

THE CRAIGHEADS' DATA ON YELLOWSTONE GRIZZLY BEAR POPULATIONS: RELEVANCE TO CURRENT RESEARCH AND MANAGEMENT

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Abstract: Various interpretations of the Craighead team data on Yellowstone grizzly bears (*Ursus arctos horribilis*) are reviewed. The Craigheads continue to favor a noncompensatory model that gives the greatest likelihood of population extinction with an increased mortality rate. McCullough (1981) found that recruitment of cubs and survivorship of juveniles were influenced by adult population size. Stringham (1983) reached most of the same conclusions by different methods. McCullough (1981), Stringham (1983), and Shaffer (1978, 1983) all reported negative relationships between adult population size (or adult males only) and percent of females producing litters and mean litter size. Time lags in the density-dependent effect of adults on cub recruitment were treated by Avrin (1976) with slightly different results. All authors have emphasized the susceptibility of grizzly bear populations to overexploitation, although the impact varies with model assumptions. Shaffer (1978, 1983) examined stochastic variables as they influence minimum viable population size.

A congruence analysis was done for the McCullough (1981) model in which parameters were run in model simulations to test model responses to observed results for the years of the Craighead study. This analysis reaffirmed the oscillatory behavior of the population and showed that oscillatory behavior decreased as the adult mortality rate increased. Great fluctuations in population parameters make assessment of the current status of the population difficult. An alternate strategy of long-term population monitoring and management based on a systematized aerial count of minimum unduplicated bears is proposed.

Int. Conf. Bear Res. and Manage. 6:21-32

The conflict over the status and management of the grizzly bear population in Yellowstone National Park began in 1967 with a disagreement between the John and Frank Craighead research team and the National Park Service biologists and administrators over the procedures for closing open-pit garbage dumps (Craighead and Craighead 1967, 1971; Cole 1971). The Craigheads recommended phasing out the dumps over a 10-year-period and simultaneously killing elk (*Cervus elaphus*) in the backcountry to attract bears away from developed areas. The Park Service chose to close dumps as rapidly as possible and did not shoot elk. Controversy quickly followed (Craighead et al. 1973, 1974; Cole 1971, 1973; Meagher 1978), and the issue was broadly reported in the press (Craighead 1973, Johnson 1973, Seater 1973, Gilbert 1976, Cauble 1977, Schullery 1980).

The current state of the population remains uncertain (Blanchard and Knight 1980, Craighead 1982, Chase 1983), as does the appropriate role of research and management. Concern about the viability of the population with apparently increased human-caused mortality means the search for a suitable research and management program is imperative.

Success of the Craighead team in gathering population data depended largely on concentration of grizzly bears at open-pit garbage dumps during the summer months. Closure of the dumps by 1971 dispersed the bears over a broader area, and despite the best efforts of the Interagency Research Team, population data are sparse and equivocal. A greatly increased effort in money and staffing may improve population estimates (Kilgore et al. 1981), but it is questionable whether accurate estimates can be

achieved or that accuracy can be achieved without deleterious impact on the population. Given this situation it is imperative to maximize understanding the best population data available, that of the Craighead research team.

The circumstances surrounding the dispersed population of today are not the same as the concentrated population studied by the Craigheads. However, the long generation time of bears results in slow evolution of traits under new selective pressures. Grizzly bears evolved to exploit concentrated food sources whenever available, so although garbage as a food source was "unnatural," the behavior of bears in taking advantage of it was perfectly natural. Therefore, while absolute values of parameters may have changed with dump closure, the relative values and patterns of responses probably remain valid. I do not mean to entirely rule out the possibility of a shift in behavioral domain, but rather to suggest that a shift seems unlikely. In the absence of alternatives, the Craighead data remain the best basis for interpreting current population results.

I wish to thank S. F. Stringham for discussions clarifying his views and M. L. Shaffer for his most helpful review and criticism of the manuscript. I am indebted to J. J. Craighead and F. C. Craighead, Jr., and their research associates for producing the excellent field data that make various interpretations worth exploring.

INTERPRETATION OF THE CRAIGHEAD DATA

The Craighead research team conducted grizzly bear population studies in Yellowstone Park from

1959 to 1970 (Craighead et al. 1973, 1974). Population size, sex, and age composition were based on censuses conducted at garbage dumps. Reproductive rates were based on recorded histories of known females and mean litter sizes. Mortality rates were estimated from age structure of a sample of known animals in 1966 and known mortalities were recorded. The purpose of this section is to review different interpretations of these data by different scientists using varying analytical methods. Readers wishing details should refer to the original publications (Craighead et al. 1973, 1974; Cole 1971; Cowan et al. 1974; Avrin 1976; Shaffer 1978, 1981, 1983; McCullough 1981; Stringham 1983).

Population Size

Craighead and Craighead (1971) believed that they were accounting for most of the bears in the ecosystem. Cole (1973), however, maintained there was a significant number of bears in the population (a "backcountry population") that was not being counted. Cowan et al. (1974) examined this issue by comparing the proportion of bears marked in the population to the proportion of marked bears dying outside of the park. If the population were completely mixed, these ratios should have been equivalent. Because marked bears were underrepresented in the mortality sample outside of the park, Cowan et al. (1974) concluded that the Craigheads' censuses were 58% efficient, and that 132 bears needed to be added to the mean population size of 177 at the garbage dumps for a total of 308. Using similar procedures, Craighead et al. (1974) concluded their censuses were 77% efficient for a total population of 229. Both estimates are subject to criticism. The ratio of marked to unmarked bears in the living population cannot be compared to the same ratio in bears found dead because the ratio in living bears was constantly changing due to marking effort and mortality, whereas the ratio in dead bears depended on the accumulation of marked and unmarked bears. Comparing the ratio of marked to unmarked dead bears inside vs. outside the park circumvents these difficulties and results in a highly significant difference between the ratios ($P \leq 0.001$) (McCullough 1981). This suggests a census efficiency of 57% for a total population estimate of 312.

Reproductive Rates

Craighead et al. (1974) treated the reproductive rate as constant from 1959 to 1967 and proposed that

it had declined after 1968 because of stress caused by garbage dump closure. Cole (1974) suggested that the relative number of cubs after 1968 was higher because young females were reproducing earlier and that because they had smaller litter sizes, the reproductive rate as expressed by mean litter size was misleading. Although this interpretation of the data is possible, no substantial evidence supports it.

Craighead et al. (1974) based their estimates of the reproductive rate on known histories of marked females, including litter sizes and interval between litters. However, the realized recruitment rate, as derived from cubs observed in the population, exceeded the rate estimated from known females (McCullough 1981). The discrepancy seems to have resulted from the marked females not being a representative sample of the females in the population.

The question of whether the reproductive rates declined after 1968 is clouded by 2 other variables. First, there was a density-dependent relationship between cub recruitment and adult population size, and the high number of adults after 1968 can account for the observed differences (McCullough 1981). Second, the evidence of a decline in reproductive rate after 1968 was based on mean litter size, and Cole's (1974) interpretation shows that this statistic is subject to several interpretations. Percent of females with litters accounted for 77% of the variance in number of cubs recruited, whereas mean litter size accounted for only 23% (McCullough 1981). Therefore, mean litter size was a weak contributor to cub recruitment and is insensitive to the true reproductive rate and recruitment of cubs.

Density Dependence (Compensation)

Craighead et al. (1974) concluded that there was no density dependence shown by their data, and they have recently reaffirmed this view (Craighead et al. 1982). In contrast, Shaffer (1978), McCullough (1981), and Stringham (1983), using different analytical procedures, independently reported statistically significant density dependence in reproductive parameters. Shaffer (1978, 1983) reported that percentage of females with litters and mean litter size were negatively correlated with adult population size. McCullough (1981) reported that the recruitment rate of cubs, yearlings, 2-year-olds, and combined juveniles (cub through 4-year-olds) all were negatively correlated with adult population size. Stringham (1983) applied different procedures but reached the same conclusion about density-dependent

effects. Furthermore, the influence of adult males is supported by similar results of an interpopulational comparison of grizzly bear populations by Stringham (1980) and manipulations of a black bear (*U. americanus*) population by Kemp (1972, 1976). The negative effect of adults or adult males on reproduction has been attributed to resource limitations due to competition or to killing of cubs by adult males and resource competition (Shaffer 1978, McCullough 1981, Stringham 1983).

The difference in methods between McCullough (1981) and Stringham (1983) do not pertain to the outcome of hypotheses testing, which is the same. Stringham criticized use of R/N on N regressions because these regressions show some negative slope in the absence of a relationship. However, this bias has long been known, and Ricker (1975:352) observed,

“However, when a relationship of some consequence does actually exist, the random component adds little to the slope of any straight line that is fitted. There is usually excellent (though not perfect) agreement between predictive regression lines fitted by this method and those fitted by direct minimization of the sums of squares of deviations from the parabola of the expression . . .”

$$Y = aX + bX^2$$

Stringham (1983) advocated using natural log transformations in regressing number of cubs (or yearlings or 2-year-olds) on number of adults or adult males according to the expression $\log_n Y = a + b \log_n X$. However, this transformation also introduces a systematic bias (Finney 1941, Baskerville 1972, Whittaker and Marks 1975, Payandeh 1981, Sprugel 1983). This bias is 10% or less, but this is equal to or greater than the biases in R/N on N regressions, and it is a debatable point as to which bias is preferable.

A criticism of the regression procedures of McCullough (1981) and Stringham (1983) is the treatment of number of adults and number of adult males on the X -axis as measured without error. If there is variance in measurement, a Type II regression model (Sokal and Rohlf 1969:481) should be applied, as was done by Shaffer (1978, 1983) for a proportion of females with litters and mean litter size. Some error was certainly present in the estimation of number of adults and number of adult males by the Craighead research team. Still, the high internal consistency of their results, with only 1 clearly impossible value,

where number of 3- and 4-year-olds greatly exceeded the sum of the 2 antecedent classes (McCullough 1981), leads me to conclude that such errors were minor. Furthermore, because Type II regressions give negative slopes (b) that are steeper than Type I (least squares) models, any negative bias in R/N on N regressions is already in the direction obtained by Type II regression models. Calculation of the Type II regression for R/N on N for cubs gave a slightly greater slope (-0.0092) than for the least squares regression (-0.0086), but the equations were quite similar (Type II, $Y = 1.1562 - 0.0092X$; least squares, $Y = 1.1057 - 0.0086X$). Comparison of observed reproductive rates for 1959–67 and 1968–70 with reproductive rates calculated from R/N on N regressions give a minor difference in slope with least squares regression being slightly more negative. Therefore, slope may have been overestimated by least squares regression and the even steeper slope of the Type II regression model seems ill advised.

Selecting the best regression method is difficult. None can be declared statistically superior because all have potential or actual biases that cannot be precisely evaluated. However, because all of them give the same result of hypothesis tests for density dependence, the selection of the preferred method can be based on pragmatic grounds: (1) do they represent a reasonable fit to the observed data and (2) do they give reasonable predictions if extended beyond the range of values included in the data set? Figures 1 and 2 show that all 3 regression methods give similar fits over the range of the observed data. Only the Craighead et al. (1974) assumption of a constant reproductive rate fails to fit the data points, because it crosses perpendicularly to the long axis of the array of data points. The 2nd criterion of projection is important in modeling the grizzly bear population to predict response to population sizes beyond the range of data points. Indeed, this is the major motivation of modeling the data. Stringham's (1983) regression equation proves unrealistic beyond the range of the data set in either direction (Fig. 2). Stringham (1983) applied dose response models (Ricker 1975) to derive predictions beyond the data set. Whether these forms of recruitment curves are realistic for bears is unknown, but they are not typical of most large mammals (Fowler et al. 1980; Fowler 1981a, 1981b). Projections of R/N on N for least squares and Type II regression models are virtually the same (Fig. 1), again reflecting the general similarity of the fit of the least squares and Type II models to the data set.

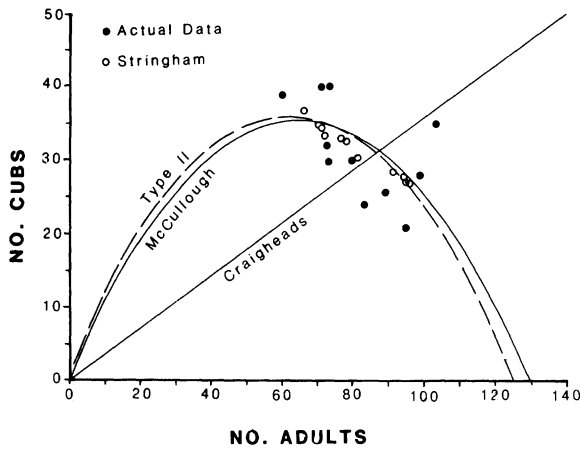


Fig. 1. Cub recruitment plotted on adult population size observed by Craighead team (closed circles) compared to different interpretations of the data: Craigheads (constant sloping line), Stringham (open circles), McCullough (solid parabola), and Type II regression (broken line parabola).

Shaffer (1978) reported that mean litter size was negatively correlated with number of adults in the year of conception, and Stringham (1983) demonstrated the same relationship for adult males. Thus, population density influenced the reproductive effort in year of conception as well as the subsequent recruitment of cubs to different ages. Stringham (1983) achieved highest correlations of recruitment with adult males in both the year of conception and the year of recruitment as cubs.

Time Lags and Oscillatory Population Behavior

The inverse relationship of juvenile recruitment and number of adults coupled with a delay of 1st reproduction to 5-year-olds (Craighead et al. 1974) inevitably results in time lags that introduce oscillatory behavior in the population. Avrin (1976), using the density-dependent recruitment equations subsequently published by McCullough (1981) and an age structure model similar to that of Craighead et al. (1974), ran simulations that resulted in a periodicity of about 20 years. McCullough (1981) concluded that including compensatory adult mortality shortened the periodicity of oscillations to about 10 years.

Sex Ratios

Craighead et al. (1974) considered the sex ratio of cubs to be 50:50 because sex ratio of the sample of 78 cubs was not different at $P = 0.05$. However, considering all juveniles, the difference in sex ratio

(60 males:40 females) was significantly different from 50:50 (McCullough 1981). Limited evidence suggested that sex ratio of cubs did not change with changes in number of adults. Knight et. al. (1982) also reported a cub sex ratio of 67 males:33 females for a sample of 24 cubs of known sex. Again the sample size is small, but the evidence suggests a male-biased sex ratio of cubs. If these data are added to the Craighead data, there is a significant difference ($P = 0.04$) from a 50:50 sex ratio of cubs. McCullough (1981) further reported that sex ratio of adults changed with number of adults, with males increasing as number of adults increased.

Influence of Climate and Food Supply

Picton (1978) reported that mean litter size of females with litters was correlated with an index of winter severity and food supply, with mean litter size declining as weather was more severe or food supply less abundant. This relationship was further explored by Picton and Knight (this volume). Inclusion of Picton's climate index with the multiple regression of percent of females with litters and mean litter size on number of cubs recruited decreased significance (McCullough 1981). At 1st, this seemed to be a contradictory result, but the explanation seems to lie in the fact that mean litter size accounts for relatively little of the total variance and includes effects of climate. Litter size is a variable that can respond

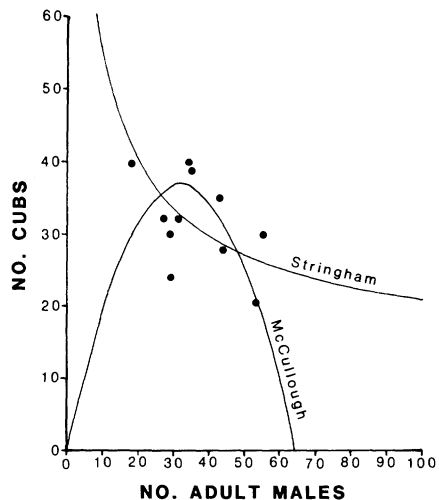


Fig. 2. Comparison of Stringham equation and McCullough equation for recruitment of cubs on number of adult males.

rapidly to local conditions, be it bad weather or good food, by reproducing females adjusting litter size up or down as circumstances dictate. Conversely, the more important variable, percent of females with litters, reflects productive state of the individual females; those with dependent offspring cannot respond by further reproductive effort, only by survivorship of previously conceived offspring. Although local conditions probably influence age at weaning, a longer time period again is involved. Primiparous females may achieve sexual maturity at an early age, which might be a more immediate response to climate. Still, percent of females with litters in any given year responds more closely and reflects environmental conditions over several years, whereas litter size can be adjusted to conditions in the year of conception.

Minimum Viable Population Size

Shaffer (1978, 1981, 1983) used the Craighead data to derive a model to test the minimum population sizes that could be maintained in the face of stochastic variation in the environment and variance in population response. He concluded that a minimum of 30–70 bears (midrange 50) was a reasonable approximation of the population size that could be sustained (i.e., not go to extinction in 100 years of simulation). Subsequent reruns of the model with corrections by Shaffer and Fred Samson have led to an upward adjustment of the estimates to 50–90 bears (midrange 70) (Shaffer, pers. commun., 1983).

However, it should be made clear that Shaffer's model does not take into account a continuing high human-induced mortality rate. All authors agree that the rate at which grizzly bears can be exploited is low, and it is a species that is easily overexploited. Unfortunately, the difference between sustainable and unsustainable exploitation involves only a few bear deaths per year (McCullough 1981). Thus, although an overexploited population appears to be adjusting through density-dependent recruitment, at the critical point where the population is reduced below the inflection point on an S-shaped (but not symmetrical) growth curve, the population declines precipitously. Shaffer's analysis (1978, 1983), which shows that populations greater than about 70 can be sustained, suggests that if an excessive mortality rate is controlled, a population of 70 or greater should be able to rebound.

CONGRUENCE ANALYSIS

If a population simulation model is derived by entering the series of fitted equations for each variable in the correct biological sequence, model runs over time should yield numerical results that mimic the observed data. Because the equations for individual sex and age classes must yield results that are compatible with the whole data set, the equations can be cross-checked for accuracy. If the model simulations and the original data are not in agreement, 1 or more equations can be adjusted to correct the errant results. This is usually done by adjusting the equations based on the weakest data or poorest fit to be compatible with those of the strongest data or best fit. The rationale is that those variables with the poorest data or greatest assumptions are more likely to be in error than those with the strongest data and fewest assumptions.

This procedure often has been referred to as "model validation," but validation, meaning to test or prove, can only come from model predictions conforming to an independent set of data. The procedure above can only test for fit of the model to the data from which it was derived, and it is circular reasoning to assume proof of predictive power.

The criteria for acceptance of the fit of the simulation model derived from the Craigheads' data were as follows:

1. Number of adults should vary from a high of approximately 100 to a low of approximately 70.
2. Total population should vary from a high of approximately 190 to a low of approximately 155.

Note that these values do not represent the extremes in the Craighead data (e.g., the highest total population recorded was 202) but rather the typical range. A model based on the extremes would "overreact." In the Craigheads' data for total population, although 6 values were above the mean and 5 below, the deviations above were less than below. Thus, the criteria values were shifted slightly below the extremes for high and low values of total population. For numbers of adults, 3 observed values were around 100, whereas only a single value (59) fell below 70, and 4 were about 70. Therefore 59 was treated as extreme and 70 was adopted. Note that there is no implication that these observed extremes were in error, although sampling error certainly was present to some degree; the point is that they appear to exaggerate the typical distribution of values. Because the criteria cannot be

stated exactly, minor discrepancies were not cause for rejection.

Simulation Procedures

Simulations began with the number of adults as an input value. The new number of adults was used as the X value to derive recruitment rates of cubs, yearlings, and 2-year-olds by regressions given in McCullough (1981) and multiplied by X to get number of recruits in the respective age classes. The number of combined 3- and 4-year-olds was derived by their relationship to the antecedent age class of 2-year-old bears in the 2 previous years (McCullough 1981). An average of 54% of these combined 3- and 4-year-olds was assigned to 3-year-olds based on extrapolation from survivorships of younger age classes to survivorship of adults based on results of Craighead et al. (1974) and Cowan et al. (1974). All values were constrained to not less than zero, rounded to the nearest whole individual, and could not exceed the number in the antecedent age class in the previous year. At each yearly iteration of the model, 4-year-olds of the previous year were assigned survival rates of adults and incorporated into the adult class. Changes in adult numbers resulting from recruitment of 5-year-olds minus adult deaths during the Craighead study period were derived from the regression of 3- and 4-year-olds/2 on change in adult population size (McCullough 1981). Because 3- and 4-year-olds were combined in the Craigheads' data, there was no objective way to sort them, and the simplest treatment was to assume they were in equal numbers. Craighead et al. (1974), Avrin (1976), and McCullough (1981) concluded that about 10 adult deaths were the average, or "background," mortality per year over the period of study despite the use of different methods of analysis. Total population was the sum of all age classes.

Gender was assigned to adults by deriving the percentage of males by the equation $Y = 5.935 + 0.4812 \times (\text{total population})$ (McCullough 1981). Because data on mortality by sex for juvenile age classes were insufficient, assignment of mortality by sex for age classes was not attempted. Nevertheless, differential mortality of male juveniles in large adult populations is necessary given an apparently constant sex ratio in cubs and predictable sex ratio shifts in adults as adult population size changes (McCullough 1981). The initial runs of the simulation using the background mortality of adults were arbitrarily started at

100 adults. The starting values were not important because the objective was to run the model until equilibrium was achieved. Therefore, so long as the starting value was great enough to avoid extinction, the same equilibrium would be achieved but at differing times. With the starting value of 100 adults, it took 27 years to reach equilibrium.

The 1st simulation resulted in number of adults and total populations higher than the values set as criteria for acceptance. These could be corrected by decreasing the recruitment rate or decreasing the slope of the regression of 3- and 4-year-olds/2 on change in number of adults. Because the analysis presented earlier for recruitment of cubs suggested that a steeper slope was not justified and because this data set was strong, this parameter was not changed. By contrast, most of the values in the 3- and 4-year-olds/2 on change in adult population clustered around the midpoints on the Y and X axes, and the survivorship of 3- and 4-year-olds was based on extrapolation from 2-year-olds to adults. Therefore, although the program steps were complex in assigning animals to 3-, 4-, and 5-year-olds, in essence, the 3- and 4-year-olds/2 on change in number of adults was changed by "rotating" the slope of the equation about the midpoint at 0 change in adult numbers (which includes a background mortality of 10 adult bears per year) until simulations gave values that matched the established criteria for number of adults and total population size. Essentially this procedure required the 3- and 4-year-old age classes to conform to the data on oscillations in numbers of cubs through 2-year-olds on 1 side and adults on the other. No other changes in the model were required.

Once the model was developed for a background mortality of 10 bears per year, higher mortalities were imposed to test the population's capability to sustain increased kills. Kills were taken from the adult segment of the population. Spreading the induced mortality over juvenile classes as well would change the result somewhat, because the increased mortality of young bears would involve a time lag in decline of the adult population. Hence, there would be a lag in the density-dependent response of cub recruitment. Therefore, it would take longer for such a model to come to equilibrium at a sustainable kill, but once there it would be similar in response to adult kill model. In kills greater than can be sustained, induced juvenile mortality would result in a slightly earlier time of extinction because of the delay in the expression of density-dependent recruitment.

Model Simulations

Equilibrium values of the model with average background mortality rates are given in Table 1 and Figure 3. The model showed oscillatory behavior with a period of 19 years. Total population varied from 191 to 149, whereas number of adults ranged from 104 to 67. Because of time lags, there were many cases where younger age classes were lower in number than older classes (Table 1).

The time lag in density-dependent recruitment, adult mortality rate, and 4 years to sexual maturity is the driving force in the oscillatory behavior of the population (Fig. 3). These variables result in a lag of 3- and 4-year-olds/2 on change in adult population as shown in Figure 4. If 3- and 4-year-olds are recruited in numbers greater than 10, the number of adults increases. The number of 3- and 4-year-olds/2 recruited reaches an upper limit of 14.5 and persists at that level until numbers of adults exceeds 100. Thereafter, 3- and 4-year-olds/2 declines, followed by a decline in number of adults as recruitment fails to replace background mortality. The adult mortality over the 19-year period ranges from 9 to 13 per year with more low values than high to give the average of 10.

Survivorships can be obtained from Table 1 for time-specific (horizontal) life tables by reading across by year and dynamic (vertical) life tables by reading

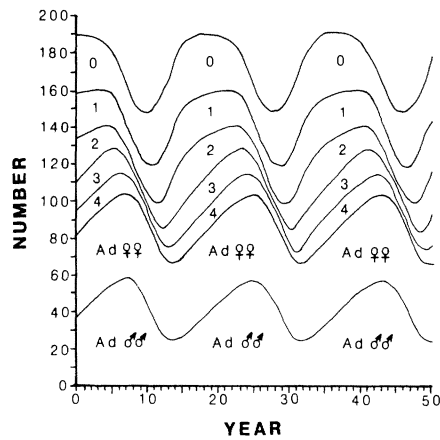


Fig. 3. Simulation of McCullough model showing sex and age composition of the population and oscillation in population numbers (stable limit cycle) with a background mortality of 10 adult bears per year. Age classes are indicated for 0-4 year old bears, and combined 5 years and older (adult) for each sex.

diagonally for year class cohorts. Time-specific tables differ from dynamic tables, as do each from adjacent tables of the same kind. This is because recruitment and survivorship are constantly changing in the stable limit cycle, and no given age structure persists for any length of time. Sex ratio of adults shifts with the oscillations (Fig. 5). Introducing a fixed number of mortalities resulted in dampening of the amplitude of oscillations (Figs. 6 and 7, Table 2), as previously

Table 1. Simulation of population size and sex and age composition over 1 oscillation of Yellowstone grizzly bear model with average background mortality.

Year	Total population	No. cubs	No. 1.5	No. 2.5	No. 3.5	No. 4.5	No. adults	No. ad. males	No. ad. females
1	191	33	24	23	16	13	82	38	44
2	190	31	23	21	16	13	86	41	45
3	190	30	22	19	16	13	90	45	45
4	188	28	20	17	16	13	94	48	46
5	186	26	18	15	16	13	98	52	46
6	181	24	16	12	15	13	101	54	47
7	173	23	14	9	12	12	103	56	47
8	164	22	13	6	9	10	104	57	47
9	155	23	12	5	6	7	102	55	47
10	150	26	13	4	5	5	97	51	46
11	149	30	16	5	4	4	90	45	45
12	152	33	20	10	5	3	81	37	44
13	158	35	23	15	9	4	72	29	43
14	168	35	26	20	13	7	67	25	42
15	178	35	27	23	16	10	67	25	42
16	186	35	27	25	16	13	70	27	43
17	188	34	26	25	16	13	74	31	43
18	190	34	25	24	16	13	78	34	44
19	191	33	24	23	16	13	82	38	44
$\bar{x} =$	175	30	20	16	13	10	86	41	45

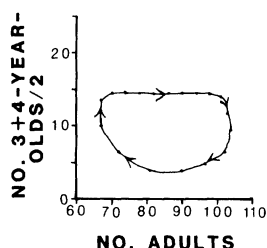


Fig. 4. Time lag in relationship of 3- and 4-year-olds recruited and change in adult population size as derived from the simulation model.

reported by Avrin (1976). Fixed mortalities of up to 10 per year resulted in a progressive dampening of oscillations, whereas 12 mortalities led to gradual extinction of the population (Fig. 6). Mortalities higher than 12 lead to increasingly rapid extinctions. This more detailed and conservative analysis (because extreme population sizes were excluded) gives about 20 as maximum sustained yield for the Craighead data, which is slightly less than 24.5 estimated by McCullough (1981). It should be remembered that because this simulation model averages the population studied by the Craigheads it is conservative. Therefore, although it mimics the behavior of the population during this period, it underestimates the extremes that are introduced in the actual data by stochastic events that result in strong or weak year classes and modify survivorship. Stochasticity lowers the accuracy of the model predictions year by year but does not influence long-term predictions, because most of the stochasticity is included in derivation of the average values for the model. However, as one approaches the maximum sustainable fixed mortality rate, stochastic events will have a large impact, because by chance, the population may be reduced below a size from which it can recover (McCullough 1979, 1984).

RELEVANCE OF THE CRAIGHEADS' DATA TO CURRENT RESEARCH

Understanding the data collected while grizzly bears were concentrated at garbage dumps gives little comfort when interpreting the current results of the Interagency Research Team (Knight et al. 1982). Few parameters can be obtained from the very dispersed current population. Mean litter size, a statistic that has been obtained, showed only a weak correlation to the actual number of cubs recruited in the Craig-

heads' data. The percent of adult females with litters, a more reliable predictor, has proven impossible to obtain in recent research. Thus the conclusion that reproductive rates have declined (Knight 1983) based on low mean litter sizes may be misleading because it might be offset by a higher percent of females with litters. This is particularly true because there was no relationship between mean litter size and percent of adult females with litters ($r^2 = 0.014$, $P = 0.71$) in the Craigheads' data.

Furthermore, the correlation of mean litter size and number of adults in the same year was negative and not quite significant. However, mean litter size is significantly negatively correlated with the number of adults in the previous year when they were bred ($P = 0.02$) (Shaffer 1978). Therefore, the trend is for high mean litter sizes to be associated with low adult population sizes and vice versa, as one would expect from a density-dependent response. A recent concern is an apparently high adult mortality rate in the ecosystem. If, in fact, the adult mortality rate is high, the reduced adult density should be reflected in high mean litter sizes. Therefore, an increase in mean litter size may be cause for concern rather than optimism, and decline cause for optimism. Given that population simulations with low mortality rates are oscillatory and those with mortality rates near the sustainable maximum are stable (Figs. 6 and 7), are not mean litter sizes with fluctuating trends over time a better sign than those showing stability over time? In conclusion, litter sizes can be interpreted as a good, bad, or indifferent sign about the status of the population. In the face of uncertainty we are forced to be prudent and interpret low mean litter size as a bad sign.

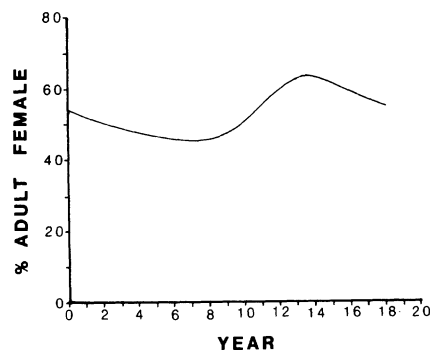


Fig. 5. Change in sex ratio in adults in the simulation model over 1 oscillation.

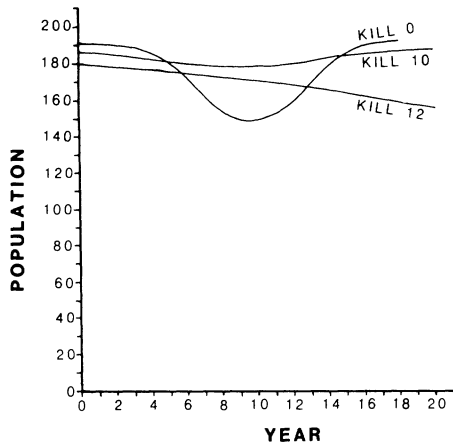


Fig. 6. Simulation showing dampening of population oscillation by imposing a sustainable kill (10 adult bears per year) and an unsustainable kill (12 adult bears per year) to the background mortality of 10 adult bears per year.

SATURATION TRAPPING FOR PETERSEN ESTIMATE

The Interagency Research Review Committee (Kilgore et al. 1981) recommended making an intensive marking effort to derive a population estimate by the Petersen estimate method. Clearly much more would be learned in such an effort in addition to the population estimate, but it would be expensive and there is some risk of the marking attempt intruding on the well-being of the grizzly bears.

Petersen estimates are quite sensitive to heterogeneity biases (White et al. 1982). Heterogeneity refers to unequal catchability and observability of sex and age classes. McCullough and Hirth (unpubl. data) have shown that for white-tailed deer (*Odocoileus virginianus*) on the George Reserve in Michigan the catchability of sex and age classes varied with deer behavior, and observability differs markedly with differential use of habitat types. All of these problems are likely to occur with Yellowstone grizzly bears.

Assuming that such difficulties can be overcome, there remains the problem of interpreting a single point estimate. Consider a point estimate of 150 or greater: this could represent any of the cases shown in Figure 6, including the case that is leading to extinction. Therefore, a point estimate verifies the population size at that point in time, but it does not give a future projection. Figures 4 and 6 show that given the slow population response and long time lags of grizzly bears, a considerable series of point estimates over time is required to determine popu-

lation behavior. The Craigheads' data are valuable because they include such a long time series. Any given year of data would have been difficult or impossible to interpret in terms of age structure, sex ratio, density dependence, or reproductive and survival rates.

In conclusion, a point estimate of grizzly bears in Yellowstone Park would be expensive, subject to bias, and likely to have broad confidence limits. Even if precise and accurate, such a point estimate would be difficult to interpret in regard to population trend. Obtaining such estimates over a sufficient period to give reliable trends would be inordinately expensive and may require an unacceptable intrusion into the bears' lives.

AN ALTERNATIVE APPROACH TO POPULATION ASSESSMENT

Because all obtainable population data are uncertain, we are being kept in a perpetual state of concern that this population may be becoming extinct. This dictates the need to find a method of monitoring the Yellowstone grizzly bear population that is sensitive to detection of serious error, that is, a method that unambiguously indicates when the population is seriously threatened.

Most thinking thus far has been directed toward deriving a point estimate of the population when, in fact, a "1-tailed" test approach may be more fruitful. It may be more valuable to know for certain that there are no fewer than *X* number of bears in the population than to have a point estimate of *X* with its estimated variance. Biologists will argue about biases in the data and statisticians about the appropriate mark-recapture model. Interest groups will argue about the variance. Thus if the estimate is 250

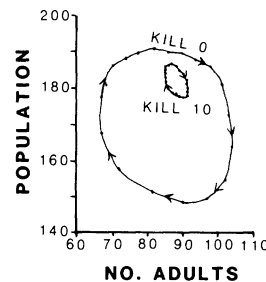


Fig. 7. Relationship of number of adults to total population showing reduction of time lag oscillation in background adult mortality (outer circle) by imposing a kill of 10 bears per year (inner circle).

Table 2. Simulation of population size and sex and age composition over 1 oscillation of Yellowstone grizzly bear model with an induced mortality of 10 bears per year.

Year	Total population	No. cubs	No. 1.5	No. 2.5	No. 3.5	No. 4.5	No. adults	No. ad. males	No. ad. females
1	187	31	22	18	16	13	87	42	45
2	186	31	21	17	16	13	88	43	45
3	185	30	21	16	16	13	89	44	45
4	184	30	20	16	15	13	90	45	45
5	182	29	20	15	15	12	91	46	45
6	181	29	19	15	15	12	91	46	45
7	180	29	19	14	15	12	91	46	45
8	179	29	19	14	14	12	91	46	45
9	178	29	19	14	14	11	91	46	45
10	178	30	19	14	14	11	90	45	45
11	178	30	20	14	14	11	89	44	45
12	179	31	20	15	14	11	88	43	45
13	179	31	21	15	14	11	87	42	45
14	180	31	21	16	15	11	86	41	45
15	182	32	22	16	15	12	85	40	45
16	183	32	22	17	15	12	85	40	45
17	184	32	22	18	15	12	85	40	45
18	185	32	22	18	16	12	85	40	45
19	186	32	22	18	16	13	85	40	45
20	186	31	22	18	16	13	86	41	45
21	187	31	22	18	16	13	87	43	45
\bar{x} =	182	31	21	16	15	12	88	43	45

bears \pm 100 (0.95 confidence level), outfitters, hunters, and sheep grazing permittees will argue that there may be as many as 350, whereas protectionists will argue that there may be as few as 150. The latter possibility will keep anyone interested in Yellowstone grizzly bears nervous, particularly if there is reason to suspect bias due to heterogeneity, or if they dwell on the luck of the draw, the 1 in 20 chance of the true value falling outside of that interval.

It is these considerations that prompt me to propose a monitoring scheme based upon a minimum, unduplicated count of bears. Based on aerial flights, Knight et al. (1980) reported unduplicated counts of 100–138 bears from 1974 to 1978. Unfortunately, these counts were confused by varying effort in flying time and area coverage. What I propose is developing a standardized set of routes and flying times to equalize the effort between years of counts of unduplicated bears. Developing the sampling system would require experimentation to determine the number of routes, number of flights replicating the routes, times of year, and so forth to optimize the cost and effort in obtaining the unduplicated count. This system could then be used year after year to monitor the size of the grizzly bear population. The unduplicated count, in conjunction with mean litter size, known mortalities, and so forth could constitute an ongoing program of affordable cost and reasonable security. As

an aside, it should be noted that some measure of effort in determining mortality is needed. The natural tendency is to watch mortality more closely when the grizzly bear population is perceived as threatened, and it is difficult to tell if there has been an actual increase in the number of mortalities or a greater proportion of mortalities has been recorded because of increased effort.

Ideally a standardized unduplicated count would be correlated with Petersen or other estimates of the population to derive a correction factor to convert the unduplicated count to total population. But the value of the unduplicated count is that it sets a bottom limit, a verified minimum number of bears present in the ecosystem. If, in fact, minimum unduplicated counts of over 100 grizzly bears—one-third to one-half of the total bears estimated to be present—can be obtained, they would ascertain the presence of a viable population. Serious changes in the counts would then be detected while there was still time to act. (This figure is above the minimum viable population suggested by Shaffer [1983].)

A MANAGEMENT STRATEGY

Here I am referring only to population management. Clearly protection and maintenance of suitable habitat underlies all that is done in the way of pop-

ulation management, and I am assuming that habitat will remain reasonably constant.

Much of the problem with population management of Yellowstone grizzly bears traces to ambiguity in estimates of population size. Whether number of mortalities is critical depends on population size. Biologists have not been able to agree on the status of the grizzly bear population, and these arguments are likely to continue given the error in population estimation. Resource managers have been confused by this situation and have been reluctant to make tough decisions that favor grizzly bears when the need for such measures is questionable, particularly because of the volatile political and economic issues associated with such decisions.

A more workable strategy might be based on a minimum unduplicated count. Biologists should be able to agree that a minimum number of bears have been documented, even though they continue to argue over what proportion of the total population the minimum represents. Assuming that such a standardized system could be developed, management plans could be tied to a threshold number of bears. As long as the unduplicated count exceeded that number, routine management practices could be followed. However, if the unduplicated count fell below the threshold number for whatever reason (an actual decline in the population or failure of bears present to be counted), stringent management policies could be implemented. Actions might include canceling grazing permits, closing bear hunting seasons in surrounding areas, increasing enforcement, and greater efforts to save and rehabilitate problem bears. Such a system should motivate users who are antagonistic or indifferent to grizzly bears to limit the number of mortalities, because depression of the grizzly bear population with resulting unduplicated counts below the threshold number would result in severe restriction on their uses of grizzly bear habitat.

Obviously this suggestion can be no more than a proposal at this time. It remains to be seen if a standardized monitoring system based on a minimum number of bears can be effectively developed and implemented. Assuming it can, negotiating a threshold number and persuading various agencies to abide by such a management system will require a rare level of statesmanship. Nevertheless, any alternative must be weighed against present practice. The current state of grizzly bear management in the Yellowstone ecosystem is hardly satisfactory and does not assure the long-term survival of the population.

LITERATURE CITED

- AVRIN, D. E. 1976. A numerical model of the Yellowstone grizzly bear population and its management implications. M.S. Thesis, Univ. Mich., Ann Arbor. 51pp.
- BASKERVILLE, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.* 2:49-53.
- BLANCHARD, B. M., AND R. R. KNIGHT. 1980. Status of grizzly bears in the Yellowstone system. *Trans. North Am. Wildl. Nat. Resour. Conf.* 45:263-267.
- CAUBLE, C. 1977. The great grizzly grapple. *Nat. Hist.* 86:74-81.
- CHASE, A. 1983. The last bears of Yellowstone. *Atlantic Monthly* 248(2):63-73.
- COLE, G. F. 1971. Preservation and management of grizzly bears in Yellowstone Park. *BioSci.* 21:858-863.
- . 1973. Management involving grizzly bears in Yellowstone National Park 1970-72. U.S. Dep. Int., Natl. Park Serv., Nat. Res. Rep. No. 7. 10pp.
- . 1974. Management involving grizzly bears and humans in Yellowstone National Park, 1970-73. *BioSci.* 24:335-338.
- COWAN, I. MCT., D. G. CHAPMAN, R. S. HOFFMANN, D. R. MCCULLOUGH, G. A. SWANSON, AND R. B. WEEDEN. 1974. Report of the Committee on the Yellowstone Grizzlies. *Nat. Acad. Sci.-NRC Rep.* 61pp.
- CRAIGHEAD, F. C., JR. 1973. They're killing Yellowstone's grizzlies. *Natl. Wildl.* 11:4-9, 17. (interview.)
- CRAIGHEAD, J. J. 1982. Satellite imagery: an alternate future. *West. Wildlands* 8(4):18-27.
- , AND F. C. CRAIGHEAD, JR. 1967. Management of bears in Yellowstone National Park. *Environ. Res. Instit. and Mont. Coop. Wildl. Res. Unit Rep. Univ. Mont., Missoula.* 113pp.
- , AND ———. 1971. Grizzly bear-man relationships in Yellowstone National Park. *BioSci.* 21:845-857.
- , J. S. SUMNER, AND G. B. SCAGGS. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources utilizing LANDSAT multispectral imagery and computer technology. *Wildlife-Wildlands Instit. Monogr.* 1. Missoula, Mont. 279pp.
- , J. R. VARNEY, AND F. C. CRAIGHEAD, JR. 1973. A computer analysis of the Yellowstone grizzly bear population. *Mont. Coop. Wildl. Res. Unit, Univ. Mont., Missoula, Mont.* 81 and 61 pp.
- , ———, AND F. C. CRAIGHEAD, JR. 1974. A population analysis of the Yellowstone grizzly bears. *Mont. For. and Conserv. Exp. Sta. Bull.* 40. Univ. Mont., Missoula. 20pp.
- FINNEY, D. I. 1941. On the distribution of a variate whose logarithm is normally distributed. *J. Royal Stat. Soc. Series B*, 7:155-161.
- FOWLER, C. W. 1981a. Density dependence as related to life history strategy. *Ecology* 62:602-610.
- . 1981b. Comparative population dynamics in large mammals. Pages 437-455 in C. W. Fowler and T. D. Smith, eds. *Dynamics of large mammal populations.* J. Wiley and Sons, Inc., New York. 477pp.
- , W. T. BUNDERSON, M. B. CHERRY, R. J. RYEL, AND B. B. STEELE. 1980. Comparative population dynamics of large mammals; a search for management criteria. Rep. No. MMC-77-20 to the U.S. Marine Mammal Comm. Natl. Tech. Inform. Serv. NTIS PB80-178627, Springfield, Va.
- GILBERT, B. 1976. The great grizzly controversy. *Audubon* 78:63-92.

- JOHNSON, A. S. 1973. Yellowstone's grizzlies: endangered or prospering? *Defenders of Wildl. News*, October:557-568.
- KEMP, G. 1972. Black bear population dynamics at Cold Lake, Alberta, 1968-70. *Int. Conf. Bear Res. and Manage.* 2:26-31.
- . 1976. The dynamics and regulation of black bear, *Ursus americanus*, populations in northern Alberta. *Int. Conf. Bear Res. and Manage.* 3:191-192.
- KILGORE, B. M., J. BEECHAM, C. JONES, J. WEIGAND, R. GOFORTH, AND M. D. STRICKLAND. 1981. Technical review of the Interagency Grizzly Bear Study Team and recommendations for future research. Rep. to the Interagency Grizzly Bear Study Team. 21pp. + appendices.
- KNIGHT, R. R. 1983. Report of the ad hoc Committee for Population Analysis. Memorandum to the Chairman of the Interagency Grizzly Bear Steering Committee. Natl. Park Serv., Mont. State Univ., Bozeman. 4pp. + illustrations.
- , B. M. BLANCHARD, AND K. C. KENDALL. 1982. Yellowstone grizzly bear investigations. Rep. of the Interagency Study Team. U.S. Dep. Int., Natl. Park Serv. 70pp.
- , ———, ———, AND L. E. OLDENBURG. 1980. Yellowstone Grizzly bear investigations. Rep. of the Interagency Study Team, 1978 and 1979. Mont. Dep. Fish, Wildl. and Parks and U.S. Dep. Int., Natl. Park Serv. 91pp.
- MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. Univ. Mich. Press, Ann Arbor. 271pp.
- . 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173-196 in C. W. Fowler and T. D. Smith, eds. *Dynamics of large mammal populations*. J. Wiley and Sons, Inc., New York. 477pp.
- . 1984. Lessons from the George Reserve. Pages 211-242 in L. K. Halls, ed., *White-tailed deer: ecology and management*. Wildl. Manage. Instit., Wash., D.C. and Stackpole Books, Harrisburg, Pa. 870pp.
- MEAGHER, M. 1978. Evaluation of bear management in Yellowstone National Park, 1977. Natl. Park Serv., Yellowstone Natl. Park. Res. Note No. 8. 18pp.
- PAYANDEH, B. 1981. Choosing regression models for biomass prediction equations. *For. Chron.* 57:229-232.
- PICTON, H. D. 1978. Climate and reproduction of grizzly bears in Yellowstone National Park. *Nature* 274:888-889.
- RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Bd. Can. Bull.* 191. 382pp.
- SCHULLERY, P. 1980. The bears of Yellowstone. Yellowstone Libr. and Mus. Assoc., Yellowstone Natl. Park, WY. 176pp.
- SEATER, S. 1973. Vanishing point: the grizzly bear. *Environ. Qual.* 4:28-34.
- SHAFFER, M. L. 1978. Determining minimum viable population sizes: a case study of the grizzly bear (*Ursus arctos* L.). Ph.D. Thesis, Duke Univ., Durham, N.C. 190pp.
- . 1981. Minimum population sizes for species conservation. *BioSci.* 31:131-134.
- . 1983. Determining minimum viable population sizes for the grizzly bear. *Int. Conf. Bear Res. and Manage.* 5:135-141.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman Co., San Francisco, Calif. 776pp.
- SPRUGEL, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64:209-210.
- STRINGHAM, S. F. 1980. Possible impacts of hunting on the grizzly/brown bear, a threatened species. *Int. Conf. Bear Res. and Manage.* 4:337-349.
- . 1983. Roles of adult males in grizzly bear population biology. *Int. Conf. Bear Res. and Manage.* 5:140-151.
- WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos Natl. Lab. Rep. LA-8787-NERP. Los Alamos, N.M. 235pp.
- WHITTAKER, R. H., AND P. L. MARKS. 1975. Methods of assessing primary productivity. Pages 55-118 in H. Lieth and R. H. Whittaker, eds. *Primary productivity of the biosphere*. Springer-Verlag, New York. 339pp.