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YELLOWSTONE GRIZZLY BEAR INVESTIGATIONS

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Written by: Richard R. Knight and Bonnie M. Blanchard

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Population Trend Estimates from Reproductive and Survival Data

by
L. L. Eberhardt

Population trend has been estimated for the Yellowstone population by using an approximation to Lotka's equation with reproductive and survival data (Eberhardt et al. 1994). The model used is:

[1]

$$\lambda^{a} - s\lambda^{a-1} - l_a m [1 - (s/\lambda)^{w-a+1}] = 0$$

Here, λ denotes the "finite population multiplier" ($\lambda = e^r$), s is a constant rate of survival for adults, l_a is survival to age of first parturition (a), w denotes the maximum age considered and m is reproductive rate, calculated as female cubs per adult female. The model is based on replacing the reproductive curve by a rectangular function (Eberhardt 1985), using an initial (a) and maximum (w) age. A maximum age of 20 was used, to compensate for likely lowered reproduction and survival rates in the older age classes. Calculations from eq. (1) are not very sensitive to the maximum age (w) used (Eberhardt 1990). The oldest female bear examined in the present study was 25 years of age, dying at that age after having had a cub. Solutions of the model for λ are obtained by iteration.

In the earlier report (Eberhardt et al. 1994) we used survival data based on bear-years of observation, the method used in prior annual reports. A bias in that approach is that radiocollars may be lost (or transmitters fail) and the individual is later recaptured and a new transmitter attached. In the earlier reports, we used the total length of time that an individual was known to be alive (i.e., the intervening time period when a transmitter was inactive was included in the period of observation). This tends to overestimate survival rates, inasmuch as other bears that lose transmitters may die shortly after "going off the air" and thus not be recorded again. Here, we use only those days of life in which a bear was actually observed by telemetry, and survival is calculated on a daily basis, and then adjusted to an annual rate, using the equation:

$$annual\ survival = \left(1 - \frac{deaths\ recorded}{bear - days\ observed}\right)^{365}$$

Data on adult female survival from bears captured before 1983 is not used here due in part to the disruption and substantial losses of bears associated with closure of garbage dumps in and near Yellowstone National Park in the early 1970s (Knight and Eberhardt 1985). More importantly, there was a substantial focus on reduction of human-caused mortalities after it became apparent that the population trend was negative (Knight et al. 1983). The survival data used for trend estimates is based on trapping conducted throughout the area by IGBST staff for the purpose of trend estimation. A number of bears caught for "management" purposes are not included in these estimates, because they belong to a high risk group. That is, they were not captured until they had become such a nuisance (by entering campgrounds, private property, etc.) that they had to be relocated. It should be noted that bears caught in "research" trapping often were caught later for "management" purposes, and these bears are included in the survival calculations.

Adult female survival was estimated as 0.943, based on 31,222 bear-days (and 5 deaths). The small sample of adult females caught initially for management purposes (7,999 bear-days) had a survival rate of 0.726 (7 deaths). Survival for subadult females caught from 1983 to date was 0.803 (8,332 bear-days; 5 deaths). Survival for all subadults caught was virtually identical (0.799). Survival for bears caught in research trapping was somewhat higher than the "management" bears, but only small samples are available if the data are broken down into subcategories, so data on all bears caught in 1983 or later is used here. Blanchard and Knight (1995) have shown that subadult females caught in management situations and relocated do not return or repeat the offense as often as adult females.

Cub survival was calculated for litters seen after emergence from the den and again as yearlings, or for cases where the adult female was observed alone the next year. Data on a total of 69 individual cubs observed in 1983 or later were used here, with 58 surviving to become yearlings for a survival rate of 0.840. The survival rate for cubs born prior to 1983 appeared to be a little higher, but is based on a smaller sample.

Survival records on adult females first caught in management operations were not included because including such high-risk bears would bias the survival estimates, so we have used only bears that were caught before they had initiated this kind of behavior. Very few bears in the Yellowstone population die of natural causes. Just 10 (11%) of 92 recorded deaths for which a cause was known died naturally. The remainder were killed by people for one reason or another, and 40% of these died in the course of management activities. Six bears died of unknown causes.

Although management activities are a major cause of mortalities, only a relatively small fraction of adult females are at high risk to death from such activities in any given year. There were 20 "management" bears in the adult female data base from 1983 through 1994, averaging less than 2 such bears caught in each year. None were radioed in 5 years, 1 in each of 3 years, 3 in 1 year, and 6 in 2 years (1986 and 1994). From the "distinct families" data (Knight et al. 1995), there is good reason to believe that the minimum number of adult females in the population each year exceeds 60, so that the average annual number of "management" bears in the population was quite surely less than 3%.

It could be argued that we should stratify the population for survival calculations, thus using the data on bears first caught in a management situation. The few bears classed as management bears each year would constitute 1 stratum and all other bears a second stratum. The problem with this is that some of the "other" bears (caught in "research" trapping) also get into management situations and are killed. Three of the 5 deaths recorded for research bears occurred in just this way. Consequently, any stratified calculation would have to be somehow adjusted for such bears, which seems very difficult to do. As noted earlier, we believe the "research" bears constitute a representative sample of the population. Nine (23%) of 39 adult females initially caught in research trapping were later caught in "management" situations. Overall mortality for management bears was 27%, so that we can calculate an expected death rate of 0.23(0.27) = 0.06, very much the same as the mortality rate of all adult female bears first caught in research trapping.

Reproductive rates in the present report are based on females aged 4 and older. This change from our earlier approach of using females aged 5 and older was instituted because it has become apparent that the Yellowstone bears do begin to have cubs at age 4. There were 20 females that were observed continuously from age 4 to the time of first parturition. The records of age of first reproduction for these bears were 5 at age 4, 4 at age 5, 6 at age 6, and 5 at age 7.

Reproductive rates can be estimated by 3 methods; (1) number of cubs born per year of observation, (2) averaging reproductive rates for individual adult females (which compensates for the fact that some females are observed for longer periods than others), (3) the average interval between parturitions divided by mean litter size. Due to the fact that individual adult bears are usually observed for only 1 or 2 such intervals, this estimate is likely to be biased because the short overall observation period makes it unlikely that the longer intervals between parturitions are observed (radiocollars are lost or transmitters fail before the next parturition). Inasmuch as all 3 methods have been used in practice, results are reported here for the 3 methods. A total of 204 bear-years of observation are available on 48 individual adult females.

Due to the prospect of some disruption of reproduction in earlier years associated with closure of garbage dumps, data for 1981 to date have been examined separately. We used 1981 rather than 1983 as cut-off date here in order to increase sample size. Results for the 3 methods are as follows:

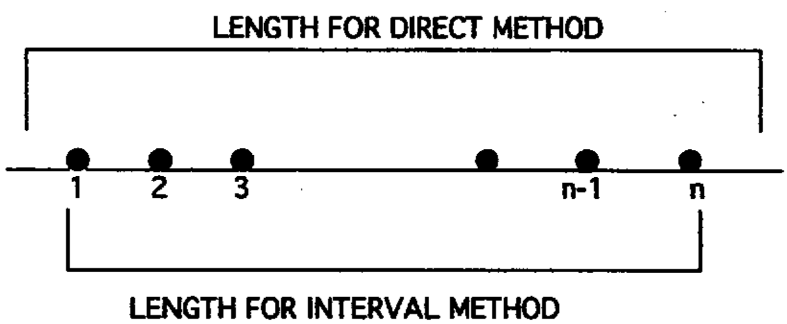
	Female cubs per bear-year	Averaging rates for individual bears	Mean interval/mean litter size
All data	0.36	0.35	0.40
1981 and later	0.35	0.35	0.40

If, instead of the mean interval between parturitions, we use the modal (most frequent) interval of 3 years, then the rate for the interval method becomes 0.37, and thus is in better agreement with the other methods. Using the modal interval reduces the bias in estimating the average interval, inasmuch as the longer intervals do not have much influence on the mode.

Unfortunately, there is no way to be sure that the sample of bear-years obtained is representative of the population. The fact that the 3 methods of estimation appear to agree is encouraging. However, another check can be made by using only data in which the interval of observation begins and ends with a parturition. The smaller sample (76 bear-years from 23 adult females) thus obtained gives the following results:

	Female cubs per bear-year	Averaging rates for individual bears	Mean interval/mean litter size
All data	0.40	0.41	0.39
1981 and later	0.40	0.42	0.40

These rates seem consistently higher than those for the full data set. A difficulty here is that the data largely encompass only a single reproductive interval per bear. Using only a few intervals can result in a bias (Eberhardt and Schneider 1994:Fig. 3). The basis for such a bias can be illustrated by the following diagram (Eberhardt and Schneider 1994:Fig. 2):



The solid points represent parturition events over time, while the length of the upper interval is l_1, and that of the lower interval is l_2. If we consider n intervals, then the basis for an estimate by the interval method consists of dividing number of cubs produced in the first n-1 litters by the overall interval length (l_2) in the diagram. To consider the source and nature of the bias, one needs to review the basis for an unbiased sample, which is a random selection of a fixed observation period (upper interval in the diagram). Random selection of the interval guarantees that location of the endpoints of the observation period is independent of the timing of the events observed (parturitions). The bias is reduced by the use of long intervals, so that l_2 becomes a better approximation to l_1. As mentioned previously, another possible source of bias arises because we may not observe the longer intervals between litters, due to the limitations of collar loss and battery life. The longest observed single interval in the Yellowstone data set is 4 years. For a simulation to illustrate the possible nature of the bias, the observed frequency of interval length has been made symmetrical, as follows:

	Observed frequency	Frequency for simulation	Cumulative distribution for simulation
1	2	2	0.0513
2	9	9	0.2820
3	17	17	0.7180
4	3	9	0.9487
5	0	2	1.0000

The simulation program draws an initial age of parturition at random in the range of ages 4 to 7, and then selects subsequent intervals at random from the above frequency distribution. These intervals can then be used to calculate a mean density of parturitions by using the equation:

$$\hat{D} = \frac{n-1}{l_2}$$

where n is the number of parturitions and l_2 is the sum of the intervals, as in the diagram above.

The symmetrical distribution of the intervals for the simulations shown above makes it evident that the expected density of parturitions is 0.333, and this is illustrated by 5,000 simulation runs with each run based on 200 intervals, which gives a mean density of 0.3335. If we consider only a single interval, the mean density in 5,000 runs is 0.3783, while using 2 intervals gives a mean density of 0.3502. Note that the data tabulated previously is for female cubs per bear-year, while the simulations only consider parturitions per bear-year. If the litter size were 2 cubs per litter (hence 1 female cub per litter) then the 2 rates would be the same. Because the mean litter size is somewhat higher than 2, one would need to decrease the observed rates somewhat to make them directly comparable to the simulated values.

A bootstrap analysis of the data gives much the same coefficient of variation for lambda (0.0393) as does the delta method (0.0384). Approximate 95% bootstrap confidence limits for λ are 0.97 to 1.12. The delta method approximation indicates that 77% of the overall variance comes from subadult survival (about 2% of that is associated with cub survival), 19% from adult survival and about 4% from reproductive rate. The estimated λ is 1.053, essentially the same rate as that reported by Eberhardt et al. (1994).

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