Footnotes

[1] Anecdotal accounts of bison adaptations were reviewed by Dary (1974). In comparing ancient and modern bison, Guthrie (1990) provides a modern, academic approach to the study of bison adaptations to their environments. In truth, we have barely begun to investigate bison behavior and physiology.

[2] Lott (2002)

[3] Christopherson et al. (1978, 1979).

[4] Personal communication, Eric Cole, biologist, National Elk Refuge.

[5] Hawley et al. (1981).

[6] On the Wichita Mountains National Wildlife Refuge, Oklahoma, and elsewhere, bison selectively forage on recently prescribed-burned patches of habitat.

[7] Gates et al. (2010).

[8] Lott (2002).

[9] Personal communication, Walter Munsterman, biologist Wichita Mountains National Wildlife Refuge.

[10] See Gard (1959) for descriptions of bison stampedes.

[11] (Jones et al. (2009).

[12] Geist (1991).

Chapter 5

Wild Bison Populations

The previous chapter described wildness in bison by focusing primarily on the characteristics of individuals. Other attributes of wildness belong, not to individuals, but to populations of bison. Populations carry the genetic diversity of a species; they have sex-age structures and social structures. Populations fluctuate in abundance through time. Populations evolve, individuals do not. Here, I explore the roles of these population characteristics of wild bison and their implications for reestablishing a few wild plains bison herds.

"Wild" and "natural" are often used words, but they are seldom well defined. I tend to use the words synonymously. A truly wild population of native animals or a truly wild ecosystem is one that exists and functions with no impact from humans. In this sense, very few wildlife are completely wild. Impacts of our huge and dispersed human population are too pervasive. (Years ago, I wrote a college text on wildlife management. Now I realize that wildlife management is somewhat an oxymoron, as suggested long ago by Aldo Leopold who advised that the value of wildlife is inverse to the artificiality of the management system that produced it.[1])

One may argue that humans have been an important factor in the evolution of bison for many centuries. Native Americans, to some extent, managed bison numbers and distribution, and used fire to manage bison habitat. This argument is used to justify some degree of human intervention with wild bison herds as being natural and acceptable.

The argument can become esoteric and unproductive. Yet, it is important. Clearly, there are degrees of "wildness" based upon the degrees of human intervention with bison management. But what degrees and qualities of wildness should influence or dictate our goals for restoring wild plains bison?

We value wild plains bison for what they are – what they have become through their history of natural selection. In this history, intervention and selection by human activities have been significant, but not dominant. Therefore, if we are to retain wildness in plains bison, we must keep them in environments where the major forces of past evolution may continue, albeit in the context of an evolving North America. Relaxation or elimination of these selective forces will result in gradual changes in bison anatomy, physiology and behavior. Moreover, replacement of natural selective forces with human interventions can cause rapid changes in bison, leading to domestication as bison adapt to a captive or semi-captive environment.

Genetic Diversity

A wild, self-contained bison population should consist of at least 2000-3000 animals. Why is that? The answer lies primarily in the complicated field of population genetics.

Before Europeans arrived, bison were widespread in North America. There were millions of bison. Considering the historic records of bison mobility, and also the tendency for bison bulls to wander far, it is likely that interbreeding among most subpopulations was widespread. With few barriers and abundant gene exchange, there may have been few areas where bison were relatively isolated, allowing local adaptations to local conditions.

However, this view of an interbreeding megapopulation of bison is likely over-influenced by a historical record that emphasizes bison on the Great Plains. The degree of isolation among historical bison herds east of the Mississippi and west of the Rocky Mountains is unknown. A comparison of genetic characteristics of bison among eastern, central and western specimens of bison would be instructive in this regard. But there are few museum specimens of eastern and western bison. Geneticists have been "surprised" by the genetic diversity remaining in today's plains bison, considering the severe genetic bottleneck of very few animals that has occurred. But all of today's plains bison seem to have originated from the central herds. We do not know what genetic resources may have been lost forever

with the passing of eastern and western plains bison.

We must begin discussion of bison genetics with definitions of several terms.

Genes and Alleles

Simply put, a gene is a portion of a chromosome that corresponds to some "unit" of inheritance.[2] Alleles are the various forms of a gene that exist within a population of animals. For each gene, an animal has obtained one allele from each of its parents. Alternative forms of alleles may cause different results in the offspring. Thus, for a gene that influences resistance to some disease, there may be alleles that favor resistance and alleles that do not.

Genetic diversity has two components: heterozygosity and allelic diversity.

Heterozygosity - and Inbreeding Depression

An animal having two different alleles for a specific gene is called heterozygous. An animal with two copies of the same allele is homozygous. For a population, the proportion of animals that are heterozygous for a particular gene is a measure of population heterozygosity. The proportion of animals that are homozygous is the population's level of homozygosity. Populations that are more genetically diverse have a greater proportion of heterozygous, rather than homozygous, genes.

Some alleles are dominant. Their effects upon inheritance are fully expressed no matter what form of the allele has been obtained from an animal's other parent. Other alleles are recessive, being expressed only when an animal has both forms of the recessive allele. To complicate matters, some alleles are co-dominant. In co-dominance, if a different allele is obtained from each parent, both are still expressed in determining traits of the offspring.

Deleterious alleles may negatively affect an animal's ability to survive or reproduce. Consequently, deleterious alleles have a reduced chance for passage to the next generation and tend to be removed from a population through natural selection. However, recessive deleterious alleles may persist within a population because, being recessive, they are not always expressed in an animal and therefore are not always exposed to natural selection. Even so, deleterious recessive alleles are generally not common in a population.

Closely related individuals, such as parents and offspring or siblings, tend to carry some of the same recessive deleterious alleles. Breeding between closely related individuals – inbreeding - increases the probability that some offspring will inherit the same deleterious recessive alleles from each parent. In this condition, homozygosity, the deleterious traits are expressed, debilitating the offspring. In addition, inbreeding reduces the probability that individuals will inherit the benefits from having multiple forms of beneficial codominant alleles. Thus, inbreeding tends to produce individuals that are inferior at survival and reproduction. Inbred mammals tend to exhibit low fecundity, reduced growth, poor juvenile survival and lowered resistance to diseases. These negative results of inbreeding are termed "inbreeding depression".

There are evolved behavioral mechanisms that minimize breeding between closely related mammals (outbreeding behavior). The relationship between population size and the effectiveness of these behavioral mechanisms has not been studied, to my knowledge. I expect these mechanisms to be less effective in smaller populations. Moreover, the behavioral mechanism to minimize inbreeding could be a genetically controlled trait that may be lost whenever natural selection is replaced or weakened by genetic drift or by artificial selection, as discussed below and in Chapter 8.

Small populations tend to accumulate closely related individuals, necessitating inbreeding. The probability of inbreeding depression in a population depends upon (1) the frequency of inbreeding among animals as determined by population size and by the effectiveness of outbreeding behavior and (2) the abundance of recessive deleterious alleles in the population (termed "genetic load").

Avoiding inbreeding depression may be accomplished by maintaining

large populations. In domestication, inbreeding can be minimized by controlling breeding and replacing male breeders frequently. This avoids sibling, father-daughter and father-niece breeding. It is common practice in commercial bison herds and in many bison "conservation" herds. (Conservation herds are defined in Chapter 10.)

Genetic load of deleterious alleles seems to vary among species of mammals. Perhaps, due to normal social habits of some species, inbreeding has been more common during recent evolution, thus exposing and eliminating most recessive deleterious alleles. There is no evidence that plains bison have an unusually high or low genetic load compared to other mammals. However, the Texas State bison herd, originating from Charles Goodnight's captive bison and now kept at Caprock State Park, has experienced pronounced symptoms of inbreeding depression. This herd originated from but 13 animals in the 1880s, apparently was maintained at fewer than 250 for 110 years, and at about 40 animals during 1997-2002. It exhibited a low birth rate and low juvenile survival, probable in-uterine mortality, and sperm abnormalities. In recent years, the herd's growth rate has been essentially zero. To relieve this problem, bison from another herd have been bred into the Caprock herd. This managed outbreeding has reduced the symptoms of inbreeding depression.

For bison, about 400 - 500 animals may be required to avoid significant inbreeding.[3] This will vary with genetic load, with factors including the sex ratio and age structure of the population, and with the effectiveness of any behavioral outbreeding mechanisms. As noted above, inbreeding in smaller bison populations can be reduced by artificially controlling which bulls are allowed to breed. However, this replaces natural selection with human decisions and can lead to some degree of domestication.

Therefore, to avoid unacceptable levels of homozygosity and the risk of inbreeding depression, wild bison herds are most prudently maintained in populations of at least 400 animals. In Chapter 11, I note that 77% of the 44 herds of plains bison that are most important for conservation of the species in the USA fail to meet this standard.

However, the standard is usually academic, since a much larger population is required to avoid significant loss of allelic diversity in bison.

Allelic Diversity - and Evolutionary Potential

Allelic diversity is usually expressed as the average number of different alleles per gene-location (on a chromosome) in a population. A population with great allelic diversity has more evolutionary potential, compared to one with less allelic diversity. Thus, the ability of a population to evolve and adapt to a new or changing environment will be compromised by having a low allelic diversity. (Think of allelic diversity as the variety of colors on an artist's pallet. If the artist must select from few colors, the options for the resulting painting are limited.)

A population may have a limited allelic diversity because it originated with very few founders. There just weren't many different alleles to start with, and beneficial mutations that may add to allelic diversity are relatively rare events. Bison herds that originated from few founders are expected to benefit from an introduction of bison from herds with different genetic histories. This brings new alleles into the herd, enhancing its allelic diversity and its evolutionary potential.

For an established population, events that may increase the relative abundance of some alleles and reduce or eliminate other alleles can occur due to natural selection, to human intervention (artificial selection), or to random chance, usually referred to as genetic "drift".

Natural selection, with no or minimal influence by humans, is the benchmark of wildness. It is discussed later in this chapter. Artificial selection, or human intervention with the natural selection process, is discussed in Chapter 8.

Genetic drift is a change in the relative frequencies of alleles in a population due to random events that occur during reproduction and survival. Thus, chance determines which alleles are passed between generations, be they beneficial or harmful alleles.

A major source of genetic drift results from separation of

chromosomes with their alleles during the formation of ova and sperm. (Most cells have the "2N" number of chromosomes. When ova and sperm are formed in cell division, chromosomes are "split", leaving the reproductive cells with the "1N" number of chromosomes. Thus, uniting an ovum and sperm will form a new organism, again with the normal "2N" number of chromosomes.)

For the most part, random chance determines which of a pair of alleles are discarded into unused ova or sperm, and which alleles an offspring will obtain from each parent. In a large population, copies of most alleles are numerously replicated in many animals. Alleles that are discarded in some matings are retained in others, and allele frequencies in the second generation of a population will closely resemble allele frequencies in the first generation. Large changes in allele frequencies are unlikely because the vagaries of chance tend to "balance out" in large populations. Thus, an allele occurring in 25% of the animals in a large reproducing population is likely to occur in very nearly 25% of the next generation. However, if the reproducing population is small, a resulting allele frequency of 20% in the next generation is not improbable due to chance. (As an analogy, it is much more likely to get 3 heads in 4 coin flips than it is to flip 75% heads in 100 coin flips.) Moreover, in a third generation, the most probable allele frequency is no longer 25%. It is 20% (that of its parents) and it may, by chance, decline again.

In this manner, allele frequencies in a population will vary across generations. While new alleles are not added in this process, alleles may decrease in frequency and may disappear from a population when none of a certain allele happens to be transmitted across two generations. It matters not whether these alleles are beneficial or deleterious at enhancing survival or reproduction in the prevailing environment.

In addition to random events in forming ova and sperm, genetic drift may occur when random environmental events remove animals or otherwise prevent them from reproducing and passing their alleles to the next generation. Any bison may be struck and killed by lightning. Any bison may stumble and break a leg, reducing its ability to survive and reproduce. Several bison may break through ice and drown. These are essentially random events that may remove beneficial alleles from a bison herd.

Given enough time, genetic drift will eventually remove some alleles from a population, reducing its allelic diversity. However, the chances that alleles will be lost are greatest in small populations and for rare alleles. Scientists debate how large a population is necessary to assure retaining a desirable amount of allelic diversity. Variation in a population's sex ratio, age structure and breeding habits will influence the rate of losing alleles by genetic drift. Computer modeling suggests that a herd of 2000-3000 bison will lose an estimated 5% of its allelic diversity during each 100 years.[4] Smaller herds will lose even more of their allelic diversity. Note, we are already into the second century with plains bison existing only in pens and almost always with herds far smaller than this standard. This rate of loss will be significant for the future of plains bison. We do not know which alleles will be lost, nor understand their effects in determining traits of future generations of bison. The rarest alleles are most in jeopardy. Significantly, that part of the bison DNA that determines an animal's ability to detect and resist disease organisms is exceptionally diverse, but contains very many rare alleles that are most susceptible to loss.[5]

Moreover, genetic drift does not have to remove an allele from <u>all</u> animals in a population to weaken the effectiveness of natural selection. Alleles that enhance the animals' fitness have a random chance to be removed from many animals before their fitness benefits are realized and expressed in rates of survival and reproduction. Thus, "fit alleles" fare no better than do "unfit alleles". This weakening of natural selection will be most important in small populations.

Beyond allelic diversity, a bison population's ability to evolve and adapt to new and changing environments will be enhanced by the occurrence of beneficial mutations that add alleles to the herd. However, beneficial mutations are rare events. Their frequency of occurrence is directly related to the number of animals in a population. Thus a population of 2000-3000 bison is the <u>minimum</u>

number of animals needed to preserve most evolutionary potential of bison for the foreseeable future. However, I hasten to note that some biologists recommend at least 5000 animals are needed to maintain genetic diversity and evolutionary potential for more than the foreseeable future.[6]

Based on our knowledge of the cattle genome, a bison carries about 22,000 genes. Most of these genes are common to all mammals and are not threatened to be lost across generations of bison. However, many thousands of genes are subject to natural selection, artificial selection, and genetic drift. Across a large bison population, some thousands of these genes are each represented by more than one form of the gene, that is, by different alleles in different animals. We know very, very little about which alleles are associated with what traits of bison, or about how alleles interact to determine bison characteristics.

A geneticist has suggested that our knowledge of bison genetics is akin to looking through one window of the Pentagon, and deducing what goes on inside. Moreover, I suggest that rather few of us have enough knowledge of genetics to find the Pentagon. With all this uncertainty, extreme prudence is justified in determining how we conserve bison for future generations.

Population Sex-age Structure

<u>Sex Ratio.</u> In a wild bison herd, there are about as many adult males as adult females. The sex ratio is near 1:1 because mortality rates are similar for bulls and cows. A result of half the population being bulls is that, outside the breeding season, there are numerous small groups of bulls scattered across the range (Fig. 5.1). These bulls are at least 3 years old and usually travel in groups of 1 to 5 animals. Some bulls wander long distances, a habit that exchanged genes among subpopulations and may have resulted in range expansions for bison in the past.

For most of the year, cows, calves, yearlings and young bulls aggregate into large herds, separate from adult bulls (Fig. 5.2). They generally use large patches of the best available forage. Implications of this sexual segregation for bison foraging efficiency, energy

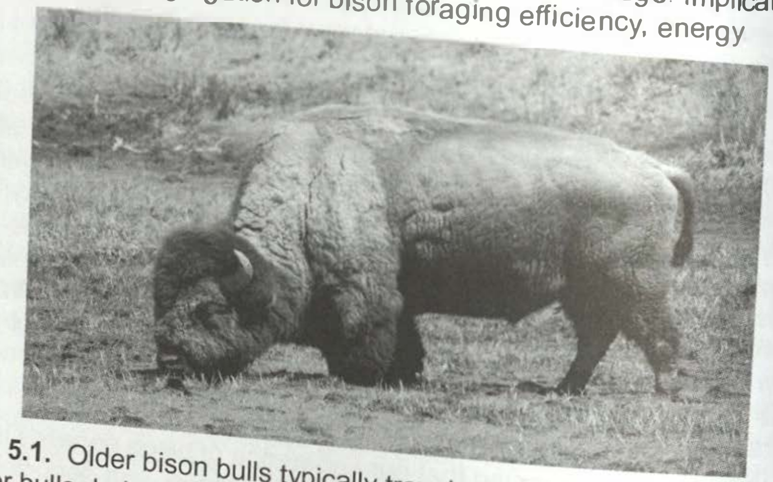

Fig. 5.1. Older bison bulls typically travel alone or with only a few other bulls during most of the year.

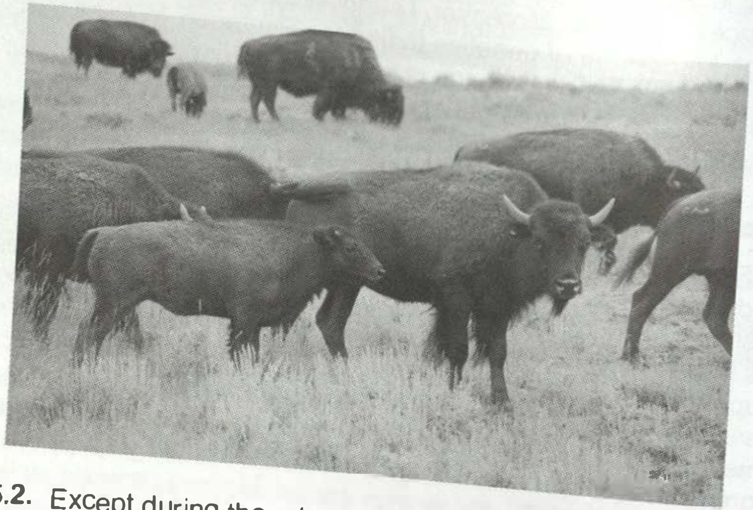

Fig. 5.2. Except during the rut, most bison travel in large mixed groups of cows, calves, yearlings and a few young bulls.

conservation, predator risk and grazing impacts on vegetation are not entirely clear. Likely, separation of small bull-groups allows a more even distribution of grazing pressure across the bison range. Small patches of quality forage are used by small groups of bulls. These patches will not support the large, mixed-sex groups; at least not without negative effects of close competition among animals. Consequently, we should expect the larger, mixed-sex groups of bison to use the largest available patches of quality forage. Moreover, separation of bulls for much of the year results in less competition for forage with their own offspring. Natural selection should eliminate bulls that reduce the fitness of their own genes in the next generation.

Largest aggregations of bison occur during the rut, or breeding season (Fig. 5.3). An even adult sex ratio results in intense competition among bulls for access to breeding cows. Early in the rut, large, dominant bulls that have proven their abilities to survive and to efficiently use forage resources will obtain most of the breeding. This is a major component of natural selection. Bulls that have proven their fitness do most of the breeding. But, in large bison herds, these dominant bulls seem to tire of the energy-expensive rutting behavior. They may leave the rutting herd, and leave the breeding of those cows that achieve late-season breeding status to less-dominant bulls. Still, with an even sex ratio in a large bison herd, there are numerous less-dominant bulls and the natural selective values of competition among them persist. Moreover, cows are known to exert some selection for mates.[7]

In commercial bison herds, only a few bulls are needed to impregnate all the cows. Consequently, production from limited forage resources is maximized by "running" more cows than bulls. The natural selection values of bull competition, and of cows selecting mates, are reduced or lost. Moreover, the potential for inbreeding is increased. This intervention with natural selection is also practiced in many of the 44 conservation herds (Chapter 11) of plains bison because (1)

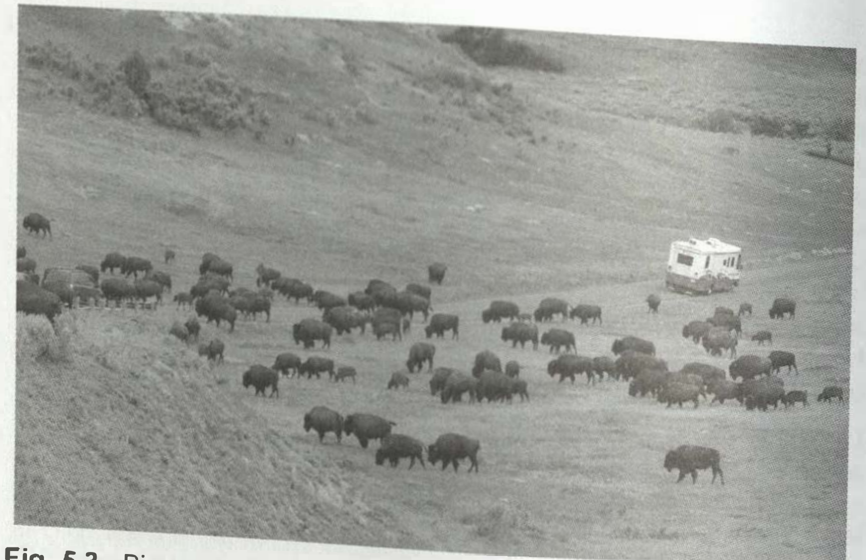

Fig. 5.3. Bison group sizes are normally largest during the rut, when old bulls join the mixed sex-age groups (R. Bailey photo).

many conservation herds are managed with incentives to produce and sell animals, just as in commercial herds; and (2) older bulls become more difficult to handle and therefore are more likely to be removed through culling at an earlier age compared to cows.

Age Structure. Age structure refers to the relative numbers of animals in each age class of a bison herd. Age classes might be year-cohorts, or – more generally – calves, yearlings, young adults, mature adults and aged animals.

Bison may live for 20 or more years. For bulls in wild herds, most breeding is accomplished by animals 8-12 years old. Cows usually produce their first calf at age 3 and may continue to produce beyond 15 years of age.

Survival and reproduction by older animals is an important component of natural selection. A bison's gene-based advantages for surviving, reproducing and leaving abundant genes in succeeding

generations will not be fully realized if the animal dies at an early age due to some random catastrophe or to artificial culling. In contrast, the advantages of the fittest bison will accumulate as the animal lives longer. Thus, having many old bison, at least 12-15 years of age, in a bison herd is an important contribution to natural selection. Artificially maintaining a young age structure reduces the effectiveness of this selection.

Age structures of wild bison herds will vary among herds and among years within herds. Bison herds living with wolves and bears usually have an older average age because calves and yearlings are more vulnerable to predation. Most increasing herds, perhaps rebounding from a few poor years of drought or severe winters, will have relatively more young animals. The sizes of calf crops and their early survival will vary among years, altering herd age structure.

On Antelope Island, Utah, a change in bison population age structure altered the herd's social structure. When the herd had been culled to maintain a younger age structure, the cow-juvenile bison normally dispersed into many small groups. After new culling practices established an older herd, the cow-juvenile bison aggregated into 2-3 large groups.[8] Implications of this change for natural selection have not been studied.

Since dominance is related to age and size of bison, the degree of competition faced by each individual can vary, not only with the number of competing animals, but with ages of competing animals. Thus, variation in herd age structure can contribute to variation of the intensity of natural selection for different survival and reproduction traits of bison. Fluctuating natural selection can be a mechanism for retaining genetic diversity in bison herds. This idea is developed more below, under "Population Fluctuations".

Competition, Dominance and Natural Selection

The social life of bison revolves around dominance and subordination. Most interactions either determine dominant and subordinate ranks, or are recognitions of already established ranks. Generally, larger and older bison are dominant over smaller and younger bison.[9] When resources are limiting, dominance enhances an animal's access to resources and therefore its fitness.

The major role of bull competition and dominance in determining reproductive success of bison bulls was discussed in Chapter 4. However, social rankings also partition access to resources among bison cows.[10]

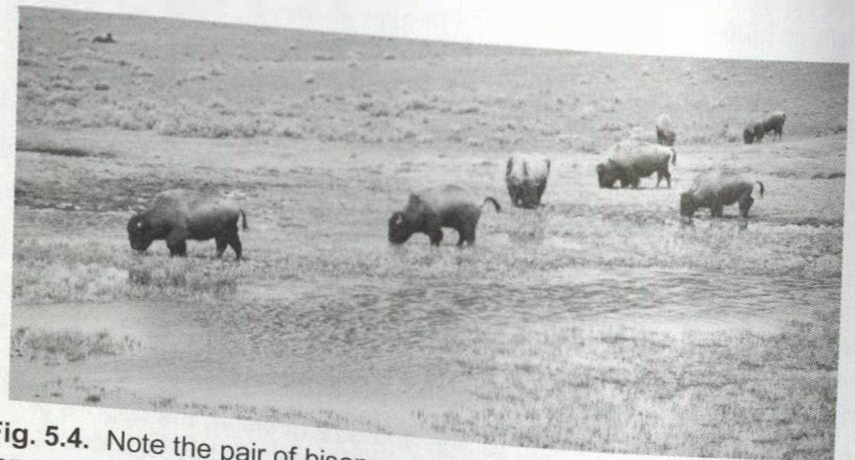

Fig. 5.4. Note the pair of bison competing for one small patch of forage near the center of the photo.

Subordinate cows have been observed to clear snow from a patch of forage, only to be displaced from their feeding crater by a dominant cow. Even in summer, during foraging bouts, dominant cows spend more time foraging and less time moving and searching for forage, compared to subordinate cows. This suggests that dominant cows have claimed and defended patches of forage with the greatest forage density (Fig. 5.4). In environments with predators, dominance may provide a cow, and perhaps her calf, with access to the safest position in the interior of the herd. Such disparities, in winter or

summer, enhance survival, growth and fat reserves of the dominant animal. This increases her ability to provide the most nutritious milk for her calf, and to attain sufficient weight to trigger ovulation and breeding in the next season. Likewise, the subordinate cow's ability to reproduce successfully is diminished. Dominance behavior therefore increases, not only the absolute number of the dominant animal's genes in subsequent generations, but – even more – the relative number in relation to genes of subordinate animals.

Population Fluctuations

In small bison herds, large fluctuations in numbers of bison should be avoided. Such fluctuations include periodic low numbers and will accelerate inbreeding and loss of genetic diversity. However natural fluctuations in population size have played an important role in determining selective forces that produced wild bison. When small herds are managed for stability of bison numbers, this component of natural selection is lost.

Stable wildlife populations are unusual. Most populations fluctuate without much notice. However, major declines and large increases are sometime obvious. Severe winters, periods of drought, periodic wildfires, and outbreaks of disease occur and fade away. Once, bison numbers responded to these vagaries of nature.

Healthy, wild bison populations fluctuate in abundance, and they live in environments where their habitat resources and their diseases and predators vary as well. However, it is not simply bison numbers; it is bison numbers in relation to the carrying capacity of their habitat that is uniquely important to the future of wild bison. Carrying capacity is the ability of the habitat to sustain a population. For large herbivores, forage quantity and quality are the most often considered elements of carrying capacity. Usually, they are the only elements considered. Carrying capacity will be determined by climatic factors such as moisture or drought that affect forage production, snow that determines forage availability, or by recent fire or recent grazing that affect available forage. Forage carrying capacity is constantly changing, within and among years.

The relationship of bison numbers to carrying capacity is termed "ecological density". A low ecological density is a few bison on abundant, quality habitat. A high ecological density is very many bison on limited or degraded habitat. In a wild bison ecosystem, bison numbers fluctuate, carrying capacity fluctuates, and ecological density varies accordingly. This natural variation is a characteristic of wildness.

I suggest that varying ecological density has been important in the evolution of wild bison. Factors of natural selection have varied in direction and degree between periods of low and high ecological density. High ecological density, often called "crunch time", generates selection for high levels of foraging efficiency, energy maintenance, and willingness to compete for forage. Aggressive bison adapted behaviorally and anatomically to cold, with stout digestive systems and energy-efficient physiologies have resulted. These characteristics are in jeopardy in most conservation herds of bison because bison numbers are maintained at artificially stable and low ecological densities. Crunch time never comes, and selection for these traits of wild bison is relaxed.

These selective factors operating at high ecological densities of bison seem obvious. But, are recurring periods of low ecological density equally important for maintaining some traits of wild bison? The answer is more speculative.

Bison bulls with a genetic tendency to divert a greater proportion of their nutritional resources toward growth of display anatomy – large horns, long beards and luxurious leg chaps – may be disadvantaged in periods of high ecological density, when a more conservative strategy is more successful, especially for survival. But they may be more successful than bison with more conservative nutritional/growth strategies during periods of low ecological density when forage is abundant and available. (Admittedly, there is much epigenetic variation in bison growth as animals respond to nutritional conditions. However, this does not preclude some gene-based variation in

growth patterns that may be exposed to natural selection.)

Implications of varying ecological density for natural selection of reproductive strategies of bison bulls are not clear. Bulls will compete aggressively for mates at either high or low ecological density. Energy-expensive competition for mates may be more intense at low ecological density when expenses can easily be recovered in the abundant foraging habitat. At high ecological density, dominant bulls may die earlier or may retire from the rutting groups relatively early, leaving some cows to be bred by less-dominant, perhaps younger bulls.

At high ecological densities, most cows do not breed until they are 2 or even 3 years old. Many do not breed every year because their physiology requires them to put on sufficient fat reserves before achieving breeding status. For each cow bison, the emphasis is to assure personal survival while producing a few, high quality calves with high probabilities for their own survival in a habitat with a high ecological density of competing bison.

In contrast, during periods of low ecological density, cows with less conservative reproduction strategies may be favored. The costs of producing a calf at an early age, or in successive years, can easily be made up in the abundant habitat. With abundant forage and few competitors, that is, low ecological density, cows with a "gambling" reproduction strategy can be successful. They gamble that breeding early before completing their own growth, or that breeding every year with perhaps less sufficient fat reserves, can still be successful. During periods of low ecological density, the gambling strategy may provide more calves and genes in the next generation than will the conservative reproduction strategy.

Thus, a fluctuating ecological density should provide alternating variation of natural selection that maintains the genetic bases for both conservative/competitive and gambling/less aggressive animals in the herd.

However, the common practice of managing bison herds at constant population sizes, usually at low ecological density, should diminish genetic diversity. The gene pool becomes specialized for living at one constant ecological density. This is a form of "stabilizing selection". Fluctuating ecological density is a much neglected aspect of wildness in plains bison conservation.

In addition to the genetic aspects of varying ecological densities of bison, I would expect the ecological functions of bison – their impacts upon plants and other animals - will vary with bison numbers and bison ecological densities. Some functions will be intensified, or reduced or lost when bison are artificially maintained at a constant number of animals. There has been little study of the implications of fluctuating bison numbers for all the other species that share grasslands with bison.

Natural Selection and Evolution

Evolution is any change across generations in the types and relative frequencies of alleles. New, beneficial and successful alleles are a rare occurrence and they contribute very slowly to evolution. However, alteration of the selective forces, including genetic drift, working on the existing array of genes in a population, may cause more rapid – though not always obvious – evolutionary changes. These changes are permanent when alleles are lost.

Bison evolution has not ended. Genetic change is most rapid in small herds subjected to a preponderance of artificial selection based on human decisions – leading to domestication. This is most obvious in commercial bison herds. But genetic change is occurring in our "conservation herds" as well. In a few studies of bison genetics, detectable changes in herd genomes have occurred in as few as 5 to 8 generations (40 to 64 years).[11] One study suggests that disease management interventions have already altered the genetic compositions of some bison herds with respect to their natural resistance to brucellosis.[12]

If we are to retain wild bison for future generations, we must address the process of evolution and the combined effects of few founders,

cattle-gene introgression, inbreeding, genetic drift and artificial selection in weakening or replacing natural selection. As we pass the bison genome to succeeding generations, we give too little thought to what this legacy will be.

Footnotes:

[1] Leopold (1933) referred to the recreational value of wildlife being compromised by artificial management, but all other wildness values (Chapter 6) are also diminished.

[2] Geneticists, bear with me. I am trying to communicate a necessary amount of genetics to the layperson. Most are familiar with "genes" and "chromosomes". "Alleles" and "loci" are unfamiliar terms, and I have avoided the latter.

[3] Gross et al. (2006) suggested 400 bison as needed to retain 90% heterozygosity over 200 years. Perez-Figueroa et al. (2010) concluded 500 bison would retain 95% heterozygosity over this period. What level of loss of heterozygosity is "significant" is a judgement call. However, we should have high standards for at least a few bison herds somewhere in the USA.

[4] Perez-Figueroa et al. (2010). The computer modeling of gene flow across generations conservatively assumes no effective outbreeding behavior in a Yellowstone bison population of this size. While some outbreeding behavior may, and probably does, exist, its role in these population genetics is unknown. In managing the only large, almost-wild population of bison south of Canada, prudence suggests accepting the implications of this study.

[5] This important region of mammal DNA related to disease resistance is termed the "major histocompatibility complex". I used the extensive review provided by Wikipedia.org for information.

[6] Traill et al. (2009). About 5000 is the estimated number of animals needed for alleles lost to genetic drift to be matched by the same

number of alleles gained through mutations. Thus, decline of allelic diversity would be 0.

[7] Lott (2002).

[8] Personal communication, Steve Bates, biologist, Utah Department of Natural Resources.

[9] Roden, C., H. Vervaecke and L. Van Elsacker. (2005).

[10] Lott (2002).

[11] Halbert et al. (2012).

[12] Seabury et al. (2005).

Chapter 6

Values of Wild Plains Bison

The several values of all wildlife are largely taken for granted by most Americans. Most of us enjoy seeing wildlife and we support wildlife conservation. Perhaps it is a part of human nature to wonder at all the diverse, colorful, interesting critters that we find near home and especially in places we refer to as "wild". Just seeing a mountain lion, grizzly bear, gray wolf – or wild bison – is a unique and memorable event for most Americans. For many, it is a once in a lifetime.

But economists and others who must track costs, benefits and values in public management plans and environmental impact statements find the pervasive "Oh wow!" attitude of Americans toward wildlife to be a bit "fuzzy" for analytical purposes. So it behooves us to analyze, "What good are wild animals?" Too often, a poor and incomplete answer to this question has diminished the future of wildlife in competition with other, often commercial, resources that compete for space on the American landscape.

I will briefly describe the types of values inherent in all wildlife, with emphasis on wild bison.

Recreational Value

Recreational value of wildlife is very personal and recognized by nearly everyone. It is the joy, wonder, excitement, fascination and accomplishment inherent in observing, feeding, hunting, fishing and studying wildlife. For family members and friends, it includes the camaraderie of experiencing the natural world together.

The above definition of recreational value of wildlife relies on human emotions in response to wildlife. Those who would push wildlife aside for usually commercial purposes often criticize this value of wildlife as too emotional – still to "fuzzy" for hard core analysis. However human life is an emotional experience. Do we discount the value of human life because it is "too emotional"?

For each of us, the recreational value of wildlife increases in