

INBREEDING IN BIGHORN SHEEP: A CASE STUDY

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ABSTRACT

The results of a study of bighorn sheep (Ovis canadensis canadensis) in Dinosaur National Monument are reviewed with emphasis on inbreeding theory. Genetic considerations are related to breeding and dispersal behavior in bighorns. The present management practice of transplanting relatively small numbers of animals is discussed.

INTRODUCTION

Inbreeding has long been suspected as a contributing factor in unsuccessful reintroductions and poor performance of small remnant populations of bighorn sheep. Berwick (1968) believed that inbreeding was partly to blame for poor performance and decreased body size in the Rock Creek, Montana herd. The value of obtaining information on the genetic composition of wildlife has been pointed out by Smith et al. (1976), and Wilson (1974) expressed the need for such information specifically in bighorns. Roberts (1979) found that 4 populations of bighorns in Colorado were genetically distinct, the importance of which has not been fully addressed. The objective of this paper is to bring together some inbreeding theory with data collected during an evaluation of a herd of bighorns in Dinosaur National Monument, and to relate this theory to some aspects of bighorn sheep biology.

Dinosaur National Monument is located in northwestern Colorado and northeastern Utah. Plant communities within the canyon habitat of the bighorns range from a riparian zone dominated by boxelder (Acer negundo) and phragmites (Phragmites communis), through sagebrush (Artemisia spp.) and pinyon-juniper (Pinus edulis and Juniperus spp.) to ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) on the canyon rims. Thirty-two bighorns from central Colorado were transplanted into Lodore Canyon, the northernmost portion of the Monument, in the winter of 1952. The National Park Service authorized a study of the herd in 1958 and 1959. The herd had increased to approximately 130 animals and occupied the length of Lodore Canyon and small contiguous portions of the Yampa Canyon and Whirlpool Canyon within the Monument (Barmore 1962). The herd was expected to occupy all of the canyons in the Monument, because all were

historic sheep range. By the mid-1970's, no range expansion outside of Lodore Canyon had occurred, and the National Park Service funded a second study of the sheep. The results of this study (Skiba 1981) will be used as an example of some of the possible effects of inbreeding in bighorn sheep.

MATERIALS AND METHODS

Access to Lodore Canyon was by raft via the Green River and on foot. Rafting provided access to portions of the canyon difficult to reach by foot and made transportation of equipment more efficient. Animals were observed with the unaided eye, binoculars and spotting scope, and placed in 8 sex-age categories (Geist 1971). Individuals were immobilized with M-99 (etorphine) for marking with collars. Collars were used to analyze movement of individuals and to estimate population size with a Peterson-Lincoln index (Ricker 1975). Some animals were equipped with radio-transmitter collars to aid in relocation. An inbreeding coefficient (Falconer 1960) for the herd was calculated based on known population data since the transplant.

RESULTS

Lamb:ewe and yearling:ewe ratios obtained in 1978 and 1979 are presented in Table 1.

Table 1. Lamb:ewe and yearling:ewe ratios of the Dinosaur National Monument bighorn herd, 1978 and 1979.

	Lamb:ewe	Yearling:ewe
1978	0.66	0.32
1979	0.82	0.43

Survival of 1978 lambs to the 1979 yearling class was calculated at 65%. Both ratios were consistent through the main field seasons of both years. Six animals were immobilized with M-99. One animal died, 4 were outfitted with radio collars, and 1 with a numbered vinyl collar. A helicopter census flight in December of 1979 resulted in a population estimate of 38. Two collared individuals had apparently died between collaring in November of 1978 and the census flight. A total of 18 animals were sighted during the flight; 1 was collared. The coefficient of inbreeding was calculated at 24%. Equations used and assumptions made about herd size and structure are presented in Appendix A.

Distribution of the herd was similar to that found by Barmore (1962). The expected range expansion had not occurred to any extent, with very few sightings of animals outside of Lodore Canyon. One ewe, recognizable due to a horn deformity was seen with a lamb in Whirlpool Canyon in August 1978 and in the same area in July 1979. She was also sighted in Lodore Canyon in November 1979. All other reports outside of Lodore Canyon were from Dinosaur National Monument visitors and were of questionable validity.

DISCUSSION

INBREEDING

The primary effect of inbreeding is to increase homozygosity, which causes a decrease in fitness (Soule 1980). The first characters to be depressed are those related to reproduction and viability of offspring (Farnsworth 1978). A generalization used is that a 10% increase in inbreeding coefficient produces a 5% depression in a trait (Soule 1980). Inbreeding has not been addressed in wild populations due to the difficulty of obtaining necessary information on breeding patterns and viability of successive generations. Ralls et al. (1979) found that inbred young were significantly less likely to survive than non-inbred young in 15 of 16 species of captive wild ungulates. Much more data are available on the effects of inbreeding in domestic animals. Effects include decreased survival of young animals to weaning in swine (McPhee et al. 1931), decreases in adult weight, litter size, and litter weight in swine (Mikami et al. 1977), decreased milk yield in cattle (Pearson et al. 1977) and decreased body size and weight in cattle (Miller et al. 1977). The salient point is that inbreeding can cause reduction in fitness of inbred individuals.

With the large number of small herds of bighorn sheep throughout the West, the potential effects of inbreeding become more important to address. In terms of introductions of animals into unoccupied habitats, the current practice (admittedly the only practical method) of transplanting small groups of bighorns only exacerbates the problem. Senner (1980) showed that a population founded with 20 individuals and maintained at 50 individuals would reach a 60% level of inbreeding (i.e., would have lost 60% of its heterozygosity) in about 90 generations. These population figures, however, are for effective population size. Effective size can be calculated with the following equation (Falconer 1960):

$$\frac{1}{N_e} = \frac{1}{4M} + \frac{1}{4F}$$

where N_e is effective population size, M is the effective number (number actually breeding) of males in the population, and F the effective number of females. Franklin (1980) suggests that to prevent short-term inbreeding problems, the effective size of a population should be greater than 50. Assuming a population structure of 60 lambs:100 ewes:40 yearlings:75 rams

(composition based on data from Bear and Jones 1973), and breeding by 50% of the rams, a population of 50 bighorns would have an effective size of about 20. The actual proportion of rams actually breeding is probably below 50%, which would further decrease the effective size. To obtain an effective size of 50 with the above demographics, the total population size would be 100. The Dinosaur herd currently consists of approximately 15 ewes, 7 lambs, 6 yearlings, and 10 rams (fall population). The effective size (assuming 50% of the rams breed) is 15. The current rate of inbreeding is approximately 1.3% per year (see Appendix A). In Colorado, population sizes range from 15 to 425. The effective population sizes probably range from 10 to 170. A total of 59 populations now exists in the state; 30 of these are currently smaller than 50 individuals. An additional 13 have between 50 and 100 individuals. While the absolute effects of inbreeding are not fully known, there is ample evidence to suggest that the continued maintenance of populations at such low levels can only be detrimental.

POPULATION RATIOS

Lamb:ewe ratios in the Dinosaur herd are generally considered to be good. Ratios of 1.00 have been found in bighorns on Wildhorse Island (Woodgerd 1964). The usual situation is for lamb crop to be less than 100 lambs per 100 ewes. The number of nonbreeding ewes is probably minimal in most populations and would have little effect on lamb:ewe ratios. The failure of most herds to reach the ideal lamb:ewe ratio has been attributed to severe weather (Smith 1954), poor forage, high density (Geist 1971), or harassment of ewes by rams (Pulling 1945). While there is no doubt these factors can and do influence the lamb crop, the effects of inbreeding can be just as important. In fact, environmental factors may increase the detrimental effects of inbreeding (or vice versa). Keller and Brinks (1978) found that different production levels had a greater than expected effect on inbred cattle. It may be wise to consider genetic causes as well as more traditional explanations when bighorn herds do not attain high lamb:ewe ratios. This is particularly true in small remnant herds which exist on areas which should have a good forage supply. In Dinosaur, assuming that all ewes were bred, prenatal and early postnatal mortality was 38% in 1978 and 18% in 1979. Inbreeding of 25% could have had an effect on the survival of embryos and lambs. While other factors could have influenced the lamb crop, inbreeding should not be overlooked.

DISTRIBUTION

Competition with domestic livestock, for both space and forage, is the most probable cause for the limited distribution of the Dinosaur National Monument bighorn sheep herd (Skiba 1981). Until 1976, cattle and domestic sheep grazed the southern end of Lodore Canyon and the western end of the Yampa Canyon. In addition, all of the suitable uplands within and surrounding the Monument were grazed (grazing in the Monument is currently being phased out). Competition with livestock may have limited the movements of the bighorn at the critical stage of range establishment.

The maintenance of this limited distribution, especially in light of the removal of livestock from the area, may be due to the pattern of dispersal in bighorns. Howard (1960) theorized that dispersal is genetically controlled. Subsequent studies have shown that there are genetic differences between dispersing and non-dispersing individuals. Dispersing types have been found in voles (*Microtus ochrogaster*) (Pickering et al. 1974) and in blue grouse (*Dendrogapus obscurus*) (Redfield 1973). Both Redfield (1973) and Myers and Krebs (1971) found that the dispersing individuals were more likely to be homozygous. If a similar genetic control of dispersal occurs in bighorn sheep, inbreeding may influence dispersal. If the dispersal genotype was homozygous, it would be expected to be more common in an inbred population. Dispersal of individuals from an already small population would only add to the problem of potential inbreeding, if no outside individuals moved into the population. The pattern of dispersal in some animals is nonrandom, with a larger than expected number remaining close to their natal area, a smaller than expected number moving an intermediate distance, and a larger than expected number moving long distances (Howard 1960). Such dispersal would be invaluable in preventing inbreeding in bighorns if all herds could receive outside individuals. This was probably the case before populations were separated to the extent they are today. Even under primeval conditions, the distribution of bighorn herds was probably discontinuous. Dispersal between groups would aid in dispersing genes and reducing inbreeding. Under present conditions, dispersal may not bring an individual in contact with another herd of sheep. Geist (1971) believed that sheep would not remain in an unfamiliar area if there were no other sheep present. In the case of a dispersing bighorn today, especially in relatively isolated herds, the animal would have the alternatives of returning to its natal area or continuing to explore. In either case, the urge to disperse exposes the animal to hazards that it would not encounter if it did not disperse, and may remove a potential breeding animal from the population. In small herds, the loss of individuals, most commonly young males in bighorn sheep (Geist 1971) would only increase the likelihood of inbreeding. Whether or not dispersal contributed to the present distribution of the Dinosaur herd is unknown. It is very unlikely that a dispersing animal from Dinosaur would find another herd or that individuals are dispersing into the population, since there are no large established herds within 100 km (there is a small recently transplanted herd, perhaps of 40 individuals, within 30 km of the range of the Dinosaur herd). While prevention of inbreeding may not be the only reason, or even a major reason for dispersal in mammals (Greenwood 1980), it is a beneficial effect. Under conditions as exist today, dispersal would be detrimental in all but the largest herds or those which are receiving outside immigrants. The primary effect would be to reduce population size and especially to reduce the size of the male segment of the population.

EFFORTS TO PREVENT INBREEDING

There are at least 3 commonly considered techniques for reducing or preventing inbreeding in transplanted bighorn sheep. The first is to

increase the size of the original transplant. There is no doubt that this would reduce the rate of inbreeding. The original size of the transplant, however, is not as important as the size at which the population is maintained over time (Senner 1980). With the cost and difficulty of trapping and transplanting large numbers of animals, follow-up management is more promising than increasing numbers of animals.

A second suggestion is to increase the proportion of males in the transplant. This is based on the fact that the numbers of the less numerous sex have a greater influence on the rate of inbreeding (see Appendix A). Since the maintenance size of the population is more important than initial transplant size, rapid population increase and maintenance of large population size are desirable. Having a large number of lambs, yearlings, and pregnant ewes would be a sounder approach than increasing the number of males.

A third technique is to transplant additional animals into the population after it has established itself. In bighorns, the effort would be most productive if males were transplanted. If the males come from a different population than the original transplant stock, more genetic variability would be added. If the additional animals come from a different population, an attempt should be made to use animals from similar habitat. Even if the males came from the same herd as the original animals, it would aid in decreasing the chances of inbreeding. From a practical standpoint, this technique is becoming more viable, at least in Colorado. All available unoccupied transplant sites are expected to be utilized within the next 5 to 10 years (W. B. Rutherford, pers. commun.). If animals are still available for transplants in the future, moving males between populations could take the place of natural dispersal. These relocations might best be accomplished by transplanting small groups of ewes and male yearlings. These yearlings might be more likely to remain in the area with the ewes than yearlings that were removed from familiar social groups. Ewes from a different stock would also contribute to genetic diversity, but a breeding male would more quickly add his genome to the population, and would likely produce more offspring than a ewe.

There are several objections to the third technique. One is the possibility of introducing disease into an established herd. Of particular concern would be viral and bacterial diseases. While this possibility does exist, the benefits of potential genetic variability probably outweigh the possible occurrence of disease. A second objection is that the imposition of males on a herd could upset the established dominance hierarchy in ram groups. This problem could be avoided by transplanting only young males. A third (and probably most valid) objection is that some herds are now genetically distinct and should be maintained in such condition. Risenhoover (1981), for example, makes a case for the existence of specialization in low-elevation herds. There is no question that distinct herds do exist today. The question is how much of the differences are naturally occurring, and how much is due to the disruptive influence of man. There is obviously a middle ground between indiscriminate mixing of

animals from differing habitats and maintaining each bighorn herd as a genetically separate entity. Approximation of natural emigration and immigration can and should be a realistic management goal. Intelligent management of bighorn sheep requires that we find and exploit that middle ground.

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APPENDIX A

CALCULATION OF COEFFICIENT OF INBREEDING

The coefficient of inbreeding for the Dinosaur National Monument bighorn sheep herd was calculated by use of 2 equations derived from Falconer (1960). These equations are:

$$(1) \quad \Delta F = \frac{1}{8 M} + \frac{1}{8 F} \quad , \text{ and}$$

$$(2) \quad F_t = \frac{1}{8 M} + \frac{1}{8 F} + \left(1 - \frac{1}{8 M} + \frac{1}{8 F}\right) F_{t-1}$$

where F is the change in the coefficient of inbreeding per generation, M is the number of males breeding, F is the number of females breeding, F_t is the coefficient of inbreeding of generation t , and F_{t-1} is the coefficient of inbreeding of the generation preceding generation t .

Assumptions were made concerning the numbers of breeding animals at various points since the introduction in 1952 (Table 2). The derivation of these numbers can be found in Skiba (1981). These numbers were used in equations 1 and 2 to determine the current coefficient in inbreeding in the Dinosaur National Monument bighorn herd.

Table 2. Assumed numbers of breeding individuals in the Dinosaur National Monument bighorn herd, 1952-1982.

Time period	Number breeding males	Number breeding females
1952-1957	4	18
1958-1962	25	49
1963-1967	25	49
1968-1972	10	22
1973-1977	10	22
1978-1982	5	15

The generation length for bighorn in Dinosaur National Monument was fixed at 5 years based on the age of the oldest rams observed (8 years) and the assumption that males began breeding at 3 years of age. The original transplant was regarded as noninbred, so equation (1) was used for the period of 1952-1957.

$$F = \frac{1}{8(4)} + \frac{1}{8(18)} = .0382/\text{generation, or}$$

.0076/year, or .046 in 6 years.

Subsequent calculations used equation (2). For the period of 1958-1962,

$$F_t = \frac{1}{200} + \frac{1}{392} + \left(1 - \frac{1}{200} + \frac{1}{392}\right) .046 = .0532$$

Continuing the calculations for the remaining time periods, the coefficient of inbreeding at the end of the period of 1963-1967 is .0604; at the end of 1968-1972, .1595; at the end of 1973-1977, .1872; and at the end of 1978-1982, .2137, or 21% inbreeding.

CONFERENCE DISCUSSION

- Q. I read a review of supplemental transplants in Colorado by Ruetherford and he concluded that they had been very unsuccessful. I can't remember exactly how many examples he had, at least 5 or 6, and the typical result of supplementing a herd that wasn't doing well was that you got a short-term increase in population and then a decline to the same level as before the supplemental transplant. I think we need to look at what data are available, where some of these things that you suggested have been tried. At least in some cases, it suggests that inbreeding may have not been the problem.
- Ans. I think that is one thing we have to keep in mind. In those cases it's probably just as likely that sheep were transplanted into poor habitat in the first place. We can't expect that inbreeding is always the only problem.