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Source: *The Journal of Wildlife Management*, Vol. 60, No. 2 (Apr., 1996), pp. 416-421
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3802244

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Received 5 July 1994.
Accepted 11 October 1995.
Associate Editor: Ryan.

HOW MANY GRIZZLIES IN YELLOWSTONE?

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Abstract: Trend data indicate that the Yellowstone grizzly bear (*Ursus arctos horribilis*) population has been increasing in recent years, after a decline induced by closure of open garbage dumps in 1970–71. Current population size appears to be approaching a level where management to curb further increases might be desirable, even though it will be highly controversial. Continual close monitoring is essential for managers to know how to safeguard the population. Estimating total population size of an endangered or threatened species should be secondary to measuring essential population parameters, but nonetheless may be necessary to avoid misunderstandings. Knowledge of survival and reproductive rates is essential if causes of a decline are to be detected and corrected.

J. WILDL. MANAGE. 60(2):416–421

Key words: grizzly bears, population estimation, population size, population trend, *Ursus arctos*, Yellowstone National Park.

When faced with uncertainty about a species, the first question administrators and the public ask is "How many are there?" This appears to be an entirely reasonable inquiry, but is usually the wrong question. The crucial questions are "Is the population increasing or decreasing?" and "Which parameters are responsible for the observed trend?" Successive measures of population size may give an indication of a trend, yet provide little or no understanding of reasons for the observed changes. Estimates of survival and reproductive rates can be used to determine population trend (Eberhardt et al. 1994) and will also serve to determine the probable cause of a trend (Knight and Eberhardt 1985).

The question of numbers often has to be approached in some fashion, and incomplete answers can result in future difficulties. Size of the grizzly bear population in the Greater Yellowstone area provides an example, described in this paper. Various popular accounts have discussed Yellowstone's grizzlies, and a large number of newspaper articles have appeared, and continue to be written. Most of these sources report the number of grizzlies now present in the area. To the best of our knowledge, not one of these numbers is based on a valid estimation scheme. Many of the estimates lie in a fairly narrow range, so that the supposed size of the population has become "common knowledge," even though erroneous. The books by Schullery (1986, 1992) provide an exception to the usual treatment, giving an excellent account of the problems of estimating the number of grizzlies in Yellowstone, and discussing the various popular perceptions in detail.

Much of the Yellowstone grizzly population apparently depended on open garbage dumps for a supplemental food supply up to 1970 and 1971, when the dumps within the Park were closed (Knight and Eberhardt 1985). This action was controversial, and many bears had to be destroyed because they invaded campgrounds and homes searching for food after closure of the dumps (Eberhardt et al. 1986). The controversy led to the formation in 1973 of the Interagency Grizzly Bear Study Team, charged with evaluating the status and trend of the population. Grizzlies are notoriously difficult to census in forested areas, and the team wound up determining reproductive and survival rates through radiotelemetry as an approach to determining trend and limiting factors. A supplemental index of abundance for assessing trend was obtained from annual tallies of adult (ages 4–5 and older) females observed with cubs-of-the-year. Substantial efforts were made to avoid duplication, so that only "distinct family" groups were recorded (Knight et al. 1995).

As the telemetry study developed, it became evident that the key to recovery of the population was adult female survival (Knight and Eberhardt 1985). Inasmuch as grizzlies typically produce young at 3-year intervals, multiplying the counts of distinct family groups by 3 gave an estimate of minimum number of adult females present. This total was used with the adult female survival rate to set a maximum allowable recorded annual mortality of adult females (2/yr). This number provided a concrete goal for the recovery effort, and ultimately was achieved by extensive interagency cooperation.

Funding for this study was provided largely by the National Park Service and the U. S. Fish and Wildlife Service. Major technical support was provided by Yellowstone National Park and the Wyoming Game and Fish Department. B. Blanchard and K. Aune reviewed the manuscript, as did two anonymous referees.

POPULATION ESTIMATES

Minimum Population Estimates

The question of total numbers continued to be raised, and at one point, the interagency committee responsible for the study made a formal request for a population estimate. When it became evident that a large trapping effort would be required, the request was withdrawn. There was nonetheless continued pressure for estimates of total numbers. A "population review" committee was convened on 4 occasions (1983, 1986, 1988, and 1994). A minimum population size estimate was developed by starting with the minimum number of adult females obtained from the "distinct family" surveys. Estimates of population composition were then used to expand the minimum number of adult females to a minimum total population size (details appear in U. S. Fish and Wildl. Serv. 1993: Appendix C). The same estimation process was repeated in the 1994 meeting. In all of these efforts, it was emphasized that the estimate is a *minimum*, but most of the popular accounts drop this caution, so that these estimates have become total population numbers.

Our most recent such estimate uses the stable age distribution of females calculated from survival data obtained by radiotelemetry (Eberhardt et al. 1994) to estimate the proportion of adult females in the female population (50.1%). Male survival rates were used to determine sex ratio from the equation:

$$\text{Proportion males in the population} = RC_f/(RC_f + C_m) = 0.453 \quad (1)$$

where $R = 1.041$ = sex ratio at birth (determined from 1,326 zoo records of sex ratio at birth, U. S. Fish and Wildl. Serv. 1993: Appendix C), and C_f is proportion of female cubs in the female population based on the stable age distribution, while C_m is proportion of male cubs in the male population, also based on the stable age distribution. Multiplying the fraction of females ($1 - 0.453 = 0.547$) by proportion of adult females (0.501) gave an estimate of 27.4% of the population being adult females. The average number of distinct family groups (Knight and Blanchard 1995) for the 1990–94 period was 22.4. Assuming a 3 year reproductive interval, this gives 67 adult females, for a minimum total population of $67/0.274 = 245$ bears.

Minimum Population Based on Ages

Because the Yellowstone population is isolated, and thus closed to immigration and emigration, an absolute minimum population estimate can be constructed from records of bears identified over the course of the study. Each bear handled is aged by tooth sectioning, so that a matrix of the years that each identified bear was in the population can be constructed. Each such bear occupies a row of the matrix, while columns represent calendar years. Each adult female bear was entered at the time it was last identified as alive, along with its ages back to the year of birth. The maximum number of females thus identified was 55 in 1986. Adding in young associated with these females and males known to be alive in 1986 gives 133 bears as the absolute minimum population for that year. The sex and age structure of these bears also indicates that about 27% of the population was composed of adult females.

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Table 1. Data from marked bears seen in distinct families used for Petersen estimates. Number of marked bears in population includes all adult females marked.

Year	No. marked in population (M)	Marked bears resighted (m)	No. in second sample (n)	Ad F population estimate
1989	16	3	14	62.8
1990	11	1	21	131.0
1992	10	0	21	241.0
1993	11	1	18	113.0
1994	10	3	18	51.3
Totals	58	8	92	599.0
Means	11.6	1.6	18.4	119.8

Estimate Using Marked Females

Each year since 1975 there have been a number of radiotagged adult females in the population. The distinct-families observations (Knight et al. 1995) provide a second sample in which the proportion marked can be determined. Because radiotagged bears are more likely to be observed (due to frequent locations by telemetry), we have not used any data in which females with cubs have been seen only through radiolocation for estimating total population size. Using the number (M) of radiotagged adult females, the number (m) of these resighted in the number (n) of distinct families tallied, Petersen estimates can be made using Chapman's bias-corrected equation (Seber 1982):

$$\hat{N} = \{[(M+1)(n+1)]/(m+1)\} - 1 \qquad (2)$$

Due to the small samples involved, data for 5 recent years (Table 1) were averaged in a Petersen estimate based on means, which simply replaces M, n, and m above by means (Eberhardt 1990). We excluded 1991, when only 3 adult females were radiotagged. An alternative estimation procedure uses the mean Petersen, in which several individual estimates are averaged. The Petersen estimate based on means gave 94 adult female bears, while the mean Petersen estimate was 120 bears. Using the factor calculated in the section on Minimum population estimates (27.4% ad F) and the average of the 2 estimates (107) suggests a total population of 390 bears.

Estimate from Distinct Families

A Petersen-type estimate can be obtained directly from the distinct family records by using the dates of sightings. Distinct families seen on or before 15 July provided the "marked" population (M), and records of distinct families seen after 15 July provided the second sample (n), in which a number (m) of the "marked" group were resighted (Table 2). Seber (1982:61) proposed that Bailey's estimate should be used for multiple resightings:

$$\hat{N} = [(M+1)(n+1)]/(m+1) \qquad (3)$$

Table 2. Data for estimating number of adult female grizzlies, using sightings before and after 15 July and Bailey's equation (eq. 3).

Year	Seen on or before 15 Jul M	Seen after 15 Jul m	Seen after 15 Jul but not marked u	$n = m + u$	Population estimate	Coef. of variation
1988	12	4	7	11	28.8	0.71
1989	12	4	4	8	21.6	0.82
1990	18	9	7	16	30.6	0.80
1991	6	3	18	21	33	0.48
1992	8	3	15	18	38	0.51
1993	12	4	8	12	31.2	0.68
1994	8	5	12	17	24	0.62
Average					29.6	
Average 1990–94					31.4	

Averaging the most recent 5 years gives 31 distinct adult females with cubs-of-the-year. Multiplying by 3 to adjust for females not having cubs-of-the year in any given year yields an average of 93 adult females, or 339 bears in the population, based on the estimate of 27.4% being adult females.

The Petersen estimates based on identification of marked bears in the distinct-family surveys are highly variable (Table 1) due to the small number of marked bears resighted in any year. The coefficient of variation of the estimates given in Table 1 is 63%, as compared to 19% for the estimates of Table 2. We thus focused our efforts to obtain confidence limits on the 1990 to 1994 population estimate of Table 2. Variance calculations for the Petersen estimate are relatively simple, using an equation given by Seber (1982:61):

$$\text{variance} = [(M^2(n+1)(n-m)]/[(m+1)^2(m+2)] \qquad (4)$$

From this one can calculate a series of high coefficients of variation (Table 2) for individual estimates. Confidence limits for an overall estimate of the total population involve the variance associated with estimating proportions of females and males [eq.(1)], as well as the variance from Petersen estimates of Table 2, thus

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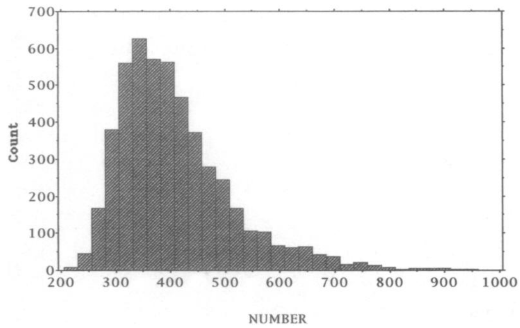

Fig. 1. Frequency distribution of 5,000 bootstrap calculations of total grizzly bear population size used to calculate confidence limits on the estimate.

leading to a complex calculation. We approached this problem using the bootstrapping technique described by Efron and Tibishirani (1993). Calculations for the proportion of adult females in the population were obtained by modifying the bootstrapping program used by Eberhardt et al. (1994) to obtain confidence limits for λ. The modifications chiefly concerned introducing male survival data (to estimate proportion of males from the stable age distribution) and sex ratio of cubs. The Petersen estimates for mean number of adult females were also bootstrapped, leading to a coefficient of variation for the mean (22%) reasonably close to that of Table 2 (19%). Combining the several sources of variation in 5,000 bootstraps yields the frequency distribution of Fig. 1, and approximate 95% confidence limits for the total population estimate (344 bears) of 260 to 660 bears. The noticeable skewness of Fig. 1 results from the Petersen estimates, as the frequency distribution of proportion of adult females is quite symmetrical. Due to this skewness, we believe that it may be appropriate to use 90% confidence limits of 280 to 610 bears, and suppose that the lower limits may be of main interest, in any case. These lower limits are somewhat higher than the 245-bear minimum total population, and about double the absolute minimum population (133 bears) based on ages.

DISCUSSION

Earlier Estimates and Recorded Mortalities

In the 1960s, bears were marked at garbage dumps, resulting in a population estimate of 229 bears (Craighead et al. 1974). A reanalysis of this data by the National Research Council (1974) yielded about the same number of bears (234). A higher number (301) appears in later correspondence among committee members (letter of 29 April 1975 from the Chairman of the committee, I. M. Cowan to G. F. Cole, Supervisory Research Biologist, Yellowstone National Park). We have been unable to locate any supporting calculations for this estimate. McCullough (1981) quotes a similar number (312 bears). The prospect that a larger population may well have existed in earlier years was raised by data collected in a black bear study by Barnes and Bray (1967), who observed only 1 marked bear in 27 grizzlies sighted. Cole (1974, 1976) also gave various estimates in the range of 300–400 bears.

The possibility of a larger grizzly population in the period before the dumps were closed is also supported by the modeling study of Eberhardt et al. (1986). They reported data on the numbers of adult females with cubs-of-the-year, adult female mortality, and litter size for the period 1959–85, and made various attempts to fit a simple difference equation model to the data, beginning with an estimate of the total number of adult females present in 1959, determined from the data of Craighead et al. (1974). Efforts were also made to use a minimum Chi-square method to fit the model to the data on adult females with cubs. These efforts suggested that a higher initial population would be required to minimize the total Chi-square.

The population model using the Craighead population estimate for its initial value exhibited a precipitous drop after the dump closures, dropping from about 65 adult females in 1965–68 to nearly 40 in 1973–74 (Eberhardt et al. 1986). Craighead et al. (1974) presented a model for the total population that showed essentially the same trend, going from a peak population of 245 grizzlies in 1967 to 136 animals in 1974. The index data (Fig. 2) do not exhibit such a dramatic drop, showing instead a shallow curve.

Current Estimates

The initial results of our study indicated a slow rate of decrease through 1980, roughly 2% per year (Knight and Eberhardt 1985). Current analyses (Eberhardt et al. 1994, Knight and Blanchard 1995, Knight et al. 1995) show a positive annual rate of change (roughly 2 to 5%). The turning point appeared to occur in the mid-

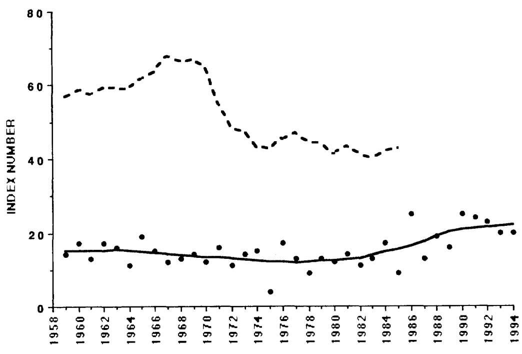

Fig. 2. Trend of a difference equation population model (upper curve) following Eberhardt et al. (1986) compared to the trend of an index based on adult females with cubs-of-the-year. Trend data (lower line) to 1975 are from Eberhardt et al. (1986), while data from 1976 to 1993 are those of Knight et al. (1995). Trend curve (solid line) calculated by the "lowess" method (Cleveland 1979).

1980s, when the policy of preventing adult female mortalities whenever feasible began to be widely observed. This policy has not been without costs in time, human resources, and public relations to the agencies, and has required continued cooperation and extra efforts. There are 2 national parks and 6 national forests covering part of the grizzly range (each with various ranger districts), and 3 states are involved, each with its enforcement and management agents. Coordination is not a simple matter. Although the grizzly population may be increasing, so has human use of its range, with continuing potential for human-bear conflicts. Relaxation of concerns about population size and trend probably will lead to an increase in bear mortalities, because it is much easier to destroy a bear than to manage sources of bear-human conflicts.

As data accumulate, it appears that we can estimate the total numbers of bears in the Yellowstone population, and thus we will have the conjunction of a perception that the population has been increasing, along with a population total appreciably higher than the estimates in current use. Consequently, research efforts may have diminishing support, and may be relegated to staff of the many agencies now involved. A few percentage points of adult survival separate an increasing from a decreasing population, so that the population could easily slide back to a decreasing trend. This might not be apparent if research and management efforts are reduced.

On the positive side, if the indications of an appreciably larger grizzly population than commonly reported are correct, several management actions need consideration. The population may be approaching an asymptotic level ("carrying capacity"). We believe that the probable indication of this event will be a decrease in subadult survival, making it desirable to intensify efforts to monitor this parameter. About 77% of the total variance in our estimate of the rate of change is associated with subadult survival (Knight and Blanchard 1995). More subadults thus need to be radiotagged in order to reduce the variability in this estimate. Our initial emphasis (Knight and Eberhardt 1985) was on adult female survival because a high adult female survival rate is essential to maintain large mammal populations having low reproductive rates.

Plans are being developed to reintroduce bears to wilderness areas not occupied since the 1920s, and it may be possible to use these "surplus" subadult females for that purpose, using those bears that move into areas where they are likely to come in conflict with human use of the area. The Wyoming Department of Fish and Game has expressed an interest in the prospect of eventually hunting grizzlies. This possibility needs to be considered as a management effort, because removal of some males may reduce competition for resources. Removal of some bears as "surplus" is difficult to justify on the basis of a density-dependence mechanism because there is little evidence of density-dependence in bear populations (Taylor 1994). Because bear-human conflict situations continue to increase, and often result in death of bears (Blanchard and Knight 1995), we believe alternate use of some bears is worthwhile.

Strong objections to any harvest are likely from those who wish to keep grizzlies in a "natural" state. The only apparent way to do this is to remove people from grizzly range. Out of 92 grizzly bear losses recorded in this study for which a cause of death could be established, just 10 (11%) were from natural causes. The remainder were killed or removed by humans (6 additional bears died of unknown causes). Capturing and moving bears has been necessary to avoid the necessity of killing bears to protect humans, but has not been highly successful (Blanchard and Knight 1995). Using surplus bears for translocations to new areas and for hunting would reduce the need for outright destruction of such bears.

Much of the evidence for a larger bear pop-

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ulation comes from the "distinct family" study. Confirmation of these indications is important in view of the implications of a higher population estimate. Due to a substantial capture heterogeneity, and the high costs, it may not be possible to use trapping to estimate population numbers. A feasible approach is immediately available, however. On several occasions in the course of the study there have been as many as 30 radiotagged bears in the population. Intensive aerial searches can locate enough bears to make an overall Petersen estimate practicable. Inasmuch as the number of bears seen in aerial searches varies with weather and forage conditions, such a survey would probably need to be run for several years to be sure of an adequate resight sample. The low rate of change in the overall population will have little effect on an estimate that combines data from several years.

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Received: 18 May 1995.
Accepted: 17 December 1995.
Associate Editor: Murphy.

 FWS_LIT_003417