Population Genetics and Wildlife Management

What is a genetically "healthy" wildlife population? How do we recognize an "unhealthy" population? And how can we maintain or promote population genetic health in wildlife management? Answers involve three complex issues of population genetics: inbreeding, genetic drift and natural selection.

> Below, indented paragraphs are additional details, examples and explanations. Many readers will not need to read all indented material. Words that may be unfamiliar to some are printed bold where they are defined.

> In discussions of wildlife population quality, terms such as genetic health, genetic integrity and genetic quality are often used. However, complete definitions are frequently lacking, probably due to the complexity of the subject, which I try to address here. Below, I propose the term "genetic adequacy", with a definition. Still, my definition depends upon the several concepts preceding it in this text.

Today's Wildlife Population Management

Most managed wildlife populations are controlled with little attention to genetic issues. This approach was sufficient when the vast majority of wild populations were large and connected across large areas of diverse habitat. Probably, most management activities had minor influences upon genetics of most populations. But today, we manage an increasing number of smaller, isolated populations – with increasing frequencies and intensities of management interventions. And this trend is accelerating into the future. Neglecting population genetics in our wildlife management is no longer justified. Genetic healths of many populations, and of some whole species, are in jeopardy.

When there is management concern for genetic health of wildlife, most attention involves two problems influenced largely by population size: inbreeding and loss of genetic diversity due to random genetic drift. Mostly, wildlife managers address inbreeding by maintaining a population size that is believed sufficient to avoid an arbitrarily chosen level of inbreeding. If there is also concern for genetic drift, a still larger population is maintained to avoid exceeding an arbitrarily chosen rate of loss of **alleles** (kinds of genes) due to drift. I have discussed these issues elsewhere in the *Essence of Wildness: Lessons from Bison*[1].

I contend our standards for allowable inbreeding and genetic drift, if addressed at all, are often "arbitrarily chosen" because these standards rarely have a strong biological basis in any understood population genetics of the local population. Standards are influenced by (1) theoretical calculations based on similar, often hypothetical populations; (2) comparing limited samples of genetic diversity between the local population and a larger population that is only assumed to be "genetically healthy"; and (3) social and environmental constraints upon the local population, when these constraints bias managers' interpretations of the genetics evidence toward conclusions that best fit the political environment and/or commonly accepted management paradigms from the past.

> Note: the negative consequences of poor genetic health may accumulate slowly, often

over timescales exceeding professional careers; whereas avoiding disputes with dominant constituents or accepted management paradigms can produce immediately convenient management solutions. Recommendations of wildlife managers may be constrained by agency policies that arise from a lack of understanding and leadership at higher levels of government. Consequently, there is little ability or incentive to explain the consequences of complex genetic issues to the public owners of wildlife. Management of a public trust resource fails due to a breakdown in the quality of trustee-public communication.

A metric for genetic drift, loss of 5% of alleles each 100 years, was first used only as a way to express this rate of loss. However, management agencies have adopted it as an acceptable rate of loss. Since we don't know what alleles are being lost, nor how they function, there is no biological basis for accepting and promoting this rate as an acceptable management goal.

Inbreeding

Often, inbreeding is ignored so long as anatomical symptoms do not occur, or – more likely – are not noticed in a wild population. However, inbreeding problems may include physiological or behavioral issues including poor biochemical balance, improper organ function, altered social behavior and susceptibility to disease. These symptoms are not easily recognized in wild populations. Obvious effects of inbreeding may be episodic, depressing survival or reproduction more during times of stress, such as a more severe winter or during a periodic disease challenge. During such periods, poor population performance is usually blamed on the environmental stressors, neglecting the interacting role of inbreeding. Lesser population-level effects of inbreeding during other years are more likely unnoticed. However, chronically poor reproductive success is easily blamed on predation, ignoring the possibility of inbreeding effects.

Obvious symptoms of inbreeding have been observed frequently in wildlife[2]. In addition, at least 2 blind bison calves have been born to a small herd that was restricted in numbers and breeding opportunities according to a research protocol designed to study quarantine effectiveness. The small Texas state bison herd had poor calf production and survival, with abnormal sperm and clear inbreeding evidence obtained in genetic analyses.

However, many populations of mammals are managed with numbers that must illicit less obvious effects of inbreeding that should compromise population performance. These include notable populations of bison, bighorn sheep and some endangered species - for which the possibility of inbreeding is often unrecognized.

Diminished resistance to disease due to inbreeding has been documented in wild and domestic populations. Infection rates, survival, and recovery times are affected by inbreeding. Inbred animals may persist longer as infective hosts, maintaining disease within a population. In wild vertebrates, inbreeding has been shown to reduce resistance to invertebrate parasites (bighorn sheep, sea lions) and to bacterial pathogens (wild boar, finches).[3]

Most recommendations are to maintain a few hundred breeding animals to avoid levels of inbreeding that will "significantly" depress reproduction and/or survival.

In 1980, it was proposed that an "effective breeding population" (Ne) of 50 would be needed to avoid a significant amount of inbreeding in a wild population. More recently, an Ne of at least 100 has been proposed for this purpose.[4]

For most wild vertebrates, Ne may be 10-30 percent of the total adult population[5], requiring an adult population size of 167-500 for an Ne of 50, or 333-1000 for an Ne of 100, to avoid negative effects of inbreeding. Four hundred animals is a commonly used compromise, without scientific basis. However, inbreeding effects are not absent in larger populations.

In Scotland, long-term intensive study[2] of a population of 1000-2000 red deer detected inbreeding effects upon calf birth weights and first-year overwinter survival of calves. Lowered birth weights occurred in calves from closely related parents - at the level of father-daughter or half-sibling parents. Overwinter survival of calves was negatively correlated with inbreeding, even to the level of first- or second-cousins as parents.

It may be argued that the lesser effects of inbreeding have little or no impact on population size because losses due to inbreeding may be compensatory; that is, the same number of animals would die each year, with or without inbreeding (the argument is that inbreeding losses replace, do not add to, other kinds of losses.) This is a risky and short-sighted argument for managers to choose. However, some small, likely inbred populations have been maintained for up to decades while we ignore losses of genetic diversity and adaptability and increasing susceptibilities of populations to eventual periods of severe stress, including disease.

Lastly, inbreeding can contribute to a weakening and replacement of natural selection, dismantling wild genomes and discarding valuable characteristics of wild populations, as discussed below.

A genome is all the alleles - forms of genes - that occur in an animal or in a population. Many animal characteristics are polygenic – they depend upon interacting sets of alleles. In these interactions, most alleles have small individual effects upon animal characteristics. Population genome quality depends upon the distribution of alleles, and of interacting sets of alleles, among animals.

Genetic Drift

Compared to inbreeding, loss of genetic diversity and, especially, decline of genome quality, due to genetic drift are recognized far less in wildlife management. Genetic drift refers to among-generation changes in a population genome that occur due to randomness, not due to any selection for or against any alleles. In all populations, random factors determine which alleles occur in successful ova and sperm. Random factors of the environment also influence survival and reproduction of many animals.

In the transfer of alleles from parent to offspring, half the parent's alleles are discarded essentially at random as pairs of chromosomes are reduced to single chromosomes in ova or sperm (the process of meiosis).

The role of randomness in environmental factors that determine which animals survive and reproduce is more complex. Removal of animals can be completely random. Some intensively controlled populations are routinely reduced with human efforts to achieve

random culling. Accidents may kill animals at random, that is with no selection for whatever alleles occur in the victims.

However, for most environmental causes of death, there must be selection for a part of the population genome, while these losses are also random for other parts of the genome. For example, losses due to highway mortality may select for alleles that enhance alertness and agility. These same losses can be random with respect to alleles that enhance energy efficiency, ease of birthing, or other functions related to survival.

(This deduction is correct only to the extent that alleles for alertness and agility do not tend to occur together with alleles for energy efficiency, etc. in a pattern called "linkage"; – or, to the extent that some functions, such as energy efficiency do not influence other functions, such as alertness. This complexity defies our attempts to model and predict genetic drift and to produce objective standards for managing drift.)

Due to random effects, some alleles will happen to increase, while other alleles happen to decrease between generations of animals. (Allele frequencies are "drifting". The frequency of an allele is the percent of animals that carry the allele.) Over long time periods, some alleles will decrease, by chance, over some number of successive generations and thus, may decline to zero and be lost from the population. The probability of losing alleles increases with time and is greater in smaller populations. Rare alleles are most at risk. With drift, loss of alleles will decrease a population's ability to adapt to future changes in its environment.

Decades ago, it was proposed that an effective breeding population (Ne) of 500 animals would be needed to offset loss of alleles due to genetic drift.[3] With Ne = 500, it was hypothesized that mutation would add viable alleles to the population at about the same rate that other alleles would be lost, thus retaining allelic diversity of the population. However, the functions of both the added and the lost alleles would remain unknown. Moreover, with an Ne of 500, effects of natural selection in favoring beneficial alleles would be relaxed; as would selection to purge the genome of mildly deleterious mutations that occur in every generation. This has led some authors to contend that an Ne in the range of 1000-5000 is necessary for long-term maintenance of population genetic quality.[3]

For large vertebrates, an Ne of 500 would require about 1667-5000 animals in a population; whereas an Ne of 1000 would require 3333-10,000!

In addition, drift diminishes genetic quality of a population for surviving and reproducing in the current environment. Random factors compete with selection to determine changes in allele frequencies across generations. Randomness is most important when selective forces of the environment are weak. Selective forces are weak in small populations living below ecological carrying capacity and relatively weak during periods between episodic stressful events such as severe winters or disease outbreaks. A dominance of random drift in determining the future population genome produces a decline in genetic quality. Selection for alleles that best suit animals for reproducing, competing and surviving in the current environment, or during periods of stress, is diminished and some of these alleles drift to become less frequent in the genome.

Note: when an allele becomes less frequent in the genome - say it occurs in only 10 percent of the population – the allele's occurrence in conjunction with other alleles with which it must interact to produce presumably valuable animal characteristics may decline to an even greater degree – perhaps in only 5 percent of the population. (Gene linkages,

the tendency of genes to be transmitted together, will reduce this latter problem. However, the frequency of gene linkages is largely unknown.)

With increasing human dominance of landscapes, more hunted wildlife populations are managed to achieve stable numbers well below ecological carrying capacity. The intentions are to maximize the number of animals produced for harvest[6], to minimize the embarrassing number of animals that may be lost during episodic periods of increased stress, or to limit wildlife impacts to human property. This low ecological density of animals weakens natural selection, largely replacing it with human harvests that are random with respect to most of the population genome. Genetic drift may become the dominant factor determining the future of the genome.

Thus, genetic drift diminishes the population's evolutionary potential for adapting to future environments; and also diminishes the population's adaptedness to the current environment by dismantling the effects of past evolution. While relatively long-term losses of genetic diversity and evolutionary potential due to genetic drift are uncommonly recognized in wildlife management, short-term dismantling of current genome quality due to drift is recognized even less.

Fitness

The concept of animal or population fitness is related to genetic health. In evolutionary biology, "fitness" is most often used to describe the success of one animal, or a class of animals within a population, at surviving, reproducing, and leaving descendants in a succeeding generation. Thus, we may compare fitness between classes of animals, such as gene-based color phases (black vs. gray wolves, brown vs. gray phases of tawny owls).

With fitness as a standard for population success, demographic parameters (reproduction, survival) are used to represent all the anatomical, physiological and behavioral traits that remain unmeasured and little understood.

Fitness is a useful concept because it can be measured directly. We can measure reproduction, survival, or the number of descendants. However, used this way, fitness is a narrower concept, compared to genetic health. Fitness describes the performances of animals at one time in one observed environment. Fitness does not imply genetic diversity, the basis of evolutionary potential. (An inbred strain of domestic animals may demonstrate great fitness in its domesticated environment; but fail miserably in the wild.)

Ecologically oriented evolutionary biologists may expand the notion of fitness and apply it to whole populations in dynamic environments. In this sense, evolution in a fluctuating environment has produced a genetically diverse population of animals that is best suited for dealing with the fluctuating opportunities and challenges of that environment. It best "fits" that environment, which I describe as its "naturally associated environment". At this level, fitness overlaps, perhaps completely, with genetic health.

Wildness and Natural Selection

Millennia of evolution and natural selection have produced wild animals. We value their wild

characteristics such as alertness, agility, hardiness in the wild, and disease resistance. However, current microevolution can alter wild genomes within a few to several decades. Therefore, a preponderance of natural selection is necessary to maintain the wild characteristics of wildlife.

I have argued[1] that natural selection is an inefficient but conservative process, because alleles are not directly or individually exposed to the environment. Consequently, natural selection is easily weakened or replaced by (1) inbreeding that causes deleterious recessive alleles to outweigh the values of beneficial alleles in some animals, such that inbreeding, not natural selection determines their survival; (2) genetic drift that replaces selection with random factors affecting some animals; (3) artificial selection by harvest or other human-caused mortality or by selective breeding; (4) human interventions such as winter feeding or vaccinations that avoid natural selection; (5) restricting population size such that limitations of the environment are avoided in most years; and (6) a monotonous environment, lacking a diversity of natural-selective factors, including effective predators and a diversity of habitat resources. Many wildlife populations have significant combinations of some, or all, these characteristics.

Some intensively hunted big-game populations are maintained well below ecological carrying capacity, often with skewed sex ratios. Natural selection associated with high ecological density, and with male aging and competition, is greatly weakened or eliminated. (Photo: Texas Parks and Wildlife Department)

Note that the types and intensities of natural selection vary greatly among sex/age classes of animals. Examples: Selection for characteristics associated with abundant reproductive success varies greatly between males and females. In males, selection for competitive behavior can vary with the age of the animal. Such variation complicates understanding and hinders the measurement of natural selection.

A wild population is influenced by a preponderance of natural selection. Without effective natural selection, we expect a redistribution of alleles across the population genome, gradual accumulation of slightly deleterious alleles, and loss of some "wild-type" alleles – the gradual and insidious process of domestication. Wild is the opposite of domestic. There is a continuum of wildness from the most domesticated to the most wild. The continuum depends upon the relative abundance of natural selection. A crude, but useful, measure of wildness is the proportion of the breeding population that dies due to natural causes.

Wildness deserves more discussion in the wildlife management profession. It is seldom considered when managers determine goals for population size or harvest levels. While there is concern for genetic diversity of some populations, there is usually no recognition of

whatever environmental factors are altering the population genome, or allowing it to drift away from a high level of adaptation to the current, but dynamic, environment. Dismantling of valuable wild genomes must be common.

Genetic Health vs. Genetic Adequacy for Wildlife

A genetically healthy population must be large enough to avoid significant inbreeding and also to maintain sufficient genetic diversity and evolutionary potential for adapting to future environmental conditions. This, alone, is sufficient for domesticated populations, but inadequate to maintain wild populations. Wildlife should be genetically healthy and also genetically wild.

I have defined[1] a genetically adequate wildlife population as being (1) large enough to avoid significant inbreeding and to maintain genetic diversity for (a) retaining wild characteristics bequeathed from past evolution and (b) retaining evolutionary potential for responding to changing environments of the future; and (2) is influenced by a preponderance of natural selection rather than by small population effects and/or by weakening of natural selection with human interventions and impacts.

A genetically adequate wildlife population is not a number; not a certain population size. It is a concept. Across ranges of population size and environmental conditions, there is no distinct point at which a population becomes adequate, such that with one less animal, or one small change in the environment, the population becomes inadequate.

The Future of Wildlife Management

Population genetic adequacy, is a far more complex concept than many users of similar terms imply. For wildlife, it is more than just genetic diversity; it involves more than just population size; it includes standards for natural selection in the population's environment. This is unsettling to wildlife managers who must explain management goals and plans to the public, and to higher level trustees in an administration or legislature. Promoting an arbitrary goal for population size is easier than discussing population genetics and evolutionary biology. But success in promoting an arbitrary number relies upon a public lack of understanding of wildness and, therefore, a public inability to judge the management program, or to judge the positions and pronouncements of elected legislators and agency leaders. Arbitrariness does nothing to reduce that lack of understanding. It is a major failure of the public-trustee relationship[7].

> I do not minimize the problems of managing wildlife genetics. A large mammal may have over 3000 genes that may vary among animals across space and time. Moreover, this variation involves a few to very many forms (alleles) for each gene. Many thousands of different alleles may occur in a wildlife population. Almost every animal has a unique combination of these alleles.

Mostly, we look at alleles simplistically. We measure allelic diversity of populations in a small number of ways. Almost always, we don't know how the alleles we measure function as very many overlapping sets of co-operating alleles to influence anatomy, physiology and behavior and ultimately, the success of populations. Too often, this immense variation among individuals and among subsets of animals, and this uncertainty, are ignored in wildlife

management. It won't be easy, but we can do better.

First, we should enhance the awareness and understanding of population genetics within our management agencies. Much of the science dealing with population genetic quality exists in esoteric journals filled with obscure jargon. There is a need to transfer this information in a simpler format to management biologists. There is an equivalent need for management biologists to seek the information.

Second, we should enhance public awareness of the issues of wildness and population genetics. In a world with competing land uses and declining amounts and diversities of wildlife habitats, we are often unable to provide genetically adequate wildlife. The public is largely unaware of these issues. Mostly, public support for or opposition to management projects is based only on resulting short-term impacts to animal numbers, with little concern for population quality. The profession of wildlife management can do more to clarify the limits and requirements for genetic adequacy, including evolutionary potential and wildness of populations. This is necessary to develop support for alleviating the problems of genetically inadequate wild populations.

We should use the term "minimum viable population" far more judiciously, if at all. Estimated minimum viable populations are really "minimally viable" populations. Emphasizing quantity of animals neglects many aspects of population quality, including diversity, wildness, and ecological functions as well as genetic quality. Promoting a single population number as the edge of viability is an illusion. Often the illusion is provided with science-credibility using computer models that have limited and imprecise input variables. Justifying management actions with pseudo-credible estimates of minimum population viability is public deception. An honest analysis of a management proposal would involve mostly qualitative descriptions of how the management action would diminish or enhance population size, distribution and all aspects of population quality – compared to alternatives.

As a legacy to the future, we should identify some populations for the goal of genetic adequacy, including wildness. For these populations, management priorities should include large, naturally fluctuating population sizes, large diverse environments, and limited management interventions to maintain a preponderance of natural selection.

We can begin with more recognition of the rare values of unimpaired ecosystems, where wildness is emphasized, particularly in our larger national parks. Too often, state agencies promote hunting in national parks, exhibiting their failure to understand the values of unimpaired ecosystems. To retain resources unimpaired for future generations is a most basic mandate of the Park Service. Proposals to vaccinate animals, use artificial birth control, and to limit numbers of wildlife within parks would impair natural selection and the wild genetic qualities of populations. In recognition of the unique values of our larger parks, state wildlife agencies should consider buffer zones with limited artificial management and control where wildlife migrate across park boundaries.

Management interventions, including harvests of animals, are most effective at enhancing genetic drift and weakening or replacing natural selection when affected populations are small. It is especially important to consider the need for interventions, and to minimize interventions, with small populations.

But with the environmental limits of today's world, we will continue to intensively manage many, often small, genetically inadequate wildlife populations. Intensive management will include periodic genetic rescue with transplants of animals. Seasonal feeding and intensive

disease management may be necessary and justified, just to maintain such populations. These will be semi-wild populations, at best. For these populations, there should be management effort to minimize the six factors, cited above, that weaken or replace natural selection. As an index to genetic adequacy, there should be periodic evaluations of the numbers of adult breeding animals that die naturally vs. numbers that succumb to human-caused mortalities.

We should stop recognizing natural mortalities only as a "waste" of animals that might have been harvested. The values of natural selection should be identified to the public. Disparaging natural mortality is "cow pasture biology", not wildlife management.

The profession of wildlife management can do more to recognize, understand and apply the concepts of population genetic adequacy. The basic concepts described above are not so difficult. Difficulty arises mainly in that there are so many complexly interacting factors that influence genetic adequacy. Moreover, the operative factors vary among populations and among times within populations. With so much uncertainty, a conservative approach – at least for selected populations with wildness goals – is to assure considerable natural mortality, maintain a diverse environment, and minimize management interventions. For the sake of the marvelous values of wildness, we can do better.

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