

PROSPECTS FOR YELLOWSTONE GRIZZLY BEARS

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Abstract: Recent analyses of data on the grizzly bear (*Ursus arctos horribilis*) population of Yellowstone National Park and its environs suggest the likelihood of a continuing decline in numbers if losses of fully adult females are not reduced. The size of the population is not known, and a simple projection model has been used to identify some inconsistencies in the available index data. Population dynamics calculations, based on Lotka's equation or a stochastic model, indicate a continuing decrease in numbers, although continued observations through radio-telemetry are needed to verify these trends. The margin between stabilizing the population and a continued decrease appears to be roughly the loss of 2 fully adult female bears per year. At present, the risk of extirpation of this population over the next 30 years appears to be small. Continued monitoring of survivorship will be needed, particularly because "recovery" of the population may be mainly characterized by a shift in the pattern of mortality, from adults to subadults, and not necessarily a reduction in absolute number of losses.

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The future of the grizzly bear population in Yellowstone National Park and its environs is uncertain and controversial. There is little question that this bear population is isolated and that human use of its habitat has been increasing steadily and will likely continue to increase into the foreseeable future. An inevitable concomitant of increased human activity is the construction of additional facilities, which undoubtedly will generate more human-bear interactions and conflicts. Improvements in habitat quality may be feasible, and some sources of conflict may be reduced in the future; however, most of the current rules and regulations designed to protect grizzly bears attempt mainly to minimize further impacts from additional development.

There is thus little reason to suppose that environmental conditions will improve for Yellowstone grizzly bears in the future, so a cautious and conservative approach is essential. Our interpretation of recent data suggests a continuing decrease in abundance (Knight and Eberhardt 1985). A reversal of that trend is feasible if the mortality rate can be sufficiently reduced, but the variety of causes and circumstances affecting mortality make such reductions difficult to achieve (Craighead et al. 1974, Knight and Eberhardt 1985). Improvements in data collection and assessment may suggest ways to reduce losses and improve knowledge of the current population status. The purpose of this paper is to update and extend some of the earlier analyses and to suggest needs for additional studies.

POPULATION SIZE AND TREND

The size of the Yellowstone grizzly bear population is unknown. Low densities, high mobility, and the species' secretive behavior make censuses in mountainous and forested areas extremely difficult. Con-

centration of a sizeable fraction of the population at garbage dumps before 1970 made marking and observation much simpler; thus estimates of population size are available for that earlier period. Tallies of the number of individual adult females accompanied by cubs are available since 1959, constituting a potential index of abundance. Ages, sizes, colors, locations, and other clues make it possible to substantially reduce the recording of duplicate observations as separate families, but it is much more difficult to determine whether some groups go unrecorded. Consequently, these counts are best regarded as an index of relative abundance of adult females. The overall indication is one of decreasing numbers (Knight and Eberhardt 1985: Fig. 5).

A Simple Population Model

Given an initial estimate of population size and a trend index, it should be possible to make some inference about recent population size. We have investigated this prospect by comparing the trend index data with data on known deaths and litter sizes through a simple difference equation model:

$$N_t = N_{t-1} + R_t - M_t \quad (1)$$

where the total number of fully adult females (N_t) in year t depends on population size 1 year earlier plus recruits (R_t) less mortalities (M_t). Because the population is defined as all females 5 years old and older, recruits are calculated as:

$$R_t = BN_{t-5}C_{t-5} \quad (2)$$

where C_{t-5} denotes litter size 5 years previously, and B is calculated as:

$$B = \frac{(\text{survival to age 5}) (\text{proportion of female cubs})}{\text{breeding interval}} \quad (3)$$

Given an initial population size, running the model requires an estimate of B , litter sizes, and records of deaths of adult females.

Craighead et al. (1974) reported a population of about 230 bears, and a National Academy of Sciences review committee concurred with this estimate but may have later considered a revision to 305 bears (cited by McCullough 1981). Craighead et al. (1974: Table 1) reported that 43.7% of the population were adults, with 53.7% of the adults being females, yielding estimates of the number of adult females ranging 54–72.

Deaths of adult females from 1959 to 1972 were reported by Craighead et al. (1974: Table 10), and the recent data (Fig. 1) were compiled in this study. Records for which age and sex were not available were prorated in accord with the fractions observed in the known categories. We do not suppose that all deaths are recorded but suspect that a fairly high fraction of losses of fully adult females may be tallied.

Efforts to reconcile the model calculations with index data (tallies of adult females with cubs, as described previously) suggest that the index data do not adequately reflect the impact of sizable losses of adult females from 1970 to 1974 (Eberhardt et al. 1986). To further illustrate the difficulty, we have assumed several constraints on the model:

1. A nearly constant adult population from 1959 to 1969 (cf. Craighead et al. 1974, Knight and Eberhardt 1985: Fig. 9).
2. A gradual decline in recent population size due to inadequate survival of adult females (cf. Knight and Eberhardt 1985 and the following discussion).
3. The actual population of adult females should exceed 3-year sums of annual tallies of females with cubs (because the breeding interval is usually somewhat greater than 3 years and we suspect some females with cubs are not counted).

Using $B = 0.025$ for 1959–67 and $B = 0.035$ for 1968–85 with the mortality and litter size data (Eber-

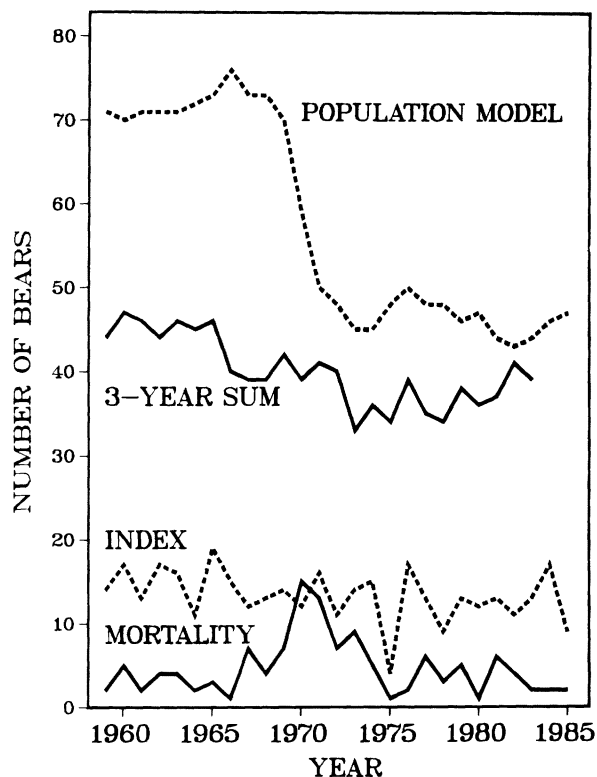


Fig. 1. Recorded mortality of adult females, annual tallies of females with cubs (Index), minimum populations of adult females (3-year sums), and projection model totals of adult female grizzly bears in Yellowstone National Park and environs.

hardt et al. 1986: Table 3) gives a calculated population trajectory consonant with these restrictions (Fig. 1).

Correlation of Mortality with the Index

An intriguing feature of the index (annual tallies of females with cubs) and mortality data (Fig. 1) is the correlation between year-to-year changes in population index and mortalities. A high hunting mortality in 1967 and the high mortality rates in 1970 and 1971, when garbage dumps were closed, make it difficult to apply "runs" tests for significance, because these unusual events would quite surely disrupt the (unknown) underlying phenomenon. Various hypotheses might be advanced for the correlation. The most likely interpretation is that varying food conditions cause adult females to range over more area in some years, thus becoming both more visible and more susceptible to being killed. Another prospect is suggested by the fact that the fluctuations in index tallies show a 2 or 3 year interval between peaks.

Thus it might be assumed that there is a degree of synchrony in reproduction, so that there are actually more females with cubs in peak years. It is then again likely that females with cubs need to forage more extensively and thus may suffer a higher mortality rate.

However, we believe it is risky to adopt an unsubstantiated hypothesis about observed behavior. The important point here is that the existence of a correlation suggests that the fluctuations of index and mortality rates are not due solely to chance and need to be investigated if the data are to be used to monitor grizzly bear populations.

POPULATION DYNAMICS

Until the advent of the white man and firearms, it is likely that adult female grizzly bears had very high rates of survival up to the age of senescence. Just how high these rates may have been may never be known with certainty, but our data suggest few deaths from natural causes during the prime of life. Food requirements and behavior patterns suggest that low bear densities probably were nonetheless maintained, which implies that subadult mortality may have regulated abundance, as seems to be the case for many species of large mammals (Eberhardt 1977). It is thus worthwhile to review overall survivorship and attempt to derive an estimate of subadult survival under primeval conditions for comparison with the present situation.

Recent Survivorship Data

Because capturing, radio-tagging, and monitoring bears are time-consuming and expensive, only small samples were available; Knight and Eberhardt (1985) used all of the available data to construct a survivorship curve. With a somewhat larger sample now available, we have examined the data for male and female grizzly bears separately.

Due to the small sample sizes, we have used pooled (weighted by sample sizes) estimates from ages 5–15 years and have combined males and females beyond age 15 because the sample of older animals is much smaller. Reproductive rates [$m(x)$] were calculated on the basis of average litter size (1.86), proportion of female cubs (0.441), and breeding interval (about 3 years), giving:

$$m(x) = \frac{1.86(0.441)}{3} = 0.273 \quad (4)$$

This rate is lower than that reported in our 1985 paper (Table 6) because there we assumed an even sex ratio of cubs rather than the ratio observed. Survivorship curves (Fig. 2) show the rather sharp divergence of males and females after the 1st few years.

With these rates, calculations from Lotka's equation yield an estimate of $r = -0.025$, indicating a gradual decrease in population size is likely under these rates. To check the calculations, we introduced the same rates into the stochastic model we used in our 1984 and 1985 studies and conducted a series of simulations for initial populations of 40 fully adult females (36 were used in the earlier study). We conducted additional runs with a starting population of 54 fully adult females (the population size estimated from the Craighead et al. [1974] data).

The results suggest much the same rate of decrease, using the average population size after 30 years. The main difference between starting with 40 fully adult females and 54 adults is that the risk of extirpation in 30 years is noticeably higher (Fig. 3) for the smaller initial population.

During additional simulations, survival in the "prime" ages (assumed to be ages 5–15) was increased in small increments until the population stabilized. Because we were uncertain about some details of the initial population, we conducted these runs for 100 years, with the 1st 30 years neglected in the

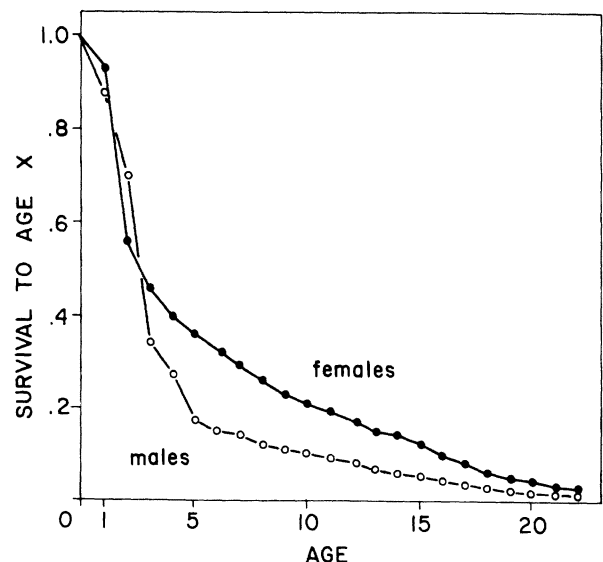


Fig. 2. Survivorship curves for male and female grizzly bears based on telemetry data through 1985. Pooled (weighted by sample size) rates were used for ages 5–15 years, and males and females were pooled for ages greater than 15 years.

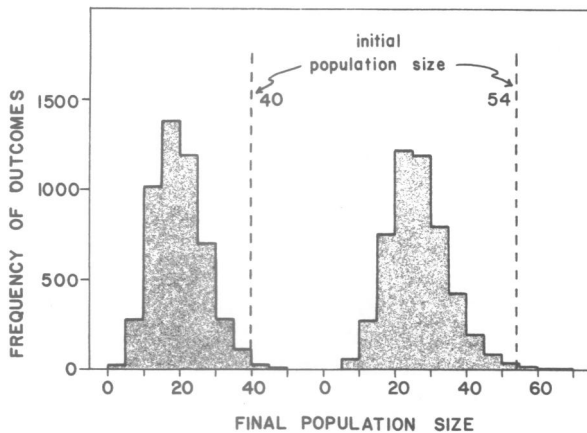


Fig. 3. Size of simulated populations of fully adult (5 years of age and older) female grizzly bears after 30 years, using the Knight and Eberhardt (1985) model and current estimates of population parameters. Vertical lines show starting populations, based on 40 fully adult females and 54 fully adult females. Frequencies are based on 5,000 simulations in each case.

analysis, assuming that period would permit the population to reach a steady state. (Unfortunately, this will not necessarily be at the level that might prevail if we knew the actual initial conditions.) These simulations suggest that an increase of about 0.04 in survivorship of the prime age classes would stabilize the population. If there are 40–50 bears in the adult female population, this translates to roughly 2 bears per year.

Survivorship Curve for Primeval Conditions

The longevity of grizzly bears is not known with much accuracy. The oldest female aged in this study was 25 years old at death, and several have been observed in their early 20's. Craighead et al. (1974: Table 9) used age 25 as the oldest age in the life table for females. The age of senescence is even less well known but has been modeled by fitting a Gompertz function to the data of Craighead et al. (1974: Table 9). This does not fit particularly well (Eberhardt 1985: Fig. 3), but it is uncertain whether the difficulty is with the data, model, or fitting process. For present purposes, we assume primeval survival in the prime age classes to be about 98% (Craighead et al. [1974] estimated about 97% survival in the 1959–69 period) and coefficients of the Gompertz function as estimated by Eberhardt (1985).

An annual reproductive rate of 0.333 female cubs per female aged 5 years and older was assumed (3 year reproductive interval, litter size of 2.0, and 50:50

sex ratio of cubs). This is a somewhat shorter reproductive interval than observed (Craighead et al. 1974, Knight and Eberhardt 1985), and a litter size intermediate between those observed with garbage dumps available for supplemental food and those observed in recent years. With these values, iterative calculations to solve the Lotka equations with a zero rate of population change (cf. Eberhardt 1985) yield survival to age 5 of about 0.25. Because the recent data on the population yield an estimate of 0.36 for that age interval, it can be seen that current subadult survivorship apparently substantially exceeds that needed to maintain a constant population level when adult survival is high.

In line with our earlier supposition that density dependence in grizzly bears may be largely a function of subadult dispersal (Knight and Eberhardt 1985), we suggest that this higher rate of survivorship to age 5 may be a form of "compensatory" response to abnormal losses of fully adult females, in the sense that subadult females may be able to occupy home ranges normally taken up by fully adult females. A weakness in this line of argument is simply that it is likely that the same factors that cause death in fully adult females are also likely to operate on subadults. Consequently, the supposed "compensation" can scarcely be regarded as a reason for complacency, particularly because reproduction depends on the fully adult females.

DISCUSSION

No doubt the most important issue at hand is whether the Yellowstone grizzly bear population has continued to decrease since closure of the garbage dumps in 1970 and 1971. The overall trend of the index (females with cubs) has declined. Our assessment of the available survivorship data suggests the decline will continue unless losses of adult females can be reduced. Reproduction in the population is simply not enough to replace the losses. Some ambiguity is introduced by the trend of recent index values, which can be interpreted as a leveling off of the trend. Unfortunately, we do not have suitable means for checking the validity of this trend indicator.

Limits of Index Techniques

The available evidence (see also Knight and Eberhardt 1984) does not suggest that the situation constitutes a major crisis. On the other hand, the evidence

does not indicate that developing a means for monitoring the population would be adequate to resolve the problem. So far as we can determine, none of the available index techniques will monitor the population closely enough to detect the very small change in adult survivorship (a few percentage points) that separate a stable and a decreasing population. The best and perhaps only way to assess survival is to monitor it directly by radiotelemetry.

Radiotelemetry, which illustrates clearly and unambiguously the fate of individual bears, demonstrates survival rates well below those reported by Craighead et al. (1974) and lower than needed to maintain a constant population level. This evidence demonstrates the need for further efforts to conserve bears. As we have already pointed out (Knight and Eberhardt 1984, 1985), the major needed management action is to reduce losses of adult females.

It also seems likely that continued or increasing marking will be needed to determine whether the available index data accurately reflect population trend. From our experience it appears that a working hypothesis about index data may be as follows. Visibility of grizzly bears varies appreciably from year to year, depending on how extensively they must forage for food. When extensive foraging is necessary, more bears are observed and deaths increase. If this hypothesis holds, much of the variability in any index based solely on observing bears or evidence of their activity is likely to be unavoidable. Because the habitat factors responsible for year-to-year variation in activity and visibility are imperfectly known, adjustments probably must be derived from observations of radio-marked bears.

Coefficients of variation of the annual tallies of females with cubs are 0.17 for 1959–66 and 0.22 for 1976–85. If it is assumed that the bear population within those periods was relatively constant, it can be argued that approximate confidence limits on an annual tally of females with cubs are plus or minus 30%–40%. Such variability makes a single year's observation of little value as a measure of trend. Although we suspect that most of the variation may be caused by changes in visibility from year to year, it may be difficult to obtain reliable correction factors.

The 2 models used here serve somewhat different purposes. The simple "projection" model provides a tool for intercomparisons of several sources of information on population trend (counts of females with cubs, litter size, and mortality records). Without independent, current estimates of population size, it

would be foolhardy to take the model outcomes as indicative of current population size. The model is useful, however, because it demonstrates inconsistencies in the data, most notably the failure of the index based on females with cubs to adequately reflect the substantial population reduction that must have resulted from the high mortality of adult females when the garbage dumps were closed in 1970 and 1971. It also suggests that the relative pattern of mortality may have changed, in that the model population appeared to increase somewhat in the early years, whereas the index did not change much (Fig. 1). This effect could, of course, alternatively be caused by a change in reporting rates of mortalities.

The stochastic model incorporates much more detail through age-specific reproductive rates, age structure, litter sizes, and so on. The same general conclusion (decreasing population size) can be reached much more simply through the Lotka equation. However, the stochastic model supplies a crucial additional feature by indicating variability in outcomes due to chance events. Over 30 years, there is a substantial spread in the outcomes of individual simulations, suggesting that if we have overestimated survival or reproductive rates, there may well be a significant probability that the population will be extirpated in the not too distant future.

There are enough uncertainties in parameter estimates and details of model structure and analysis to make us skeptical of precise interpretations of model outcomes. Calculating a "probability of extinction" or a "minimum viable population size," although desirable, is fraught with uncertainty. We prefer to suggest that the data do not demonstrate a crisis, but to also note that the margin between the present indications of slow decline and crisis may be very small — just a few bears per year. We thus suppose that prudence demands pessimism. Nonetheless, our analysis is somewhat more optimistic than the earlier results (Knight and Eberhardt 1984, 1985). Also, the reported adult female mortality has been lower in the last few years (Fig. 1).

Future Research Needs

A feature of the situation that needs more study is that the Yellowstone grizzly bear population has little room to expand. "Recovery" under these conditions may have a dimension not usually contemplated by wildlife managers. We do not know what the carrying capacity for the existing range may be

but suppose it could be less that when a dependable supplemental food supply was available at garbage dumps. In addition, we do not yet know how well bears may eventually use the large elk (*Cervus elaphus*) population in Yellowstone.

In any case, if recent losses of fully adult females are stemmed and the population stabilizes, this equilibrium condition may be accompanied by increased losses of subadults, perhaps most evidently on the periphery of the occupied range. These deaths will largely result from human-bear interactions because that is the most likely fate of a subadult bear moving away from occupied ranges. In short, the difference between a population on its way to extinction and one successfully occupying an island in a sea of humanity may be one that can be distinguished only through continued and accurate assessments of the population. It is likely that "recovery" of the population may not be recognized as such by many observers, if judgments are based only on total recorded mortality.

As "dump" bears disappear from the population, their replacements are smaller, mature later, and have a lower reproductive rate as a result of the changed habitat (Blanchard, this volume). We hope they will be better predators and more adept at avoiding humans (and thus less often seen). Simplistic views of

recovery to conditions that existed before dump closures are not realistic. We suspect that the price for maintaining the Yellowstone grizzly bear may be continuing close and detailed surveillance and that stringent management policies for limiting adult female mortality will need to be implemented, enforced, and maintained.

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