MONITORING GRIZZLY BEAR POPULATION TRENDS

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Abstract: A simple difference equation model was developed to provide additional perspective on observed mortality and trend data on Yellowstone grizzly bears (*Ursus arctos horribilis*). Records of mortalities of adult females from 1959 to 1985 were utilized, in conjunction with data on females with cubs. The overall downward trend of observed numbers of females with cubs generally agrees with the model calculations but does not adequately reflect mortality from 1970 to 1974. The model may be useful in developing a composite index of population trend.

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Even under the best conditions, grizzly bear populations exhibit very low densities. Grizzlies are highly mobile, often secretive, and occupy extremely large home ranges. To date no satisfactory method of censusing has been developed. In consequence of the precarious status of these bears over much of their range in the coterminous United States, indicators of population trends are urgently needed. Very likely it will be necessary to develop some sort of composite measure, as no single index has been demonstrated to be wholly suitable.

A stochastic model of the Yellowstone population indicates that the balance between a stable population and a continued decline may be determined by death or survival of as few as 2 of the "prime" adult females (Knight and Eberhardt 1985). Considering that this key population segment (adult females) may amount to about 40–50 individuals dispersed over an area of approximately 20,000 km^2, it is unlikely that any index or census method can provide sufficient accuracy to determine year-to-year trends. Because most of the available methods do not measure a single component of the population, shifts in age and sex ratios also may tend to obscure trends in the adult female segment of the population.

Available evidence suggests that the Yellowstone population is continuing a decline initiated in about 1970 (Knight and Eberhardt 1984). Presently, average annual mortality of adult females apparently exceeds the level at which population stability can be expected (Knight and Eberhardt 1985). Clearly, the 1st priority of research and management must be to reduce mortality. If this can be achieved, then continued monitoring of the population is essential. The present report seeks to evaluate possible utility of some potential elements in a composite index of population abundance.

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STUDY AREA AND METHODS

The study area is roughly centered on Yellowstone National Park but includes about 20,000 km^2, an area about 2× the size of the park. Portions of 5 national forests in 3 states (Idaho, Mont., and Wyo.) are included. The area is essentially a large basin encircled by mountain ranges with elevations from about 1,600 to 2,400 m and is about 70% forested. Winters are long and cold and summers are short and cool.

The present study, which began in 1973, utilizes a range of observational methods from aerial relocation of telemetered bears to detailed studies of habitats. Mortality data were obtained through telemetry; continued contacts with staff of the many agencies involved; and interviews with ranchers, sheepherders, outfitters, and others. Further details of the study area and methods are available in Knight and Eberhardt (1985).

Approach

The approach taken was to examine the simplest prospective model (a difference equation) of dynamics of the adult female population. The model was used to construct a possible popu-

Table 1. Prorating of unknown and partially unknown grizzly bear mortalities in the Yellowstone National Park area, 1973–85.

Year	Total	Adult females	Subadult females	Males	Unknown	Partially unknown[a]	Prorated	
							Adult	Subadult
1973	21	4	2	4	11		5	
1974	16	4	1	8	2	1 SA	1	
1975	3	1		1	1			
1976	6	1	1	3		1 A	1	
1977	18	6	1	11				
1978	10	2		6	1	1 A	1	
1979	11	2		2	7		3	
1980	10	1	2	6		1 SA		
1981	16	5	1	6	2	2 SA	1	1
1982	17	4	2	9		2 SA		1
1983	6	2	1	3				
1984	11	2	3	6				
1985	13	2	2	2		7 SA		3
Totals	158	36	16	67	24	15	12	5

[a] SA = subadult and A = adult.

lation trajectory based on observed mortality and litter sizes. The observed trend of a population index was then contrasted with the model outcome. Besides helping to put the data and needs in perspective, the model also may provide a framework for developing an index for monitoring population trends into the future.

The model used was:

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

where t denotes time in years, N_t represents current size of the adult (≥5 years) female segment of the population, R_t denotes 5-year-old recruits to the female population (born at $t-5$), and M_t denotes total mortality of adult females in year t. Recruits were calculated from:

$$R_t = Q_5 C_{t-5} N_{t-5}, \quad (2)$$

where C_{t-5} denotes litter size 5 years previously and Q_5 represents survival from the age at which litter size is observed (about 6 months of age) to age 5, multiplied by the proportion of female cubs, and divided by breeding interval.

Mortality Data

The mortality data used for 1959–72 were reported by Craighead et al. (1974:table 10), and the data for 1973 to the present were tabulated in the present study. Mortalities for which age and sex were not known were prorated as follows:

1. Tables containing the recorded deaths of adult females, subadult females, and males were prepared. For the 1973–85 period (Table 1) there were 119 such bears (30.3% adult females, 13.4% subadult females, and 56.3% known to be males).

2. The remaining 39 bears (24 completely unidentified and 15 for which age class was reported) were prorated by the above percentages. This yielded 12 adult females and 5 subadult females that then were distributed in approximate proportion to the numbers of "unknown" mortalities (Table 1).

The same procedure was used for the 1959–72 data. In this case 264 "known" mortalities contained 22.4% adult females, 17.0% subadult females, and 60.6% males. There were 24 completely unknown mortalities and 54 with partial information. These were prorated in the same manner as above (Table 2). Craighead et al. (1974:table 12) also prorated losses of unknown sex and age, but in several years their corrected table contains fewer adult females than does the table of known mortalities (their table 10). Consequently, we recalculated estimates to provide consistency in the approach.

Two features of the overall mortality data (Table 3) are of special interest. One is the appreciably higher fraction of adult females in the 1970–85 data (83/286 = 0.290) as compared to 1959–69 (41/214 = 0.192), before the garbage dumps were closed. A comparison by year appears in Figure 1. The other is the relative scarcity of subadult females (38.9% of female mortalities). According to the survivorship data of Knight and Eberhardt (1985:table 6), one would expect about 70% of the female mortalities to be in subadult classes, whereas the

Table 2. Prorating of unknown and partially unknown grizzly bear mortalities in the Yellowstone National Park area, 1959–72.

Year	Total	Adult females	Subadult females	Males	Unknown	Partially unknown[a]	Prorated	
							Adult	Subadult
1959	12	1	2	7	1	1 A	1	
1960	24	4	2	8	1	2 A, 7 SA	1	3
1961	21	1	4	9	1	1 A, 4 SA, 1 F	1	2
1962	15	4	5	5		1 SA		
1963	15	3	2	8		2 SA	1	
1964	12	1	1	7		3 SA	1	1
1965	15	3	2	9	1			
1966	13			7	4	2 SA	1	1
1967	43	3	1	17	6	2 A, 3 SA, 11 F	4	4
1968	21	2	3	11	3	1 A, 1 SA	2	
1969	23	6	3	12		1 SA, 1 F	1	
1970	53	13	11	23	1	5 SA	2	
1971	48	11	6	24	5	1 A, 1 SA	2	1
1972	27	7	3	13	1	1 A, 2 SA		1
Total	342	59	45	160	24	54	17	13

[a] SA = subadult, A = adult, and F = female.

data of Craighead et al. (1974) suggest about 60%.

RESULTS

Calculations for the model of equations (1) and (2) depend on an estimate of the initial population size, survivorship to age 5, litter sizes (Table 3), cub sex ratio, and adult female mortality. Craighead et al. (1974:15) estimated an average population of 229 bears. A National Academy of Sciences review committee report essentially agreed with this estimate, giving a population size of 234 bears (Natl. Acad. Sci. 1974:21). Craighead et al. (1974:table 1) reported 43.7% of the population as adults and field observations that indicated that 53.7% of the adults were females, giving 54 adult females in the total of 230 bears.

We do not suppose that all adult female mortalities are recorded, having suggested that perhaps as much of 50% of all mortalities go unreported (Knight and Eberhardt 1984). Various efforts thus were made to utilize a correction factor for unreported losses in the model. However, none of the outcomes seemed to be more useful or realistic than calculations based simply on the observed data.

An initial estimate of Q_5 was based on data reported by Knight and Eberhardt (1985) who gave survivorship to age 5 as 0.254 (table 6), breeding interval as about 3.2 years (p. 328), and proportion of female cubs as 0.408 (p. 326):

$$Q_5 = (0.254)(0.408)/3.2 = 0.032.$$

Therefore data for the model include: (1) an initial (1958) population size of 54, (2) observed adult female mortalities and cub litter sizes (Table 3), and (3) the coefficient, Q_5. Calculations then proceed according to equations (1) and (2). The results may then give an indication of the likely general trend of the adult female population and seem especially useful in suggesting the approximate relationship between mortality and recruitment over time (calculated recruits in the model were rounded off to the nearest integer). The model calculations can be compared with the observed trend data (observed number of presumably different females with cubs) through a transformation of the population estimates from the model to the scale of the index data (Table 3). This was accomplished by multiplying each entry by the ratio of the sum of all index values divided by the sum of all population estimates generated by the model. Therefore, the model was used to generate expected values for the counts of females with cubs from marginal totals as is done in the usual 2-way Chi-square table.

Chi-square calculations also can be used to estimate the coefficient (Q_5) by varying it until a minimum total Chi-square is obtained. For an initial population of 54 adult females a value of $Q_5 = 0.040$ gives the minimum Chi-square value (20.2). The process can be carried a step further and used in an attempt to estimate both parameters (initial population and Q_5). In this case it turns out that the total Chi-square de-

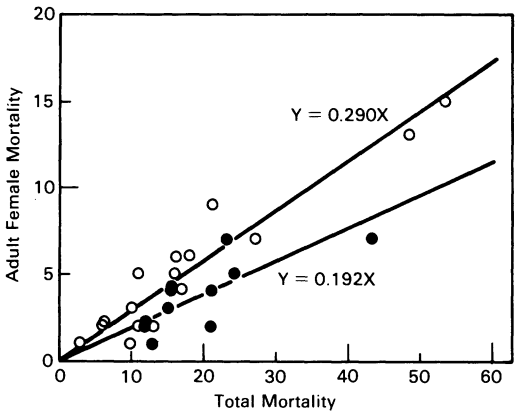

Fig. 1. Recorded mortalities of adult female grizzly bears as a function of total mortality for 2 time periods. Upper line shows ratio of total adult female mortality to total recorded mortality for 1970–85, the lower line shows the corresponding ratio for 1959–69. Yearly observations denoted by symbols (● = 1959–69 and ○ = 1970–85).

creases slowly with increasing values of the initial population so that unique estimates of both parameters are not obtained. To illustrate the outcome a curve for an initial population of 162 bears, which gives $Q_5 = 0.011$, is included (Fig. 2). The projected population values for an initial population of 54 bears and $Q_5 = 0.036$ are shown in Figure 3, along with index values (annual tallies of females with cubs) and mortalities of adult females.

The 2nd curve in Figure 3 shows a "minimal" population estimate based on successive 3-year sums of the index. Because grizzlies typically reproduce at 3-year intervals, this total should roughly approximate the number of adult females present at the beginning of a 3-year interval if this interval holds for all bears. In reality some females with cubs may escape observation, the breeding interval is somewhat longer than 3 years, and younger adults may not reproduce as frequently as the "prime-aged" females. These possible biases may be offset by the possibilities that some of the supposedly nonduplicated observations may actually be repeated records of the same adult female, and the likelihood of rebreeding if cubs are lost, or offspring are weaned as yearlings, plus the mortality of some of the adult females seen in the 1st and 2nd years.

DISCUSSION

The very simple model (eq. 1 and 2) requires a minimum of data but depends on the deceptive compression of 3 essential parameters into 1 constant (Q_5). Small changes in this coefficient result in substantial changes in the calculated population trajectory, particularly in the most recent years. Because there are no recent independently derived population estimates with which to "calibrate" the model, we believe it should mainly be used to assess consistency of the trend data provided by tallies of females with cubs (Fig. 3 and Table 3).

In general, we believe that the model is presently most useful as a device for approximating the effect of the observed mortality pattern. Perhaps the main value of the modeling exercise is a demonstration of the substantial likely impact of the mortality in 1970–74, a feature not evident in the trend index provided by the tallies of females with cubs. The upper panel of Figure 2 shows that the "best" fit of the model to trend data (tallies of females with cubs) is

Table 3. Adult female grizzly bear mortalities, cub litter sizes, and females with cubs in the Yellowstone National Park area, 1959–85. Mortality rates were obtained as described in text. Litter sizes and females with cubs are from Craighead et al. (1974:table 8) for 1959–73; remaining data are from present study.

	Mortalities				
Year	Total	Adult females	Subadult females	Litter size	Females with cubs
1959	12	2	2	1.86	14
1960	24	5	5	2.06	17
1961	21	2	6	2.31	13
1962	15	4	5	2.29	17
1963	15	4	2	2.5	16
1964	12	2	2	2.18	11
1965	15	3	2	2.11	19
1966	13	1	1	2.13	15
1967	43	7	5	2.5	12
1968	21	4	3	2.46	13
1969	23	7	3	2.0	14
1970	53	15	11	1.75	12
1971	48	13	7	1.94	16
1972	27	7	4	2.00	11
1973	21	9	2	1.86	14
1974	16	5	1	1.73	15
1975	3	1	0	1.50	4
1976	6	2	1	1.88	17
1977	18	6	1	1.92	13
1978	10	3	0	2.0	9
1979	11	5	0	2.23	13
1980	10	1	2	1.92	12
1981	16	6	2	1.92	13
1982	17	4	3	1.82	11
1983	6	2	1	1.69	13
1984	11	2	3	1.76	17
1985	13	2	5	1.78	9

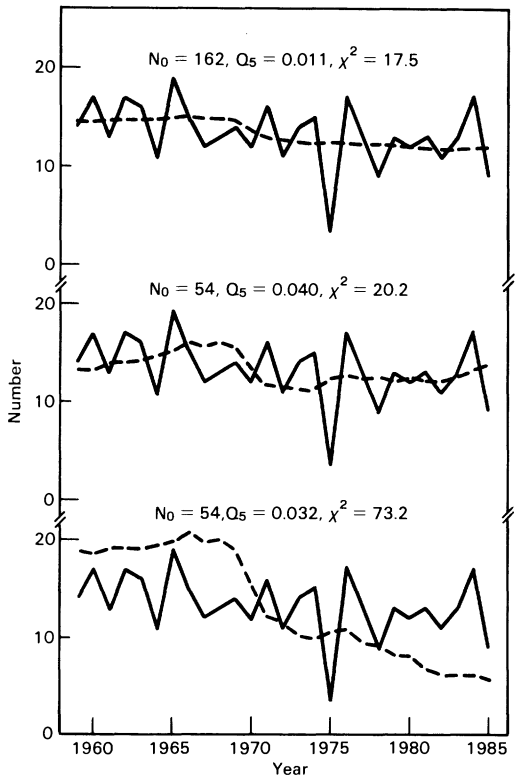

Fig. 2. Comparisons of observed number of female grizzly bears with cubs and expected values generated from the projection model, 1959–85. Initial population sizes (N_o), values of coefficient (Q_5) used in model, and Chi-square values for fit of model to observations are shown for each curve (see text for details).

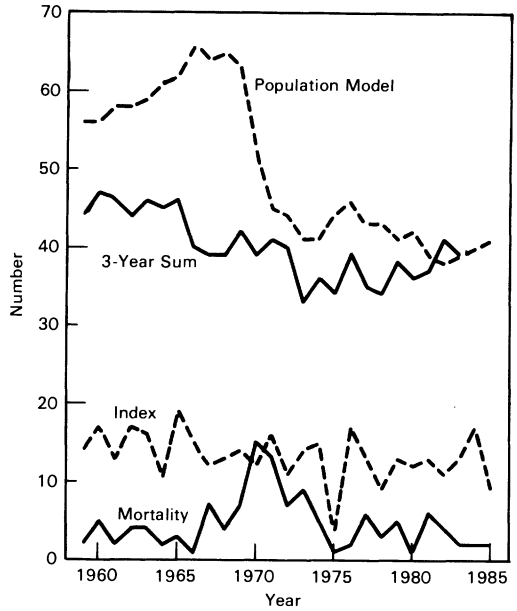

Fig. 3. Calculated grizzly bear populations from a difference equation model (upper curve), 3-year sum of females with cubs (2nd line), individual annual observations of females with cubs (3rd line), and recorded annual mortality of adult females (bottom line). Three-year sums of females with cubs are plotted at 1st year of 3-year intervals because this approximates the number of adult females present at that time.

achieved at unreasonably high initial population values (in this example an initial population 3× that actually estimated). Such a high initial population value tends to reduce the impact of high mortalities in 1970 and 1971 (Fig. 3). The model then becomes little more than a device for smoothing the observed index data. Poorer fits are obtained in the lower panels (Fig. 2) by virtue of the fact that the initial population is small enough to be substantially influenced by the higher mortalities (Fig. 3).

Circumstances under which the index was obtained changed sharply in 1969–70. Previously, garbage dumps were readily available to grizzlies and tallies of females with cubs presumably came mainly from the dump censuses (Craighead et al. 1974). In 1970, the dumps were closed, no doubt causing substantial behavioral alterations (as evidenced by the heavy 1970–73 mortality, Fig. 3). Also, records of females with cubs were obtained by a different system at that time (largely park ranger reports). By 1974, when the present project began extensive field operations, the surviving bears presumably had begun to adapt to the changes, and collection of data on females with cubs was supplemented by extensive aerial observations, trapping, and radiotelemetry.

It seems likely that the increased proportion of adult females in the 1970–85 mortality, as compared to 1959–69 (Fig. 1), reflects a real change in relative survival. Certainly the estimates of survivorship were much lower for recent years (Knight and Eberhardt 1985:table 6) than they were for the earlier period (Craighead et al. 1974:table 12). Subadults clearly were not adequately represented in the recorded mortality.

A 2nd useful purpose of the model may lie in devising a population index that does not depend so heavily on an unknown constant. A "recruitment index" based on the product of number of females with cubs and litter size has a trend that is not influenced by an arbitrary constant because such a constant need only serve to scale the curve down to a level roughly in

accord with present knowledge of population parameters. This scaling is important only if one attempts a numerical contrast of recruitment with mortality. In our present state of knowledge we can only suggest that the relationship is qualitatively correct (i.e., the available evidence suggests a decreasing trend in the population since 1970 [cf. Knight and Eberhardt 1984:fig. 1]), whereas Craighead et al. (1974) reported an increasing trend prior to 1970 and predicted sharp reductions in numbers after dump closures.

Technically, all a recruitment index accomplishes is some smoothing of the index provided by tallies of females with cubs plus incorporating the litter size data. It is essentially just a tally of cubs observed. However, we believe the qualitative aspects are important, because some direct perspective on mechanics of population change is provided.

The model of equations (1) and (2) is a well-known difference equation leading to simple exponential growth if rates hold constant. In recent years, it has become customary to incorporate a density-dependence term in such a model, often as an added term in equation (2). Inasmuch as the current level of the Yellowstone grizzly population is clearly well below historical densities, we do not suppose that a density-dependent term would have much effect on the population trajectory. Further, as discussed by Knight and Eberhardt (1985), we believe that such an arbitrary function will serve mostly to confuse the issues.

A number of other techniques for monitoring population trends have been investigated during the course of the present study. Aerial counts made while relocating radio-telemetered bears have been somewhat erratic but essentially suggest a relatively constant recent population (Knight and Eberhardt 1985:fig. 3). One season's trial (1983) of intensive aerial counts, using 3 aircraft working at the same time, failed to locate enough bears to make the results worthwhile. Efforts at capture-recapture estimates based on aerial counts have been unsatisfactory thus far. Some limited investigations of bait stations have not been very promising but require much more effort than has been possible thus far.

Another trend indication that needs further investigation depends on data on the amount of area used by grizzlies over long time periods. Location maps of recorded mortalities for an earlier period (Craighead 1980) and from recent years (obtained in the present study) suggest a distinct reduction of area over which mortalities were reported so that recent mortalities are appreciably closer to park boundaries. It is possible that some of the change in spatial distribution of mortalities may be associated with cessation of legal hunting of the population in 1974. Changes in the distributional patterns of bears observed in aerial surveys have been qualitatively evident and also need further study.

Our overall conclusion about other possible trend indicators is that none of those studied thus far have been very satisfactory. Consequently, further improving our understanding of the index data discussed here is of considerable importance.

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