

DETERMINING MINIMUM VIABLE POPULATION SIZES FOR THE GRIZZLY BEAR¹

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Abstract: A stochastic computer simulation is presented for use in determining the relationship of population size to extinction probabilities for populations of grizzly bears (*Ursus arctos*). Published data on numbers, age, sex, reproduction, and mortality for the grizzly bear population of Yellowstone National Park were used to develop and test several simulation models. The results indicate that, for the Yellowstone grizzlies, 35 to 70 bears constitute a minimum viable population (the smallest population with a 95% probability of surviving at least 100 years). Minimum area requirements for populations of this size range from 700 to 10,000 km.²

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To preserve the grizzly bear in the northern Rockies, the U.S. Fish and Wildlife Service has proposed designation of over 5,000,000 ha of public domain in Montana, Wyoming, Idaho, and Washington as "critical habitat" for the species. This has triggered opposition from various interest groups and focused attention on the question of how much habitat the grizzly bear needs to survive (Fischer 1977).

This is one example of an increasingly frequent scenario—a widely distributed species becoming confined to small fragments of its former range. Aside from any systematic deterioration in the quality of remaining habitat, such fragmentation exposes remnant populations to higher extinction rates. This is due to the increasing importance of chance events and environmental variation with decreasing population size in determining population persistence. The effect of these factors is to introduce a stochastic component into the process of extinction.

This stochastic component of extinction requires that preservation be viewed as the probability of persistence relative to some time frame and some set of conditions. What time frame to use and what level of stochasticity to anticipate in determining preservation probabilities is open to question. For purposes of illustration I define a minimum viable population as the smallest isolated population having at least a 95% probability of

surviving at least 100 years. Given this definition, the objective of this paper is to illustrate how minimum viable population size may be estimated for the grizzly bear through use of computer simulations that incorporate the effects of chance events and environmental variation.

DEVELOPMENT OF THE MODELS

Data Analyses

Due to variability between grizzly bear populations, it was necessary to develop the simulation based on information for 1 population. The population chosen was that of Yellowstone National Park and surroundings. Data on this population were gathered over a 12-year period (1959–70) and provided the most detailed information and longest continuous record available for any grizzly bear population (Hornocker 1962; Craighead and Craighead 1965, 1971, 1972; Craighead et al. 1969, 1974, 1976; Craighead 1976).

Distribution of the Variables.—Six variables (Table 1) were defined from the data of Craighead et al. (1974). Distributions of the variables were checked using the rankit method (Sokal and Rohlf 1969). Average litter sizes and adult, subadult, and total population sizes were normally distributed. Mortality rate was normally distributed after transformation to \log_e scale. Percent of females reproducing was not normally distributed.

Serial Correlations.—Runs tests (Sokal and Rohlf 1969) were used to check for trend or oscillation in the variables. None of the variables differed significantly ($P \geq 0.05$) from a random sequence.

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Table 1. Variables describing the Yellowstone grizzly bear population, 1959 to 1970 (derived from data of Craighead et al. 1974).

| | Variable | Mean | Standard deviation | Sample size |
|-----|---------------------------------------|------|--------------------|-------------|
| MR | Overall population mortality rate (%) | 16.6 | 8.0 | 11 |
| PR | Adult females reproducing (%) | 30.4 | 7.0 | 10 |
| ALS | Average litter size | 2.21 | 0.23 | 11 |
| A | Adult population size | 81 | 13 | 12 |
| SA | Subadult population size | 96 | 18 | 12 |
| T | Total population size | 177 | 15 | 12 |

Density-Dependence.—Density-dependence is here defined as the significant correlation between a population parameter and population size (assuming the area used by the population remains constant). Simple correlations were done between pairings of mortality rate, percent reproducing, and average litter size versus adult, subadult, and total population sizes. Pearson's product-moment correlation coefficients were calculated when both variables in a pairing were normally distributed; otherwise, Kendall's coefficient of rank correlation was used (Sokal and Rohlf 1969). These correlations were done both within years and for a 1-year time lag (e.g., average litter size in 1960 versus adult population size in 1959). Only 2 of the correlations were significant. Both percent reproducing and average litter size were negatively correlated ($P \leq 0.10$ and $P \leq 0.05$, respectively) with adult population size at the time of breeding. For use in the simulation, functional relationships of these variables to density were estimated by regression analyses. Because the data were subject to sampling error, Model II regression lines were fitted by Bartlett's Three-Group-Method (Sokal and Rohlf 1969). The resulting relationships were:

$$PR = 59.9 - 0.37(A); s = 6.0; r^2 = 0.34 \quad (1)$$

$$ALS = 3.09 - 0.01(A); s = 0.19; r^2 = 0.38 \quad (2)$$

where PR = percent of females ≥ 4.5 years reproducing, ALS = average litter size, A = adult population size at time of breeding, s = standard deviation around the regression, and r^2 = coefficient of determination.

Cross-Correlations.—To determine if there was any relationship between the parameters of mortality and reproduction, aside from density-dependence, residuals from the above regressions were compared to each other and to residuals from a regression of mortality rate on adult population size. The residuals were first checked for distribution and trend or oscillation as described above. None of the paired residuals were significantly correlated.

Structure of the Simulation

The simulation approach used was a discrete approximation to the continuous process of population dynamics. For each cycle (equivalent to 1 year) population size was determined as the number of individuals (by sex and age) surviving from the previous year plus the number of cubs (by sex) that entered the population. If population size dropped below a specified extinction threshold in less than 100 cycles, the population was considered extinct. A simplified statement of the basic algorithm is given in Table 2. Numerous variations in the simulation were available for testing the effects of various factors on extinction probabilities. A brief description of the simulation's major features, components, and their variations follows.

Continuous/Discrete Population Size.—Two versions of the simulation were available. One version treated population size as a continuous variable, the other as a discrete (integer) variable. In the latter version a pseudo-random number generator was used to determine the survival and reproductive success of each individual and the sex of cubs. This mimicked the effects of chance events and introduced 1 level of stochasticity into the simulation.

Environmental Variation.—Yearly variation in mortality rate, percent reproducing, and average litter size were taken to reflect environmental variation. Such variation represented another level of stochasticity. In those simulation models that incorporated such variation, yearly values of the variables were determined as follows:

$$X(I) = \bar{X} + (s)(d) \quad (3)$$

where $X(I)$ = this year's value of the variable, \bar{X} = mean value of the variable, s = standard deviation of the variable, and d = a standard normal deviate ($\bar{X} = 0.0$, $s = 1.0$).

Based on the results of the data analyses, separate random sequences of standard normal deviates were generated for each variable.

Survivorship—Two options were available for the survivorship component. With Option I-S the mortality rate was held constant at 16.6% (Table 1). With Option IV-S mortality varied as a truncated \log_e -normally distributed variable with mean and standard deviation (converted to \log_e scale) as given in Table 1.

Once mortality rate was set, sex/age-specific mortality (q_x) and survivorship (p_x) schedules from Craighead et al. (1974) were scaled to yield this rate. Both q_x and p_x values were constrained to lie within the range 0.0–1.0. After sex/age-specific mortality and survivorship rates were set, the number of survivors from the previous year's population were determined. Once this procedure was completed, each class was incremented to become the next age class for the current year.

Reproduction—The reproduction component also had 2 options. With Options I-R, percent reproducing and average litter size exhibited only density-dependent variation from year to year. With Option IV-R these variables exhibited both density-dependent and density-independent (environmental) variation.

Under Option I-R yearly values for the 2 variables were determined by use of Eqs. (1) and (2). Under Option IV-R Eqs. (1) and (2) were used to generate the mean values of percent reproducing and average litter size employed in Eq. (3). In this case the standard deviations used in Eq. (3) were those from regressions of percent reproducing and average litter size on density from Eqs. (1) and (2).

A scaled adult population density was required when simulating populations of equivalent density but different absolute size than that for which the regression relationships were derived. When this scaled population density was outside the range of densities for which the regressions were determined, the density-dependent values of percent reproducing and average litter size were held constant at the bound (upper or lower) value.

After percent reproducing and average litter size were set, the number of cubs entering the population was determined. Cubs were distributed by sex on the basis of a M:F ratio of 50:50.

In the small populations simulated, it was possible that sexually mature females might be pres-

Table 2. Simplified statement of the simulation algorithm.

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BEGIN
  Read in basic data (population and survivorship rates by sex/age
  group; standard deviations of mortality rate, percent reproduc-
  ing, average litter size; seed numbers for pseudo-random num-
  ber generator — PRNG
  Use PRNG to generate 50 100-year patterns of variation in mortal-
  ity rate, percent reproducing, average litter size
  Replication counter = 0
  Extinction counter = 0
  WHILE (replication counter.LE.50) DO
    BEGIN
      Increment replication counter
      Year = 0
      Extinct = false
      WHILE (year.LE.100) and (extinct = false) DO
        BEGIN
          Increment year counter
          Determine mortality rate
          Scale sex/age-specific survivorship values to yield mortality
          rate
          Use PRNG to determine survivors promoted to next sex/
          age class
          Determine density-equivalent population
          Determine percent reproducing and average litter size
          Use PRNG to determine females reproducing
          Use PRNG to round off number of cubs produced
          Use PRNG to determine sex of cubs
          Sum sex/age classes to get total population
          Sum females  $\geq$  4.5 years
          IF (sum.LE.0) THEN BEGIN
            Extinct = true
            Increment extinction counter
          END
        END
      END
    END
  END
  Percent survive = extinction counter/50
  WRITE initial population size, percent survive, average survival time
  END
    
```

ent in the absence of male counterparts. The simulation was structured so that, if no males \geq 4.5 years of age were present in last year's population, no cubs entered this year's population.

Extinction Thresholds.—Two extinction thresholds were tested. The 1st was reached when there were no females \geq 4.5 years of age in the population. This is a conservative estimate, but given the importance of adult females to the survival of their young, it should be the safest index of extinction. Nevertheless, some immature females might survive and, provided males were present, begin to reproduce. To test this, a 2nd extinction threshold was reached when no individuals remained of 1 of the sexes.

Simulation Models

From the various versions and options available, 4 models were defined for testing. These

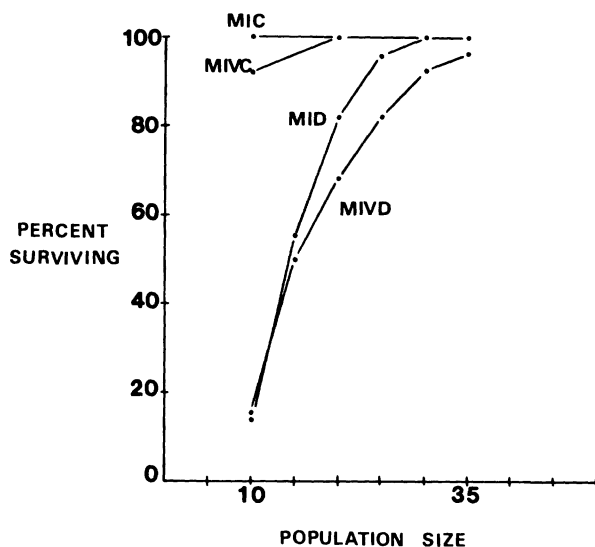


Fig. 1. Percent of 50 replicates surviving 100-year test period for the 4 basic simulation models. Results are for the 1st extinction threshold (no females ≥ 4.5 years). Models I-C and I-D held mortality rate constant and incorporated only density-dependent variation in reproduction. Models IV-C and IV-D incorporated density-independent (environmental) variation in mortality rate and both density-dependent and independent variation in reproduction. The suffixes C and D refer to continuous and discrete versions of the simulation, respectively.

are described below. The suffixes C and D refer to the continuous and discrete versions of the simulation, respectively.

Model I-C and I-D.—These models used Option I-S for survivorship and Option I-R for reproduction. Thus, no environmental variation was included. These models served as controls against which those models that included environmental variation were compared. As with the model pairings described below, comparison of the continuous and discrete versions allowed testing the effects of chance events on population survival.

Model IV-C and IV-D.—These models used Option IV-S for survivorship and Option IV-R for reproduction. These were the “real-world” models in which density-independent (environmental) variation affected mortality and reproductive success was affected by both density-dependent and density-independent variation. Thus, these models recreated the patterns of variation in population dynamics revealed from analyses of the Yellowstone population data.

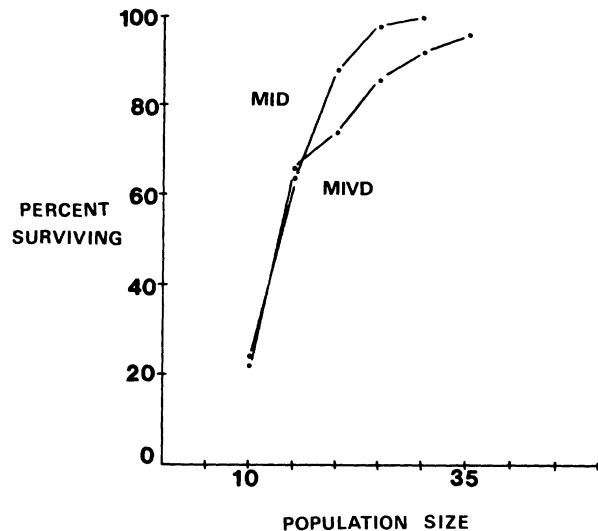


Fig. 2. Percent of 50 replicates surviving 100-year test period versus population size for Models I-D and IV-D. The results are for the 2nd extinction threshold (all remaining individuals of same sex).

RESULTS WITH THE MODELS

To estimate minimum viable population sizes for the grizzly bear, continuous (C) and discrete (D) versions of Models I and IV were each run for 50 replicates of population sizes ranging from 10 to x (in increments of 5 individuals; x equals the population size at which 95% of the replicates survived the 100-year test period). Statistics computed were number and percent of populations surviving and becoming extinct, and average survival time of the latter. These statistics were computed for both extinction thresholds.

The major feature of the results was the difference between minimum viable population estimates from continuous versus discrete versions of the simulation. In the continuous versions of Model I and IV (MI-C and MIV-C), 92–100% of the populations of 10 bears survived the test period. Such levels of survival were not achieved in discrete versions below population sizes of 25 (MI-D) or 35 (MIV-D) (Fig. 1). Greater differences in estimates from continuous to discrete versions than from Model I to Model IV indicated that chance events affecting the survival and reproduction of individuals played the major role in extinctions of such small populations. Never-

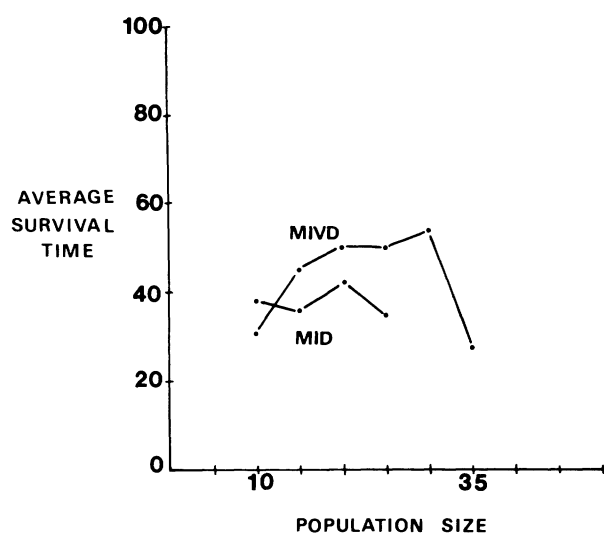


Fig. 3. Average survival time versus population size for those replicates not surviving the 100-year test period. Results are for Models I-D and IV-D using the 1st extinction threshold (no females ≥ 4.5 years).

theless, environmental variation was an important additional component of extinction (Figs. 1 and 2).

The choice of extinction thresholds made little difference in the overall results. In all cases, the 1st extinction threshold (no females ≥ 4.5 yrs.) yielded lower population survival than the 2nd threshold (no survivors of 1 sex), but the differences were minor (Figs. 1 and 2.)

Average survival times for those populations that became extinct were not strongly related to population size (Fig. 3). This was due to the fact that, as percent of populations surviving increased, average survival time could have been strongly influenced by either a short- or long-lived population. Nevertheless, for both discrete versions there was an initial tendency for average survival time to increase with population size, as was expected. Again, the choice of extinction thresholds did not affect the outcome.

The most remarkable and sobering feature of this portion of the results was the relatively high survival times for populations even when their probability of surviving was quite low. For example, using Model IV-D, a population of 10 bears had only a 16% chance of surviving the 100-year test period, yet the average survival time for the 42 populations that became extinct was 31 years (Fig. 3).

Because it incorporated the effects of both chance events and environmental variation, Model IV-D was used to provide the basic estimate of minimum viable population size. Using the first extinction threshold, Model IV-D provided an estimate of 35 bears as the smallest isolated population having at least a 95% chance of surviving for at least 100 years (Fig. 1).

Sensitivity Analyses

Numerous assumptions were made to derive parameter values and their relationships, or to structure the simulation. The effects of these assumptions were tested by running a number of additional simulations with appropriate modifications in one or more of the simulation's inputs or components. In each case a Model IV-D with an initial population of 35 was run for 50 replicates. Depending on the outcome of the initial run, larger or smaller populations (in increments of 5) were run for each modification until a new minimum viable population was determined. The results of these analyses showed that the initial estimate of minimum viable population size was fairly stable with respect to the majority of modifications tested (Table 3). Of the 18 modifications tested, 6 did not alter the initial estimate. Two modifications decreased and 4 increased the initial estimate only slightly (± 5). Only 4 modifications altered the original estimate of minimum viable populations by more than 5 individuals. A slight increase (10%) in mean mortality rate coupled with a slight decrease (10%) in the means of percent reproducing and average litter size had the greatest effect, doubling the initial estimate from 35 to 70. A slight (10%) increase in mean mortality rate alone also had a substantial impact on the initial estimate, raising it to 50. Both a change in age at first reproduction for females from 4.5 to 6.5 years and use of the cub sex ratio of 59M:41F measured by Craighead et al. (1974) increased the initial estimate of minimum viable population size from 35 to 45 bears.

The measured cub sex ratio of 59M:41F was based on yearly samples, but sample sizes were small (Craighead et al. 1974). Most females in the Yellowstone population did first reproduce at 4.5 years of age (Craighead et al. 1969, 1976). Reproductive data are more easily gathered and probably more reliable than mortality data, at least in this case. Thus, of the 4 modifications

Table 3. Results of analyses of the simulation's sensitivity to modifications in parameter values of relationships, or in the simulation's structure. The 1st column lists the modification made in a Model IV-D simulation and the 2nd column lists the new minimum viable population that resulted. All results are for the 1st extinction threshold (no females \geq 4.5 years).

| Modification | Minimum viable population |
|---|---------------------------|
| $\overline{MR}^a + 10\%$ | 50 |
| $\overline{PR} - 10\%$ | 35 |
| $\overline{ALS} - 10\%$ | 35 |
| $s_{MR} + 10\%$ | 40 |
| $s_{PR} - 10\%$ | 40 |
| $s_{ALS} - 10\%$ | 40 |
| $\overline{MR} + 10\%$, $\overline{PR} - 10\%$, $\overline{ALS} - 10\%$ | 70 |
| $s_{MR} + 10\%$, $s_{PR} - 10\%$, $s_{ALS} - 10\%$ | 40 |
| $VAR(MR, PR, ALS) / 2^b$ | 30 |
| Cub sex ratio = 59M:41F | 45 |
| Correlated environmental variation | 35 |
| Density-dependent dispersal | 30 |
| Old age distribution | 35 |
| Young age distribution | 35 |
| Density-independent reproduction | 35 |
| Age at females' 1st reproduction = 6.5 years | 45 |

^a \overline{MR} , \overline{PR} , \overline{ALS} refer to mean values and s_{MR} , s_{PR} , s_{ALS} refer to standard deviations of mortality rate, percent reproducing, and average litter size, respectively.

^b Variance in MR, PR, and ALS reduced by half.

which had a substantial impact on the initial estimate of minimum viable population size, the possible underestimate of mean mortality rate caused the greatest concern. Because of this, the initial estimate of minimum viable population size of 35 was raised to 50 for the Yellowstone population.

Minimum Area Requirements

To translate the estimates of minimum viable population size into minimum area requirements necessitated some measure of density or average area requirements of individual bears. Review of the literature revealed that average area requirements for individual grizzly bears ranged from about 20 to 150 km² (Shaffer 1978). For the Yellowstone population, the range was approximately 50 to 80 km² (Shaffer 1978). The simulation provided a range of minimum viable population sizes of 35 to 70 bears, with 50 as the most likely estimate for the Yellowstone population. Multiplying the range of area requirements by the range of minimum viable population sizes yielded a range of 700 to 10,500 km² as minimum area

requirements for the species overall and 2500 to 4000 km² for the Yellowstone population. Clearly, minimum area requirements, like minimum viable population sizes, will vary depending on the characteristics of each population.

DISCUSSION

It is important that the simulation and results presented here be interpreted with caution. Though the data base for the Yellowstone grizzly bears was the best available, there were problems with using it in such a simulation exercise. Ten to 12 years is a small sample size for determining distributions of the basic parameters. Long-term cyclical behavior is virtually impossible to detect with such a short data base. In addition, from the information available, it was impossible to separate sampling variation from true variation in the basic population parameters. The variances and standard deviations derived in the data analyses and used in the simulation were based on the assumption that the data were error-free — which is unlikely. Though analyses of the data showed that reproductive parameters were significantly correlated (negatively) with adult population density at the time of breeding, such analyses cannot prove a cause-effect relationship. Only longer data bases of increased detail and greater precision can resolve these weaknesses.

Aside from the above noted weaknesses, certain other aspects of the simulation should be viewed skeptically. For example, in the standard versions of the simulation both the percent of females reproducing and average litter sizes stabilized at fairly high values at high population densities. If, in reality, these parameters continued to decline, or ceased altogether, at densities outside the range for which the density-dependent relationships were determined, the simulation's outcome could have been altered substantially.

Another problem concerns the distribution of variation in mortality rate throughout the population. Although the simulation employed age-specific survivorship and mortality rates, variation in the overall mortality rate was distributed amongst the various age classes in about the same proportion.

Jonkel and Cowan (1971) reported that the majority of yearly variation in mortality for the black bear (*Ursus americanus*) population they

studied occurred in the subadult age classes. Alteration of the simulation to reflect such a pattern could also have altered estimates of minimum viable population size. To determine this would have required information on the variances associated with the mean age-specific mortality and survivorship rates given in the life table of Craighead et al. (1974). This information is usually omitted when researchers publish life tables. It should not be.

An additional weakness of the simulation was lack of consideration of the genetic factors (e.g., inbreeding depression, founder effect, genetic drift) that might affect population survival at low population levels. Again, lack of adequate information precluded testing the effects of such factors.

Clearly, the work presented here must be viewed as a rough "first-cut." Resolution of the above noted weaknesses would probably result in larger estimates of minimum viable population size. Therefore, the results presented here can only be interpreted as the bare minimum population sizes to ensure even short-term survival for populations of this species.

Any attempt to transfer the results obtained here to other populations of the species must recognize that grizzly bear populations vary in numerous important population parameters (e.g., age at first reproduction, cub sex ratio, average litter size, etc., Pearson 1975, Shaffer 1978), and that such variations can have substantial impacts on estimates of minimum viable population size. Therefore, both minimum viable population sizes and their minimum area requirement should be based on detailed information from the population of interest. As such information becomes available, the simulation outlined here can be

employed as 1 tool to provide more reliable assessments of minimum viable population sizes and their minimum area requirements.

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Note: Recent work with the simulation presented here indicates two systematic errors were inadvertently overlooked. One error involved the use of the pseudo-random number generators; the other was due to small populations drifting well above carrying capacity. These errors have been corrected and the new estimate for a minimum viable population is 50–90 bears. This corresponds to a new estimate of minimum area requirements of 1000–13, 500 km².