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Demographic Considerations in Reintroduction Programs of Bighorn Sheep [1]

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Lenarz M. S. & Conley W., 1980: Demographic considerations in reintroduction programs of bighorn sheep. Acta theriol., 25, 7: 71—80 [With 1 Table & 3 Figs.].

The disappearance of bighorn sheep (*Ovis canadensis*) populations in western North America has stimulated several attempts at reintroducing bighorn onto historic ranges. Many of the early attempts failed because of an ignorance of bighorn behavior and demographic characteristics. Utilizing survival and fertility data available from the literature, a series of computer simulations were run to answer the question: »what is the optimum number and sex and age composition for sheep to utilize in a reintroduction attempt?«. The optimum age at which to transplant sheep of both sexes is three years. The optimum number of females to use in a founding population is dependent on the desired rate of increase. A sex ratio of one is neither necessary nor desirable in the initial population.

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INTRODUCION

North American bighorn sheep (*Ovis canadensis*) inhabit the Rocky Mountain Cordillera from the periglacial regions of central British Columbia to the hot deserts of northern Mexico. Throughout this range, bighorn populations have declined or disappeared since the arrival of western man (Buechner, 1960). As early as 1939, attempts were made to restock bighorn on historic ranges (Woodgerg, 1964). These early attempts, however, produced limited success.

The lack of success in reintroducing sheep can be attributed to at least two causes. First, the social system of bighorn has evolved to allow for the transfer of important behavioral patterns of habitat utilization (Geist, 1971). These patterns include information on seasonal ranges, mineral licks and lambing areas. The success of reintroduced populations is in part dependent on the founding members discovering

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new areas which fulfill these requirements. Geist (1974) discussed methods which may be utilized to imprint lambs with this information.

Second, early reintroduction attempts utilized sex and age classes of sheep that were available. Bighorn have a relatively low reproductive potential and the lack of success in some early attempts may have been because of too small a founding population. Today, however, several state and federal organizations have captive populations from which groups can be selected to maximize the potential of a successful transplant. In this paper we address the question: »what is the optimum number and sex and age composition of bighorn sheep to reintroduce onto a historic range?«

SURVIVAL AND FERTILITY SCHEDULES

There are several sources of survival information available for bighorn sheep including Geist (1971), Hansen (1967) and Woodgerg 1964). Hansen (1967) provided the most extensive set of data which was derived from 374 ewe and ram skulls collected between 1946 and 1964. A sheep's age at death can be determined by counting the annuli present on the horns. This technique is accurate for males but provides only a minimum age for females (Geist, 1966). The number of individuals that died at a specific age x are summed to represent D_x. Although problems exist with this type of data (Murphy & Whitten, 1976), the long interval over which these skulls were collected incorporates many years of varied environmental impact and thus the survival values (l_x) derived from these data represent mean survival values. The survival values in Table 1 are defined as:

$$l_x = \frac{n_x}{n_0} \tag{1}$$

with

$$n_0 = \sum_{x=0}^{\omega} D_x \tag{2}$$

and

$$n_x = n_0 - \sum_{x=0}^{x-1} D_x \tag{3}$$

The lower case ω denotes the last age class that contains individuals. Survival values represent the probability that an age 0 individual will survive to enter the xth age class and n_x represents the number of individuals in the xth age class. Hansen (1967) did not present separate data for ewe and ram skulls and thus the combined data confound possible sex-specific survival schedules for both sexes. In the absence of evidence to the contrary, we have assumed similar survival patterns for both sexes.

Hansen (1967 : 698) began his survival curve with age two individuals because of the small number of lamb and yearling skulls collected. The l_0 and l_1 values listed in Table 1 represent the mean lamb and yearling survival rates discussed by Hansen (1967 : 697).

Fertility values (m_x) shown in Table 1 represent the expected number of daughter offspring produced by an age x to $x+1$ female that produces

Table 1

Life table generated from data provided in Hansen (1965).

x	l_x	l_x*	p_x	m_x	B_x	v_x
0	1.000	1.000	0.500	0.000	0.000	1.268
1	0.500	0.500	0.750	0.000	0.000	2.594
2	0.214	0.375	0.989	0.000	0.000	3.540
3	0.212	0.371	0.987	0.500	0.800	3.661
4	0.209	0.366	0.989	0.500	0.800	3.276
5	0.207	0.362	0.964	0.500	0.800	2.871
6	0.199	0.349	0.945	0.500	0.800	2.516
7	0.189	0.330	0.900	0.500	0.800	2.183
8	0.169	0.297	0.905	0.500	0.800	1.911
9	0.153	0.269	0.862	0.500	0.800	1.592
10	0.132	0.232	0.805	0.500	0.800	1.293
11	0.107	0.187	0.591	0.500	0.800	1.009
12	0.063	0.110	0.518	0.500	0.800	0.884
13	0.032	0.057	0.368	0.500	0.800	0.755
14	0.012	0.021	0.286	0.500	0.800	0.720
15	0.003	0.006	0.334	0.500	0.800	0.703
16	0.001	0.002	0.000	0.500	0.800	0.720

* Survival values after yearling survival increased.

offspring (Conley, in press a). Since twinning is extremely rare and the sex ratio at birth is equal to one (Geist, 1971) a ewe will produce an average of 0.5 female lambs per year after reaching reproductive age.

The proportion breeding (B_x) listed in Table 1 represents the percentage of age x to $x+1$ females that produce offspring (Conley, 1978). This value varies according to age (Geist, 1971) and environmental conditions, but accurate information is not available. Hansen (1967 : 697) reported an average of 70 lambs per 100 ewes. This value may be biased, however, since male yearlings are nearly indistinguishable from adult ewes (Geist, 1971; Hansen, 1965). The B_x values listed in Table 1 were arbitrarily raised to 0.80 for $x \geqslant 3$ years to account for this bias.

Bighorn ewes normally do not reach sexual maturity until their third season (Streeter, 1970; Geist, 1971). In a captive population (Deming, 1955) and in a reintroduced population (Woodgerg, 1964), bighorn ewes gave birth to lambs at two years of age. Although it is possible that ewes in a reintroduced population will begin breeding a year early, all simulations were run with ewes reaching sexual maturity at three years, to generate conservative estimates.

POPULATION SIMULATIONS

All simulations were conducted using a FORTRAN IV version of a modified Lotka model (1956) as discussed by Conley (1978). This model calculates population size (N) at time t based on constant l_x and m_x functions where:

$$N_t = \sum_{x=0}^{\omega} n_{x,\ t} \tag{4}$$

$$n_{x+1,\ t+1} = n_{x,\ t}\ p_x \tag{5}$$

The probability that an individual that entres the xth age clas will survive to enter the $x+1$ age class at time $t+1$ is:

$$p_x = 1 - \frac{l_x - l_{x+1}}{l_x} \tag{6}$$

and the number of new females entering the population at time t is:

$$n_{0,\ t} = \sum_{x=1}^{\omega} n_{x,\ t}\ m_x\ B_x \tag{7}$$

In the majority of simulations, two optimal routines were utilized. First, in order to simulate a small founding population in a more realistic manner, we incorporated a stochastic age-specific survivorship function. A uniformly distributed random number ($0.0 \leqslant r \leqslant 1.0$) was drawn for each individual in the population at time t. If this number was smaller than the p_x value, that individual survived to enter the $x+1$ interval.

The model as discussed above (eqs. 4 through 7) treats all individuals in the population as females with the implicit assumption that sufficient males are available for breeding. This model was altered to include males in the total population by:

$$N_t = \sum_{x=1}^{\omega} n_{x,t,1} + \sum_{x=0}^{\omega} n_{x,t,2} \tag{8}$$

where 1=females and 2=males and with new young given by

$$n_{0,t,1} = \sum_{x=1}^{\omega} n_{x,t,1}\, m_x B_x \tag{9}$$

and

$$n_{0,t,2} = \sum_{x=1}^{\omega} n_{x,t,1}\, m_x B_x \tag{10}$$

for females and males respectively. A complete description of this model is given by Conley (1978).

An artifact of the mathematics in the Lotka model reduces the initial number of individuals in the population prior to reproduction. To overcome this bias in the simulations, the appropriate number of lambs (according to the fertility schedule) were added to the population at time $t=0$ to simulate pregnant ewes.

During initial simulations utilizing the l_x and m_x functions discussed above, a problem became apparent. The finite rate of increase (λ) was only 0.946 which represents a declining population. Any attempt at utilizing these data to simulate a reintroduction attempt was doomed to failure. To alleviate this problem the l_2 value (yearling survival) was raised to 0.375 which raised lambda to 1.023. The yearling survival rate discussed by Hansen (1967) is considerably lower than that described by Geist (1971) and Woodgerg (1964). Since two-year-old sheep are difficult to distinguish from adult ewes, the l_2 value is more questionable than other values.

OPTIMUM AGE

The optimum age at which to transplant sheep must take into account the survival and fertility functions characteristic of that population. An older ewe may have a better chance of conceiving a lamb (Geist, 1971) but will contribute less to population numbers because of a lowered life expectancy. Fisher (1958) utilized survival and fertility functions to calculate the reproductive value, v_x, which, in discrete form is:

$$\frac{v_x}{v_0} = \frac{\lambda^x}{l_x} \sum_{y=x}^{\omega} \lambda^{-y}\, l_y m_y \tag{11}$$

Reproductive value represents the expected contribution to future population growth of a female aged x and her expected offspring, expressed relative to the contribution of a female aged 0, where $v_0=1$. Reproductive values calculated from Hansen's data are listed in Table 1.

The optimum age at which to transplant bighorn is 3 years of age according to Fisher's reproductive value (Table 1). To illustrate the effect of transplanting various ages of sheep, a series of simulations were run in which the founding population was composed entirely of a single age class of ewes. These simulations were deterministic and utilized only the one-sex model. Figure 1 illustrates the effect of utilizing different age classess in the initial population. Population size was higher throughout the simulation using the three-year-old ewes, as was predicted.

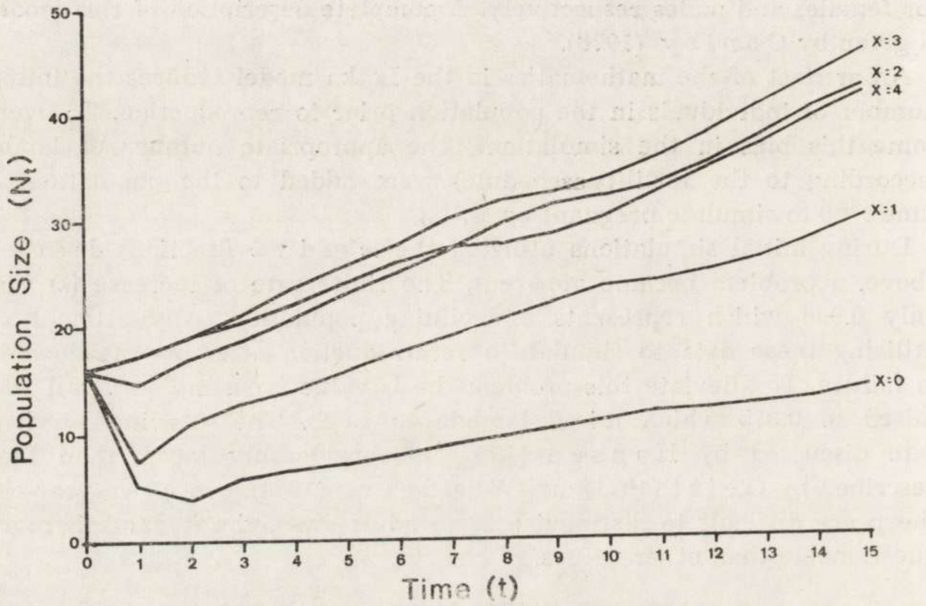

Fig. 1. Simulations of founding populations composed entirely of age x individuals.

OPTIMUM NUMBER

A total of 100 simulations were run utilizing the stochastic p_x and the two sex model. Initial population size ranged from 5 to 25 pregnant females in steps of five with only one ram per group. A total of 20 simulations were run for each of these groups. All ewes and rams in these groups were age three individuals. The results of these simulations are summarized in Figure 2.

All of the populations in Figure 2 continued to increase, since the λ associated with the l_x and m_x functions utilized, is greater than one. The mean number of individuals added to the population per year, however, varies substantially and is a function of the number of ewes in the founding population (Figure 3). Population size at $t=11$ varies substantially within groups and results from use of the stochastic survival function. Theoretically, as population size increases, the stochastic function approximates the deterministic function. At low population numbers, however, this stochastic process tends to simulate natural mortality in a more realistic manner. Figure 3 illustrates the range of possible rates of increase for each of the initial populations.

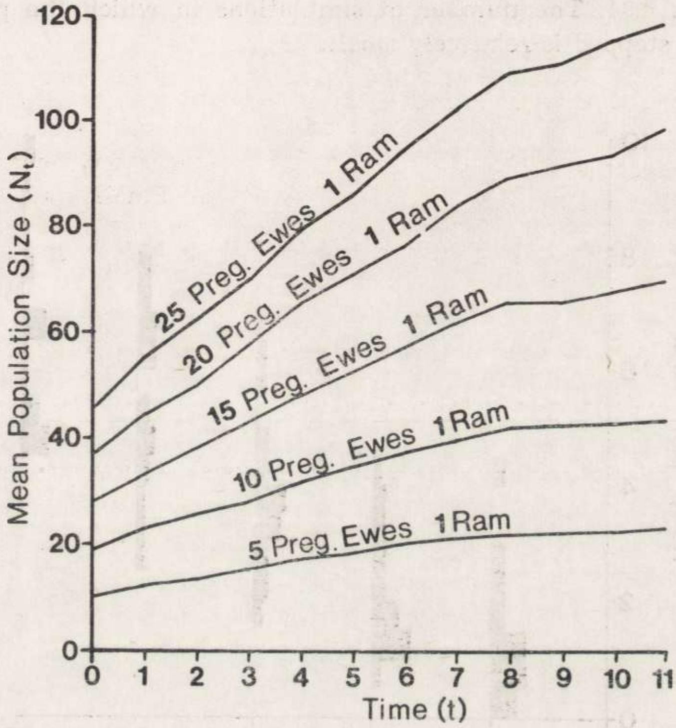

Fig. 2. Simulations of founding populations containing different number of ewes.

The optimum number of ewes to utilize in a reintroduction attempt is dependent on the goals of the project. In the majority of simulations, the populations doubled in size every six to seven years. Although it is possible to start a viable population with as few as five ewes and one ram, the population will offer little to consumptive or non-consumptive users of wildlife for many years.

OPTIMUM SEX RATIO

Only one ram was utilized in all of the simulated founding populations. The two-sex model used in these simulations is designed to stop if the number of males in the population decreases below one individual. In all 100 simulations, the number of rams did not decrease to this level. The model, however, does not take into account the age of sexual maturity in males and thus it is possible that during some simulations the population was »kept alive« by sexually immature rams. The probability that the single age three ram will survive to enter the sixth age class (at which time the first male lambs will have reached sexual maturity) is 0.94. The number of simulations in which the population would have stopped is relatively small.

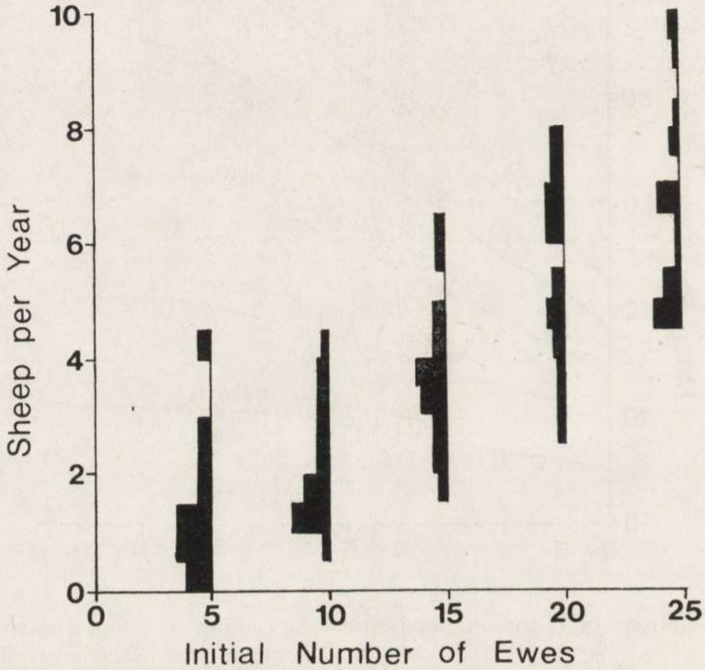

Fig. 3. Number of sheep added to the population per year according to initial population size.

In an actual reintroduction attempt, however, it would be advisable to introduce additional rams to preclude the possibility of loosing the only viable ram and to increase the genetic diversity of the founding population. The addition of rams to the founding population will not appreciably increase population size in the future. An even sex ratio in the initial population is not necessary nor desirable, since ewes are more valuable for increasing population size.

DISCUSSION

Demographic models such as the one utilized for these simulations are not designed to predict population size at some future time. Population demography encompasses a complex set of relationships between individuals in the population and their environment. To assume that a model can predict a specific outcome assumes that all of the complex relationships are incorporated into the model. This is neither possible nor desirable. The power of models lies in their ability to illustrate the importance of one or more variables in the demographic process.

The results of these simulations illustrate three concepts that are important to any reintroduction program. First, utilize young sheep that have reached sexual maturity, rather than lambs or yearlings. Second, utilize as many ewes in the founding population as is economically feasible. Finally, an equal sex ratio in the founding population is not necessary and is in fact a waste of resources.

Demographic responses as presented here do not consider potential effects of inbreeding depression. If a population is to be started from a very few individuals, they should be unrelated, and consideration should be given to the need for continued introduction of unrelated individuals subsequent to the initial stocking. Such a procedure would help insure the maintainence of maximum genetic variability.

These results may be combined with the methods suggested by Geist (1974). An initial transplant of male and female lambs imprinted with the important habitat utilization patterns could be supplemented after three to four years with a large number of ewes and a few rams.

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WARUNKI DEMOGRAFICZNE PROGRAMU REINTRODUKCJI *OVIS CANADENSIS*

Streszczenie

Po zniknięciu populacji *Ovis canadensis* z zachodniej części Ameryki Północnej dokonano kilku prób reintrodukcji tego gatunku w jego historycznych granicach. Próby te nie powiodły się ze względu na nieuwzględnianie behawioru owcy kanadyjskiej i jej charakterystyki demograficznej. Wykorzystano dane literaturowe o przeżywalności (Tabela 1) i płodności do stworzenia sztucznego modelu, który odpowiedziałby na pytanie jaka powinna być optymalna liczba osobników oraz skład wiekowy i płciowy stada owiec użytego do reintrodukcji (Ryc. 1—3). Okazało się, że optymalny wiek zalecany dla owiec obu płci wynosi 3 lata. Optymalna liczba samic użyta do odbudowy populacji jest zależna od żądanego poziomu wzrostu tej populacji. Stosunek płci 1 : 1 nie jest ani konieczny ani nawet pożądany, ponieważ samice są bardziej wartościowe dla wzrostu stada.