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Phenotypic Effects of Cattle Mitochondrial DNA in American Bison

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Abstract: *Hybridization between endangered species and more common species is a significant problem in conservation biology because it may result in extinction or loss of adaptation. The historical reduction in abundance and geographic distribution of the American plains bison* (Bison bison bison) *and their recovery over the last 125 years is well documented. However, introgression from domestic cattle* (Bos taurus) *into the few remaining bison populations that existed in the late 1800s has now been identified in many modern bison herds. We examined the phenotypic effect of this ancestry by comparing weight and height of bison with cattle or bison mitochondrial DNA (mtDNA) from Santa Catalina Island, California (U.S.A.), a nutritionally stressful environment for bison, and of a group of age-matched feedlot bison males in Montana, a nutritionally rich environment. The environmental and nutritional differences between these 2 bison populations were very different and demonstrated the phenotypic effect of domestic cattle mtDNA in bison over a broad range of conditions. For example, the average weight of feedlot males that were 2 years of age was 2.54 times greater than that of males from Santa Catalina Island. In both environments, bison with cattle mtDNA had lower weight compared with bison with bison mtDNA, and on Santa Catalina Island, the height of bison with cattle mtDNA was lower than the height of bison with bison mtDNA. These data support the hypothesis that body size is smaller and height is lower in bison with domestic cattle mtDNA and that genomic integrity is important for the conservation of the American plains bison.*

Keywords: Catalina Island, height, hybridization, introgression, mtDNA, weight

Efectos Fenotípicos del ADN Mitocondrial de Ganado en el Bisonte Americano

Resumen: *La hibridación entre especies en peligro y especies más comunes es un problema significativo en biología de la conservación porque puede resultar en la extinción o pérdida de adaptación. La reducción histórica de la abundancia y distribución geográfica del bisonte americano* (Bison bison bison) *y su recuperación en los últimos 125 años esta bien documentada. Sin embargo, la introgresión de ganado doméstico* (Bos Taurus) *en las escasas poblaciones remanentes de bisonte que existían a fines del siglo XIX ha sido identificada en muchas manadas actuales de bisonte. Examinamos el efecto fenotípico de esta ascendencia mediante la comparación del peso y altura de bisontes con ADN mitocondrial (ADNmt) de ganado o bisonte de la Isla Santa Catalina, California, (E.U.A.), un ambiente nutricionalmente estresante para bisontes, y de un grupo de bisontes machos de la misma edad de Montana, un ambiente nutricionalmente rico. Las diferencias*

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ambientales y nutricionales entres estas 2 poblaciones de bisontes fueron muy grandes y demostraron el efecto fenotípico del ADN mt de ganado doméstico en bisontes en un amplio rango de condiciones. Por ejemplo, el peso promedio de machos de 2 años de Montana fue 2.54 veces mayor que el de machos de la Isla Santa Catalina. En ambos ambientes, los bisontes con ADNmt de ganado tenían menos peso en comparación con bisontes con ADNmt de bisonte, y en la Isla Santa Catalina, la altura de bisontes con ADNmt de ganado fue menor que la altura de bisontes con ADNmt de bisontes. Estos datos soportan la hipótesis de que el tamaño corporal es menor y la altura es menor en bisontes con ADNmt de ganado y que la integridad genética es importante para la conservación del bisonte americano.

Palabras Clave: ADNmt, altura, hibridación, introgresión, Isla Catalina, peso

Introduction

Hybridization between endangered species and more common species may result in extinction (Rhymer & Simberloff 1996; Allendorf et al. 2001; Wolf et al. 2001). In addition, hybridization with a species that has undergone domestication selection, such as feral carnivores (dogs, cats), ungulates (pigs, goats), game birds (galliforms, waterfowl), and crop plants, may result in disruption of adaptation in threatened or endangered species (Randi 2008). In some cases, introgression may result in obvious morphological changes, such as the presence of dog dewclaws in wolves (*Canis lupus*) in Italy (Randi 2008), but in other instances, in which the level of introgression is low or a number of generations in the past, detection of the morphological effects of introgression is difficult. Although it is not our task here, we recognize that hybridization has often played a natural and important role in evolution and may increase the probability of long-term survival of endangered species.

Although the American plains bison (*Bison bison bison*) once numbered in the tens of millions in North America (Shaw 1995), they almost became extinct in the late 1800s and early 1900s. Bison survived this population bottleneck as a small wild herd in Yellowstone National Park, which had only 23 animals in 1902 (Meagher 1973), and as small herds on 5 private ranches. The exact number of founder animals from these 5 herds is unknown, but estimates suggest the total number of founders for the present-day population was <100 (Hedrick 2009).

Bison in these ranch herds were deliberately crossed with domestic cattle (*Bos taurus*) in an attempt to introduce bison traits, such as meat quality and quantity, hardiness, and disease resistance, into breeds of beef cattle (Boyd 1914; Goodnight 1914). Genetic evidence of this century-old introgression is present in many public, nongovernmental organization, and private bison herds (e.g., Polziehn et al. 1995; Ward et al. 1999; Halbert & Derr 2007). In general, the level of cattle ancestry in bison for autosomal microsatellite markers is <1% in herds maintained for conservation purposes (Halbert & Derr 2007). In contrast, cattle ancestry in bison for maternally inherited mitochondrial DNA (mtDNA) is much higher than for autosomal genes, and for 22 herds that have been surveyed for both markers, the overall level of cattle mtDNA ancestry is 23 times that of autosomal cattle ancestry (Hedrick 2010).

It is difficult to make interspecific crosses between these 2 species, and although the ranchers were able to cross bison males (bulls) and domestic cattle females (cows), the reciprocal cross was not possible because bison females were very reluctant to mate with domestic-cattle males (Hedrick 2009). In these initial crossbreeding experiments, all the offspring were female (although sterile F_1 males were subsequently reported), a result consistent with Haldane's rule, "...when in the F_1 of two different animal races one sex is absent, rare or sterile, that sex is the heterozygous sex" (Haldane 1922). The F_1 females could then be backcrossed to bison males, and a majority of these 75% bison-ancestry offspring were females. As a result, both the F_1 and first backcross-generation progeny had 100% cattle mtDNA and 50% and 25% autosomal cattle ancestry in the F_1 and first backcross generations, respectively. In other words, the differential level of mtDNA and autosomal ancestry is consistent with the success of these crosses although other factors, such as selection and chance, also appear to contribute (Hedrick 2010).

Recently, the complete mtDNA sequence of bison identified 642 fixed synonymous (nonamino-acid changing) and 86 fixed nonsynonymous (amino-acid changing) differences between bison and domestic cattle mtDNA out of 16,325 total nucleotides (Douglas et al. 2011). From these data and those of Achilli et al. (2008), it is estimated that bison and the ancestor of domestic cattle diverged 1–2 million years ago, which is consistent with the information discussed above about prereproductive and postreproductive isolation between the species.

For closely related species, specific regions of the genome may have variants that have the same fitness in both species, fit in one species and not in the other, or unfit in both species. For example, it is generally assumed that most variants at microsatellite loci are neutral with respect to each other within a species and that microsatellite variants at loci used to estimate ancestry are not selectively different between species. There are examples in which variants have a detrimental effect on fitness in closely related species (Sackton et al. 2003) or in which variants have a positive effect on fitness in closely related species (Song et al. 2011).

Today a pivotal bison conservation issue is the extent and effect of cattle ancestry on the long-term recovery of bison (Marris 2009). Recent suggestions that cattle ancestry should be identified and reduced in conservation bison herds (Gates et al. 2010) are controversial because there are no known direct observations of a phenotypic effect from cattle ancestry in bison and selection to eliminate cattle ancestry in bison could reduce genetic variation at associated loci that do not have phenotypic effects. We examined whether cattle mtDNA reduces both weight and height of bison in a free-roaming population with poor nutrition or weight in a controlled population with good nutrition.

Methods

Populations

Fourteen American plains bison were introduced in 1924 to Santa Catalina Island (hereafter, Catalina Island or Catalina), one of the Channel Islands off the coast of southern California (U.S.A.), for the filming of a silent movie called *The Vanishing American* (Vogel et al. 2007). These bison were left on the island after filming finished, and the herd was subsequently supplemented with 45 additional bison, 10 in 1934, 23 in 1968–1971, and 12 in 1996. Although Catalina is not within the range of native bison (bison did not exist in southern California) and does not have any native ungulates, the bison herd grew to about 400 in the 1960s and reached a peak of 524 animals in 1987 (Sweitzer et al. 2005). Since 1969, more than 2000 bison have been exported to the mainland United States, and in 2009 a reproductive vaccination program (contraception) was started to reduce the effect of high bison numbers on native vegetation and maintain the herd at around 150 to 200.

The environmental conditions on the island for bison are considered harsh, nutritionally poor, and marginal (Lott & Galland 1987; Sweitzer et al. 2003). For example, adult males and females on Catalina Island weighed only 427 and 321 kg on average, 46.4% and 35.9% less than adult males and females, respectively, from the Theodore Roosevelt National Park in North Dakota and the National Bison Range in Montana (Sweitzer et al. 2003). In bison roundups (in which bison are brought into corrals) on Catalina Island in 2004 (48 males and 50 females) and 2009 (97 males and 134 females) blood samples were taken for genetic analyses, age was estimated, and body weight and height (only in 2009) were measured. We also used weight-gain data collected during the 2011 roundup on 36 of the same animals measured in 2009.

The other bison population we examined was from a feedlot on a private ranch in Montana within the native bison range. All 618 animals in the feedlot were young males (bull calves). They were fed a high-nutrition diet and were weighed 8 times at 90- to 120-day intervals over 26 months. Some reduction in number in this cohort over time was attributable to culling, natural death, and sale.

Genetic Analyses

For DNA collection, we applied approximately 1 mL of whole blood to FTA cards (Whatman, Newton Center, Massachusetts) and collected tail hair follicles from each animal. We conducted polymerase chain reaction (PCR) amplifications with either cutout sections of the FTA cards that contained blood, following manufacturer's suggestions, or from DNA isolated from hair follicles, following the protocol of Schnabel et al. (2000). We performed PCR amplification in 5-mL reactions on a GeneAmp PCR System 9700 thermal cycler (Applied Biosystems, Foster City, California). We determined mtDNA type (domestic cattle or bison) following the methods of Ward et al. (1999) and archived all genetic samples at Texas A&M University, College Station, Texas.

Statistical Analyses

We analyzed weight of the Catalina Island animals to assess the effects of sex, mtDNA type, and year of sampling, with age as a covariate, because weight distribution differed between the 2 collection years. We used natural log of weight (ln[wt]) as our response variable, but back-transformed the resulting least-squares means for ease of interpretation and comparison. The linear model for ln(wt), calculated with the generalized linear model (GLM) procedure in SAS 9.2 (SAS Institute, Cary, North Carolina), was

$$\begin{aligned}\ln(\mathrm{wt}) = {} & \mathrm{age} + (\mathrm{age})(\mathrm{yr}) + (\mathrm{age})(\mathrm{sex}) + \mathrm{sex} + \mathrm{mt} \\ & + (\mathrm{sex})(\mathrm{mt}) + (\mathrm{yr})(\mathrm{sex})(\mathrm{mt}), \qquad (1)\end{aligned}$$

where age was the age in years estimated from horn wear, overall body condition, and incisor tooth wear when visible (Fuller 1959), yr (year) was 2004 or 2009, sex was female or male, and mt was bison mtDNA or cattle mtDNA.

In addition, we analyzed association of height (h) at rump of bison sampled in 2009 with sex and mtDNA type with the linear model

$$\mathrm{h} = \mathrm{age} + \mathrm{mt} + \mathrm{sex} + (\mathrm{mt})(\mathrm{sex}). \qquad (2)$$

Thirty-six animals were weighed in both 2009 and 2011. For these data, we fit the linear model

$$\mathrm{gain} = \ln(2009\mathrm{wt}) + \mathrm{sex} + \mathrm{mt}, \qquad (3)$$

where gain is the difference in weight (wt) between 2009 and 2011 and ln(2009wt) is the logarithm of the 2009 weight.

For the feedlot population, we used a mixed-effects linear model to examine the effects on body weight (response variable) of the covariates sampling time (a surrogate for age), mtDNA type (bison or cattle), and the

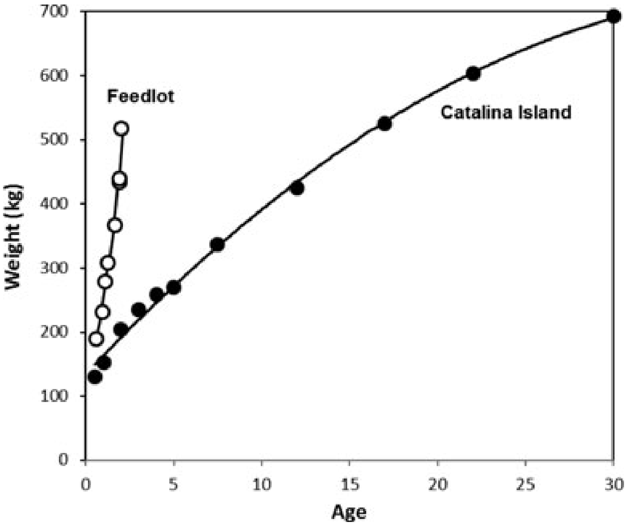

Figure 1. Mean weight of male bison from Catalina Island (shaded circles) and from the feedlot (unshaded circles) at different ages (years).

interaction of sampling time and mtDNA type. We modeled sampling time as an ordered categorical variable and mtDNA type as a dichotomous categorical variable. We modeled sample time and mtDNA type as fixed effects and individual animals as a random effect to account for repeated measures over time. We included the interaction of sample times with mtDNA type in the model. We used Sidak's method for post hoc tests of effects of mtDNA type among years.

Results

Santa Catalina Island

Our sample included 329 animals from Catalina Island and 618 from the feedlot. Comparison of the weight of males in these groups of bison demonstrates the very large effect of nutritional differences in the 2 environments (Fig. 1). For example, the average weight of 2-year-old males from Catalina Island was 204 kg, whereas the average weight of 2-year-old feedlot males was 518 kg, 2.54 times as much. The Catalina males were on average 17 years old when they reached a similar size of 524 kg. In other words, the males from the feedlot environment were substantially larger than Catalina Island males at the same age.

Of the animals examined on Catalina Island, 52.3% had bison mtDNA and 47.7% had cattle mtDNA (an earlier estimate of autosomal ancestry from cattle in the Catalina Island herd was only 0.6% [Hedrick 2009]). After controlling for age, year, and sex, bison with cattle mtDNA weighed 7.8% less than bison with bison mtDNA ($F_{1,318} = 6.42, p = 0.012$) (Fig. 2). In addition, females with cattle mtDNA weighed significantly less than females with bison mtDNA ($t = 2.49, p = 0.013$). None of the other comparisons by sex and year between bison with bison mtDNA and bison with cattle mtDNA were statistically significant—owing most likely to small sample sizes in some of the categories. However, bison with bison mtDNA were heavier than bison with cattle mtDNA in all comparisons (Fig. 2).

Bison heavier than 450 kg or judged to be extremely old were not sampled in 2004 because these animals were to be removed from the island. Sampling was more exhaustive in 2009, when a complete census of the herd was desired, and resulted in greater average age in 2009 than in 2004. Age structure, by sex and year, was bimodal except for males in 2004.

The model given in Eq. 1 explained 75.2% of variance in ln(wt). Age and its interactions with sex and year were highly significant (age, $F_{1,318} = 516.7, p < 0.001$; age × yr, $F_{1,318} = 8.45, p = 0.004$; age × sex, $F_{1,318} = 31.7, p < 0.001$) and explained 58.5%, 2.4%, and 13.1% of variation in ln(wt), respectively. The effects of sex and mtDNA

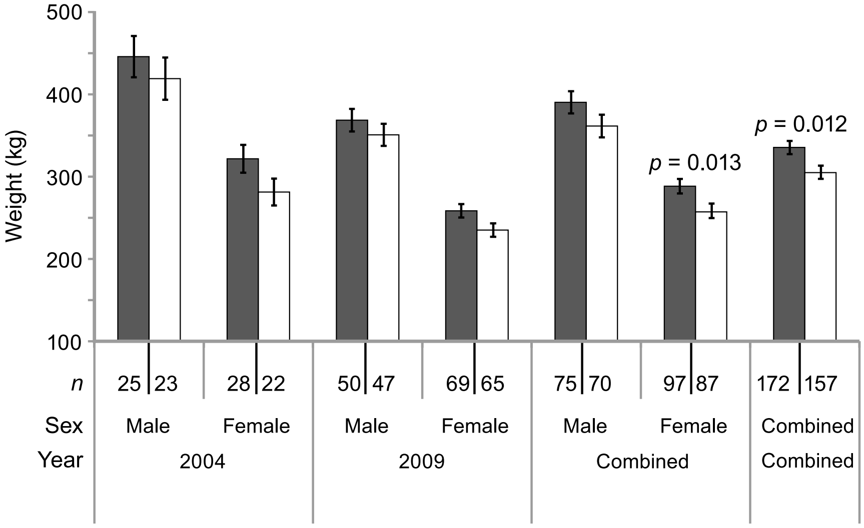

*Figure 2. Mean weight (SE) for male and female bison from Santa Catalina Island with bison mtDNA (shaded bars) or cattle mtDNA (open bars) for samples from 2004 and 2009, for 2004 and 2009 combined, and for combined males and females and years (*n*, sample size;* p*, statistical significance when <0.05).*

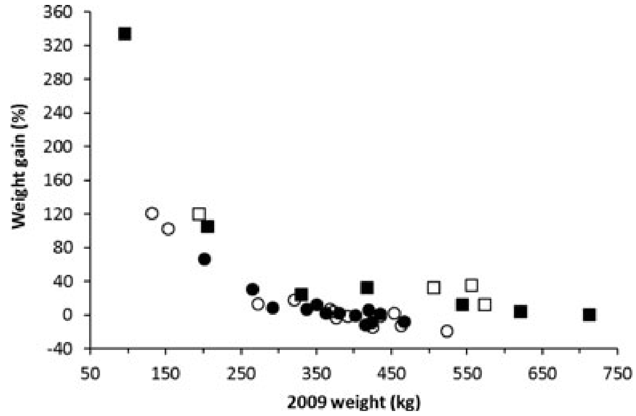

Figure 3. Weight gain in bison from Santa Catalina Island from 2009 to 2011 (circles, females; squares, males; shaded symbols, with bison mtDNA; unshaded symbols, with cattle mtDNA). Weight gain calculated as 100×[(2011weight − 2009weight)/2009weight].

type were small and roughly equal, and were significant components of weight variance once the dominant effect of age was removed (sex, $F_{1,318} = 7.85, p = 0.005$, 2.2% of adjusted ln[wt] variance; mt, $F_{1,318} = 6.42, p = 0.012$, 2.1% of adjusted ln[wt]variance).

In 2009 we measured the heights of 219 bison on Santa Catalina Island, and the linear model in Eq. 2 explained 58.8% of variance in height. The association of height with both age and sex was statistically significant (age, $F_{1,214} = 254.2, p < 0.0001$; sex, $F_{1,214} = 73.3, p < 0.0001$), and bison mtDNA type had a significant positive effect on height ($F_{1,214} = 4.26, p = 0.040$). Least squares mean heights, adjusted for age and sex, were 125.7 cm (SE 1.2) for bison with bison mtDNA but 123.1 cm (SE 1.2), for bison with cattle mtDNA, a 2.1% difference. The height of females with bison mtDNA (121.0 cm [SE 1.4]) was significantly different from the height of females with cattle mtDNA (117.1 cm [SE 1.5], $t = 2.32, p = 0.02$), but heights of males with different types of mtDNA were not significantly different (bison mtDNA, 130.5 cm [SE 1.5]; cattle mtDNA, 129.1 cm [SE 1.5], $p = 0.48$). For all comparisons, bison with bison mtDNA were taller than bison with cattle mtDNA.

For the animals weighed in both 2009 and 2011, the percentage of weight gain over this 2-year period was a decreasing exponential function of initial weight ($F_{1,34} = 170.1, p < 0.0001$) and did not differ for bison with bison mtDNA and bison with cattle mtDNA (Fig. 3). The linear model in Eq. 3 explained 85.8% of weight gain and was significant (model $F_{3,34} = 68.8$, $p < 0.0001$). Sex was significantly associated with weight gain ($F_{1,34} = 47.9$, $p < 0.0001$), but weight gain and mtDNA type were not significantly associated ($F_{1,34} = 0.01, p = 0.94$).

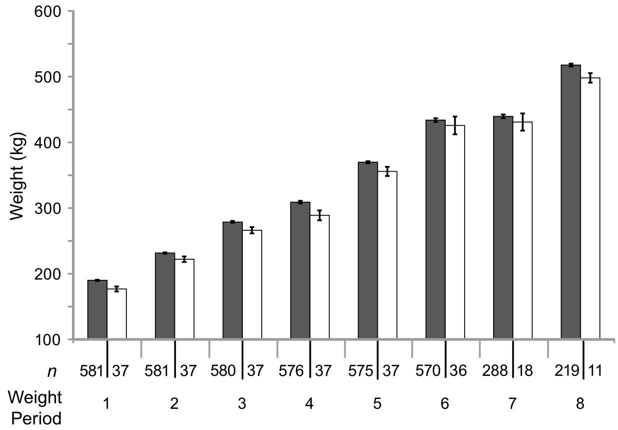

*Figure 4. Mean weight (SE) every 90–120 days for young bison males with bison (shaded bars) or cattle (unshaded bars) mtDNA from a feedlot in Montana (U.S.A.) (*n*, sample size). The weight periods were between 90 and 120 days apart. All differences in weight between animals with bison mtDNA and cattle mtDNA were statistically significant (*p* < 0.05), and over all weight periods bison with bison mtDNA were significantly heavier than bison with cattle mtDNA (*p* < 0.01).*

Feedlot

In the high-nutrition, feedlot study, we determined the type of mtDNA of 618 young, age-matched young bison males. Of these animals, 94.0% had bison mtDNA and 6.0% had cattle mtDNA. (Although autosomal cattle ancestry was not estimated for this herd, a number of similar herds examined had autosomal cattle ancestry between 1% and 2% [J.D., unpublished].) The percentages of the 2 types of mtDNA remained the same throughout the study except for the last weight period, when there were only 230 animals remaining and the percentage with bison mtDNA increased to 95.2%.

For each of the 8 sampling periods, the average weight of bison with bison mtDNA was significantly greater ($p < 0.05$) than that of bison with cattle mtDNA (Fig. 4). In addition, bison with bison mtDNA were significantly heavier than bison with cattle mtDNA over all weight periods ($p < 0.003$). mtDNA type was not associated with the rate of weight gain over the 26 months but was associated with the initial (weaning) weight; mean difference was 13 kg (7%). The animals with cattle mtDNA continued to weigh less than animals with bison mtDNA, and at the end of the 26 months, bison with cattle mtDNA weighed 19.5 kg (4%) less than bison with bison mtDNA.

Discussion

Cattle ancestry may affect phenotypic traits or fitness in herds of bison maintained for conservation. These effects may be exacerbated because cattle have undergone long-term selection by humans, whereas bison have been generally free of artificial selection except in commercial herds.

The extent of cattle ancestry in individual bison and bison herds has been estimated by autosomal microsatellite loci and mtDNA sequence variation, which are generally thought to be neutral markers and to have no phenotypic or fitness effects. However, our results show that mtDNA from cattle has a phenotypic effect on bison and that bison with cattle mtDNA are consistently smaller in both nutritionally poor and nutritionally rich environments. In other words, it appears that cattle mtDNA is associated with lower body weight in bison across all populations of bison maintained for conservation, even under quite different environmental conditions.

In general, it is assumed that for the ordinary range of values there is a positive relation between fitness-related traits, such as body size, and fitness (Robertson 1955). However, whether variation in body weight resulting from bison or cattle mtDNA translates into significant differences in fitness for bison across their range or in particular environments, such as Catalina Island, remains an open question. Results of some studies demonstrate a correlation between male reproductive success and body mass or age, which is strongly correlated with body mass (Wilson et al. 2002; Bowyer et al. 2007), whereas results of other studies show no such correlation (Wolff 1998). The correlation between body mass and reproductive success of females appears to be variable, depending on the environment and other factors that determine dominance hierarchy (Rutberg 1983; Lott & Galland 1987; Vervaecke et al. 2005). It seems prudent to minimize the risk of potentially detrimental phenotypic effects of cattle mtDNA introgression into bison.

Hedrick (2009) states that in bison "Reduction of cattle ancestry by culling animals with known cattle mtDNA is generally appropriate and could eliminate cattle mtDNA from herds..." "In herds with high cattle mtDNA levels, great care should be taken to retain bison variation at nuclear loci if there is selective culling to reduce cattle mtDNA." Furthermore, most, if not all, established bison populations maintained for conservation are routinely culled on the basis of various criteria (e.g., disease status, age, body conformation, hair color, horn size, head size, and behavior). Overall, culling animals on the basis of mtDNA status may be more reasonable and defensible than use of other criteria with unknown genetic bases.

Detrimental mtDNA mutants may be primarily specific to males because selection cannot act against maternally inherited mtDNA in males (Frank & Hurst 1996), a phenomenon called the "mother's curse" (Gemmell et al. 2004). In the Catalina Island bison, the difference in weight was significant between females but not between males (although in the same direction in males). In the feedlot study, only young males were sampled, and they differed significantly in weight. In other words, we have no strong evidence that selection against cattle mtDNA in bison is male specific as posited by the mother's curse hypothesis. Of course, if the fitness difference occurs in females, as it appears to in the Catalina Island population, then selection can act against these maternally inherited variants from cattle and reduce their frequency in bison.

The frequency of cattle mtDNA in Catalina Island bison is higher than in most bison herds maintained for conservation (Vogel et al. 2007), although cattle-ancestry estimates of mtDNA and autosomal microsatellite loci on Catalina Island are not theoretically inconsistent with founding cattle ancestry, subsequent gene flow, and selection against both cattle mtDNA and autosomal ancestry (Hedrick 2010). Conversely, it is possible that the nutritionally poor environment of Catalina Island favors smaller animals and, consequently, bison with cattle mtDNA. We are examining this hypothesis by evaluating the relative reproductive success of bison with bison mtDNA and those with domestic cattle mtDNA.

The initial difference in weight between young males in the feedlot with cattle mtDNA and those with bison mtDNA may reflect the effects of maternal mtDNA genotype on birth weight and early growth, of mtDNA genotype of young on birth weight or early growth, or both. However, these mtDNA effects are completely correlated, and we cannot distinguish between them on the basis of our data. Weight gain for Catalina bison between 2009 and 2011 did not differ by mtDNA type but was highly affected by initial weight in 2009 (Fig. 4). This result suggests that the size difference between the 2 mitochondrial types in the population was established early in life.

American bison, with a population bottleneck in the late 1800s and hybridization with domestic cattle around 100 years ago, provide an opportunity to test whether genetic introgression from another species affects phenotype. We found that cattle mtDNA was associated with a reduction in overall body size. The cattle genome and the nearly completed bison genome, could be used to identify the effects of specific regions of the autosomal cattle genome on phenotypic traits or fitness in bison.

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