

EFFECTIVE POPULATION SIZES FOR BIGHORN SHEEP

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Abstract: Determination of effective population size allows conceptualization of the effects of population size and demography on rates of genetic drift and inbreeding. To better understand the extent to which genetic factors may be affecting population viability, we estimated effective population size for bighorn sheep (*Ovis canadensis*) with varied population histories. For 13 populations of bighorn sheep in Wyoming, Montana and South Dakota, we found ratios of effective population size to actual population size ranging from 0.23 to 0.42, and averaging 0.33. This suggests that bighorn sheep populations should be kept at total sizes of over 150 to avoid short-term loss of genetic variability. Effective population size provides a conceptual framework for considering the management of bighorn sheep populations, especially those that are small or isolated.

The importance of genetic factors in the management of free-ranging wildlife populations is being increasingly recognized (Soulé 1986), especially where populations are small, have undergone bottlenecks, or are isolated (Leberg 1991). Genetic variability is important in contributing to population viability, and assumes 2 forms: allelic variability and heterozygosity. Allelic variability refers to the kinds and frequencies of genes that occupy specific positions (loci) on chromosomes. Allelic variability is important in part because it provides the basis for adaptation to local environments; without it, selection cannot occur. Heterozygosity refers to the ways in which dissimilar alleles are paired at loci, and reflects an intrinsic taxon-specific value as well as recent breeding history. Examples of factors that affect recent breeding history are genetic exchange among populations, and the breeding system within a population (Falconer 1981).

In very small populations, variability often is reduced. More specifically, variability is lost at low values of effective population size (N_e), the size of an idealized population (one with panmictic breeding, an even sex ratio, and no variation in size over time) that has the same rate of drift as the population of concern (Falconer 1981). In these populations, heterozygosity is reduced primarily by inbreeding, or breeding among close relatives, whereas allelic variability is

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reduced primarily by drift, or the changes in allele frequencies that occur as a result of the random sampling of gametes to form zygotes (Falconer 1981). Both allelic variability and heterozygosity undergo reductions at increased rates at low levels of N_e , and these reductions are undesirable from the standpoint of population persistence.

Genetic variability has been alleged to affect population performance of bighorn sheep (DeForge et al. 1979, Skiba and Schmidt 1982) because of the high insularity and low N_e of many populations (Schwartz et al. 1986). In captive-born bighorn sheep, lamb survival was 34% less in inbred lambs than in non-inbred lambs (Sausman 1984). Horn growth has been correlated with population history in bighorn sheep by Stewart and Butts (1982), who found that herds in Montana that had undergone bottlenecks of population size (N) < 60 had lower cumulative horn growth to age 3.5 years than did herds that had maintained $N \geq 150$. In other ungulate species, allozyme variability has been shown to be positively correlated with reproductivity (Johns et al. 1977), fetal growth rate (Cothran et al. 1983), longevity (Chesser et al. 1982), and antler size (Scribner et al. 1989). Others have dismissed the importance of loss of genetic variability to bighorn sheep populations because interpopulation movements are difficult to detect and may be relatively common (Schwartz et al. 1986).

Predictions of population viability rely on species-specific knowledge of N_e . However, estimation of N_e is problematic, particularly for polygamous species hunted for only one sex, such as the bighorn sheep. This paper attempts to estimate N_e for bighorn sheep using aerial survey data for 13 populations from Wyoming, Montana, and South Dakota, and discusses the potential conceptual importance of effective population size in managing bighorn sheep.

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METHODS

We analyzed demographic data for bighorn sheep herds in Wyoming, Montana, and South Dakota obtained from aerial surveys (Wyoming Game and Fish Department completion reports 1975-1990) and from periodic surveys by other agencies to estimate N_e . We adjusted for unequal sex ratios of breeders with the formula:

$$N_e = \frac{4N_fN_m}{N_f+N_m}$$

where N_f is the number of breeding females and N_m is the number of breeding males (Crow and Kimura 1970). We adjusted for the effect of changes in N over time with the formula:

$$\frac{1}{N_e} = \frac{1}{t} \left(\frac{1}{N_{e_1}} + \frac{1}{N_{e_2}} + \frac{1}{N_{e_t}} \right)$$

which uses a harmonic mean of estimates of N_e over time to emphasize years of low population size (Crow and Kimura 1970). The number of breeding females was estimated by multiplying the number of adult ewes observed by the post-harvest proportion of ewes accompanied by lambs. The number of males was estimated by multiplying the number of adult rams (with $\geq 1/2$ curl horns) by 0.66. This proportion represents the midrange between the value (0.33) reported by Hogg (1987) to be the dominant breeders of estrous ewes, and 100%, which is possible given that sub-dominant rams also mate (Hogg 1987). From these calculations, we obtained estimates of N_e/N for each year. N_e may be reduced by overlapping populations, but we had too few data on age-specific reproduction and mortality to address this issue. We assumed no significant gene flow among native herds, which likely is violated for some herds we studied. Such gene flow would tend to increase N_e to an extent influenced by the gender of dispersers in polygamous species (Chesser 1991). To assess the effect of changes in the number of breeding rams or in lamb/ewe ratios, N_e also was estimated by reducing the number of breeders of each sex by 50%. Inbreeding coefficients (F) were estimated by the formula of Crow and Kimura (1970):

$$F = \frac{1}{2N_e}$$

RESULTS AND DISCUSSION

We estimated that the mean N_e/N for all populations was 0.33 (range = 0.23 - 0.42), which resulted in N_e values from 36 to 326 in native herds (Table 1). All introduced herds had $N_e < 50$. In calculating N_e/N , if the number of breeding rams or the lamb/ewe ratio was reduced by 50%, mean N_e/N decreased to 0.21. Rate of inbreeding was $< 1\%$ in all native herds except in a small remnant herd in the Teton Mountains, where it was 1.4% (Table 1). Reintroduced herds had inbreeding rates ranging from 1.0 - 4.6%. Because our estimated N_e/N ratios varied by a factor of almost 2, herd-specific estimates should be used to address any herd-specific question. Importantly, estimates of N_e from aerial observations may be confounded by herd-specific biases in locating ewe/lamb or ram cohorts.

Our estimates of herd-specific N_e values suggest that the transplanted herds and the Teton herd are at risk of losing genetic variability over the short-term, and that several native herds may be at long-term risk. To manage for the maintenance of genetic variability over the short term, Franklin (1980) recommended an $N_e \geq 50$, which would keep the inbreeding rate $< 1\%$. For bighorn sheep, this requires $N \geq 150$, given a mean N_e/N of 0.33. Therefore, herds that have $N < 150$ should be expected to lose variability over generational time. Persistently small populations may fail to grow, even in the presence of adequate habitat, if their reproductivity becomes impaired by the phenotypic changes

Table 1. Population histories of native and transplanted bighorn sheep herds from Wyoming and neighboring states. Population estimates are from records of the Wyoming Game and Fish Department and the South Dakota Department of Fish, Parks and Wildlife. N_e represents the effective population size, N the population size and F the inbreeding coefficient. The N_e/N ratio is the average value derived from aerial survey data 1975-1990.

Location	Year of Transplants	Founder N	1990 N	N_e	N_e/N	F
<u>Native</u>						
Clark's Fork, WY	n.a.	n.a.	520	129	0.33	0.004
Trout Peak, WY	n.a.	n.a.	668	79	0.39	0.006
Wapiti Ridge, WY	n.a.	n.a.	968	154	0.27	0.003
Yount's Peak, WY	n.a.	n.a.	827	130	0.23	0.004
Franc's Peak, WY	n.a.	n.a.	1146	326	0.39	0.002
Jackson, WY	n.a.	n.a.	525	184	0.40	0.003
Tetons, WY	n.a.	n.a.	100	36	0.36	0.014
<u>Founder</u>						
Whiskey Mtn., WY	n.a.	n.a.	1070	207	0.28	0.002
<u>Transplant</u>						
Bighorn Canyon, WY/MT	1973	8	90	11	0.42	0.046
Douglas Creek, WY	1970	41	131	48	0.27	0.010
Custer State Park, SD	1965	12	145	21	--	0.024
Encampment River, WY	1976-77	69	60	25	0.31	0.020
Laramie Peak, WY	1964-82	129	53	25	--	0.020

caused by inbreeding (Sausman 1984). Franklin's (1980) suggested $N_e > 500$ to reduce genetic loss over the long term would necessitate maintaining bighorn populations of over 1530, an estimate larger than any herd size in Wyoming. This assumes little or no exchange of animals among these herds.

The objective of genetic management of bighorn sheep populations should be to minimize the loss of naturally-occurring genetic variability, rather than to maximize genetic variability through outcrossing to distant herds. For the large native herds, this may be most effectively accomplished by maintaining habitat corridors to permit continued migration between adjacent herds, which will increase the N_e of both populations involved. Habitat improvements to increase carrying capacity also should be considered. Maintaining or restoring genetic variability should be considered for persistently small or reintroduced herds. Theoretically, an immigration rate of 1 per generation can prevent allele fixation (Wright 1978). However, Lacy's (1987) models showed that 5 immigrants per generation were required to retain at least 90% of long-term genetic variability. These values provide a range for managers to consider in planning supplemental transplants. Chesser (1983) found that inbreeding in polygynous species is more rapidly countered when males that can impregnate several females are introduced. This suggests the importance of rams of breeding age in both initial and supplemental transplants. Transplant size also is important because it determines initial inbreeding levels and the time necessary to expand to population sizes with high persistence probabilities.

Genetic factors should be considered along with vegetation, topography, weather, disturbance and disease when assessing and managing bighorn sheep populations. Management of small or isolated herds to achieve goals of N_e rather than of N would place the management of these herds into the theoretical framework of conservation biology, which could suggest new solutions to old problems. For example, the effects of hunting only large-horned rams may warrant further consideration. In simulations of grizzly bear (*Ursus arctos*) populations, different hunting regimes resulted in values of N_e/N ranging from 0.24 to 0.32 (Harris and Allendorf 1989). Similarly, Ryman et al. (1981) estimated that N_e/N of moose (*Alces alces*) would range from 0.24 to 0.36 under different hunting regimes.

The role of genetic variability within and among populations of bighorn sheep should be considered if populations are to persist, expand, and have long-term viability with low management costs. Management decisions may need to rely on genetic theory because diagnostic tools are not yet available. If habitat fragmentation and herd isolation are not offset by corridors for dispersal or supplemented gene flow, then genetic variability and population viability may be compromised.

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