POTENTIAL GENETIC EFFECTS OF

SMALL POPULATION SIZE IN

WILDLIFE

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ABSTRACT

To be most effective, a program of game management must recognize that
a wildlife species is not genetically uniform. Moreover, the genetic
quality of a population is subject to degradation if care is not taken to
assure its quality. This paper discusses some sources of genetic quality
and steps which may be taken to assist in its preservation.

INTRODUCTION

Wildlife managers are paying increasing attention to the genetic
quality of the populations they manage. Yet current practices fall far
short of producing the advantages that would result from optimal genetic
management. There are several bona fide reasons for this lag. First, an
appreciation of the genetic diversity present in natural populations has
only recently been developed. Second is the difficulty in resolving the
biological significance of this diversity. Third, the curricula of
wildlife management trainees has not emphasized genetics.

Wildlife management has rightly emphasized habitat improvement as a
means for improving the quality of the species in question. The value of
this approach, when properly applied, is incontrovertible. However,
another important component of the species-habitat system is the genetic
quality of the population. An understanding of the nature of this
component of the system together with the ability to manipulate it, could
pay great dividends. The manager's work could be made more productive and,
perhaps, at less expense. The genetic lessons learned by breeders of
domestic livestock are readily applicable to many problems with wildlife.
Failure to exploit the potential values of genetic management would be
unjustified.

In working out practical procedures for genetic management, the first problem is to determine the kinds and extent of genetic diversity present in the species. Some differences may be relatively simple, e.g., those between snow geese and blue geese. These are referred to as qualitative traits. At the phenotypic level they are usually so rare, or of such small biological significance, that they are of little value as tools in wildlife management. However, at the biochemical level discrete differences such as those seen in different forms of enzymes or other proteins may be valuable in evaluating the genetic structure of populations.

In contrast to simple qualitative variation, quantitative differences are of much more interest to the game manager because such traits as reproductive performance, growth rates, and stature fall within this category. Unfortunately, the genetic basis of these traits is not as clear-cut as with qualitative traits. Moreover, in general, environmental effects appear to be more important in the determination of the definitive phenotypes in these cases. Nonetheless, they are of such importance that the extra effort required to tease out the role of the genes in the quantitative traits is well repaid. For example, feed efficiency, rate of gain and egg production in chickens have all been vastly improved through the application of the proper techniques of genetic management.

Genetic diversity is maintained by the action of four factors; mutation, gene flow, normalizing selection and large, stable population size. Mutation typically results in the introduction of a small, steady flow of new genetic material into the gene pool. Admittedly most of these newly arisen variants are soon lost from the population simply due to chance even if they do not convey a disadvantage on the carrier. However, some few, usually those conveying some slight advantage or with effects nearly neutral as compared to the pre-existing alleles, will be retained or even increase in the gene pool. Hence they contribute to the maintenance of genetic diversity.

Gene flow was long considered to be a major source of genetic diversity. It has its basis in migration, i.e., animals migrating from one population and being incorporated into the breeding stock of another population would introduce "foreign" genetic materials. The extent of gene flow in natural population was examined by Raven and Ehrlich (1970) and they concluded that it was far less significant force in maintaining diversity than has been previously assumed (Mayr 1963). Fortunately, for the game manager, the ability to transplant stocks permits him to use artificial gene flow much more effectively than might occur in natural populations.

Normalizing selection describes the situation in which those individuals lying near the mean of the population distribution leave relatively more offspring in the next generation than those lying near

either extreme. The effect of such selection is to maintain the structure of the population in its present state. Since individuals lying near the mean are usually heterozygous at more loci than those at the extreme, then normalizing selection acts to maintain genetic diversity by tending to keep contrasting alleles in the gene pool. Without doubt, this is the most important mechanicsm responsible for maintaining diversity.

The reason large, stable population size tends to maintain diversity is that under these circumstances genetic drift cannot be very effective. Genetic drift is an outcome of small population effects. Imagine flipping a penny ten times. A result of 7 heads and 3 tails would be no great surprise, but it would be a 20 percent deviation from the expected 5:5 ratio. Next, imagine a trial of 100 flips. A result of the same percent deviation, i.e., 70 heads and 30 tails would lead you to suspect something was wrong with the coin. In just the same way, variation in genetic structure of populations can be affected by the number of trials. A large stable population of 1000 individuals would have 2000 gametes drawn every generation to form the next generation. A population of 10 would result from only 20 gametes. Other factors being ignored, the expected proportion of the gametes drawn in each case would be predicted by the proportions of the various alleles present in the preceeding generation. However, in small populations, the potentiality for deviations from expectations are greater than in large populations. Consequently, changes in allelic frequencies simply due to the accidents of gametic sampling are expected to occur more often in smaller than in larger populations. This phenomenon, called genetic drift, has potentially dangerous consequences in wildlife management. It is one mechanism by which the genetic diversity of a population may be degraded.

So far we have discussed the nature and maintenance of genetic diversity, but have not specifically addressed the issue of its biological significance. It might initially appear that a genetically homogeneous, phenotypically uniform stock might be more easily managed than one with greater diversity. But let us examine the consequences of reducing diversity by considering inbreeding. Inbreeding of close relatives is a very effective way to reduce the range of genetic heterogeneity in a population since it tends to eliminate certain alleles and increase the proportions of their alternates. One of the most often cited cases of reduction of fitness is seen in corn (Zea mays) (Neal 1935).

Figure 1 shows the effects of inbreeding on yield. Not only plants, but animals also show these effects as shown by the work of Albolanalp (1974). Some of his data are presented in Table 1.

The data in Table 1 were derived from lines which were only 25 percent inbred. Yet, the reduction of quality in important traits is obvious. Note also the rather striking differences when comparing chickens and turkeys with quail and chukars. The two former species have been under domestication for a long period and have undergone extensive inbreeding during this period. This would have exhausted part of their genetic

diversity and consequently reduced the potential for further inbreeding depression. The quail and partridge are nearer the natural condition and the drastic effects on these species should be noted by those who would attempt genetic management of wild species. They are much more subject to the degradative effects of inbreeding than species which have a long history of domestication.
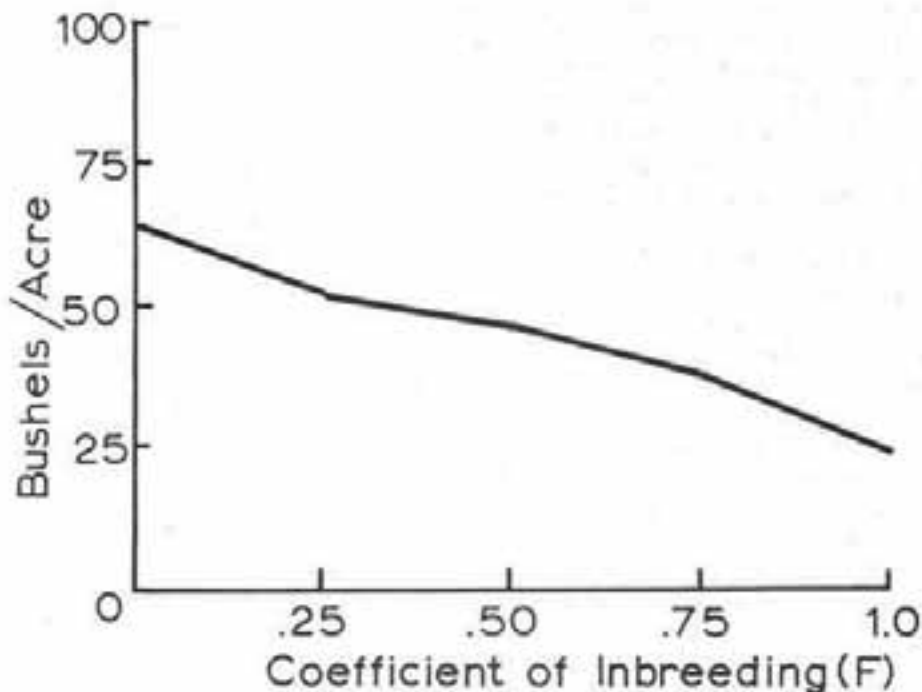

Figure 1. Relationship between inbreeding coefficient and yield in corn (Data from Neal, 1935).

Table 1. Effects of inbreeding on four species of galliform birds. (Outbreds = 100)

Trait	Chicken	Turkey	Japanese Quail	Chukar Partridge
Hatchability	90.0	83.4	72.2	71.3
Fertility	59.1	98.9	79.2	71.1
Female viability	94.3	90.7	81.5	92.1
Egg production	90.4	89.5	83.9	84.1
Total reproduction	74.4	61.6	35.9	34.1
Mean inbreeding depression	1.183	1.938	4.098	4.303

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The reciprocal effect of inbreeding depression is called heterosis, or hybrid vigor. Although a number of matings between species do produce highly vigorous offsprings, e.g., the mule, this type of hybrid (interspecies) is of little relevance to game managers. The hybrid vigor we refer to is that resulting from crossing different strains of one species. The literature of plant and animal breeding is replete with examples. Everyone is now familiar with the great impact the use of hybrid corn has made on American agriculture. Although records of natural hybrids are abundant, data on the relative vigor of these organisms is seldom gathered. Yet, laboratory experiments comparing heterozygotes and homozygotes in fruit flies (Wallace 1981) suggest that the phenomenon of heterosis is generally applicable in most animals. Two field studies are relevant to this problem. Sinoh and Zouros (1978) determined that higher levels of heterozygosity were associated with greater growth rates in oysters (Crassostrea). Batttaglia (1958) crossed two forms of the copepod crustacean, Tisbe reticulata, and showed that the heterozygotes have higher survival than either of the homozygotes. The gains from cross-breeding beef cattle suggest that ungulates are no exception to the increase of vigor resulting from outbreeding.

POPULATION SIZE AND INBREEDING

Effective breeding population (N_e) is a term used by Wright (1948) to denote a statistic useful in predicting the potential effects of population size and structure upon the variance in gene frequencies in succeeding generations. Its significance can be understood by considering a few examples. First, if the numbers of the two sexes contributing gametes to the next generation are unequal, say as in harem formers, the contribution of the breeding males will be disproportionately greater than each of the females, i.e., the males will be more "important" genetically. The N_e in this instance can be calculated by the following equation:

$$Ne = \frac{4N_m \times 4N_f}{N_m + N_f} \qquad (1)$$

Where N_m and N_f are the numbers of males and females, respectively. For example, a band of sheep which has 20 ewes and two rams would have an effective breeding size of only 7.27 instead of 22.

Another situation causing N_e to be misleadingly small is when population numbers vary during different generations. This would exist not only with cycles of abundance, but during periods of population growth. For example if a population of 10 parents were to triple in numbers of reproductives, in four succeeding generations, the value of N_e would be calculated from the equation:

$$\frac{1}{Ne} = \frac{1}{t} \frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_3} \dots \frac{1}{N_t} \qquad (2)$$

Where t represents the number of generations and N_1, N_2 etc. represent the numbers in each generation. In the example cited, the effective

breeding population over this interval turns out to be aporoximately 33.5. It is far less than one might have assumed since the final population was 810. The reason again is the disproportionate representation of the genes of certain individuals. In this case they are the original generation.

One measure of inbreeding is the probability that the two alleles an individual receives at a given locus are identical by descent. That is, that they are both copies of a specific, single gene present in some individual ancestor. It should be noted that an organism could be homozygous, i.e., having both alleles at a locus identical, but if they were derived from unrelated ancestors this does not represent inbreeding as used here. The degree of inbreeding in a population is denoted by F, the coefficient of inbreeding. This value can be calculated in a number of different ways and techniques for doing so are shown in a number of tests on population genetics (for example, Falconer 1960; Spiess 1977). For our present purpose, suffice it to say that values of F could range from zero in a totally outbred situation to 1 in the case of complete, total inbreeding, e.g., the offspring resulting from monoploids.

Now let us turn to an examination of the relationship between effective breeding population and inbreeding. Frankel and Soule (1981) following Wright (1931), showed the loss of heterozygosity in a population as a change in the inbreeding coefficient of the population. This amounts to the equivalent of an increase in inbreeding. Hetrozygosity is lost at a rate given by the expression:

$$\triangle F = \frac{1}{2N_c} = \frac{1}{8N_m} + \frac{1}{8N_f} \qquad (3)$$

Where F is the change of inbreeding coefficient and the other notations is as in (1).

One of the rules of good genetic management employed by the breeders of domestic animals is to permit no more than 1 percent increase in inbreeding per generation. This substituting into equation 3:

$$2 N_e = \frac{1}{.01}$$

$$N_e = 50$$

Thus if the number in each sex reproducing were 25 of the F would not exceed the 1 percent per generation ceiling. However, with unequal sex ratio, as is typical in many ungulate species, the situation is a bit more complex. If the sex ratio of reproductive adults were, say 5:1, then, for example a population of 15 males would require 75 females for F to be no more than 1 percent. Moreover, some quick calculations would show that 15 would be approximately the minimal number of males in a population wherein the 1 percent limit per generation would not be exceeded. At numbers lower than this, the number of females required begin to skyrocket toward biologically unrealistic levels.

DISCUSSION

In view of the foregoing, several questions concerning the genetic management of wildlife stocks spring immediately to mind. Among them are:

1. If inbreeding is so deleterious and such a likely outcome of small population effects, how is it that any of the small bands of wildlife have survived?

2. What can be done to counter the potential deleterious effects of inbreeding?

3. Would not outbreeding, by introducing new individuals from other populations, tend to reduce the fitness local populations had achieved through a history of natural selection?

4. In establishing a new population in a previously unoccupied area, how many individuals should be moved?

Considering these questions en seriatim, first, why have any small bands survived? The answer must naturally be equivocal because the effects of drift are not uniformly predictable. The very name suggests that there is no systematic effect from this factor. However, it may be that some of these organisms, e.g., small bands of sheep or goats have undergone a prior history of inbreeding, like the chickens and turkeys alluded to earlier and consequently do not suffer as much inbreeding depression as they might otherwise. In view of the social structure of the species, they would be expected to have lower N_e than species which are monogamous. If the assumption that they are already rather highly inbred is true, this does not invalidate the proposition that they would benefit from outbreeding. Reference to Figure 2 shows the relationship of inbreeding and continued consanguineous matings.

Note how the increment in F diminishes as the generations proceed. If a population is already at, say generation 15, continued inbreeding for an additional 15 generations will have a relatvely small effect on F as compared to the foregoing 15 generations. Conversely, outbreeding after the 15th generation of inbreeding would be expected to produce a dramatic reversal of inbreeding depression. In fact, the resulting hybrid vigor should be relatively greater in the first generation of outbreeding than in the ensuing generations. So, despite the fact that some organisms might survive in the face of high levels of inbreeding, these are the populations which may respond most favorably to outbreeding. This possibility should be considered for exploitation.

The answer to the first question immediately suggests an answer to the second, i.e., what can be done to counter inbreeding depression? The answer is to outbreed by introducing unrelated animals into the small isolated stocks. The number required to offset the effects of drift is surprisingly small. Wright (1931) proposed that the introduction of one outside individual into a population every generation is adequate to offset the effects of drift.
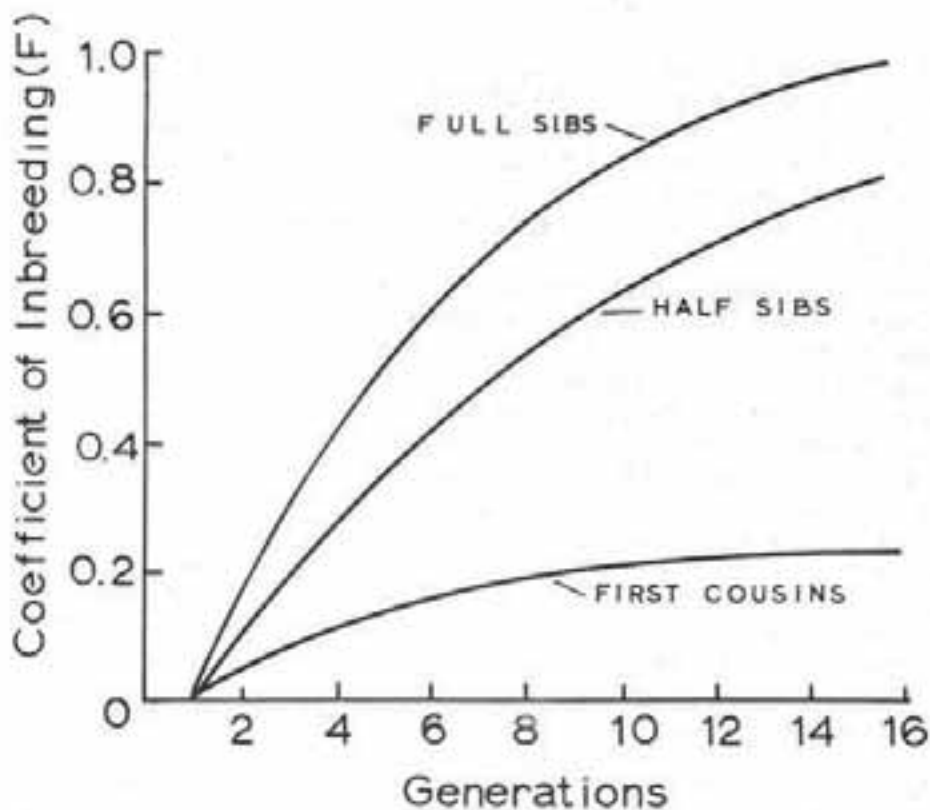
Figure 2. Effect of difference breeding systems on inbreeding coefficient.

The third question concerns the disruption of an adapted population by introducing individuals from other stocks. The question is valid, but when all factors are considered the problem is, on balance, a relatively small one. Most large mammals are more closely adapted to the general niche than they are to the specific set of physical and biotic parameters in their immediate environment. Such factors as general vigor, fecundity and disease resistance are general adaptations, not adaptations to a particular geographic area. Consequently, the special (local) adaptedness is not nearly so important in these socially and physiologically well buffered animals. Any slight diminution in special adaptedness caused by the introduction of new indivduals is likely to be more than offset by the increase in the fitness of general adapted traits. Moreover, selection should continue to act to eliminate the undesirable alleles which reduced special adaptedness. So, unless the depression caused by introduction was truly extreme, the population's genetic quality would be improved at little net cost.

In introducing new individuals, the problem of disease control should be given a great deal more attention than the attenuation of fitness.

In answering the last question (size of a new colony?) several constraints must be considered. Naturally, available fiscal and biologic resources are primary concerns. With respect to genetic quality, the number to be transplanted is not quite so important as the genetic structure of the transplanted animals and the prospects for their numerical expansion. If they have come from an inbred stock, they would be less likely to be successful than those derived from a genetically heterogeneous population. If they are from a population of the latter type, and have the prospect for rapid numerical increase, large numbers are not so important. There is no absolute threshold value for adequate and unadequate numbers, but a group of 15-20 which actually participate in breeding can transmit a healthy fraction of the genetic diversity of the parent population to the newly established colony. If there were inequality in the sex ratio the N_e would be reduced according to the equation given previously. But if the population expanded quickly enough even this problem would become inconsequential. The point to be made here is that we should not attempt to establish colonies in habitats extensve enough to contain relatively large populations. Otherwise, we must expect to play genetic nursemaids every generation or so.

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