Estimation of Effective Population Size of Grizzly Bears by Computer Simulation

Fred W. Allendorf, Richard B. Harris, and Lee H. Metzgar

Abstract. We present a new method to predict the rate at which small populations will lose genetic variation and apply it to the grizzly bear (Ursus arctos). The simulation model is a discrete-time, stochastic computer program that follows the life-history and kinship of each individual. We determined heterozygosity by calculating the inbreeding coefficient of individuals, pedigree $F$, which is the probability that two genes at a locus in an individual are identical by descent from an allele in the foundation population. Thus, $F$ provides an exact measure of heterozygosity, $H=(1-F)$, at selectively neutral loci over the entire genome.

We estimate the genetically effective population size to be approximately 25% of total population size under a wide variety of demographic conditions. However, the introduction of even a few bears per generation from other populations greatly increased the effective population size. We conclude that many extant populations of grizzly bears can only be maintained by intensive management that includes movement of bears among currently isolated populations.

INTRODUCTION

The fragmentation and isolation of populations is of increasing concern in management of endangered species. Loss of genetic variation in isolated populations of large mammals is especially serious because of their low population densities and high spatial requirements. Thus, even the largest protected reserves may be too small to maintain genetically viable populations of large mammals (Soulé et al., 1986; Belovsky, 1987).

The most useful concept to estimate the expected rate of loss of genetic variation is effective population size ($N_e$). Knowledge of effective population size allows prediction of the expected time when reduced genetic variation is likely to threaten continued existence of an isolated population. In spite of universal agreement about the importance of effective population size for making management decisions (Soulé, 1980), considerable confusion persists about its estimation in natural populations. This is especially true for large mammals because of their complex demographics and numerous departures from the genetically "ideal" population.

In this paper, we introduce a new method for estimating $N_e$ by computer simulation in a consideration of grizzly bear (Ursus arctos) populations. An estimation of the rate of loss of genetic variation in grizzly bear subpopulations is needed in order to determine population sizes required to maintain genetically viable subpopulations. Moreover, it is also important to determine what management actions can be taken to reduce the rate of loss of genetic variation in the remaining subpopulations.

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The United States Endangered Species Act of 1975 declared the grizzly bear to be a threatened species. The number of grizzly bears in the contiguous 48 states has declined from an estimated 100,000 in 1800 to less than 1,000 at present (Servheen, 1985). Similarly, the range of the species within this area is now less than 1% of its historic range. The current verified range of the grizzly bear is approximately five million hectares in six separate subpopulations in four states (Servheen, 1985).

The reduction in range has isolated subpopulations as continuous habitat was divided and movement corridors disappeared. Population decline accelerated because these isolated subpopulations were small and subject to stochastic demographic influences. Current recovery goals for the remaining subpopulations are based upon estimates of the minimum viable population (MVP) size that has a 95% probability of survival for 100 years (Allendorf & Servheen, 1986).

Current estimates of MVP for the grizzly bear are based upon a comprehensive series of computer simulations of demographic structure (Shaffer & Sampson, 1985; Shaffer, 1983). Recovery targets for four of the six subpopulations are 70–90 individuals (U.S. Fish & Wildlife Service, 1982). The genetically effective population size ($N_e$) of such subpopulations is far short of the recommended effective number of approximately 500 that is necessary to maintain evolutionarily significant quantities of genetic variation (Lande & Barrowclough, 1987). These $N_e$ are also likely to be lower than that of the generally accepted minimum number of 50 necessary to avoid serious loss of genetic variation in the short term (Soulé, 1980).

Well known studies with domestic animals have shown that loss of genetic variation has a variety of harmful effects on development, reproduction, survival, and growth rate. Studies with a variety of species in zoos indicate that similar effects probably occur in wild populations of animals (Ralls et al., 1986; Ralls et al., 1988; Ralls & Ballou, 1986). For example, natural populations of lions (*Panthera leo*) that have lost genetic variation through recent population bottlenecks have more developmentally abnormal sperm and lower testosterone concentrations than adjacent populations that have not lost genetic variation through a bottleneck (Wildt et al., 1987). Thus, subpopulations within the recovery targets of 70–90 individuals will lose genetic variation at a rate likely to decrease their expected longevity.

**THE MODEL**

The rate of loss of genetic variation generally has been measured by change in average heterozygosity per individual per locus ($h$). Heterozygosity is expected to be lost at an approximate rate of $(1/2N)$ per generation in the theoretical “idealized” population of $(N/2)$ males and $(N/2)$ females that are all equally likely to contribute a sperm or egg to the next generation (Wright, 1969). However, a wild population of $N$ individuals will lose heterozygosity much faster than the rate of $(1/2N)$ expected in the ideal population. For example, unequal sex ratios, fluctuations in population size, and non-random reproductive success of individuals will all increase the rate of loss of heterozygosity.

Sewall Wright (1969, p. 211) defined effective population size ($N_e$) as whatever must be substituted in the formula $(1/2N)$ to describe the actual loss in heterozygosity. A variety of methods provide estimates of $N_e$ under different violations of the assumptions of the ideal population (Wright, 1969). Several problems restrict application of these estimations to wild populations. First, these formulas cannot be combined to estimate rate of loss of genetic variation in a wild population in which all of the assumptions are not likely to hold. Second, many of the parameters needed to estimate $N_e$ with these formulas are virtually impossible to estimate in wild populations. In addition, most populations do not consist of a single random mating group. Existing formulas for estimating $N_e$ have not been
designed to incorporate effects of gene flow between geographically separated local populations. The simulation model was a discrete-time, stochastic computer program that followed the history and kinship of each individual. Values of parameters used in the simulations were taken from studies of grizzly bear populations in Montana, Wyoming, and British Columbia (Harris & Allendorf, 1989; Harris & Metzgar, 1987a,b). The simulation model is described in a paper in which we evaluated published techniques to estimate effective population size (Harris & Allendorf, 1989).

Four events occurred during a simulation year: breeding, natural mortality, birth, and weaning of juveniles. At each event, an individual's fate (e.g., dying) was determined by comparing its sex and age-specific probability with a random number from a uniform (0,1) probability distribution (Harris & Metzgar, 1987a,b). We performed 50 replicates for each combination of parameter values. Each replicate lasted 100 years; the first 24 years were omitted from the regression analysis to provide a delay of 2–3 generations in which loss of heterozygosity became asymptotically linear.

We determined heterozygosity with the algorithm of Boyce (1983) to calculate the inbreeding coefficient of individuals, pedigree $F$, which is the probability that two genes at a locus in an individual are identical by descent from an allele in the foundation population (Wright, 1969). Thus, $F$ provides an exact measure of heterozygosity, $H = (1 - F)$, at selectively neutral loci over the entire genome. We estimated the rate of loss of heterozygosity by regressing the natural logarithm of $H$ in newborns on time measured in generations. Effective population size was estimated by solving for $N_e$ using the rate of loss of heterozygosity per generation of $1/(2N_e)$ ($N_e = 1 / (-2m + 2)$, where $m$ is the slope of the natural log of mean heterozygosity of the newborn cohort on time, measured in generations). The mean inbreeding coefficient of newborns was calculated at five year intervals, rather than each year, to save computing time.

RESULTS AND DISCUSSION

A critical, but poorly known, component for estimating $N_e$ is the distribution of the reproductive contribution among males. We simulated three male mating systems with the intent of embracing the range of actual values: (1) random, in which adult males were picked at random (with replacement) to be sires; (2) our best estimate, in which adult males of a prime age group (8–18 years) had greater probabilities of being sires; and (3) extreme, in which there was an extreme advantage to prime age males. We detected surprisingly little effect of changing the distribution of male reproductive success on rate of loss of genetic variation (Table 1).

The rate of loss of genetic variation through time depends upon both $N_e$ and mean generation interval because $1/(2N_e)$ is the expected rate of loss per generation. Therefore, results are presented (Table 1) by two measures: the ratio of effective to census population size ($N_e/N$), and the amount of variation expected to be lost in 100 years. The former measure varies more because the amount of variation lost depends upon both the $N_e/N$ ratio and the mean generation time. In general, conditions that lower $N_e/N$ tend to lengthen mean generation intervals (Table 1).

Table 1. Results of simulations showing mean generation interval, $N_e/N$ ratio, and total percent loss of heterozygosity ($H$) in 100 years in grizzly bear populations of mean size of $N=100$.

<table>
<thead>
<tr>
<th>Male mating</th>
<th>Generation (years)</th>
<th>$N_e/N$</th>
<th>Loss of $H$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random</td>
<td>10.0</td>
<td>0.311</td>
<td>15.6</td>
</tr>
<tr>
<td>Estimate</td>
<td>10.8</td>
<td>0.280</td>
<td>15.8</td>
</tr>
<tr>
<td>Extreme</td>
<td>11.1</td>
<td>0.260</td>
<td>16.4</td>
</tr>
</tbody>
</table>
We first tested for effects of population size on the ratio between effective and census population size using three different mean census sizes: 50, 100, and 200. We found no indication of an effect of population size on the population size ratio (Harris & Allendorf, 1989). We selected a population size of 100 to carry out the main body of simulations.

Our results suggest that the effective population size of grizzly bears is approximately 25–30% of census size (Table 1). This estimate may be high because of other factors in real populations that our simulations did not consider. A dominance hierarchy among breeding males is one such factor. All males of a given age had equal probability of reproductive success in our simulations. Dominance hierarchies within males of similar age may further reduce effective population size.

Thus, even fairly large isolated subpopulations, such as the 200 or so bears in Yellowstone National Park, United States, are vulnerable to harmful effects of loss of genetic variation. A moderate decrease in genetic variation in this population may decrease reproductive rates, further reducing population size and, in turn, accelerating the rate of loss of genetic variation. Artificial movement of bears among naturally isolated subpopulations is required to decrease the rate of loss of genetic variation. We therefore extended our simulations to determine the amount of gene flow needed to reduce the rate of loss of genetic variation in subpopulations to an acceptable level.

Gene flow was incorporated by introducing three year-old males or females that were assumed to be unrelated to all other animals in the population. Once introduced into a population, an immigrant had the same sex and age-specific life-history probabilities as other bears in the population; thus, not all introduced bears reproduced. These simulations were done with the random male mating system.

The introduction of a few bears greatly reduced the rate of loss of genetic variation (Table 2). For example, introduction of one male bear per year (approximately 10 per generation) increased mean \( N_e \) from 31 to 194 (Table 2). This agrees with analytic results that have shown that one migrant per generation is expected to limit genetic divergence among subpopulations (Wright, 1969). Those results have also indicated that the effectiveness of gene flow is determined by the number, not the proportion, of individuals exchanged among subpopulations. Accordingly, our results apply to subpopulations of other sizes.

Introduction of males caused a greater increase in \( N_e \) than females. This occurred because of the greater variability in male mating success. A few exceptionally successful introduced males had a pervasive effect on the pedigree of relationships. However, introduced males in nature may be less likely to be incorporated successfully into a population than females because of the greater movement of young males. Thus, these results may overstate the benefits of introducing males rather than females.

Our results support the notion that even large and protected reserves are too small to maintain viable populations of large mammals if they are isolated (Soulé et al., 1986; Belovsky, 1987). Genetically viable populations can only be maintained in such reserves by artificial exchange among reserves. However, even if all available isolated preserves are genetically connected, there is insufficient habitat available for many species (Ralls & Ballou, 1986). A combination of protected natural habitat preserves and ex situ preservation in zoos will become necessary for many species. Zoos will allow an increase in total

<table>
<thead>
<tr>
<th>Immigrants per generation</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>5</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>31.1</td>
<td>36.6</td>
<td>40.7</td>
<td>67.2</td>
<td>123.6</td>
</tr>
<tr>
<td>Males</td>
<td>31.1</td>
<td>42.5</td>
<td>49.6</td>
<td>113.2</td>
<td>194.2</td>
</tr>
</tbody>
</table>
number of animals to be maintained and can also serve as sources for individuals to be used in gene exchange programs.

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LITERATURE CITED