed genes. Several hypotheses or scenarios related to these factors will be examined below that may be important in making the frequency of cattle mtDNA markers higher than cattle autosomal markers in bison.

First, incipient reproductive isolation between the species can differentially influence the ancestry for the two types of genes. This is because when only crosses between bison bulls and domestic cows are successful, virtually all  $F_1$ s are females, and nearly all fertile backcrosses to bison are also females, the ratio of mitochondrial to autosomal cattle ancestry is expected to be greater than unity. Second, selection against autosomal cattle variants in bison may also result in lower autosomal than mtDNA cattle ancestry. If no bison cows are successfully used, then the mtDNA is only from cattle so that no selection against cattle mtDNA in bison would be possible. Third, if some bison cows were successfully used so that there were both cattle and bison mtDNA (gene flow of bison mtDNA into the population), then selection against both autosomal cattle genes and mtDNA from cattle in bison would be possible. Finally, chance effects in the form of small population size or population bottlenecks may increase the variance in the estimated autosomal ancestry over different loci.

## Background data

The level of cattle ancestry has now been estimated in a number of bison herds (Halbert *et al.* 2005; Halbert &

Derr 2007), but only four federal conservation herds (Grand Teton National Park, Sully's Hill National Game Refuge, Yellowstone National Park, and Wind Cave National Park) appear to not have any detectable cattle ancestry for either mtDNA or autosomal microsatellite markers that are specific to cattle. On the other hand, in some other herds, the level of cattle ancestry estimated from mtDNA is quite high, much higher than that from autosomal microsatellite loci (usually 14 diagnostic loci, that is, loci that have nonoverlapping sets of alleles in the two species, have been used in this estimation).

Table 1 gives the estimates of cattle ancestry for the six herds with cattle mtDNA ancestry estimates  $>10\%$  and the average for 16 other herds. The most extreme difference between the mtDNA and autosomal markers is for the Williams Ranch herd from Texas with 100% cattle mtDNA and no detected autosomal cattle markers. Nearly as extreme is that for the Houserock Ranch Herd from Arizona (this includes the related Raymond Ranch herd), which has estimated 97.5% cattle mtDNA and 1.9% autosomal ancestry. Although this herd has been a management problem for Grand Canyon National Park (Minard 2003) and now appears to have high cattle ancestry (Wakeling 2006), it continues to be used for 'buffalo' hunting. Over all these 22 surveyed herds, there is on average 13.9% mtDNA cattle ancestry and 0.6% autosomal cattle ancestry for a ratio of 23.2 mtDNA/autosomal cattle ancestry. Of course, the estimate of the autosomal cattle ancestry is the average of 14 unlinked loci while that for mtDNA is only from one locus. This should result in much less variance in the estimate for autosomal ancestry than mtDNA ancestry, all other things being equal.

## Interspecific crosses and backcrosses

The interspecific cross between cattle and bison is difficult, and the early ranchers could generally cross only bison bulls to domestic cows, the reciprocal cross was not possible because bison cows would not mate with domestic bulls (see discussion and references in

Herd name	Location	mtDNA (N)	Autosomal (N)	Ratio (mt/A)
Williams Ranch (WR)	Texas	1.000 (11)	0.000 (11)	$\infty$
Houserock Ranch (HR)	Arizona	0.975 (40)	0.019 (40)	51.0
Santa Catalina Island	California	0.449 (98)	0.006 (98)	74.8
Custer State Park	S. Dakota	0.206 (34)	0.015 (39)	13.7
Maxwell Game Refuge	Kansas	0.180 (39)	0.011 (40)	16.4
Texas State Bison Herd	Texas	0.167 (36)	0.000 (40)	$\infty$
16 other herds		0.0053	0.0050	1.1
All 22 herds		0.1392	0.0060	23.2
20 herds (not WR or HR)		0.0543	0.0056	9.7

**Table 1** Estimated cattle ancestry for mtDNA (mt) (ranked in order) and autosomal (A) genes (sample size  $N$ ) for the six herds with more than 10% cattle mtDNA and 16 other herds that have been surveyed (Hedrick 2009; data from Ward *et al.* 1999; Halbert *et al.* 2004, 2005; b; Wakeling 2006; Vogel *et al.* 2007; C. Penedo, personal communication)

Hedrick 2009). Further, from the interspecific cross between the bison bulls and domestic cows, virtually all the offspring were female, that is, there were no viable male offspring (see discussion in Hedrick 2009). This observation is consistent with Haldane's rule, 'When if the  $F_1$  of two different animal races one sex is absent, rare or sterile, that sex is the heterozygous sex' (Haldane 1922), suggesting significant reproductive isolation has occurred between the two species. From recent molecular genetic studies of whole mtDNA sequence, it is estimated that bison and the ancestor of domestic cattle diverged approximately two million years ago (Achilli *et al.* 2008), suggesting that there should be significant reproductive isolation between these two species.

$F_1$  females could then be backcrossed to bison bulls, and nearly all of these progeny with 25% cattle ancestry and 75% bison ancestry were again females. Sometimes, 75% bison ancestry bulls could be produced but such offspring were generally not fertile (Boyd 1914).

What are the consequences of the ancestry of these initial crosses for genes with maternal (mtDNA) and autosomal modes of inheritance? Table 2 gives the expected proportion of cattle ancestry for mtDNA and autosomes over these first two generations. For the cross between bison bulls and domestic cows, the offspring have 100% cattle mtDNA ancestry and 50% autosomal cattle ancestry. For the backcross progeny of a bison bull to  $F_1$  cow cross, there is again 100% mtDNA cattle ancestry and only 25% autosomal cattle ancestry. In other words, these first two crosses result in a predicted fourfold excess of cattle mtDNA ancestry compared to autosomal ancestry. This of course assumes that there is no paternal leakage of bison mtDNA from the bison male parents into the offspring (Sutovsky *et al.* 2004).

Although we will not discuss it further here, the expected proportion of paternally inherited cattle Y chromosomes is 0% from these crosses. Consistent with this prediction, no cattle Y chromosomes have been

observed in these herds with either cattle mtDNA or microsatellite markers (Ward *et al.* 2001).

If there is continued backcrossing of the progeny to bison bulls for  $t - 1$  generations, then the expected mtDNA ancestry remains at 100% and the expected autosomal ancestry becomes  $(1/2)^t$  (Table 2). In other words, if only bison bulls are used, high mtDNA cattle ancestry is retained, and autosomal cattle ancestry is reduced fairly quickly (Fig. 1). After five and six generations of backcrossing, the autosomal cattle ancestry is expected to be reduced to 1.56% and 0.78%, respectively. Or perhaps, more realistically after several generations, all the animals may have mated at random, and the cattle mtDNA ancestry would have stayed stay at 1.0 and the cattle autosomal ancestry would not have been reduced further. In this case, other factors, such as selection against autosomal cattle genes as discussed later, would have been necessary to reduce the autosomal cattle ancestry to the levels observed.

If bison cows were used, then bison mtDNA would have been introduced. Therefore, to result in near 100% cattle mtDNA and low autosomal cattle ancestry, such as those found for the Williams Ranch and Houserock Ranch herds, then only bison bulls and no bison cows could have been successfully introduced. In other words, in these herds we can assume that a scenario that includes substantial gene flow of bison mtDNA is not likely.

### Selection against autosomal regions

Another scenario that could contribute to a large difference in mtDNA and autosomal ancestry is to have selection against the autosomal regions with cattle markers. It is possible that diagnostic markers may be enriched for microsatellite loci that are linked to loci that have been selected differentially between the species. To examine this, assume that after the third generation in a population as given in Table 2, matings were

**Table 2** The proportion of cattle ancestry for mtDNA (mt) and autosomal (A) genes from an interspecific cross between bison bulls and domestic cows and for progeny of the backcrosses (BC) to bison bulls in subsequent generations

Generation	Cross	Bull × cow	Cattle ancestry		
			mtDNA	Autosomal	Ratio (mt/A)
1	Interspecies	Bison × domestic	1.0	0.5	2.0
2	Backcross to male bison	Bison × $F_1$	1.0	0.25	4.0
3	Backcross of generation 2 progeny to male bison	Bison × BC	1.0	0.125	8.0
$t$	$t - 1$ generations of backcross matings to progeny of the previous generation	Bison × BC	1.0	$(1/2)^t$	$2^t$

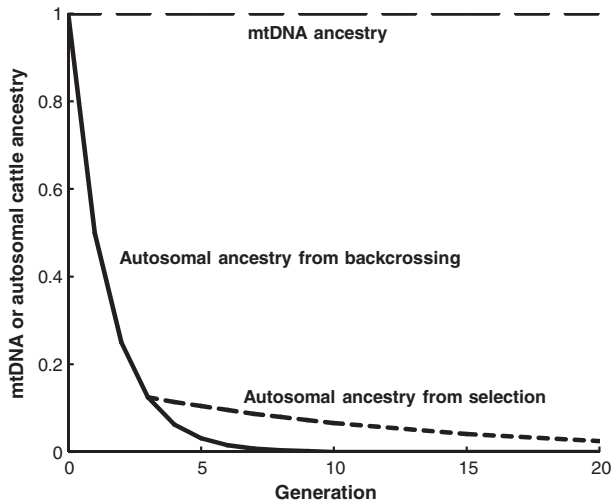


Fig. 1 The proportion of mtDNA cattle ancestry from backcrossing or selection against autosomal cattle genes (long broken line) and the proportion of autosomal ancestry from backcrossing (solid line) or selection against autosomal cattle genes (short broken line).

between progeny bulls and cows with 12.5% autosomal cattle ancestry (and 100% cattle mtDNA). At this point, there is no possible selection against the cattle mtDNA because there is no bison mtDNA present but selection is possible against autosomal cattle genome regions. As a simple example, assume that at gene *A* the bison allele *A<sub>b</sub>* and the cattle allele *A<sub>c</sub>* have frequencies in generation *t* of  $1 - q_t$  and  $q_t$ . Here and later, we will assume different alleles in bison and cattle so that the frequency of the cattle allele in bison is equal to the proportion of cattle ancestry in bison. If selection is additive, then for this autosomal region, the genotypes *A<sub>b</sub>A<sub>b</sub>*, *A<sub>b</sub>A<sub>c</sub>*, and *A<sub>c</sub>A<sub>c</sub>* have relative fitnesses of 1,  $1 - s/2$ , and  $1 - s$ , respectively. For additive selection, the number of generations that it takes for an allele to decrease from  $q_0$  to  $q_t$  is

$$t \approx \frac{2}{s} \left[ \ln \frac{q_0(1 - q_t)}{q_t(1 - q_0)} \right] \tag{1a}$$

(Hedrick 2010), and this expression can be rewritten as

$$q_t \approx \frac{q_0}{q_0 + e^{st/2}(1 - q_0)} \tag{1b}$$

Using expression (1b), if selection starts after the second backcross generation in Table 2 so that  $q_0 = 0.125$ , and we assume that  $s = 0.2$  and that the total number of generations, including the first three without selection, is 20 (about 120 years with a mean generation length of 6 years in these captive or managed herds),

then after 20 generations the frequency of the cattle allele (also the proportion of cattle ancestry) is 0.025 (Fig. 1). The generation length may be longer, based on the average age of reproduction in wild herds (Berger & Cunningham 1994), so that the number of generations may be less, and the selection necessary to result in this amount of change would be larger. In other words, given the initial crosses in Table 2, and then random mating among the subsequent progeny and selection against the cattle genome regions, the mtDNA cattle ancestry is still 100%, and the expected autosomal cattle ancestry is only 2.5%. Such a scenario could explain the joint mtDNA and autosomal ancestry observed in the Williams Ranch and Houserock Ranch herds. In other words, given the starting point discussed earlier, scenarios in which the amount of selection against autosomal ancestry is less than suggested here are very unlikely to have generated the proportions of cattle mtDNA and autosomal ancestry observed.

### Selection against both mtDNA and autosomal regions

For several of the populations, cattle mtDNA ancestry is not near 1.0 but is still much larger than the autosomal ancestry. For example, how can the 44.9% mtDNA cattle ancestry and the 0.6% autosomal cattle ancestry in the Santa Catalina population be explained? One possibility is gene flow from pure bison after the first three generations of crosses and then subsequent selection against both the mtDNA and autosomal ancestry.

Before we discuss this model, let us mention some body size data from Santa Catalina bison with bison or cattle mtDNA (D. Hedgecock, personal communication). In this instance, bison bulls with cattle mtDNA were 10.6% smaller than bison bulls with bison mtDNA, and bison cows with cattle mtDNA were 7.4% smaller than bison cows with bison mtDNA. In other words, assuming larger size is associated with higher fitness, then bison with cattle mtDNA appear to have lower fitness than bison with bison mtDNA.

In this model of gene flow and selection, let the allele frequency after one generation of gene flow be

$$q' = q(1 - m) + q_m m$$

where *m* is the proportion of migrants (bison) and  $q_m$  is the allele frequency of the cattle allele in the bison migrants. If we assume that for mtDNA,  $q = 1.0$ ,  $m = 0.2$  and  $q_m = 0.0$ , then  $q' = 0.8$  (the proportion of cattle ancestry is reduced and bison mtDNA is introduced). For the autosomal markers, assume that  $q = 0.125$ ,  $m = 0.2$ , and  $q_m = 0.0$ , then  $q' = 0.1$  (cattle ancestry is also reduced).

For the haploid mtDNA marker, assume that the fitnesses are 1 and  $1 - s$  for mtDNA haplotypes  $H_b$  and  $H_c$  from bison and cattle, respectively. In this case, using the approach given earlier

$$q_t \approx \frac{q_0}{q_0 + e^{st}(1 - q_0)} \quad (2)$$

Therefore, the expected frequency of the mtDNA after 20 total generations using this equation, assuming  $s = 0.1$ , is 0.423 (Fig. 2), similar to that observed in Santa Catalina Island herd. For the autosomal markers using expression (1b) and assuming  $s = 0.2$  as earlier, after 20 total generations the expected proportion of cattle ancestry is 0.02 (Fig. 2), also consistent with that for the Santa Catalina Island sample. Again, if the generation length is longer so that the number of generations is less, then to have this reduction in autosomal ancestry, selection would need to be larger.

The original source of the bison introduced to Santa Catalina Island (Goodnight Ranch in Texas) is thought to be the same as that of the Texas State Bison Herd (Vogel *et al.* 2007), which has an estimated cattle mtDNA frequency of 0.167 (Halbert *et al.* 2004). In other words, it is possible that some of the original Santa Catalina Island females had bison mtDNA or that later augmentation (Sweitzer *et al.* 2005) may have included female bison with bison mtDNA in this herd. Overall, scenarios that exclude gene flow of bison

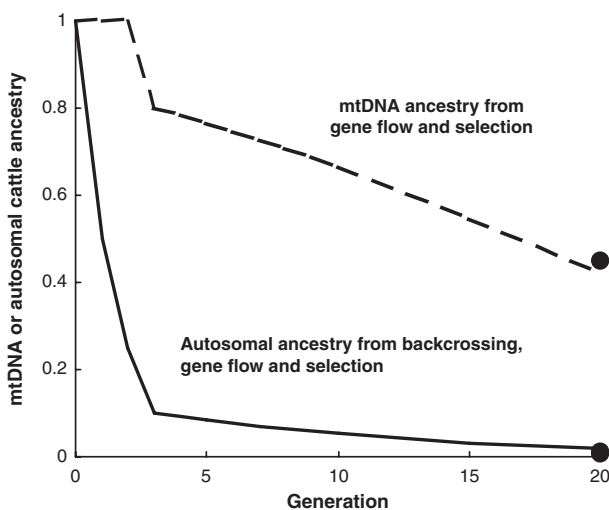


Fig. 2 The proportion of mtDNA cattle ancestry from gene flow and selection against cattle mtDNA (broken line) and the proportion of autosomal ancestry from backcrossing, gene flow, and selection against autosomal cattle genes (solid line). The closed circles indicate the observed mtDNA and autosomal ancestry on Santa Catalina Island.

mtDNA and exclude selection against both cattle mtDNA and autosomal genes are unlikely to have generated the observed pattern of variation in the Santa Catalina Island herd.

### Chance effects

There is rather large variation over the autosomal loci examined in cattle ancestry, with many herds having only one locus indicating cattle ancestry and the frequency of this cattle allele is often 10% or more (Table 3). It is not clear whether this variation over loci can be the result of chance ancestral effects or that selection operating differentially on the regions marked by these loci has occurred. In Table 3, the herds are ranked by their mean estimated autosomal ancestry and the sample variance ( $s^2$ ) over 14 loci (only 12 loci for the Houserock Ranch herd) is given. The ratio of the standard deviation ( $s$ ) to the mean ( $a$ ) cattle ancestry is much greater than unity for most herds and averages 3.17, suggesting high variation in ancestry over loci.

Some of these herds are related and have the same cattle allele in high frequency. For example, four of the populations, Badlands NP, Neal Smith National Wildlife Refuge, T. Roosevelt NP – N, and T. Roosevelt NP – S, were found entirely or in part with animals from Fort Niobrara NP. These five populations have allele 197 at locus BM4307 as the only, or major, cattle allele with frequencies in these herds of 0.136, 0.135, 0.163, 0.115, and 0.135. If we only use Fort Niobrara NP to represent this group of five herds, then the average  $s/a$  for the remaining seven herds is 2.93, only slightly lower.

On the other hand, the largest number of autosomal loci having cattle ancestry is for the Houserock Ranch and the Custer State Park herds. For the Houserock Ranch herd, 5 of the 12 loci examined showed cattle ancestry with allele frequencies of 0.125, 0.050, 0.0375, 0.025, and 0.025. For the Custer herd, 6 of 14 loci showed cattle ancestry with allele frequencies of 0.045, 0.040, 0.040, 0.027, 0.026, and 0.026. Both the Houserock Ranch and Custer State Park herds appear to have had founders from multiple sources (Wilson & Strobeck 1999; Wakeling 2006), so that cattle alleles from different loci might be expected, resulting in lower  $s/a$  values.

The maximum value that  $s/a$  can take is when only one of the loci has a cattle allele. The sample variance when only one of  $n$  loci has a cattle allele frequency value of  $a_i$  (and the  $n - 1$  rest of the loci have 0 cattle ancestry) is

$$s^2 = \frac{1}{n-1} \left[ (a_i - a)^2 + (n-1)a^2 \right] = \frac{a^2}{n} \quad (3a)$$

**Table 3** The mean ( $a$ ) and sample variance ( $s^2$ ) of autosomal cattle ancestry over 14 diagnostic loci for 11 herds (12 loci for the House Rock Ranch herd) ordered by mean ancestry, giving the  $s/a$  ratio and the frequency of the cattle alleles in each herd (NP – National Park, N – north, S – south) (based on data from Halbert *et al.* 2005; Wakeling 2006; Halbert & Derr 2007)

Herd name	Cattle ancestry			Cattle alleles
	Mean ( $a$ )	Variance ( $s^2$ )	$s/a$	
Houserock Ranch	0.022	0.0014	1.69	0.125, 0.050, 0.038, 0.025, 0.025
Finney Refuge	0.018	0.0027	2.88	0.188, 0.064
Custer State Park	0.015	0.0004	1.29	0.054, 0.040, 0.040, 0.027, 0.026, 0.026
Badlands NP	0.012	0.0014	3.06	0.136, 0.032
T. Roosevelt NP-N	0.012	0.0019	3.74	0.163
Maxwell Refuge	0.011	0.0013	3.43	0.138, 0.012
Neal Smith	0.011	0.0013	3.34	0.135, 0.016
Fort Niobrara	0.010	0.0013	3.74	0.135
T. Roosevelt NP-S	0.008	0.0009	3.74	0.115
Wichita Mountains	0.006	0.0006	3.74	0.090
National Bison Range	0.003	0.0001	3.74	0.038

Therefore,

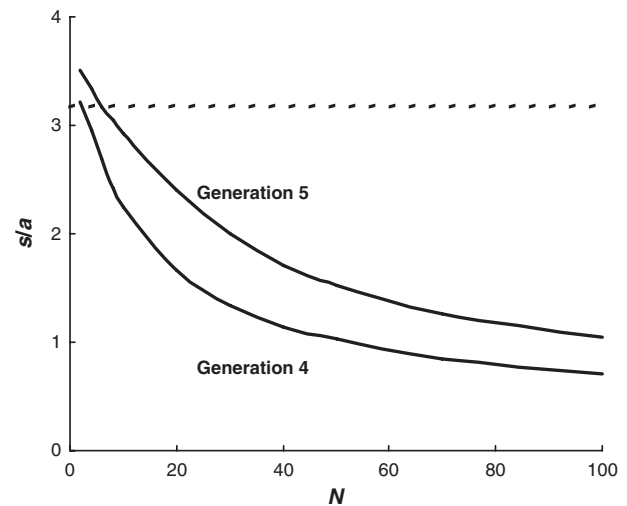
$$s/a = \frac{a/n^{1/2}}{a/n} = n^{1/2} \quad (3b)$$

Interestingly, this ratio is independent of the allele frequency of the cattle allele  $a_i$ . For 14 loci,  $s/a = 3.74$ , the observed value of  $s/a$ , the observed value for a number of herds given in Table 3.

What kind of ancestral pattern can result in such a high value of  $s/a$ ? As an example, let us assume that there are backcrosses as given in Table 2, starting with the generation with 0.25 cattle ancestry (as a result, the generation number in this section is two later than that used in Table 2), but that each generation there are only  $N$  offspring (half of each sex). If this backcrossing continues for four or five generations, then the expected cattle ancestry is 0.0156 and 0.0078, respectively, bracketing most of the observed cattle ancestry values in Table 3.

Figure 3 gives the expected value of  $s/a$  for 5000 simulations of samples of 14 loci for different numbers of progeny ( $N$ ) each generation. Only when  $N$  is very small is the value of  $s/a$  as high as that observed. However, it is unlikely that  $N$  was this small continuously for the first four or five generations, making this scenario unlikely unless, for example, there was high variance in reproductive success among individuals over all these generations.

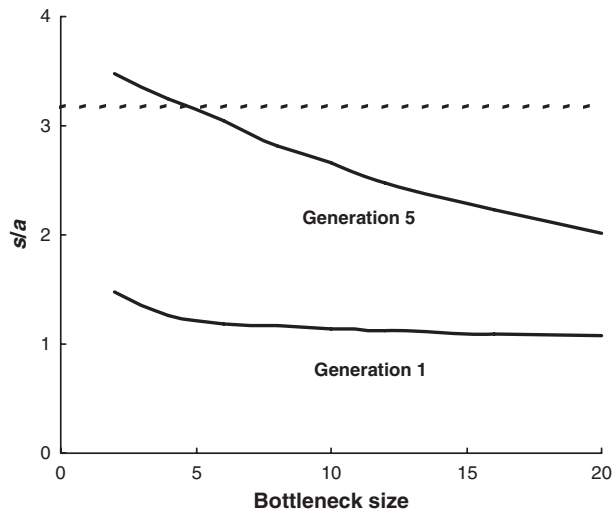
Another possibility is that there was a bottleneck for one (or more) generation(s) that resulted in high  $s/a$  values. To examine this, again 5000 simulations were carried out with a one-generation bottleneck of different sizes either in the first or last generation (generation 1 or 5), and  $N$  was 100 in all other generations. When the



**Fig. 3** The average (of 5000 simulations of 14 loci each) ratio of the standard deviation to the mean ( $s/a$ ) cattle ancestry after four and five generations of backcrossing when there is a finite number of progeny ( $N$ ). The broken line indicates the mean observed value of  $s/a$  over 11 herds.

bottleneck was in generation 1, there was little effect on  $s/a$ , even when the bottleneck size was only 2 (Fig. 4). On the other hand, when the bottleneck was in generation 5, there was a large effect on  $s/a$ , even when the bottleneck was larger.

The difference between the effect of an early or late bottleneck can be understood by realizing that in generation 1, the expected frequency of the cattle allele is 0.125, while in generation 5, it is only 0.0078. In the latter case, for example if  $N = 4$ , then nearly all loci will have a frequency of 0.0 after the bottleneck, and only a few will have a frequency of  $1/2N = 0.125$ . When only one of 14 loci in a simulation has a frequency of 0.125,



**Fig. 4** The average (of 5000 simulations of 14 loci each) ratio of the standard deviation to the mean ( $s/a$ ) cattle ancestry after one-generation bottlenecks of different sizes in generations 1 or 5. The number of progeny in the other generations is 100. The broken line indicates the mean observed value of  $s/a$  over 11 herds.

then  $s/a = 3.74$ , and the estimate of cattle ancestry is not unlike that observed for the herds given in Table 3. On the other hand, if the bottleneck is in generation 1 when the expected frequency of the cattle allele is 0.125, then it is much more likely that more than one locus out of 14 will show cattle ancestry, and the level of  $s/a$  will be much lower. Overall then, chance effects from a bottleneck after the cattle ancestry had already been reduced to a low level could have resulted in the high observed variance over loci and high  $s/a$  values, and differential selection over loci need not be invoked.

## Conclusions

Conservation herds of plains bison have low amounts of cattle ancestry (generally about 1% or less), and most of this ancestry is the remnant of crosses made over a century ago by five ranchers attempting to improve their cattle by introducing bison traits. However, the amount of cattle ancestry for maternally inherited mtDNA is much higher than that for autosomal microsatellite loci in many contemporary herds, unlike the predicted estimates if all crosses were equally successful.

A major factor that appears to contribute to this difference is the differential success of interspecies crosses and backcrosses and that female progeny from these crosses have a higher survival. However, it appears unlikely that the highest ratios of mtDNA to autosomal ancestry can be explained alone by this and subsequent

backcrossing to bison bulls. It appears that in addition, selection against the autosomal cattle regions in bison probably contributed to a reduction in the amount of cattle autosomal ancestry compared to mtDNA ancestry.

Further, in some cases, selection against cattle mtDNA in bison may have been important. Some unpublished data show that bison with cattle mtDNA are smaller than bison with bison mtDNA, consistent with potential selection against cattle mtDNA in bison. Further, male bison with cattle mtDNA showed a larger relative reduction in body size than female bison with cattle mtDNA consistent with the hypothesis that males may suffer more deleterious effects of mtDNA dysfunction because they do not transmit it to their offspring (Frank & Hurst 1996; Sackton *et al.* 2003). Finally, chance history appears to have played a role in the high variation of cattle ancestry over the autosomal markers examined. Using a simulation model, the high variation over loci appears consistent with a bottleneck(s) in generations after the amount of cattle ancestry had been reduced to a low level. Further examination of the cattle genome in bison may shed light on whether these markers, or their associated regions, are indeed neutral.

Current studies using genome-wide arrays of SNPs developed in cattle may help clarify the factors influencing cattle ancestry in bison. For example, such studies could identify neutral autosomal regions, so that the amount of cattle ancestry not influenced by selection could be estimated. Further, cattle regions that are higher or lower in frequency in bison than the average could indicate cattle regions that are selectively advantageous or disadvantageous in bison. Finally, using both historical and genomic information, knowing in detail this ancestry may allow identification of cattle ancestry resulting from the five different ranchers responsible for introducing cattle ancestry into bison. This could then be used, in combination with genomic bison information, to estimate the proportion of the contemporary population that descends from the different ranch herds and potentially determine the number of effective founders that contributed to the bison herds surviving today. These data could then be used to design breeding strategies to maintain genetic variation in the conservation herds of bison.

The detailed examination of cattle ancestry in bison may provide general information about the process of reproductive isolation in species with recent common ancestors. Because the cattle genome has now been sequenced, loci that contribute to either prezygotic or postzygotic reproductive isolation could potentially be identified, providing information both on the number and types of loci, and even the role of mtDNA–nuclear interactions, involved in this process. In other words,

this unintended experiment in evolution may be the source of important genetic information on general speciation processes. Further, this example may provide general insight into the fate of DNA introgressed into a related species, the effects of natural hybridization, and other related evolutionary phenomenon that would be difficult to examine on the magnitude and time scale provided by the example of cattle introgression into bison.

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