Wildl. Soc. Bull. 13:223–228, 1985

NEW ESTIMATES OF MINIMUM VIABLE POPULATION SIZE FOR GRIZZLY BEARS OF THE YELLOWSTONE ECOSYSTEM

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A minimum viable population (MVP) is the population size that has a 95% chance of surviving for 100 years (Shaffer 1978, 1981). Shaffer used estimates of population parameters for grizzly bears (*Ursos arctus horribilis*) obtained by Craighead et al. (1974) to develop a population model and estimate the MVP by computer simulation.

Our research estimated the MVP for grizzly bears using data gathered since 1975 under the direction of the Interagency Grizzly Bear Study Team (U.S. Dep. Inter. 1982*a*) and compared the results with those of Shaffer. The data were reduced to the following summary parameters: mortality rates (age- and sex-specific), reproductive rates, mean age and sex structure, and estimates of the variances for the rates. Shaffer's model was modified to reflect the relationships found in the new data. Computer simulations were run to determine MVP estimates, the sensitivity of MVP estimates to changes in the population parameters, and the influence of environmental and demographic stochasticity on the MVP estimates.

METHODS AND PARAMETER ESTIMATES

Shaffer's (1978) model used data gathered from 1959 to 1970. Data used for this project were based on research conducted from 1975 to 1982 (Knight et al. 1975, 1977, 1978, 1980, 1982; Knight and Blanchard 1981, 1983; Knight, unpubl. data) using radiotelemetry methods to learn the fate of individual bears.

Using the cementum annuli method, the oldest bear recorded was 25 years old. Thus, 26 age-classes were used in simulations with cubs being the first age-class.

Sample sizes for bears in each age- and sex class whose fates were known were small. Thus, the data were pooled to give an average estimate for the study period, 1975–1982. Annual mortality rates were estimated by dividing the number of radio-marked bears that died in each age- and sex class by the number of radio-marked bears that entered that age- and sex class. Several (7) bears were suspected to have died but were not confirmed as mortalities. We calculated a lower mortality estimate (Case 1) excluding these suspected mortalities, and a higher estimate (Case 2) including them.

Because sample sizes were small, mortality estimates were averaged for age-classes 3 through 14 years by taking 5 year-class moving averages (Kendall 1973). A single mortality rate was calculated for age-classes 15–26. The age-specific mortality rates appear in Table 1.

The smoothed estimates of mortality rates precluded calculating variances by age- and sex class. Thus, a mortality rate was calculated for all bears by year, and variance in yearly rates (Table 2) was used in the simulations (Shaffer 1978).

Shaffer (1978) estimated reproductive rates by dividing average litter size by average length of the reproductive cycle. Alternately, we divided the number of radio-marked adult females (age ≥5 years) into the number of cubs that they produced in a given year. The mean and standard deviations for the population reproductive rate were calculated using the formulas for a simple random sample (Table 3).

The percentage of animals in each age- and sex class (ages 1–11) was estimated assuming the age at first capture to be a random sample of the population (Table 4). For age-classes 12–26, the classes were combined and the percentage per class was estimated by constructing a right triangle with an area equal to the estimated total percentage of animals ages 12–26 and the base length equal to the number of classes (Fig. 1). The percentage in each class was estimated from the area above each age interval, insuring a smooth age-distribution curve even though the sample sizes were small for some older ages.

Table 1. Estimates of grizzly bear mortality rates in the Yellowstone ecosystem.

Age-class	Case 1 (lower mortality)		Case 2 (higher mortality)	
	Males	Females	Males	Females
1[a]	.110	.110	.110	.110
2[a]	.111	.200	.111	.333
3	.212	.090	.261	.147
4	.212	.115	.239	.172
5	.189	.115	.217	.145
6	.117	.098	.167	.098
7	.050	.138	.100	.138
8	.040	.178	.073	.178
9	.040	.153	.113	.153
10	.040	.113	.113	.113
11	.107	.080	.147	.080
12	.107	.080	.147	.080
13	.117	.100	.117	.100
14	.117	.100	.117	.100
15–26[b]	.167	.267	.167	.267

[a] R. R. Knight (unpubl. data, 1982).
[b] All numbers for age-classes 15–26 were pooled.

THE MODEL

The simulation model of Shaffer (1978) estimated MVP as the initial population size that survived for 100 years in 48 out of 50 computer trials. Environmental variation (stochasticity) was simulated by generating a sequence of 100 random numbers that were normally distributed around the estimate of a given parameter. This simulates a random sequence of "good," "bad," and "average" years. Reproductive and survival rates were allowed to vary independently of each other and from year to year because relationships or patterns in the data were not detected. Demographic variation was simulated by considering the fate of each bear individually in the computations. A uniformly distributed random number between 0.0 and 1.0 was obtained for each bear; if the number was below the appropriate mortality rate, the animal was removed (died). The sex ratio for cubs was also allowed to vary

Table 2. Estimates of yearly mortality rates for grizzly bears in the Yellowstone ecosystem.

Years	Case 1 (lower mortality)	Case 2 (higher mortality)
1975	.0	.0
1976	.125	.125
1977	.174	.269
1978	.174	.174
1979	.071	.071
1980	.100	.129
1981	.162	.225
1982	.107	.107
$\bar{x} \pm$ SD	.131 ± .0405	.157 ± .0697

Table 3. Estimates of the average reproductive rates (ARR) for grizzly bears in the Yellowstone ecosystem.

Years	ARR
1976	.714
1977	.818
1978	.444
1979	.625
1980	.714
1981	.727
1982	1.125
$\bar{x} \pm$ SD	.738 ± .207

Table 4. Estimated percentage of grizzly bears in each age- and sex class in the Yellowstone ecosystem.

Age-class	Males	Females
1	.105	.059
2	.093	.066
3	.089	.059
4	.077	.043
5	.053	.035
6	.031	.024
7	.023	.024
8	.019	.017
9	.020	.020
10	.016	.012
11	.016	.004
12	.004	.007
13	.004	.007
14	.004	.006
15	.004	.006
16	.003	.005
17	.003	.005
18	.003	.004
19	.002	.004
20	.002	.003
21	.002	.003
22	.002	.002
23	.001	.002
24	.001	.002
25	.001	.001
26	<.001	<.001
Totals	.578	.422

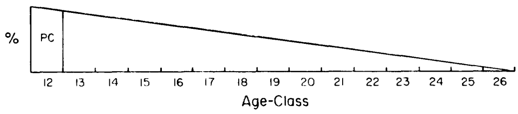

Fig. 1. The age-class triangle for age-classes 12 to 26. The total area of the triangle equals the percentage of bears in age-classes 12 to 26. The percentage of bears in each age-class (PC) equals the area above that age-class.

normally about the mean ratio of 50:50. The number of cubs produced was estimated stochastically for each year; cubs were assigned to be either male or female by generating a uniformly distributed random number between 0.0 and 1.0 for each animal. Numbers <0.5 indicated male cubs. Shaffer (1978) considered simulations including both environmental and demographic variations to be more realistic, thus both were included in the basic model used for this project.

Shaffer's original simulations were repeated to verify that the program was operating correctly on our computer system. Shaffer's program entered the initial age structure directly for each age- and sex class. Bears in our program were assigned to individual age-classes differently. We calculated the cumulative percentage for each age-class and generated a uniformly distributed random number between 0.0 and 1.0 for each bear. The bear was assigned to the age-class with the cumulative percentage that contained the generated number. For example, if the number generated was .5349 and the cumulative percentages for age-classes 1 through 5 were .15, .25, .47, .83, and 1.0, respectively, the bear was assigned to age-class 4. This procedure resulted in initial populations in which bears were randomly distributed rather than an initial population where the number of bears in the age-classes is a deterministic monotonic decreasing function of age.

Shaffer's program did not limit the size of the population through time, a problem which he acknowledges (Shaffer, pers. commun.). Thus, the population grew to large sizes in some simulations. Our program limited the size of the population to 300 bears, a management objective for the population (U.S. Dep. Inter. 1982*b*). Excess bears were removed in the same manner that bears were assigned to the initial population.

The values of environmental parameters were restricted to realistic ranges. Mortality rates were restricted to a range of 0.0–1.0. Average reproductive rate was restricted to the range calculated from the telemetry data, 0.444 to 1.125.

THE SIMULATIONS

We ran 3 sets of simulations comprising 2 cases each. The first case used the lower and the second case the higher mortality estimates. We considered 2 thresholds of extinction. First, the population became extinct when all adult females died, thus assuming that all younger females also would perish. The second threshold was reached if all bears of either sex died. Output included the percentage of trials where the population did not become extinct, the number of bears removed, and the percentage of trials with a population larger than the initial population. The MVP was estimated by starting with a small initial population (usually $n = 30$), which was increased by 10 for Case 1 and 25 for Case 2 until 95% (>47 of 50) of the trials indicated that the population survived 100 years. The second set of simulations examined the sensitivity of the MVP estimates by decreasing the average reproductive rate by 10%. The sensitivity of the estimates to environmental variation was examined by setting the standard deviations of the parameters equal to 0.0. Finally environmental and demographic variations were removed so that the average conditions persisted over all years.

RESULTS

The MVP was 40 bears for Case 1 vs. 125 bears for Case 2 (Table 5). On the average,

Table 5. Number of simulated populations ($n = 50$) surviving thresholds 1 and 2, and the number of animals removed.

	Initial population size	No. populations surviving		Average no. of bears removed per simulation
		First threshold	Second threshold	
Case 1	30	47	47	324
(lower mortality estimates)	40[a]	49	50	473
	50	50	50	532
Case 2	75	37	39	0
(higher mortality estimates)	100	44	45	21
	125[a]	48	49	35
	150	47	48	26
	175	47	47	51
	200	49	50	68
	225	48	48	98
	250	49	49	117
	275	50	50	150

[a] MVP estimate.

324–532 bears were removed for Case 1 vs. 0–150 for Case 2. The percentages of simulated populations where the final population size was larger than the initial population ranged from 92% (initial $n = 30$) to 100% (initial $n = 40$) for Case 1 and from 20% (initial $n = 275$) to 38% (initial $n = 100$) for Case 2. Estimates of this parameter were unstable in Case 2.

The second set of simulations indicated that a drop in the average reproductive rate of 10% would increase the MVP to 50 bears for Case 1 and to 225 bears for Case 2. Removing the environmental variation did not affect the MVP estimate for Case 1 but dropped the Case 2 estimate to 100 bears.

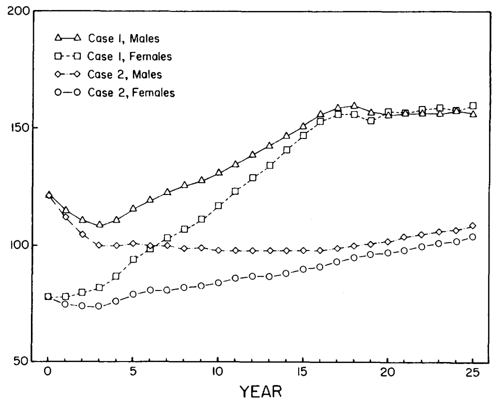

Fig. 2. Simulated grizzly bear numbers with environmental and demographic variations removed.

In the third set of simulations (both demographic and environmental variations were removed), populations in both cases increased from an assumed initial 180 bears to >300 in <100 years (Fig. 2). For Case 1, the population increased about 3.7%/year. The population increased about 1.4%/year for Case 2.

DISCUSSION

If the lower mortality estimate is correct, our results approximate those of Shaffer (1978). The MVP estimate of 40 bears (Case 1) compares to Shaffer's estimate of 35 bears. However, if the higher mortality estimate represents the true situation, the MVP estimate is about 3.5 times larger (125 bears). The addition of a few mortalities can drastically change the population dynamics of the bears and result in an unstable population. The effect of these extra mortalities is also reflected in a decrease in the number of bears removed and the number of trials in which the populations increased.

Decreasing the average reproductive rate increased the MVP estimate by only 10 bears for Case 1 vs. 100 bears for Case 2. Removing the environmental variation did not influence MVP estimates, as the Case 2 estimate decreased only 25 bears.

The simulated bear populations increased in both cases when environmental and demographic variations were removed. Also, almost all trials resulted in an increase in population numbers (Case 1). This would seem to indicate that, on the average, the population was increasing. Assuming the simulations using the higher mortality estimates were correct, this tendency to increase can be reversed easily.

The radio-collared bears were considered a random sample of the whole population. Conceivably the collared bears may be more representative of problem bears, which are more likely to be subjected to management action. Thus, our mortality estimates may be biased upward. Also, genetic effects and natural catastrophes have been ignored due to a lack of quantitative information (Shaffer 1978). These factors could alter the actual MVP substantially.

SUMMARY

We simulated the effects that environmental and demographic variations have on the size of a minimum viable population for the grizzly bear in the Yellowstone ecosystem. Parameters were based on radiotelemetry data collected from 1975 to 1982. The sensitivity of the MVP estimates to changes in reproductive rates and removal of environmental and demographic variations was examined.

We conclude that mortality rates have greater influence on the simulated populations than reproductive rates. Although the simulated populations increased using average values for the parameters, consecutive years of high mortality, low reproduction, or too many male cubs could reverse this trend. Based upon our simulations, we conservatively estimate that a minium of 125 bears should be maintained to ensure high probability of a viable grizzly bear population for 100 years in the Yellowstone ecosystem.

Acknowledgments.—We thank the Interagency Grizzly Bear Study Team and specifically R. R. Knight for making unpublished data available for this study. M. L. Shaffer provided a copy of his program and advice on modifications.

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Received 6 April 1984.
Accepted 2 December 1984.

Wildl. Soc. Bull. 13:228–233, 1985

NUISANCE CANADA GOOSE PROBLEMS IN THE EASTERN UNITED STATES

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Canada geese (*Branta canadensis*) have increased in numbers in North America during the past 50 years. This expansion has resulted in goose-inflicted damage to many grain and green forage crops in rural areas (Horn 1949, Bossenmaier and Marshall 1958, Hunt and Bell 1973, Sugden 1976, Clark and Jarvis 1978, Hunt 1984). Recently, an increasing number of complaints has come from suburban and urban areas where geese forage on lawns located in parks, beaches, golf courses, country clubs, and backyards (Hawkins 1970, Laycock 1982). Even low numbers of geese can damage the grass and litter areas with their defecations. High densities of feces reduce the esthetic value and recreational use of these areas (Fig. 1) and are often perceived as health hazards. Droppings from large flocks of geese can also contribute to the over-fertilization of small lakes and reservoirs. This study addresses the history, extent, and severity of nuisance goose problems through surveys of water companies in Connecticut and golf courses throughout the eastern United States.

METHODS

Questionnaires were sent in 1982 to the managers of every water company in Connecticut to determine if geese were perceived as reducing water quality. Lists of water companies were provided by the Connecticut Department of Environmental Protection. Questionnaires also were sent to golf course managers in each state east of the Mississippi River to determine if goose defecations and damage to lawns were considered problems. Addresses of golf course and country club managers were obtained from the membership rolls of the Golf Course Superintendents Association of America (GCSAA). For each eastern state, we sent questionnaires to 12 randomly selected golf course managers listed on the GCSAA rolls as being affiliated with a golf course; however, we could locate only 6 active addresses for managers in New Hampshire and 9 each in Delaware and Mississippi.

Questionnaire packages included a cover letter and self-addressed return envelope. After 3 weeks, nonrespondents were sent a second questionnaire. Questionnaires sent to each group were similar, with some questions altered to suit each group.

The questionnaires were designed to be as neutral as possible. Recipients were first asked whether any Canada geese spent time on their property last year, and whether they enjoyed having the geese present. Respondents responding positively to the latter question were asked to answer 1 set of questions; those responding negatively were directed to a second set. Respondents who did not enjoy geese were asked how much damage the Canada geese were doing, what year geese first became a problem, what techniques had been used to alleviate the problem, and what their opinion was on a number of potential solutions to this problem. All recipients were asked the number of geese on the property during an average winter, spring, summer, and fall day last year, and whether hunters were allowed on the property. Copies of the cover letters and questionnaires can be obtained from the authors.

RESULTS

Survey of Connecticut Water Companies

Forty-three percent of the 73 Connecticut water companies returned the questionnaire