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Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates

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The trend of the Yellowstone grizzly bear (*Ursus arctos horribilis*) population was estimated using reproductive rates calculated from 22 individual females and survival rates from 400 female bear-years. The point estimate of the rate of increase was 4.6%, with 95% confidence limits of 0 and 9%. Caution in interpreting this result is advised because of possible biases in the population parameter estimates. The main prospects for improving present knowledge of the population trend appear to be further study of possible biases in the parameter estimates, and the continued use of radiotelemetry to increase the number of samples on which the estimates are based.

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L'évolution de la densité de la population de Grizzlis de Yellowstone (*Ursus arctos horribilis*) a été estimée par détermination des taux de reproduction calculés pour 22 individus femelles et des taux de survie de 400 femelles-années. L'estimation ponctuelle du taux d'augmentation est de 4,6% (limites de l'intervalle de confiance de 95% situées à 0 et 9%). L'interprétation de ces résultats demande de la prudence, puisqu'il peut s'introduire des biais dans l'estimation des diverses variables démographiques. L'identification des biais qui peuvent fausser les estimations des variables et l'utilisation de la radiotélémétrie pour augmenter l'importance des échantillons sur lesquels sont basées ces estimations semblent les meilleurs outils à utiliser pour améliorer nos connaissances sur l'évolution des populations.

[Traduit par la Rédaction]

Introduction

The future of the Yellowstone grizzly bear population remains uncertain and controversial. The population is isolated and human use of its habitat has increased rapidly and can be expected to continue to increase at an accelerating rate. Although recent regulations to minimize mortality have been largely successful, conflicts with humans remain the main source of mortality (Knight and Eberhardt 1984). Human encroachment on habitat contributes to both direct and indirect mortality. In the face of these difficulties, close monitoring of the population is essential. An interagency research team was formed in 1973 and has attempted to develop monitoring methods since then (Eberhardt et al. 1986). Radiotelemetry data for this study have been collected since 1975.

It soon became evident that estimating the total population size would require a very large and continuing capture–recapture effort. This approach has not been mounted owing to cost and intrusion factors. Attempts at devising population trend indices have been hampered by the secretive habits and high mobility of grizzlies. Tallies of separate families with cubs of the year ("unduplicateds") seemed to show the most promise as trend indicators (R.R. Knight and L.L. Blanchard, submitted for publication), but these are substantially influenced by annual moisture conditions: in good years, bears remain in heavy cover and are difficult to see, while in dry years, they must forage more extensively and become more visible (Knight et al. 1988).

The best monitoring scheme devised thus far has depended on determining reproductive and survival rates by radiotelemetry. Estimates of these rates can be used to determine rate of change for the population. The main drawback is th data accumulate slowly. Also, there are prospects of bi associated with the difficulties of maintaining contact wi individual bears either through loss of radios or battery fa ure. Another problem has been the lack of confidence lim on the reported rate of change. The present paper presents t most recent results, along with confidence limits on the r of population increase. These limits were obtained by t statistical technique of bootstrapping.

Methods

Study area

The study area is centered on Yellowstone National Park. encompasses roughly twice its area, or about 20 000 km^2. It inclu portions of the states of Idaho, Montana, and Wyoming, and parts 5 National Forests. Elevations range from 1600 to 3300 m o extensive central plateaus surrounded by mountains. The climate characterized by long cold winters and short cool summers. The a is mostly (75%) forested and is in the subalpine zone, with lodgep pine (*Pinus contorta*) dominated stands. Douglas-fir (*Pseudots menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) are comm dominants on high-relief topography in the area.

Populations of ungulates in the area provide a supplemental s source for grizzlies, particularly as carrion during many sp periods. The largest and most extensively distributed ungulate p ulation is that of elk (*Cervus canadensis*), and smaller population bison (*Bison bison*), mule deer (*Odocoileus hemionus*), and mo (*Alces alces*) are also rather widely distributed. The food habits the grizzly population have been studied extensively (Mattson et 1991).

TABLE 1. Ages at first parturition for Yellowstone grizzly bears observed in two time periods

Age	1959–1970	1974–1992
4		5
5	11	5
6	1	11
7	3	6
8	1	1
Total	16	28

Model

The model used to estimate the rate of change of the Yellowstone grizzly population is an approximation to Lotka's equation proposed by Eberhardt (1985), and presented here as a polynomial:

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

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 at first parturition (a), w denotes the maximum age considered, and m is the reproductive rate, calculated as the number of 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 a 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.

Reproductive rate

In previous reports (Knight and Eberhardt 1985, 1987) we have used a fixed reproductive interval (3 years) based on field data. Mean litter size and sex ratio were then incorporated to estimate an average rate. As more reproductive data accumulated, it seemed desirable and feasible to avoid the assumption of a fixed interval, and to use an estimate based on the average number of cubs per bear-year. We used only data from adult females for which we had a complete record of one or more reproductive cycles, a cycle generally being defined as the interval between successive parturitions. Because we use age 5 as an average date of first reproduction and a fixed average rate of reproduction (m in eq. 1) at age 5 and beyond, we have arbitrarily defined the cycle that includes the first birth as beginning at age 5 and ending at the second parturition. In calculations, each cycle includes one litter, so data on the last litter observed do not enter into the computation of an average reproductive rate (but are used to estimate cub survival). It is assumed that 50% of the cubs are female.

Survival rates

Survival was calculated as

$$[2] \quad s = 1 - \frac{\text{recorded deaths}}{\text{bear-years observed}}$$

for cubs, subadults (ages 1–4), and adults (5 years and older). The data for cubs and subadults are combined to estimate survival to age 5, using

$$[3] \quad l_a = s_0\, s_1^{4}$$

where s_0 denotes cub survival and s_1 the subadult rate. The latter was based on pooling all data on subadults, but individual rates were also calculated for all 4 subadult classes. The product of these 4 rates is essentially the same as s_1^{4}.

Bootstrap confidence limits on the rate of increase

The statistical technique of bootstrapping (Efron and Gong 1983) was used to obtain confidence limits on λ using eq. 1. Four different files contain the field data for cub survival, subadult survival, adult survival, and reproductive rate. Each such file was sampled randomly with replacement using the observed sample size. Rates needed for eq. 1 were calculated from the sample data and used to calculate λ. The process was then repeated 2000 times and the resulting frequency distribution of values of λ was used to provide approximate 95% confidence limits by excluding 2.5% at each end of the distribution.

Variance estimates from the delta method

The bootstrap confidence limits have appeared to give quite satisfactory results in Monte Carlo simulations (L.L. Eberhardt, unpublished data), but the technique does not provide direct measures of the relative importance of the 4 component estimates. We have thus resorted to the delta method (Seber 1982), which provides an estimate of the variance of a function, $g(x)$, from

$$[4] \quad V[g(x)] \doteq \Sigma V(x_i)\left(\frac{\partial g}{\partial x_i}\right)^2$$

In the present study, values of the individual variances, $V(x_i)$, were obtained for each component estimate from the bootstrapping procedure described above. The partial derivatives were obtained by implicit differentiation of eq. 1, which gives

$$\frac{\partial\lambda}{\partial s} = \lambda\left[(w-a+1)\, l_a m\lambda\left(\frac{s}{\lambda}\right)^{w-a+1} - s\lambda^{a}\right] / sA$$

$$[5] \quad \frac{\partial\lambda}{\partial l_a} = m\lambda^2\left[\left(\frac{s}{\lambda}\right)^{w-a+1} - 1\right] / A$$

$$\frac{\partial\lambda}{\partial m} = l_a\lambda^2\left[\left(\frac{s}{\lambda}\right)^{w-a+1} - 1\right] / A$$

where $A = (w-a+1)\, l_a m\, \lambda\left(\frac{s}{\lambda}\right)^{w-a+1} + \lambda^{a}(as - s - a\lambda)$

Results

Age at first reproduction

In the Yellowstone area, first births typically occur at age 5, 6, or 7. However, in recent years we have had several records of bears known to be 4 years of age at first reproduction. Reproduction is recorded for litters seen in the summer. Table 1 brings up-to-date the record of ages at first parturition reported by Knight and Eberhardt (1985).

Parameter estimates

Records on one or more reproductive cycles were available for 22 adult females, yielding a rate of 0.328 female cubs per female each year. Survival data were available for 37 litters containing 93 cubs (both sexes), for a rate of 0.845. Mean annual survival of 48 subadult females (106 bear-years) was 0.887, while records on 58 adult females (247 bear-years) gave an annual survival rate of 0.923.

Estimate of λ and confidence limits

An iterative solution of eq. 1 with the above parameter estimates gave λ = 1.046. Two thousand bootstrap samples gave a frequency distribution (Fig. 1) for which 95% confidence limits on λ are about 1.00 – 1.09 when the "percentile" method for obtaining bootstrap confidence limits, in which the limits are taken as points that cut off about 5% of the "tails" of the distribution, is used (cf. Fig. 1). The coefficient of variation of the bootstrapping data was 0.022 and the standard deviation was 0.023. Using this standard deviation yields essentially the same 95% confidence limits as those obtained from the frequency distribution.

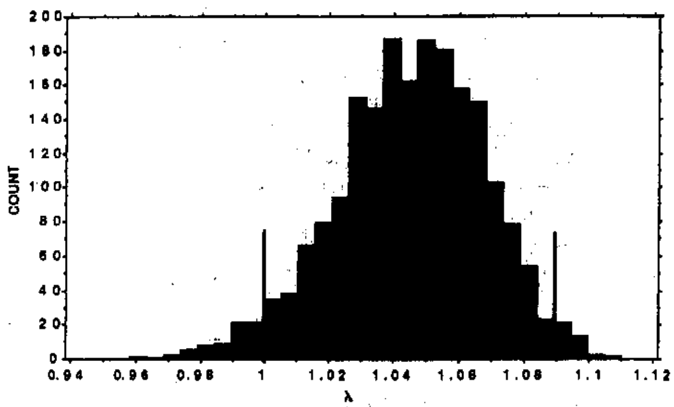

FIG. 1. Frequency distribution of 2000 bootstrap samples of λ for the Yellowstone grizzly bear population. Vertical lines show approximate 95% confidence limits.

Variance estimates from the delta method

Using the delta method (eq. 4) with variance estimates from the bootstrapping yielded a coefficient of variation of λ of 0.0216, essentially the same as the value obtained by bootstrapping. Values of the partial derivatives evaluated at the parameter values (Table 2) indicate, as might be expected, that adult survival is the most important determinant of the rate of increase of the population, with reproductive rate the next most important factor and subadult survival somewhat less important than reproductive rate.

Components of variance (expressed in Table 2 as proportions of the total variance) indicate that adult survival and survival to age 5 contributed about equally to overall variance, while variation in the reproductive rate was responsible for only about 10% of the overall variance. If the delta method is applied to eq. 3 with the variances for cub survival and mean subadult survival recorded in the bootstrapping, the result indicates that about 10% of the variance component for survival to age 5 is cub survival.

Discussion

The major finding of the present study is that the Yellowstone grizzly bear population appears to be increasing. The wide 95% confidence interval on λ (1.00–1.09) suggests that caution be used in interpreting this finding. There is also a significant prospect of bias in the parameter estimates. As the safety of individual bears has been the paramount consideration in trapping operations, radios are attached somewhat loosely, so loss of radios is a continuing problem. Ear tags and lip tattoos aid in maintaining identification of individuals. Trapping is conducted annually, and frequently "targets" particular individuals whose radio has been lost or has failed. Radio losses and the longevity of grizzlies necessitate the use of bear-years to estimate survival in eq. 2. Consequently, only 19 of the 58 individuals used to estimate adult survival were followed until death. Thus, further study of possible biases in the estimates is needed.

Earlier reports from the present study indicated a population decreasing at the rate of about 2.5% per year. In the first such report (Knight and Eberhardt 1985) the small number of records available forced us to combine males and females to estimate subadult survival. As the sample size increased with time, it became evident that male survival to age 5 is substantially less than that of females (Fig. 2 in Knight and

TABLE 2. Components of variance and partial derivatives for eq. 1

Source	Proportion of variance	Partial derivative
Adult survival	0.443	0.567
Survival to age 5	0.460	0.200
Reproduction	0.097	0.320
Total	1.000	

Eberhardt 1987). The larger sample now available indic a higher survival rate for subadult females, and yield estimate of λ greater than unity. The substantial e required to capture, radio-tag, and monitor bears means data accumulate very slowly, so the records used here compass all bears successfully monitored since trap began in 1975.

Use of eq. 1 to estimate λ implies the assumption of a st age distribution. We have aged bears throughout the st and have not observed any major changes in age struct Moderate changes in initial age structure have a minor ef on the rate of increase in simulations (L.L. Eberh unpublished data). Reproductive rates appear to h remained reasonably steady over the term of the study. only substantial fluctuation in mortality occurred from 1 to 1973 following the closure of open garbage dumps in area (Fig. 1 in Knight and Eberhardt 1987).

Presently, the main prospects for improving knowledg the population trend appear to be further study of poss biases in the estimates, and the continued use of ra telemetry to increase the number of samples on which estimates are based. If the population is actually increas and continues to do so, the limited habitat available ultimately result in cessation of population growth. This most likely be evident first in subadult survival (Eberh 1977). Thus, one might suppose that subadult survival sh be emphasized in monitoring. This expectation is fur supported by the fact that the variance component subadults in Table 2 is about as large as that for adu Because the estimates for subadults are based on a sho observation period (4 years at most), tagging more subad may increase precision more rapidly than tagging equivalent number of adults. Cub survival is also include the rate for subadults, but as noted in the Results sectio contributes only about 10% to the variance componen survival to age 5.

Continual assessment of adult survival is essential, as i the most important single factor determining λ. This indicated by the values of the partial derivatives in Tabl which show that changing adult survival has the grea influence on the values of λ. One can, of course, observe t effect without calculating partial derivatives by manipulat values of the parameters in eq. 1. The partial derivatives needed mainly for determining relative contributions to overall variance of the estimate of λ through eq. 4.

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