

# Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates

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**Abstract:** Using survival and reproduction data obtained from radio-tracking 23 adult female, 24 subadult female, 49 yearling, and 44 cub grizzly bears (*Ursus arctos*) in the Flathead River drainage of British Columbia and Montana, we estimated the finite rate of population increase ( $\hat{\lambda}$ ) from 1979 to 1994 at  $1.085 \pm 0.026$ , with  $\approx 95\%$  confidence limits of  $1.032-1.136$ . Estimated annual survival rates were  $0.946 \pm 0.026$  for adult females,  $0.931 \pm 0.038$  for subadult females,  $0.944 \pm 0.039$  for yearlings, and  $0.867 \pm 0.050$  for cubs (rates for cubs and yearlings represented both sexes). The estimated annual reproduction rate and age at first parturition were  $0.422 \pm 0.042$  female cubs per female and  $6.44 \pm 0.45$  years, respectively. We found that uncertainty in  $\hat{\lambda}$  was mostly attributable to uncertainty in survival rates (76.7%), with subadult (47.5%) and adult (21.9%) survival contributing the largest portions. These results indicated that to reduce uncertainty in  $\hat{\lambda}$ , further research on grizzly bears in our study area should focus on improving estimates of adult and subadult female survivorship. Other demographic variables are not as important in estimating the grizzly bear population trend in the North Fork of the Flathead River drainage.

**Résumé :** Des données sur la survie et la reproduction ont été obtenues chez 23 femelles adultes, 24 femelles subadultes, 49 jeunes de 1 an et 44 petits du Grizzli (*Ursus arctos*) munis d'émetteurs radio dans le bassin de la Flathead en Colombie-Britannique et au Montana; ces données ont permis d'estimer le taux de croissance  $\hat{\lambda}$  de la population de 1979 à 1994 à  $1,085 \pm 0,026$  avec un intervalle de confiance de  $\approx 95\%$  situé entre 1,032 et 1,136. Les taux de survie annuels ont été estimés à  $0,946 \pm 0,026$  chez les femelles adultes, à  $0,931 \pm 0,038$  chez les femelles subadultes, à  $0,944 \pm 0,039$  chez les jeunes de 1 an, et à  $0,867 \pm 0,050$  chez les petits de l'année (dans ces deux derniers cas, il s'agit de jeunes des deux sexes). Le taux annuel de reproduction a été évalué à  $0,422 \pm 0,042$  petit femelle par femelle et l'âge à la première parturition, à  $6,44 \pm 0,45$  ans. L'incertitude qui entoure  $\hat{\lambda}$  est surtout attribuable à l'incertitude qui entoure les taux de survie (76,7%) et c'est la survie des subadultes (47,5%) et celle des adultes (21,9%) qui ont le plus d'impact. Ces résultats indiquent que pour remédier à l'incertitude qui entoure  $\hat{\lambda}$ , les recherches sur les grizzlis dans cette région doivent s'attarder à trouver un moyen d'obtenir des estimations plus précises de la survie des femelles adultes et subadultes. Les autres variables démographiques n'ont pas autant d'impact sur l'estimation de la population de grizzlis du bras nord de la fourche du bassin de la Flathead.

[Traduit par la Rédaction]

## Introduction

Although considered threatened (Servheen 1990), grizzly bears in the Northern Continental Divide Ecosystem (NCDE) of Montana have the highest probability of persistence of any population in the continental U.S.A. Not only does the NCDE have the most bears, it is also adjacent to British Columbia and Alberta, so its grizzly population is linked to those of the rest of the continent (U.S. Fish and Wildlife Service 1993). The grizzly bear linkage zone in southern Canada is vital to the long-term health of the NCDE population, but it may be in jeopardy because in some places it is only  $\approx 50$  km wide. Our study area in the North Fork of the Flathead River drainage (NF Flathead) encompasses a large portion of this linkage zone; consequently, its habitats and grizzly population are important for the maintenance of U.S. bears. Grizzly bears have been studied in the NF Flathead

since 1975. Several aspects of their ecology in this area have been reported, including behavioural responses to human activities (McLellan and Shackleton 1988, 1989a, 1989b), population characteristics (McLellan 1989a, 1989b, 1989c), and diet (McLellan and Hovey 1995). The present focus of the study is on continued monitoring of the population so that its status and potential influence on the NCDE and adjacent populations can be assessed.

Caughley (1977, p. 53) believed that the "demographic vigour" of a population could be measured by its survival-fecundity rate of increase ( $r_s$ ). He defined this measure as the exponential rate at which a population will change if it has a stable age distribution appropriate to its current schedules of age-specific survival and fecundity. Several researchers have estimated  $r_s$  or its antilogarithm, the finite rate of increase ( $\lambda = e^{r_s}$ ), to assess the status of grizzly populations (e.g., McLellan 1989c; Eberhardt et al. 1994; Wielgus and Bunnell 1994; Wielgus et al. 1994). Other than that reported by Eberhardt et al. (1994), however, these estimates did not include a measure of uncertainty. The growth rates were determined from point estimates of survival and reproduction rates so they too were only point estimates. Using

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data from 1979–1987, McLellan (1989a, 1989b, 1989c) estimated several population characteristics of NF Flathead grizzlies, including rates of increase, survival, and reproduction. In this paper, we had three objectives: first, to update  $\hat{\lambda}$  and provide estimates of standard error and bias using an additional 7 years of data (1979–1994) on radio-tracked female grizzlies and their offspring; second, to quantify the relative importance of the survival and reproductive variables that determined our estimate of  $\hat{\lambda}$  and its precision; and third, to identify the key demographic parameters on which continued research should focus.

## Methods

### Study area

The study was located in a  $\approx 3000\text{-km}^2$  area of the North Fork of the Flathead River drainage in British Columbia and Montana ( $49^\circ\text{N}$ ,  $114^\circ 30'\text{W}$ ). The river flows southward through the 4–10 km wide valley at elevations from 1550 to 1025 m, crossing the Canada–U.S.A. border at 1200 m. The surrounding topography consists of flat benches and rolling hills bordered by subranges of the Rocky Mountains that rise to  $>2900$  m. The climate is characterized by short cool summers and long cold winters with heavy snowfall. During the first half of this century, wildfires burned most of the study area. More recently, bark beetle (*Dendroctonus ponderosae* and *D. obsesus*) infestations killed many trees that have since been clear-cut. Lower elevations in the study area were a mosaic of young, nonmerchantable lodgepole pine (*Pinus contorta*), immature western larch (*Larix occidentalis*), and spruce (*Picea engelmannii*  $\times$  *glauca*); low-gradient riparian areas; marshes and dry meadows; and numerous clearcuts and roads. In mountainous areas, forests contained mixtures of spruce, subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), and subalpine larch (*L. lyallii*). Early-successional burns, avalanche paths, alpine meadows, selective cuts and clearcuts, roads, and rock outcrops were also common in the mountains. The species diversity of large mammals was among the highest on the continent and abundant populations of ungulates in the area were an important food source for bears during the spring and fall (McLellan and Hovey 1995). The Canadian portion of the study area is the largest unsettled drainage in southern Canada; the U.S. portion, however, contained  $\approx 100$  permanent and seasonal residents. Hunting of grizzlies was permitted in the study area, but regulations varied among years and jurisdictions. Grizzlies were also killed illegally in both countries (McLellan 1989b).

### Capture and monitoring

The methods of capture and handling of bears for our study were approved by Simon Fraser University's Animal Care Committee and met the standards of principles and guidelines set by the Canadian Council on Animal Care. Trapping of grizzly bears was conducted each year from May to July and from September to November using Aldrich foot snares or culvert traps. Most of the trapping was confined to a  $\approx 264\text{-km}^2$  area, but efforts were concentrated within a  $\approx 164\text{-km}^2$  area (McLellan 1989a). Captured bears were immobilized to allow handling and then ear-tagged and tattooed for permanent identification. To determine age, we removed a premolar from subadult and adult bears. Bears were classified as cub ( $<1$  year), yearling (1–2 years), subadult (2–5 years), or adult ( $\geq 6$  years) and then fitted with motion-sensitive radio collars designed to drop off within 3–5 years for adults and 1–2 years for younger bears.

Each year during bears' active season (May to November), the locations of all radio-collared individuals were determined from fixed-wing aircraft at  $\approx 1\text{-week}$  intervals. The study area's high

road density ( $\approx 69\text{ km} \cdot 100\text{ km}^{-2}$ ) provided widespread access that enabled us to locate most bears from the ground every 1–10 days. Information on reproduction rates, including age at first parturition, the period between litters (interbirth interval), and number of cubs per litter (litter size), was collected by tracking female bears over several years. Mortality of cubs was assumed if they were no longer observed with their mothers. This was also assumed in the case of yearlings, except where we observed loss of an entire yearling litter during the breeding season (a common time of family breakup). All recorded mortalities were classified as either known, when the carcass was examined, or suspected, when the carcass was not recovered but there was sufficient circumstantial evidence to indicate that a death had occurred (e.g., finding a collar cut off, rumours of a bear being killed after the radio signal of one that had been frequently located near areas occupied by humans stopped being received).

### Estimating the population growth rate

We estimated  $\hat{\lambda}$  for the NF Flathead grizzly bear population using Eberhardt's (1985) version of Lotka's equation (Eberhardt et al. 1994) with a modification that included yearling survival:

$$[1] \quad 0 = \lambda^a - S_a \lambda^{a-1} - S_c S_y S_s^{a-2} m \left[ 1 - \left( \frac{S_a}{\lambda} \right)^{w-a+1} \right]$$

where  $S_a$  is adult survival rate,  $S_s$  is subadult survival rate,  $S_y$  is yearling survival rate,  $S_c$  is cub survival rate,  $a$  is age at first parturition,  $m$  is reproduction rate (number of female offspring per female), and  $w$  is maximum age. All of the parameters represent values for females only. Estimates of population growth were obtained by changing  $\hat{\lambda}$  iteratively until the absolute value of expression 1 was  $\leq 0.0001$ . By using eq. 1, we assumed that the population's age distribution was stable. Our observations and trapping records did not indicate any major changes in age structure.

### Estimating annual survival rates

Eberhardt et al. (1994) estimated annual survival rates ( $\hat{S}$ ) of grizzly bears using the following equation:

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

They calculated the number of bear-years observed as the difference in time between the year a bear was first captured and the year it was last observed (L. Eberhardt, personal communication). However, during our study and the Yellowstone study as well (L. Eberhardt, personal communication), monitoring of some bears could not be maintained because their collars either dropped off or failed or the batteries expired. Because several of these bears were recaptured, the data contained records of individual bears that repeatedly entered and left the study samples.

Given these data, we believe that survival estimates based on eq. 2 will be biased and lead to inflated estimates of survival rates and population growth. The method used by Eberhardt et al. (1994) added intervening periods between recaptures even when collar loss prevented detection of mortality. Consequently, survival estimates based on their method will be biased toward survivors because only surviving bears can be recaptured (White and Garrott 1990, pp. 224–225).

The use of eq. 2 with radio-tracking data also implies that the hazard function (Lee 1980) within the annual interval is constant. It is likely, however, that survival rates for periods when bears are denned are different from those when bears are active. Moreover, grizzlies in our study area were hunted each spring. To account for potential seasonal differences in the hazard functions, we used the following Kaplan–Meier product limit estimator (Kaplan and Meier

1958) to determine annual survival rates for each age-class except cubs:

$$[3] \quad \hat{S}_i = \prod_{j=1}^{n=52} \left[ 1 - \left( \frac{D_{ij}}{R_{ij}} \right) \right]$$

where  $D_{ij}$  is number of recorded deaths and  $R_{ij}$  is number of animals at risk for age-class  $i$  during week of the year  $j$  ( $j = 1$  (January 1–7),  $j = 2$  (January 8–14), ...,  $j = 52$  (December 25–31)).

We applied eq. 3 to our data using the following procedure. For each bear, periods of radio-tracking were partitioned into week of the year. The sample at risk ( $R_{ij}$ ) was increased by 1 for every week that a bear was radio-tracked. Bears that were tracked > 1 year had 1 record added to  $R_{ij}$  for every year they were monitored during week  $j$ . If the bear died,  $D_{ij}$  was also increased by 1. Bears that lost radio collars during week  $j$  were treated as censored and  $R_{ij}$  was reduced. If they were recaptured, they were added to the sample at risk as a new record. Because bears in our study were not radio-collared simultaneously, we treated the radio-tracked sample as a staggered-entry design (Pollock et al. 1989).

Our procedure for estimating annual survival rates can be characterized as a modified Kaplan–Meier method that accounts for left (staggered entry) and right (lost collars) truncated data, with samples pooled across years.

The annual survival rate of cubs was calculated as 1 minus the division of cub deaths ( $D_c$ ) and number of cubs observed ( $R_c$ ) (i.e.,  $1 - (D_c/R_c)$ ). Use of this simple, binomial estimate could be applied only to cubs because this was the only age-class for which we always assumed that the disappearance of an individual meant that it was dead. To prevent introducing a bias, our calculations of cub survival used only cubs of mothers that were radio-tracked for the entire year. Records of cubs whose mothers were tracked < 1 year were ignored whether or not cubs died.

### Estimating reproduction rate

The annual reproduction rate ( $\hat{m}$ ) of female grizzlies can be estimated from observations of the number of cubs they produced and their interbirth intervals. We used this information with the following equation to estimate  $\hat{m}$  as the mean of each adult female's reproductive rate:

$$[4] \quad \hat{m} = \frac{\sum_{i=1}^n \frac{\sum_{j=1}^p L_{ij}}{\sum_{j=1}^p B_{ij}}}{n} 0.5$$

where  $j$  is an observation of paired litter size ( $L$ ) and interbirth interval ( $B$ ) data from the reproductive history of female  $i$ ,  $p$  is the number of observations of  $L$  and  $B$  recorded for female  $i$ , and  $n$  is the number of females. We assumed that the sex ratio of cubs was 50:50 and used data only from females that were tracked for at least one complete reproductive cycle (i.e.,  $\geq 1$  interbirth interval). For each female, data on litter size and interval were treated as paired in that the interval used reflected the period of care given the litter ( $L$ ) plus the period of recovery before the next parturition.

Of the three methods of estimating reproduction rate discussed by McLellan (1989c), we used eq. 4 because it did not give more weight to individuals that were radio-tracked longer or to those with shorter interbirth intervals. However, because eq. 4 used data only from females that were monitored for  $\geq 1$  interbirth interval, it could have been biased against including females with reproductive cycles longer than the period for which they were monitored (McLellan 1994).

### Estimating age at first parturition and longevity

In solving eq. 1 for  $\hat{\lambda}$ , we estimated the parameter,  $\hat{a}$ , as the mean of observations of age at first parturition. To account for the potential of reduced productivity in the oldest age-classes, we fixed the parameter,  $\hat{w}$ , at 20 years. This procedure is the same as that used by Eberhardt et al. (1994), and the value of 20 years is not significantly different from the mean of 21.3 years determined from a review of 22 other grizzly populations (Wielgus et al. 1994).

### Estimating correlations between parameters

Several life-history parameters of female mammals are known to covary (Harvey and Nee 1991). To guide our methods in estimating  $\hat{\lambda}$ , we investigated potential correlations between  $\hat{S}_a$ ,  $\hat{a}$ , and  $\hat{m}$  and between interbirth interval and litter size. For each pair of variables except  $\hat{S}_a$  and  $\hat{a}$ , Spearman's rank correlation coefficients ( $r_{SR}$ ) and their significance were determined. We could not evaluate the correlation between  $\hat{S}_a$  and  $\hat{a}$  because none of the females for which age at first parturition had been observed had died.

Because eq. 3 cannot be used to estimate survival rates of individuals ( $\hat{S}_{ai}$ ), a modified Trent–Rongstad (Trent and Rongstad 1974) estimator was used in the correlation analyses:

$$[5] \quad S_{ai} = e^{(-365(\text{Fate}_i/T_i))}$$

where  $\text{Fate}_i = 0$  (lived) or 1 (died) and  $T_i$  is the number of days female  $i$  was radio-tracked.

Using data representing individuals that were radio-tracked for at least one complete reproductive cycle and assuming a 50:50 sex ratio of cubs, we calculated mean annual reproduction rate for each adult female ( $\hat{m}_i$ ) as

$$[6] \quad \hat{m}_i = \frac{\sum_{j=1}^p L_{ij}}{\sum_{j=1}^p B_{ij}} 0.5$$

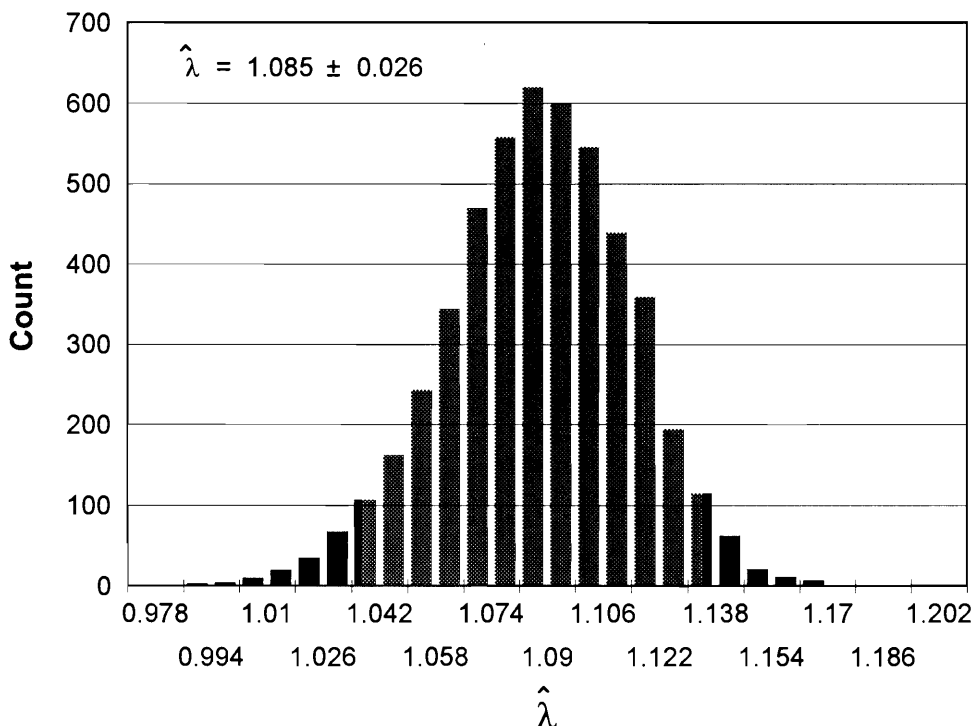
where  $j$  represents a paired litter size ( $L$ ) and interbirth interval ( $B$ ) record from the reproductive history of female  $i$ . Depending on the female, values of  $p$  ranged from 1 to 5.

### The bootstrap procedure for estimating bias and standard errors

We used bootstrapping (Efron and Gong 1983) to estimate bias and standard errors for  $\hat{\lambda}$ , survival rates, reproduction rate, and age at first parturition. Bootstrapping is a computer-intensive method where some statistic (e.g., bias or standard error) of a parameter is estimated from several (usually  $\geq 200$ ) random subsamples of the original data (Efron and Gong 1983; Manly 1991). This technique assumes that the observed data are an empirical representation of the distribution of the parameter of interest. We chose the bootstrap rather than the jackknife method (Tukey 1958) because the results of the jackknife only approximate those of the bootstrap (Efron 1979). Moreover, the bootstrap method can produce more accurate estimates of error than traditional, Fisher-based methods, and is asymptotically efficient in that it will produce accurate answers for large samples regardless of the underlying population (Efron and Tibshirani 1993, pp. 394–395).

Bootstrapping was performed using a computer program (BOOTER 1.0 © F. Hovey) and two data files. The first file contained information on each bear's age-class, the period it was radio-tracked, age at first parturition, and fate (i.e., whether it lived or died). The second contained information on each adult female's reproductive history and included data on litter sizes and interbirth intervals. Using these data files as input, the program first estimated values of each of the parameters using observed data. It then recal-

**Fig. 1.** Frequency distribution of 5000 bootstrap subsamples of  $\hat{\lambda}$  (finite rate of population increase) for the NF Flathead grizzly bear population ( $\hat{\lambda} = 1.085 \pm 0.026$ ). Darker bars show  $\approx 95\%$  confidence limits of  $1.032 \leq \hat{\lambda} \leq 1.136$ . Data were collected from 1979 to 1994.



culated each parameter estimate from uniform random subsamples of the data that were taken with replacement. The number of records included in each sample equalled the number of observations. This process was repeated 5000 times and an output file containing estimates of each parameter was produced. Standard errors of parameter estimates were calculated from the output file as the standard deviation of bootstrap replicates and  $\approx 95\%$  confidence limits were determined from the 2.5 and 97.5 percentiles (Efron and Tibshirani 1993). We determined statistical bias for each parameter as the difference between its estimate and the mean of the bootstrap replicates (Efron and Tibshirani 1993).

Correlation analysis revealed that litter size and interbirth interval were significantly related ( $r_{SR} = 0.592$ ,  $n = 15$ ,  $P \leq 0.001$ ). Females with large litters tended to have either longer periods of parental care or longer periods of recovery between births or both. To account for this correlation, we estimated  $\hat{m}$  by using only paired observations of litter size and interbirth interval data. Because several females had  $> 1$  paired records, **BOOTER** randomly selected only 1 record from a female's reproductive history. This method allowed us to include the variation in the components of reproduction rate in our estimate of the standard error of  $\hat{m}$ . During each bootstrap iteration, the total number of records sampled equalled the number of females observed.

In estimating survival rates of yearlings, subadults, and adults, **BOOTER** randomly selected observations of periods of radio-tracking for individuals within each age-class. Records of bears with  $> 1$  radio-tracking periods were treated as independent so that the total number of records sampled equalled the number of radio-tracking periods observed.

#### Estimating the relative contribution of each parameter to $\hat{\lambda}$ uncertainty

The complexity of eq. 1 indicates that the value and uncertainty of its 7 parameters may affect the value and uncertainty of  $\hat{\lambda}$  differently. Knowledge of each parameter's influence on  $\hat{\lambda}$  may help

guide further research on population processes of bears by identifying the key parameters that contributed most to  $\hat{\lambda}$  and its precision. To obtain this information, we used the delta method. This method estimates the variance,  $V$ , of a function,  $g(x)$ , as

$$[7] \quad V(g(x)) = \sum_{i=1}^n V(x_i) \left( \frac{\partial g}{\partial x_i} \right)^2 + 2 \sum_{i=1}^{n-1} \sum_{j>i}^n \text{cov}(x_i, x_j) \left( \frac{\partial g}{\partial x_i} \right) \left( \frac{\partial g}{\partial x_j} \right)$$

where  $n$  represents the number of random variables  $x$  ( $x_i, x_{i+1}, \dots, x_n$ ) and  $\text{cov}[x_i, x_j]$  the covariance of  $x_i$  and  $x_j$  (Seber 1982). We calculated the variance,  $V(\hat{x}_i)$ , of each parameter estimate,  $\hat{x}_i$ , in eq. 1 from the bootstrap output file described previously. Following Eberhardt et al. (1994), partial derivatives of  $\hat{\lambda}$  with respect to each parameter ( $\partial \hat{\lambda} / \partial \hat{x}_i$ ) were determined and then, using eq. 7, we estimated the variance of  $\hat{\lambda}$ ,  $V(\hat{\lambda})$ , and calculated the relative contribution,  $C_i$ , of each parameter estimate to this variance as

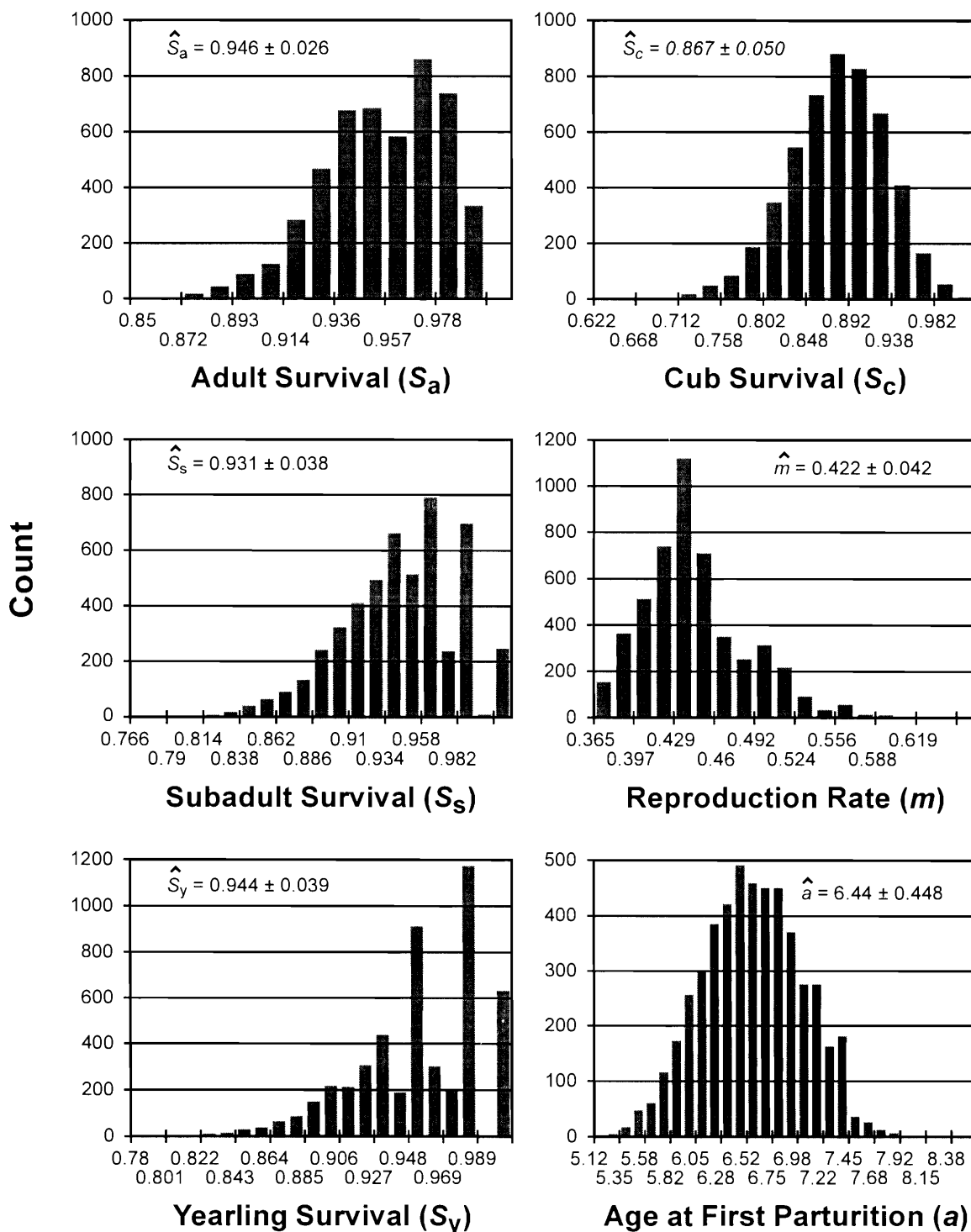
$$[8] \quad C_i = \left[ \frac{V(\hat{x}_i) \left( \frac{\partial \hat{\lambda}}{\partial \hat{x}_i} \right)^2}{V(\hat{\lambda})} \right] 100$$

Because we did not find significant correlations between parameter estimates ( $\hat{S}_a$  and  $\hat{m}$ :  $r_{RS} = 0.546$ ,  $n = 8$ ,  $P \leq 0.161$ ;  $\hat{m}$  and  $\hat{a}$ :  $r_{RS} = 0.304$ ,  $n = 5$ ,  $P \leq 0.619$ ), that portion of eq. 7 treating covariance was ignored (i.e., set to zero).

#### Results

During our study, 23 adult female, 24 subadult female, and 14 yearling grizzly bears were captured and monitored for a total of 118.1 radio-tracking-years. Thirty-five yearlings and 44 cubs were also monitored by tracking their mothers. Other than the mature offspring of radio-tracked females, no

**Fig. 2.** Frequency distributions of 5000 bootstrap subsamples of demographic variables used to estimate uncertainty in  $\hat{\lambda}$  (finite rate of population increase).



unknown adult female grizzlies were captured within our trapping area after 1982.

The middle  $\approx 95\%$  of  $\hat{\lambda}$  values produced by the bootstrapping procedure ranged from 1.032 to 1.136 (Fig. 1), indicating that from 1979 to 1994, the grizzly population was increasing, with a  $\hat{\lambda}$  of  $1.085 \pm 0.026$ . Only three adult females, three subadult females, and one yearling died in 69.8, 43.3, and 24.7 radio-tracking-years, respectively; con-

sequently, annual survival rates for these age-classes were high ( $\geq 0.931$ ; Table 1). Estimated annual survival rates were  $0.946 \pm 0.026$  for adult females,  $0.931 \pm 0.038$  for subadult females,  $0.944 \pm 0.039$  for yearlings, and  $0.867 \pm 0.050$  for cubs. Annual reproduction rate and age at first parturition were  $0.422 \pm 0.042$  female cubs per female and  $6.44 \pm 0.45$  years, respectively.

Except for cub survival, distributions of bootstrap repli-

**Table 1.** Estimates of demographic variables used to determine uncertainty in the finite rate of increase ( $\hat{\lambda}$ ) of grizzly bears from the NF Flathead River drainage in British Columbia and Montana (data were collected from 1979 to 1994).

Parameter <sup>a</sup>	Sample size <sup>b</sup>	Estimated value	Estimated bias <sup>c</sup>	Estimated standard error <sup>d</sup>	Bootstrap variance	$\frac{\partial \hat{\lambda}}{\partial \hat{x}_i}$ <sup>e</sup>	Percentage of $\hat{\lambda}$ variance explained <sup>f</sup>
$S_a^g$	23, 29	0.946	0.0001	0.026	0.000672	0.4725	21.91
$S_s$	24, 33	0.931	0.0007	0.038	0.001456	0.4727	47.47
$S_y$	49, 50	0.944	-0.0007	0.039	0.001506	0.1049	2.42
$S_c$	44	0.867	-0.0007	0.050	0.002552	0.1142	4.86
$m$	8, 5 <sup>h</sup>	0.422	0.0090	0.042	0.001809	0.2347	14.55
$a$	9	6.444	0.0032	0.448	0.200772	-0.0173	8.79
$w$	Fixed	20.0				-0.0021	
$\lambda$	5000	1.085	0.0021	0.026	0.000691 0.000685 <sup>i</sup>		100.00

<sup>a</sup>Parameters used in solving Eberhardt's (1985) version of Lotka's equation, with our modification, which includes yearling survival:

$$0 = \lambda^a - S_a \lambda^{a-1} - S_c S_y S_s^{a-2} m \left[ 1 - \left( \frac{S_a}{\lambda} \right)^{w-a+1} \right]$$

where  $S_a$  is adult female survivorship,  $S_s$  is subadult female survivorship,  $S_y$  is yearling survivorship,  $S_c$  is cub survivorship,  $m$  is the reproduction rate (number of female cubs per female),  $a$  is the age at first parturition,  $w$  is the maximum age of an adult female, and  $\lambda$  is the finite rate of population increase.

<sup>b</sup>The first number indicates the number of grizzlies studied and the second indicates the number of periods during which grizzlies were radio-tracked. In estimating survival rates, we used the second number as the number of observations.

<sup>c</sup>Estimated bias in the parameter estimate calculated as the mean of the bootstrap replicates minus the parameter estimate.

<sup>d</sup>Estimated standard error of the parameter estimate calculated as the standard deviation of the bootstrap replicates.

<sup>e</sup>Partial derivation of  $\hat{\lambda}$  with respect to parameter estimate  $\hat{x}_i$ .

<sup>f</sup>Percentage of variance ( $C_i$ ) in  $\hat{\lambda}$  explained by parameter estimate  $\hat{x}_i$  and its variance  $V(\hat{x}_i)$ :

$$C_i = \left[ \frac{V(\hat{x}_i) \left( \frac{\partial \hat{\lambda}}{\partial \hat{x}_i} \right)^2}{V(\hat{\lambda})} \right] 100$$

<sup>g</sup>Estimated annual survival rate:

$$\hat{S}_i = \prod_{j=1}^{n=52} \left[ 1 - \left( \frac{D_{ij}}{R_{ij}} \right) \right]$$

where  $D_{ij}$  is the number of recorded deaths and  $R_{ij}$  is the number at risk observed by radiotelemetry for age-class  $i$  during week of the year  $j$ . The annual cub survival rate was estimated as  $1 - (D_i/R_i)$ , where  $R$  is the number of cubs observed.

<sup>h</sup>Information from eight females provided paired interbirth interval and litter size data with a maximum of 5 records for one female. During each bootstrap iteration,  $\hat{m}$  was calculated as

$$\hat{m} = \frac{\sum_{i=1}^8 \left( \frac{L}{B} \right)_{ij}}{8} 0.5$$

where  $L$  is the litter size and  $B$  is the interbirth interval for a randomly selected record  $j$  obtained from the reproductive history of a randomly selected female,  $i$ .

<sup>i</sup>Estimated variance in  $\hat{\lambda}$  calculated by the delta method.

cates for survival rates were slightly skewed to the left and truncated at values near 1 (Fig. 2). This type of distribution was expected given the few mortalities we observed. The bootstrap replicates for cub survival rate, age at first parturition, and reproduction rate appeared to be normally distributed (Fig. 2).

Estimated statistical biases in our parameter estimates were small (Table 1). In each case, the ratio of estimated bias to standard error was  $<0.25$ ; consequently, bias corrections to parameter estimates and their confidence limits can be ignored (Efron and Tibshirani 1993). The potential bias associated with the use of eq. 4 to estimate  $\hat{m}$  was not a seri-

ous problem with our data. Of 14 females that provided observations of litter size, only 4 did not provide an observation of interbirth interval. This result was caused by loss of radio collars rather than by long interbirth intervals. The four bears were monitored for an average of only  $1.46 \pm 0.22$  years, a period significantly less than the mean interbirth interval of  $2.8 \pm 0.14$  years.

Partial derivatives ranged from 0.4727 to  $-0.0021$ , subadult survival having the largest value and maximum age the smallest (Table 1). The variation in  $\hat{\lambda}$  obtained from the bootstrap replicates was almost the same as that obtained from the delta method (0.000691 vs. 0.000685). Using the latter estimate, most of the uncertainty was attributable to sampling variation in survival rates (76.7%), subadult and adult survival accounting for 69.4% of the total. Sampling variation in reproduction rate and age at first parturition, on the other hand, contributed only 14.6 and 8.8% to the total, respectively (Table 1).

## Discussion

Our analyses showed that from 1979 to 1994, the NF Flathead grizzly population was increasing. The  $\hat{\lambda}$  value of 1.085 is nearly identical with the value of 1.084 that McLellan (1989c) determined from data collected between 1979 and 1987. The uncertainty in  $\hat{\lambda}$  was largely due to sampling variation in survival rates. Age at first parturition and reproduction rate contributed little to uncertainty in  $\hat{\lambda}$ . The small contribution (only 14.6%) and partial derivative of the reproduction rate indicates that the choice of methods of calculating this parameter, as discussed by McLellan (1989c), is not critical to improving estimates of precision for  $\hat{\lambda}$ . Given the relatively small partial derivative of maximum age, altering this parameter would have had little effect on our estimate of population growth rate.

Published rate-of-increase estimates for grizzly bear populations are rare. Of those that have been determined, our estimate is the highest. The  $\lambda$  value for Yellowstone grizzlies, for example, was estimated at 1.046, with  $\approx 95\%$  confidence limits between 1.00 and 1.09 (Eberhardt et al. 1994). Comparing this rate with the one we estimated for NF Flathead grizzlies, however, is difficult because Eberhardt et al. (1994) calculated survival rates using eq. 2. As a result, we suspect that their determination of  $\hat{\lambda}$  is inflated. Stable population growth was estimated for grizzlies in both the Kananaskis area of southwestern Alberta ( $\hat{\lambda} = 0.99-1.01$ ; Wielgus and Bunnell 1994) and the Selkirk Mountains of British Columbia and Idaho ( $\hat{\lambda} = 1.00$ ; Wielgus et al. 1994). These rates, however, were point estimates based on small sample sizes; it is likely that 95% confidence limits about these estimates would be relatively broad and encompass  $\hat{\lambda}$  values both less than and greater than 1.

Our  $\hat{\lambda}$  estimate of 1.085 suggests that there should have been 3.4 times as many grizzly bears in the study area in 1994 as there were in 1979. Population estimates between 1979 and 1986 indicated that grizzlies were increasing at approximately the calculated rate even though their density was relatively high (McLellan 1989a). Changes in population size between 1987 and 1994 have not been determined, but it appears that net emigration of both male and female bears may be reducing the rate of increase (F.W. Hovey and B.N. McLellan, unpublished data).

Despite 15 years of study and monitoring of 117 different grizzly bears for  $>137$  radio-tracking-years,  $\approx 95\%$  confidence limits on  $\hat{\lambda}$  are still wide ( $\pm 4.8\%$ ). This uncertainty further emphasizes the difficulty of estimating grizzly bear population trends in forested habitats where standard wildlife census methods cannot be applied. To reduce uncertainty in the estimate of growth rate, further research on the NF Flathead grizzlies should focus on improving estimates of survivorship of adult and subadult females. This may be achieved by increasing sample sizes and monitoring these age-classes. Because we assumed that the population was at equilibrium and that demographic parameters were not changing in time (temporal variation) or space (spatial variation), the estimates of error we derived considered only sampling variation (i.e., error in estimation of unknown parameters); process variation (spatial or temporal) was not treated. Consequently, our error estimates contain both types of variation. Although sampling variation can be reduced by using larger samples, better estimates of process variation in the population dynamics of grizzlies in our study area can be achieved only by extending the study period.

Our research was focused in a relatively small area. This intensity enabled us to monitor most of the female bears in the trapping area; we did not capture any unknown adult females after 1982. Cochran (1977) showed that as the size of a sample from a finite population approaches the size of the population from which it was drawn, the standard error of any variable of interest decreases. Applying such finite population corrections to our standard errors would have reduced the estimates substantially. The problem with performing such adjustments, however, is that the value they provide is based on a population that occurred, in part, by chance. Because bear populations are subject to stochastic events,  $\hat{\lambda}$  values determined from point estimates or finite population corrections may not reflect ecological conditions or future trends. Therefore, estimates regarding population processes should treat samples as if they were drawn from an infinite population, regardless of the size of the population sample. When using radio-tracking data, the bootstrapping procedure introduced by Eberhardt et al. (1994) provides improved estimates of population trend in bears because it accounts for sampling variation in demographic parameters and provides an estimate of error.

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