

**ESTIMATING THE NUMBER OF FEMALES WITH CUBS-OF-THE-YEAR IN THE YELLOWSTONE GRIZZLY BEAR POPULATION:  
Are maximum-likelihood estimates that assume equal sightability conservative?**

**Final report submitted to the U. S. Fish and Wildlife Service. 1999.**

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**Abstract:** Annual mortality limits for the Yellowstone grizzly bear population are calculated as a function of the number of females with cubs-of-the-year (FCOY), which has previously been estimated as the number of such animals actually observed ( $\hat{N}_0$ ). Lewontin and Prout's (1956) maximum likelihood estimator ( $\hat{N}_{MLE2}$ ) has been proposed by Boyce *et al.* (1998) as a more realistic alternative to  $\hat{N}_0$ .  $\hat{N}_{MLE2}$  assumes all animals are equally sightable, and is positively biased at small sample sizes and negatively biased as heterogeneity of individual sighting probabilities increases. Examining counts of FCOY for 1986-1998, we compared a suite of estimators to determine whether  $\hat{N}_{MLE2}$  is likely to yield conservative estimates of the number of

FCOY in the Yellowstone population.

Comparisons of uncorrected and bias-corrected versions of a closely related maximum likelihood estimator showed no evidence of small sample bias when applied to these data. Ratios of sample size to estimated population size similarly indicated little potential for small sample bias. Comparisons with six nonparametric estimators showed nonparametric estimates were consistently larger than  $\hat{N}_{MLE2}$ , whereas Monte Carlo results showed most estimates should have been comparable if samples had been drawn from a population that was, in fact, comprised of  $\hat{N}_{MLE2}$  individuals with equal sighting probabilities. Observed “best”-order jackknife, lower bound, and sample coverage estimators exceeded expected values under the null (homogeneous) model for 3 ( $P = 0.10$ ), 4 ( $P = 0.03$ ), and 6 ( $P < 0.001$ ) of the 13 years examined, respectively. These patterns are consistent with the hypothesis of heterogeneous sighting probabilities. We concluded that  $\hat{N}_{MLE2}$  was negatively biased by variations in individual sighting probabilities and is, therefore, likely to yield conservative estimates of the number of FCOY in the Yellowstone grizzly bear population for 1986-1998. Two caveats are discussed: (1)  $\hat{N}_{MLE2}$  should not be used to assess population trend, due to likely changes in the degree of variation among individual sighting probabilities over time, and (2) use of a biased estimator to ensure conservatism is fraught with non-trivial practical and philosophical issues. Overall, we believe an unbiased estimator with valid confidence limits should be preferred over  $\hat{N}_{MLE2}$ , and recommend that such an estimator be sought.

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Criteria for recovering the grizzly bear (*Ursus arctos*) in the lower United States include annual limits on mortalities (U.S. Fish and Wildlife Service 1993). These limits are calculated as

a function of the number of females with cubs-of-the-year (FCOY) present in the population over a three-year period. Previously, the number of FCOY has been estimated as the number of unique FCOY actually observed during a given year. To the extent that criteria for distinguishing different FCOY are conservative (*cf* Knight *et al.* 1995), and because it is highly unlikely that all such animals will be seen in a given year, this approach clearly underestimates the true number of FCOY in the population. Indeed, using this approach, estimates of the number of FCOY for a given year may be determined primarily by sample size, suggesting that annual mortality limits may be driven largely by factors such as agency budgets or annual differences in habitat-use patterns, rather than changes in the underlying population. More scientific estimates are clearly desirable.

Many statistical methods are potentially applicable to this problem and have been compared elsewhere (e.g., Otis *et al.* 1978, Pollock *et al.* 1990, Wilson and Collins 1992, Lee and Chao 1994). Studies of these methods typically emphasize unbiased estimation of population size. In this case, however, it is important not to overestimate the number of FCOY, as this could lead to setting unsustainably high mortality limits. Two approaches might be used to achieve conservative estimates of the number of FCOY: (1) calculate some lower confidence bound to an unbiased estimate, or (2) use an estimator that is negatively biased. Our charge was to determine whether the maximum likelihood estimator (MLE) proposed by Boyce *et al.* (1998) is negatively biased and, therefore, likely to yield conservative estimates of the number of FCOY in the Yellowstone grizzly bear population. Three general concerns should be noted at the outset. First, the approach of using a negatively biased statistical method to ensure conservative estimates is encumbered with non-trivial philosophical and practical baggage. We address this

more fully in our discussion. Second, although we compare population estimates obtained using different statistical methods, our study was designed only to determine whether the estimator in question is likely to be conservative. No “best” estimator should be inferred from our results. Finally, we assume that the criteria for distinguishing among different FCOY are either accurate or conservative, so that the number of animals identified is less than or equal to the number truly observed. Although we believe this assumption is reasonable, it has been challenged by Mattson (1997) and merits additional scrutiny that is beyond the scope of this study.

Boyce *et al.* (1998) suggested that a MLE, based on the assumption that all family groups have an equal probability of being sighted, may yield useful estimates of the number of FCOY in a given year. The sampling model assumed by this estimator is equivalent to model  $M_0$  of Otis *et al.* (1978). As shown below, the MLE of Boyce *et al.* is mathematically identical to Lewontin and Prout’s (1956) MLE, and functionally equivalent to Darroch’s (1958) MLE. Consequently, many of the properties of this estimator are well known. For example, this method tends to underestimate population size when sighting probabilities vary among individuals (Lewontin and Prout 1956), although it is robust to modest deviations from this assumption (Chao and Lee 1992). In the Yellowstone area, it is improbable that all family groups are equally sightable. For example, about 60% of sightings of FCOY are reported by ground-based observers (whose observations should favor bears that inhabit areas near to or visible from roads or trails), while both ground and aerial observations are biased toward animals in open habitats. It is, therefore, reasonable to suggest that this MLE may yield improved, yet conservative, estimates of the number of FCOY in the Yellowstone population. However, two important caveats exist concerning this estimator: (1) it tends to overestimate population size

when sample size is small (Darroch and Ratcliff 1980), and (2) it becomes conservative only as sighting probabilities become more heterogeneous (Lewontin and Prout 1956, Otis *et al.* 1978). It is, therefore, prudent to ask whether sample sizes are large enough, and sighting probabilities heterogeneous enough, so that the proposed estimator yields conservative estimates in this instance.

To gauge the effects of sample size and heterogeneity of sighting probabilities on estimates of the number of FCOY in the Yellowstone grizzly bear population, we made two qualitative comparisons. These were limited to the period 1986-1998 due to concerns that earlier data may not be comparable. First, we compared uncorrected and bias-corrected versions of Darroch's (1958) MLE. If estimates for the 1986-1998 period were inflated due to small sample sizes, then uncorrected estimates should be substantially greater than bias-corrected estimates (Darroch and Ratcliff 1980). Second, we compared estimates obtained using the MLE under model  $M_0$  with those obtained using nonparametric methods. We show that, if sighting probabilities were homogeneous, the MLE and nonparametric estimates should be generally comparable, whereas the nonparametric estimates should tend to be larger if sighting probabilities were heterogeneous. A confounding factor in the second comparison is that many nonparametric estimates may be positively biased at moderate sample sizes; thus, differences of the kind predicted under heterogeneous sighting probabilities might be attributable, instead, to sample-size effects. We distinguished among these possibilities using Monte Carlo methods to evaluate whether observed differences might reasonably be expected, given actual sample sizes and the population structures implied by the MLE estimates under model  $M_0$ .

## **METHODS**

## General Problem and Notation

The sampling model we used approximates the true sampling scheme, in which reports of FCOY come from observers employing various methods (ground-based observation, trapping, systematic fixed-wing observations, or fixed-wing observations made incidental to other work). Because the sampling period associated with each of these methods varies considerably (or is undefined), we used the sighting of an individual FCOY as the sample unit. The problem of estimating population size from repeated sightings of unique individuals may then be generalized as a special case of the more commonly used model in which multiple individuals may be sighted during a given sampling period (e.g., Otis *et al.* 1978).

Suppose that after randomly drawing  $n$  individuals from a population of size  $N$  (where  $N$  is unknown), we observe  $s_n$  unique individuals. The probability of sighting and recording the  $i$ th individual during any particular sampling event is  $\pi_i$  and probabilities for all  $N$  individuals are given by  $\boldsymbol{\pi} = (\pi_1, \pi_2, \dots, \pi_N)$ ,  $\sum_{i=1}^N \pi_i = 1$ . In our sample, individuals were observed with frequency  $\mathbf{n} = (n_1, n_2, \dots, n_N)$  (but we do not know the identity of the  $N - s_n$  animals for which  $n_i = 0$ ). The number of different individuals observed exactly  $j$  times was  $f_j$  and  $\mathbf{f} = (f_1, f_2, \dots, f_n)$ . Also, we may record the index variable  $I$ , such that  $I_{i,k} = 1$  if the  $i$ th individual was first observed in the  $k$ th sample ( $1 \# k \# n$ ) and  $I_{i,k} = 0$ , otherwise; except that  $I_{i,n+1} = 1$  if the  $i$ th individual was not observed in any of the  $n$  samples (but, again, we do not know the identity of the  $N - s_n$  animals for which  $I_{i,n+1} = 1$ ). The number of previously unobserved individuals detected during the  $k$ th sampling event is given by  $x_k = \sum_{i=1}^N I_{ik}$ , and the complete sequence of numbers of new individuals recorded during the  $n$  sampling events is given by  $\mathbf{x} = (x_1, x_2, \dots, x_n)$ . Because a

sample consists of a single individual, each  $x_k$  value must be either zero or one. Important relationships among variables include  $n = \sum_{i=1}^S n_i = \sum_{j=1}^n j f_j$ , and  $s_n = \sum_{j=1}^n f_j = \sum_{k=1}^N x_k$ . The problem is to estimate  $N$  using only the information in  $\mathbf{f}$  or  $\mathbf{I}$ , where  $\mathbf{I}$  is the matrix of  $I_{i,k}$  values.

In this idealized sampling model, all information about population size is obtained from the  $n$  randomly selected individuals. For the Yellowstone grizzly bear population, observations of radio-marked FCOY made during radio-relocation flights provide additional information from non-randomly selected individuals. In particular, observations of otherwise unobserved FCOY may be added to  $s_n$  to improve the estimate of minimum population size. We refer to this estimate as  $\hat{N}_0$ , and note that  $\hat{N}_0 \geq s_n$ .  $\hat{N}_0$  provides a natural lower bound for estimating  $N$  and is the estimator that has been used previously to set annual mortality limits. The goal is to improve upon  $\hat{N}_0$  while minimizing the risk of overestimating  $N$ . To state our objective more formally, we asked whether the method proposed by Boyce *et al.* (1998) is likely to yield an estimate of the number of FCOY ( $\hat{N}$ ), such that  $\hat{N}_0 < E(\hat{N}) \leq N$ , where  $E(\hat{N})$  is the statistical expectation for  $\hat{N}$ .

### The Estimators

Our evaluation used comparisons among eight estimators of two basic types: (1) MLE's of  $N$  that assume homogeneous sighting probabilities (i.e.,  $\pi_1 = \pi_2 = \dots = \pi_N = 1/N$ ), and (2) nonparametric estimators of  $N$ , which make no assumption about the distribution of  $\pi_i$  values. Within the latter group we included methods for estimating a *lower bound* for  $N$ . Such estimators have received relatively little attention, but should provide inherently conservative estimates of  $N$  in situations where one wishes to minimize the possibility of overestimating  $N$ .

Details of the estimators follow.

*Parametric estimators.*—As the most mathematically tractable case of the general problem posed above, estimation of  $N$  under the assumption of homogeneous  $\pi_i$  values has received considerable attention, yielding a host of similar estimators. Lewontin and Prout (1956), Darroch (1958), and McNeil (1973) found that, under the hypothesis of homogeneous sighting probabilities, the statistical expectation for  $s_n$  is approximately

$$E(s_n) \approx N[1 - e^{(-n/N)}]. \quad (1)$$

Darroch (1958), Arnold and Beaver (1988), and Boyce *et al.* (1998) derived the exact form,

$$E(s_n) = N \left[ 1 - \left( \frac{N-1}{N} \right)^n \right]. \quad (2)$$

Using  $s_n$  as an estimate of  $E(s_n)$ , solutions to Eqs. (1) or (2) have been taken as the MLE of  $N$  by various authors. We refer to this estimate as  $\hat{N}_{MLE1}$  and calculated it as the solution to Eq. (2).

Darroch and Ratcliff (1980) calculated the bias of  $\hat{N}_{MLE1}$  as

$$E(\hat{N}_{MLE1} - N) = \frac{1}{2} \lambda^2 (e^\lambda - 1 - \lambda)^{-2}, \quad (3)$$

where  $\lambda = n/N$ . They recommended using Eq. (3) to iteratively correct for bias until  $\hat{N}_{MLE1}$  converges to within a specified tolerance. We used tolerance = 0.001 and reference the resulting bias-corrected estimate as  $\hat{N}_{MLE(B)}$ .

Lewontin and Prout (1956) derived the MLE of  $N$  as the solution to



This same result was obtained independently by McNeil (1973). Boyce *et al.* (1998) obtained the MLE of  $N$  as the solution to

$$\frac{n}{\hat{N}} = \sum_{i=\hat{N}-s+1}^{\hat{N}} \frac{1}{i}. \quad (4)$$

where  $s_{i-1}$  is the number of unique animals observed after examining  $i - 1$  randomly selected individuals. Because each  $x_i$  must equal either one (the sighting of a new animal) or zero (the animal was sighted previously), it may be shown that Eqs. (4) and (5) are equivalent by

$$\frac{n}{\hat{N}} = \sum_{i=1}^n \frac{x_i}{\hat{N} - s_{i-1}}, \quad (5)$$

observing that

$$\sum_{i=1}^n \frac{x_i}{\hat{N} - s_{i-1}} = \sum_{i=0}^{s-1} \frac{1}{\hat{N} - i} = \sum_{i=\hat{N}-s+1}^{\hat{N}} \frac{1}{i}.$$

This reaffirms the conclusion (Lewinton and Prout 1956, Otis *et al.* 1978) that, given homogeneous  $\pi_i$  values, all information relating to  $N$  in the sample is contained in  $s_n$ . We refer to solutions to Eqs. (4) or (5) as  $\hat{N}_{\text{MLE2}}$ . Boyce *et al.* devised a bias correction for  $\hat{N}_{\text{MLE2}}$ , but we did not consider it in this analysis because it is graphic-based.

*Nonparametric estimators.*—Among nonparametric methods, we first examined Chao's (1984) estimate of a *lower bound* for  $N$ , given by

$$\hat{N}_{\text{Chao1}} = s_n + \frac{f_1^2}{2f_2}. \quad (6)$$

Under Eq. (6),  $E(\hat{N}) \leq N$  (Chao 1984), which does not ensure  $\hat{N} \leq N$  in all cases, but should provide an inherently conservative approach to estimating  $N$ . We also considered a similar bias-corrected form developed by Chao (1989). Where the sample unit is the individual animal, Chao's (1989) estimator is given by (Wilson and Collins 1992)

$$\hat{N}_{\text{Chao2}} = s_n + \frac{f_1^2 - f_1}{2(f_2 + 1)}.$$

Burnham and Overton (1978, 1979) devised a jackknife estimator ( $\hat{N}_{Jk}$ ), of the general form

$$\hat{N}_{Jk} = s_n + \sum_{i=1}^k \alpha_{ik} f_i, \quad (7)$$

where  $\alpha_{ik}$  is a coefficient in terms of  $n$ , and  $\alpha_{ik} = 0$  when  $i > k$ . Theoretically, estimates of order  $k = 1$  to  $n$  may be calculated from Eq. (7), but variance increases rapidly with  $k$  so that, in practice,  $k$  is small (Burnham and Overton 1979). We considered the first-order jackknife estimator ( $\hat{N}_{J1}$ ), as well as a "best"  $k$ th-order jackknife estimator. Burnham and Overton (1979) suggested two methods for choosing a "best" value for  $k$  for a particular study. Because Keating and Quinn (1998) found little difference between them, we considered only their first method, which evaluates estimates of order  $k = 1$  to 5 (Table 1), as follows. Beginning with  $k = 1$  and proceeding to subsequently higher values of  $k$ , test the null hypothesis that  $E(\hat{N}_{Jk+1} - \hat{N}_{Jk}) = 0$ , versus the alternative hypothesis that  $E(\hat{N}_{Jk+1} - \hat{N}_{Jk}) \neq 0$ . When no significant difference is observed, further testing ends and  $\hat{N}_{Jk}$  is taken as the "best" jackknife estimate. We reference the resulting  $k$ th-order estimate as  $\hat{N}_{Jk1}$ . The test is based on the statistic

$$T_k = \frac{\hat{N}_{Jk+1} - \hat{N}_{Jk}}{[\hat{\text{var}}(\hat{N}_{Jk+1} - \hat{N}_{Jk} | s_n)]^{1/2}},$$

$$\hat{N}_{SCi} = \frac{s_n}{\hat{C}_i} + \frac{n(1 - \hat{C}_i)}{\hat{C}_i} \hat{\gamma}^2,$$

$$\hat{\text{var}}(\hat{N}_{Jk+1} - \hat{N}_{Jk} | s_n) = \frac{s_n}{s_{n-1}} \left[ \sum_{i=1}^n (b_i)^2 f_i - \frac{(\hat{N}_{Jk+1} - \hat{N}_{Jk})^2}{s_n} \right],$$

where

and  $b_i = \alpha_{ik+1} - \alpha_{ik}$ .  $T_k$  is evaluated using  $P$  values determined from a table of the standard normal distribution.

Chao and Lee (1992) proposed an estimator based on sample coverage ( $C$ ), where  $C$  is

$$\hat{C}_1 = 1 - \frac{f_1}{n},$$

the sum of the  $\pi_i$  values for the  $s_n$  individuals actually observed in the sample. Most recently (Lee and Chao 1994), they estimated  $C$  as either

$$\hat{C}_2 = 1 - \frac{f_1 - 2f_2}{n(n-1)}.$$

or

They then estimated  $N$  as

where  $i = 1$  or  $2$ , and  $\gamma$  is a measure of the coefficient of variation of the  $\pi_i$ 's, with  $\hat{\gamma}^2$

calculated as

$$\hat{\gamma}^2 = \max \left\{ \hat{N} \sum_{i=1}^n \frac{i(i-1)f_i}{n(n-1)} - 1, 0 \right\}.$$

Calculation of  $\hat{\gamma}^2$  requires an initial estimate of  $N$ . Following Chao and Lee (1992), we used Darroch and Ratcliff's (1980) estimator,  $\hat{N}_{DR} = s_n / \hat{C}_i$ , which assumes homogenous  $\pi_i$  values. We did not consider the bias correction proposed by Chao *et al.* (1993; see also Colwell 1997) because sightings were not unduly dominated by particular family groups.

### Data Collection and Analysis

Sightings of grizzly bear family groups in the Yellowstone ecosystem were examined for 1986-1998. For each year, unique family groups were distinguished per Knight *et al.* (1995). Observations of radio-collared animals made during radio-location flights were used to calculate the minimum number of FCOY known to exist in the population each year ( $\hat{N}_0$ ), but were excluded from statistical estimates of  $N$  because such sightings were non-random. Sightings were summarized by year as the number of unique family groups seen once, twice, etc. Total numbers of FCOY for each year were then estimated using each of the methods described above.

$$\hat{N}_{T,t} = \frac{\sum_{i=t-2}^t (\hat{N}_i - m_i)}{0.274}, \quad (8)$$

Estimates of total population size in year  $t$  ( $N_{T,t}$ ) were calculated as

where  $\hat{N}_i$  is the estimated number of FCOY in year  $i$ , and  $m_i$  is the number of known human-

caused mortalities of adult females in year  $i$ . Implied limits for known human-caused mortalities for year  $t$  were then calculated as  $0.04\hat{N}_{T,t}$ , and limits for known human-caused mortalities of females were calculated as  $0.012\hat{N}_{T,t}$  ( $= 0.3 * 0.04\hat{N}_{T,t}$ ).

To evaluate whether  $\hat{N}_{MLE2}$  was positively biased due to small sample sizes, we examined differences between uncorrected and bias-corrected forms of  $\hat{N}_{MLE1}$ , which is derived from the same underlying model and yields similar results. If biologically significant small-sample biases existed, then substantial differences between the uncorrected and bias-corrected estimates should be evident. As a further check, we examined the ratio  $\lambda = n/N$ . Darroch and Ratcliff (1980) found that the expected positive bias of  $\hat{N}_{MLE1}$  becomes quite small as  $\lambda$  approaches or exceeds one; thus, a  $\lambda$ -value much less than 1 may indicate a potentially significant positive bias in  $\hat{N}_{MLE1}$ . We estimated  $\lambda$  as  $\hat{\lambda} = n/\hat{N}_{MLE1}$ , which should foster conservative conclusions about the adequacy of sample sizes, since  $\hat{\lambda}$  will underestimate  $\lambda$  if  $\hat{N}_{MLE1} > N$ .

If sighting probabilities ( $\pi_i$  values) are heterogeneous rather than homogeneous,  $\hat{N}_{MLE2}$  will be negatively biased (Lewontin and Prout 1956, Otis *et al.* 1978) and, thus, yield conservative estimates of the number of FCOY. We sought evidence of heterogeneity by comparing  $\hat{N}_{MLE2}$  with nonparametric estimates of  $N$ . The premise of this comparison is that the different methods should yield similar estimates of  $N$  if sighting probabilities were, in fact, homogeneous, whereas nonparametric estimates should tend to be larger if sighting probabilities were significantly heterogeneous. We evaluated this premise using Monte Carlo methods, as

described below.

A confounding factor in this comparison is that nonparametric estimates may be positively biased at moderate sample sizes; thus, they may be larger than  $\hat{N}_{MLE2}$  due to sample-size effects rather than heterogeneous sighting probabilities. To distinguish effects of heterogeneity from those of sample size, we used Monte Carlo methods to evaluate whether observed nonparametric estimates exceeded expected values under the null model implied by  $\hat{N}_{MLE2}$  and the observed sample size,  $n$ , for that year. For each year, we drew 1000 Monte Carlo samples, each of size  $n$ , from a homogenous population equal in size to the value of  $\hat{N}_{MLE2}$  (rounded to the nearest integer) calculated for that year. For each Monte Carlo sample, we estimated  $N$  using all nonparametric estimators. For each estimator, we examined the resulting 1000 Monte Carlo estimates to determine the probability of obtaining an estimate greater than or equal to the estimate calculated from the actual field data. Under the null hypothesis of  $\hat{N}_{MLE2}$  animals with homogeneous sighting probabilities, and at the  $\alpha = 0.10$  level, estimates based on field data should exceed Monte Carlo expectations in no more than 2 of the 13 years. Failure to fall within expected limits and frequencies was regarded as evidence that field samples were not drawn from an underlying population of size  $\hat{N}_{MLE2}$  with homogeneous sighting probabilities. In turn, this would imply that the underlying sighting probabilities were heterogeneous and that  $\hat{N}_{MLE2}$  was negatively biased.

## RESULTS

Maximum likelihood and nonparametric estimates of numbers of FCOY in the Yellowstone grizzly bear population were calculated for the 1986-1998 period, together with

population sizes and mortality limits implied by these estimates (Table 2). Numbers of FCOY actually observed ( $\hat{N}_0$ ) ranged from 13 to 35, while female mortality limits based on  $\hat{N}_0$  ranged from 2.0 to 4.0. In contrast,  $\hat{N}_{MLE2}$  yielded estimates of the number of FCOY that ranged from 16.7 to 42.2, and implied female mortality limits of 2.2 to 4.7. For all years except 1986,  $\hat{N}_{MLE2}$  was greater than  $\hat{N}_0$ , despite the additional (telemetry-based) information incorporated into  $\hat{N}_0$ .

Comparisons of uncorrected and bias-corrected forms of  $\hat{N}_{MLE1}$  yielded little evidence of biologically significant small-sample biases. Differences between uncorrected and bias-corrected forms of  $\hat{N}_{MLE1}$  were generally small (range = 0.0 to 0.8; mean = 0.4  $\forall$  0.3 [sd]). Also, the ratio  $\hat{\lambda} = n/\hat{N}_{MLE2}$  was  $>1$  for 12 of the 13 years examined; for the remaining year (1995),  $\hat{\lambda} = 0.87$ . Comparisons with bias-corrected estimates were specific to  $\hat{N}_{MLE1}$ , as we did not examine a bias-corrected form of  $\hat{N}_{MLE2}$ . However,  $\hat{N}_{MLE1}$  and  $\hat{N}_{MLE2}$  derive from the same underlying model and assumptions (*cf* Lewontin and Prout 1956), and differed by  $\neq 0.6$  in all years, suggesting that results for one can reasonably be applied to the other. Overall, we concluded that there was little evidence of biologically significant small-sample biases in estimates calculated using  $\hat{N}_{MLE2}$ .

Although  $\hat{N}_{Chao2}$  yielded the lowest estimates of any method for numbers of FCOY in 1990, 1993, 1994, 1996 and 1998, MLE's tended to be smaller than nonparametric estimates (Table 2, Fig. 1). They also yielded the lowest estimates of total population size and, hence, the lowest mortality limits for all years except 1994, when the estimate of total population size based

on  $\hat{N}_{\text{Chao2}}$  was slightly smaller (Table 2). This reflects the fact that estimates of total population size are based, essentially, on three-year running averages of estimated numbers of FCOY, and indicates that MLE's were *consistently* less than nonparametric estimates even though particular nonparametric estimates might be smaller for some years.

The fact that nonparametric estimators tended to be greater than MLE's was not attributable to biases in the nonparametric estimators. Monte Carlo tests showed that, under the sampling situation implied by  $\hat{N}_{\text{MLE2}}$  and  $n$ , the nonparametric methods we examined should have yielded estimates of numbers of FCOY that were more comparable to the MLE's than was actually observed (Table 3, Fig. 2). Evidence of deviations from expected values based on Monte Carlo tests varied somewhat among estimators (Table 3), but overall, supported this conclusion. At the  $\alpha = 0.10$  level, observed values exceeded expected values under the null (homogeneous) model in 4 of 13 years for  $\hat{N}_{\text{Chao1}}$  and  $\hat{N}_{\text{Chao2}}$  ( $P = 0.03$ ), 2 years for  $\hat{N}_{\text{J1}}$  ( $P = 0.24$ ), 3 years for  $\hat{N}_{\text{JK1}}$  ( $P = 0.10$ ), and 6 years for  $\hat{N}_{\text{SC1}}$  and  $\hat{N}_{\text{SC2}}$  ( $P < 0.001$ ) (Table 3). Overall, the observed pattern, in which nonparametric estimates tended to be greater than  $\hat{N}_{\text{MLE2}}$ , was inconsistent with the hypothesis of populations of size  $\hat{N}_{\text{MLE2}}$  with homogeneous sighting probabilities.

## DISCUSSION

Small sample size may cause  $\hat{N}_{\text{MLE2}}$  to be positively biased, while variations in individual sighting probabilities result in negative biases. The question we addressed was whether, on average,  $\hat{N}_{\text{MLE2}}$  is likely to yield conservative estimates of the number of FCOY in



the Yellowstone grizzly bear population. Two conclusions were important in this regard. First, positive and biologically significant biases due to small sample sizes generally were not evident when applying  $\hat{N}_{MLE2}$  to the 1986-1998 data. This conclusion follows from the relatedness of  $\hat{N}_{MLE2}$  and  $\hat{N}_{MLE1}$ , and the observation that uncorrected and bias-corrected versions of  $\hat{N}_{MLE1}$  yielded comparable results in most years, whereas substantial differences would be expected if sample sizes had exerted a significant effect on estimator performances. It is further supported (*cf* Darroch and Ratcliff 1980) by the observation that  $n/\hat{N}_{MLE2} > 1.0$  for 12 of the 13 years examined. Lack of small sample bias in most years does not imply that corrections for such biases should not be undertaken or that larger sample sizes would not be highly beneficial. Corrections are a prudent and conservative measure (Darroch and Ratcliff 1980). For this reason,  $\hat{N}_{MLE(B)}$  may be preferred over  $\hat{N}_{MLE2}$ , although we note that the two methods yielded quite similar results for the 1986-1998 data. Also, larger sample sizes are generally helpful for narrowing confidence limits (but see comments below) and improving our understanding of the degree to which sighting probabilities vary among individuals.

Second, we concluded that  $\hat{N}_{MLE2}$  was negatively biased by heterogeneous sighting probabilities among individuals. This conclusion follows from the observation that nonparametric population estimates were consistently larger than  $\hat{N}_{MLE2}$ , whereas Monte Carlo results demonstrated that estimates should have been more comparable (given observed sample sizes) if samples had been drawn from populations that were, in fact, comprised of  $\hat{N}_{MLE2}$  individuals with equal sighting probabilities (Fig. 2). This conclusion was further supported by

the fact that 5 of the 6 nonparametric estimators we examined exceeded expected values under the null (homogenous) model more often than expected ( $P \neq 0.10$ ).

Overall, we concluded that  $\hat{N}_{MLE2}$  is likely to yield conservative estimates of the numbers of FCOY in the Yellowstone grizzly bear population during 1986-1998, primarily due to negative biases resulting from heterogeneous sighting probabilities. Assuming that the estimated proportion of adult females in the population (0.274, see Eq. 8) is correct, it follows that calculations of mortality limits based on  $\hat{N}_{MLE2}$  should be similarly conservative. Comparisons of observed mortalities versus mortality limits calculated using  $\hat{N}_{MLE2}$  indicate that human-caused mortalities during 1988-1998 were within acceptable limits, except for 1990 and 1995 (Fig. 3).

Population trend among Yellowstone grizzly bears has been a contentious issue (Eberhardt *et al.* 1994, Boyce 1995, Pease and Mattson 1999) and it is tempting to examine  $\hat{N}_{MLE2}$  values for evidence of trends. We believe, however, that such an evaluation is inappropriate. Given observed sample sizes, the magnitude of the bias in  $\hat{N}_{MLE2}$  is determined largely by the degree of heterogeneity in individual sighting probabilities. In turn, the degree of heterogeneity may have changed with the distribution of sampling effort over time; e.g., increased attention to moth sites in recent years may have reduced heterogeneity in sighting probabilities, thereby reducing the bias in  $\hat{N}_{MLE2}$ . To support trend evaluations, an estimator that is relatively robust to such changes should be used.

Finally, we offer the following cautionary notes regarding use of  $\hat{N}_{MLE2}$ : (1) we do not

know the *degree* to which population estimates and mortality limits based on  $\hat{N}_{MLE2}$  are conservative, and (2) to the extent that  $\hat{N}_{MLE2}$  is conservative, calculated confidence limits are invalid. These concerns are not trivial, as the magnitudes of the biases and uncertainties inherent in  $\hat{N}_{MLE2}$  may be biologically and managerially significant. For this reason, we believe that an unbiased estimator with valid confidence limits should be sought. Conservatism may then be built into the decision-making process by using some lower confidence bound to estimate total population size and calculate mortality limits. Such an approach appropriately makes conservatism (and the degree of conservatism) an explicit and informed managerial choice, and allows for a more detailed evaluation of risks associated with different management alternatives. Unfortunately, this study was devised only to evaluate the performance of  $\hat{N}_{MLE2}$ . Performances of the nonparametric estimators we considered cannot be inferred beyond the narrow conditions of our Monte Carlo test. More extensive Monte Carlo work is needed to identify those estimators that are most accurate, precise, and robust to variations in the distribution of sighting probabilities. The design and funding of such work is now being actively pursued as a follow-up to this study.

#### **ACKNOWLEDGMENTS**

We thank S. Cherry, L. H. Metzgar, and G. C. White for reviewing and commenting on an earlier draft of this report.

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**Table 1.** Jackknife estimators of population size,  $\hat{N}_{jk}$ , for order  $k = 1$  to 5, where  $s_n$  is the number of unique individuals observed after  $n$  samples, and  $f_i$  is the number of individuals observed exactly  $i$  times (after Burnham and Overton, 1979).

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$$\hat{N}_{j1} = s_n + \left( \frac{n-1}{n} \right) f_1$$

$$\hat{N}_{j2} = s_n + \left( \frac{2n-3}{n} \right) f_1 - \left( \frac{(n-2)^2}{n(n-1)} \right) f_2$$

$$\hat{N}_{j3} = s_n + \left( \frac{3n-6}{n} \right) f_1 - \left( \frac{3n^2-15n+19}{n(n-1)} \right) f_2 + \left( \frac{(n-3)^3}{n(n-1)(n-2)} \right) f_3$$

$$\hat{N}_{j4} = s_n + \left( \frac{4n-10}{n} \right) f_1 - \left( \frac{6n^2-36n+55}{n(n-1)} \right) f_2 + \left( \frac{4n^3-42n^2+148n-175}{n(n-1)(n-2)} \right) f_3$$

$$- \left( \frac{(n-4)^4}{n(n-1)(n-2)(n-3)} \right) f_4$$

$$\hat{N}_{j5} = s_n + \left( \frac{5n-15}{n} \right) f_1 - \left( \frac{10n^2-70n+125}{n(n-1)} \right) f_2 + \left( \frac{10n^3-120n^2+485n-660}{n(n-1)(n-2)} \right) f_3$$

$$- \left( \frac{(n-4)^5 - (n-5)^5}{n(n-1)(n-2)(n-3)} \right) f_4 - \left( \frac{(n-5)^5}{n(n-1)(n-2)(n-3)(n-4)} \right) f_5$$


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**Table 2.** Estimates of numbers of females with cubs-of-the-year ( $\hat{N}_{\text{♀}}$ ) and total population size ( $\hat{N}$ ), together with calculated total ( $M$ ) and female ( $M_{\text{♀}}$ ) mortality limits implied by the estimates. Estimates are based on  $n$  replicated sightings of unique family groups and were calculated using each of eight different methods. The number of FCOY actually observed ( $\hat{N}_0$ ) is shown for comparison and may be based on  $>n$  sightings because  $\hat{N}_0$  uses additional data from non-random sightings of radio-collared animals. Estimates of total population size and mortality limits are not given for 1986 and 1987 because calculations of these values require data for the current and previous two years, whereas these analyses considered only data for 1986-1998.

Method	1986 ( $n = 82$ )				1987 ( $n = 20$ )				1988 ( $n = 36$ )				1989 ( $n = 28$ )			
	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$
$\hat{N}_0$	25.0	C	C	C	13.0	C	C	C	19.0	193.4	7.7	2.3	16.0	167.9	6.7	2.0
$\hat{N}_{\text{MLE1}}$	24.9	C	C	C	17.2	C	C	C	20.3	212.8	8.5	2.6	17.2	192.3	7.7	2.3
$\hat{N}_{\text{MLE1(B)}}$	24.8	C	C	C	16.6	C	C	C	20.1	210.2	8.4	2.5	17.0	188.9	7.6	2.3
$\hat{N}_{\text{MLE2}}$	24.3	C	C	C	16.7	C	C	C	19.8	207.0	8.3	2.5	16.7	186.6	7.5	2.2
$\hat{N}_{\text{Chao1}}$	28.9	C	C	C	20.2	C	C	C	23.1	248.9	10.0	3.0	18.9	219.7	8.8	2.6
$\hat{N}_{\text{Chao2}}$	27.5	C	C	C	17.3	C	C	C	21.2	226.1	9.0	2.7	17.5	196.9	7.9	2.4
$\hat{N}_{\text{J1}}$	30.9	C	C	C	18.6	C	C	C	23.8	253.2	10.1	3.0	20.8	223.4	8.9	2.7
$\hat{N}_{\text{Jk1}}$	30.9	C	C	C	18.6	C	C	C	23.8	253.2	10.1	3.0	20.8	223.4	8.9	2.7
$\hat{N}_{\text{SC1}}$	32.0	C	C	C	20.2	C	C	C	21.7	255.2	10.2	3.1	24.1	233.8	9.4	2.8
$\hat{N}_{\text{SC2}}$	31.9	C	C	C	19.5	C	C	C	21.5	251.2	10.0	3.0	23.4	227.7	9.1	2.7



**Table 2.** (continued)

Method	1990 ( $n = 49$ )				1991 ( $n = 62$ )				1992 ( $n = 37$ )				1993 ( $n = 30$ )			
	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$
$\hat{N}_0$	25.0	204.4	8.2	2.5	24.0	222.6	8.9	2.7	25.0	255.5	10.2	3.1	20.0	244.5	9.8	2.9
$\hat{N}_{\text{MLE1}}$	25.7	216.0	8.6	2.6	26.4	238.3	9.5	2.9	34.9	302.9	12.1	3.6	26.1	311.6	12.5	3.7
$\hat{N}_{\text{MLE1(B)}}$	25.5	214.2	8.6	2.6	26.4	236.9	9.5	2.8	34.1	299.4	12.0	3.6	25.4	306.4	12.3	3.7
$\hat{N}_{\text{MLE2}}$	25.1	210.3	8.4	2.5	25.9	232.6	9.3	2.8	34.4	297.2	11.9	3.6	25.5	306.0	12.2	3.7
$\hat{N}_{\text{Chao1}}$	26.1	234.0	9.4	2.8	44.2	310.8	12.4	3.7	45.5	407.8	16.3	4.9	22.0	400.2	16.0	4.8
$\hat{N}_{\text{Chao2}}$	25.0	217.9	8.7	2.6	37.8	278.3	11.1	3.3	40.5	362.2	14.5	4.3	21.1	355.3	14.2	4.3
$\hat{N}_{\text{J1}}$	28.9	253.3	10.1	3.0	34.8	293.5	11.7	3.5	37.6	355.0	14.2	4.3	25.7	350.9	14.0	4.2
$\hat{N}_{\text{Jk1}}$	28.9	253.3	10.1	3.0	42.6	322.0	12.9	3.9	47.2	418.4	16.7	5.0	25.7	414.3	16.6	5.0
$\hat{N}_{\text{SC1}}$	25.7	246.3	9.9	3.0	34.6	293.2	11.7	3.5	48.6	382.7	15.3	4.6	24.5	385.9	15.4	4.6
$\hat{N}_{\text{SC2}}$	25.5	242.4	9.7	2.9	34.5	289.8	11.6	3.5	47.6	378.0	15.1	4.5	23.9	379.6	15.2	4.6

**Table 2.** (continued)

Method	1994 ( $n = 29$ )				1995 ( $n = 25$ )				1996 ( $n = 45$ )				1997 ( $n = 65$ )			
	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$
$\hat{N}_0$	20.0	215.3	8.6	2.6	17.0	175.2	7.0	2.1	33.0	219.0	8.8	2.6	31.0	262.8	10.5	3.2
$\hat{N}_{\text{MLE1}}$	27.1	299.6	12.0	3.6	29.3	268.1	10.7	3.2	42.7	325.2	13.0	3.9	33.8	353.2	14.1	4.2
$\hat{N}_{\text{MLE1(B)}}$	26.4	291.9	11.7	3.5	28.0	258.4	10.3	3.1	41.9	314.8	12.6	3.8	33.7	345.1	13.8	4.1
$\hat{N}_{\text{MLE2}}$	26.6	294.0	11.8	3.5	28.8	262.6	10.5	3.2	42.2	319.7	12.8	3.8	33.3	347.7	13.9	4.2
$\hat{N}_{\text{Chao1}}$	23.8	311.3	12.5	3.7	59.3	350.5	14.0	4.2	39.3	409.8	16.4	4.9	41.1	476.5	19.1	5.7
$\hat{N}_{\text{Chao2}}$	22.5	285.1	11.4	3.4	43.0	283.3	11.3	3.4	37.5	339.6	13.6	4.1	38.8	402.5	16.1	4.8
$\hat{N}_{\text{J1}}$	26.7	306.6	12.3	3.7	29.5	266.1	10.6	3.2	42.7	324.2	13.0	3.9	41.8	383.0	15.3	4.6
$\hat{N}_{\text{Jk1}}$	26.7	341.6	13.7	4.1	48.6	335.8	13.4	4.0	42.7	394.0	15.8	4.7	41.8	452.8	18.1	5.4
$\hat{N}_{\text{SC1}}$	26.1	340.4	13.6	4.1	56.3	357.4	14.3	4.3	42.0	417.5	16.7	5.0	41.5	477.4	19.1	5.7
$\hat{N}_{\text{SC2}}$	25.5	332.1	13.3	4.0	54.9	347.7	13.9	4.2	41.4	407.7	16.3	4.9	41.3	469.0	18.8	5.6

**Table 2.** (continued)

Method	1998 ( $n = 75$ )			
	$\hat{N}_{\text{♀}}$	$\hat{N}$	$M$	$M_{\text{♀}}$
$\hat{N}_0$	35.0	335.8	13.4	4.0
$\hat{N}_{\text{MLE1}}$	38.2	393.2	15.7	4.7
$\hat{N}_{\text{MLE1(B)}}$	38.1	389.5	15.6	4.7
$\hat{N}_{\text{MLE2}}$	37.7	387.6	15.5	4.7
$\hat{N}_{\text{Chao1}}$	37.7	405.0	16.2	4.9
$\hat{N}_{\text{Chao2}}$	36.9	387.7	15.5	4.7
$\hat{N}_{\text{J1}}$	43.9	442.8	17.7	5.3
$\hat{N}_{\text{Jk1}}$	43.9	442.8	17.7	5.3
$\hat{N}_{\text{SC1}}$	41.2	429.8	17.2	5.2
$\hat{N}_{\text{SC2}}$	40.9	425.4	17.0	5.1

**Table 3.** Monte Carlo evaluation of five nonparametric estimators given a population of size  $N$ , sample size  $n$ , and homogeneous sighting probabilities. Values for  $N$  were determined as the estimate  $\hat{N}_{MLE2}$  for that year (rounded to the nearest integer value), while  $n$ -values are equal to observed sample sizes for each year.

Values calculated for each estimator include the mean estimate ( $\bar{\hat{N}}$ ) given the model population and sample size, root mean square error (RMSE) of the estimate, observed estimate ( $\hat{N}$ ) of the number of FCOY for that year and estimator, and the 1-tailed probability [ $P(\hat{N})$ ] of obtaining an estimate  $\geq \hat{N}$ , given the model population and  $n$ .  $\bar{\hat{N}}$ , RMSE, and  $P(\hat{N})$  were determined from 1000 Monte Carlo simulations for each year.

Year	$N$	$n$	$\hat{N}_{Chao1}$				$\hat{N}_{Chao2}$				$\hat{N}_{J1}$			
			$\bar{\hat{N}}$	RMSE	$\hat{N}$	$P(\hat{N})$	$\bar{\hat{N}}$	RMSE	$\hat{N}$	$P(\hat{N})$	$\bar{\hat{N}}$	RMSE	$\hat{N}$	$P(\hat{N})$
1986	24	82	24.6	2.636	28.9	0.046	24.0	1.352	27.5	0.019	25.8	2.467	30.9	0.001
1987	17	20	20.1	9.851	20.2	0.376	17.1	6.017	17.3	0.397	18.1	3.321	18.6	0.482
1988	20	36	21.5	5.752	23.1	0.270	20.0	3.730	21.2	0.301	22.7	3.952	23.8	0.423
1989	17	28	18.7	6.559	18.9	0.314	16.9	3.881	17.5	0.337	19.1	3.405	20.8	0.327
1990	25	49	26.1	4.879	26.1	0.414	24.9	3.590	25.0	0.435	28.3	4.619	28.9	0.456
1991	26	62	27.1	4.486	44.2	0.009	26.1	3.065	37.8	0.007	29.3	4.268	34.8	0.025
1992	34	37	37.4	15.336	45.5	0.188	33.9	9.561	40.5	0.189	35.0	4.585	37.6	0.308
1993	26	30	29.1	12.070	22.0	0.774	26.0	7.762	21.1	0.742	27.3	4.185	25.7	0.641
1994	27	29	30.1	12.460	23.8	0.726	26.7	7.773	22.5	0.702	27.7	4.057	26.7	0.603
1995	29	25	34.2	17.607	59.3	0.065	29.0	10.259	43.0	0.078	27.2	4.303	29.5	0.330
1996	42	45	44.9	14.541	39.3	0.640	41.7	10.255	37.5	0.610	43.0	5.231	42.7	0.518
1997	33	65	34.1	5.576	41.1	0.074	32.9	4.290	38.8	0.074	37.3	5.557	41.8	0.116
1998	38	75	39.1	5.484	37.7	0.554	37.9	4.506	36.9	0.555	43.1	6.393	43.9	0.454

**Table 3.** (continued)

Year	$N$	$N$	$\hat{N}_{JK1}$				$\hat{N}_{SC2}$				$\hat{N}_{SC2}$			
			$\bar{\hat{N}}$	RMSE	$\hat{N}$	$P(\hat{N})$	$\bar{\hat{N}}$	RMSE	$\hat{N}$	$P(\hat{N})$	$\bar{\hat{N}}$	RMSE	$\hat{N}$	$P(\hat{N})$
1986	24	82	25.9	3.033	30.9	0.006	24.2	1.131	32.0	<0.001	24.1	1.122	31.9	<0.001
1987	17	20	19.8	7.335	18.6	0.502	19.7	7.320	20.2	0.360	19.0	6.831	19.5	0.362
1988	20	36	23.3	6.671	23.8	0.428	21.0	3.517	21.7	0.361	20.8	3.395	21.5	0.358
1989	17	28	20.1	6.783	20.8	0.338	18.0	3.684	24.1	0.057	17.7	3.535	23.4	0.061
1990	25	49	28.9	7.624	28.9	0.461	25.8	3.388	25.7	0.489	25.6	3.301	25.5	0.456
1991	26	62	30.0	8.941	42.6	0.015	26.6	2.393	34.6	0.004	26.4	2.350	34.5	0.004
1992	34	37	39.2	12.516	47.2	0.222	37.1	9.662	48.6	0.085	36.4	9.255	47.6	0.085
1993	26	30	30.2	10.585	25.7	0.647	28.5	8.056	24.5	0.695	27.9	7.647	23.9	0.694
1994	27	29	30.7	9.841	26.7	0.630	29.8	8.848	26.1	0.651	29.1	8.359	25.5	0.643
1995	29	25	32.7	11.466	48.6	0.078	33.6	13.084	56.3	0.068	32.5	12.318	54.9	0.068
1996	42	45	48.1	14.473	42.7	0.583	45.2	10.470	42.0	0.585	44.5	10.030	41.4	0.576
1997	33	65	38.3	10.139	41.8	0.130	33.8	3.605	41.5	0.031	33.6	3.532	41.3	0.030
1998	38	75	44.0	11.212	43.9	0.455	38.8	3.862	41.2	0.247	38.6	3.791	40.9	0.253

**Fig. 1.** Estimated numbers of female grizzly bears with cubs-of-the-year (FCOY) in the Greater Yellowstone population, 1986-1998, calculated using eight different parametric and nonparametric estimators. Numbers of FCOY actually observed are shown for comparison. Curves were fitted using a LOWESS smoothing function with tension = 0.6. Methods used to calculate estimates in (A) assumed all family groups were equally likely to be seen, while those in (B) through (D) made no assumption about relative probabilities of seeing different family groups.

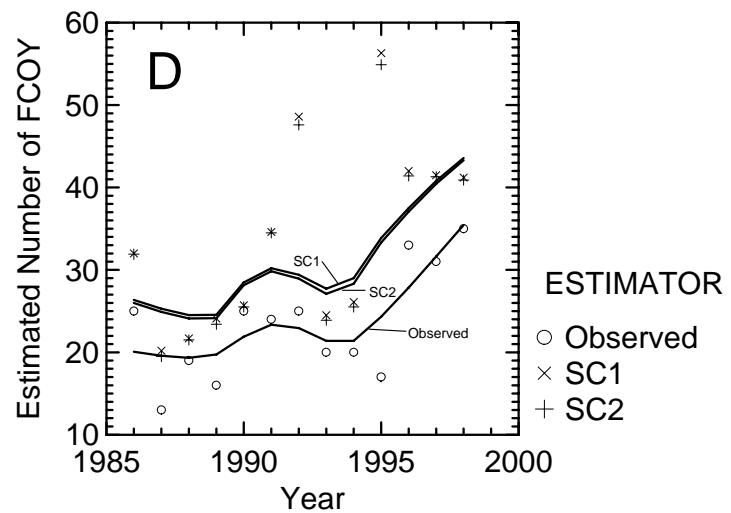
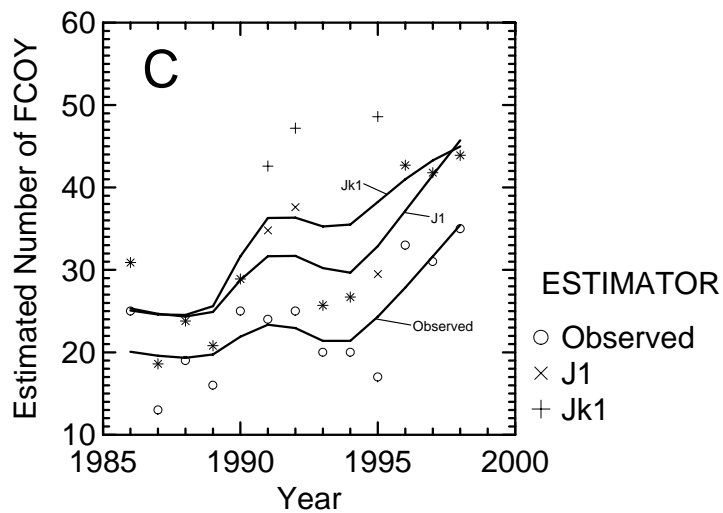
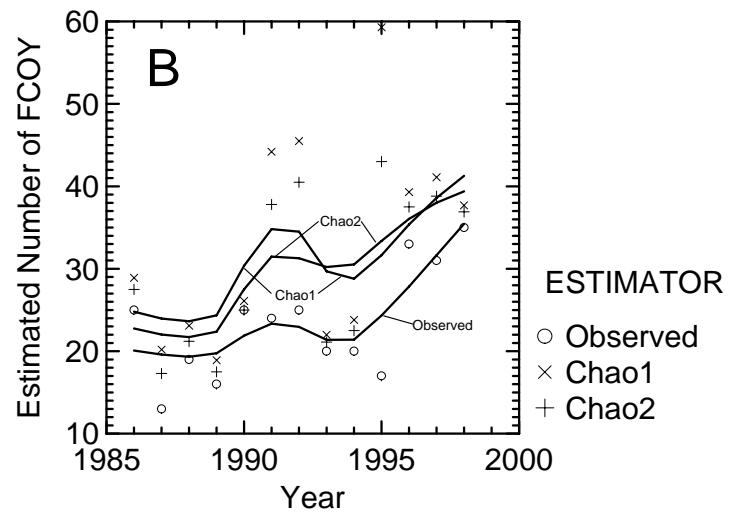
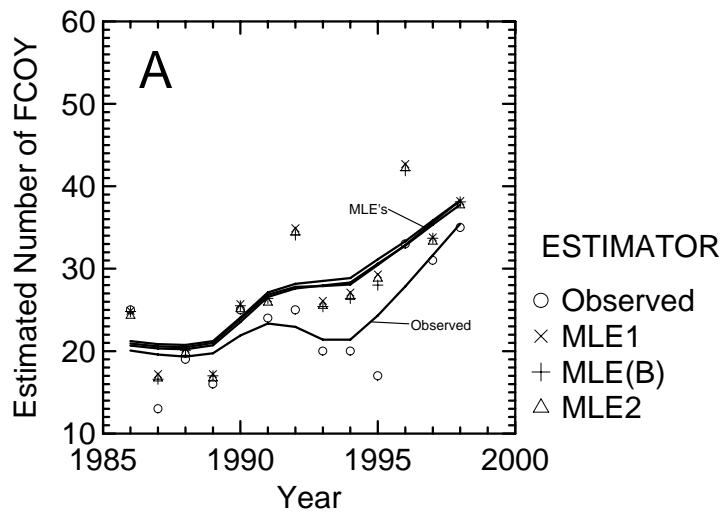


Fig. 1

**Fig. 2.** Monte Carlo estimates of expected values of (A) maximum likelihood, (B) lower bound, (C) first- and  $k$ th-order jackknife, and (D) sample coverage estimators of population size. Estimates in (A) assume all individuals have an equal probability of being sighted, while those in (B) through (D) are nonparametric and allow sighting probabilities to vary among individuals. Estimates were based on 1000 simulations for each year. Simulations assumed that (1) true population size was equal to the estimate obtained using  $\hat{N}_{MLE2}$  (see text, Table 2), (2) all individuals had an equal probability of being seen, and (3) sample size was equal to the observed sample size for that year. Results show that, given observed sample sizes and a population of  $\hat{N}_{MLE2}$  equally sightable individuals, the parametric and nonparametric (especially  $\hat{N}_{Chao1}$ ,  $\hat{N}_{Chao2}$ ,  $\hat{N}_{SC1}$ , and  $\hat{N}_{SC2}$ ) estimators should have yielded quite similar population estimates. As in Fig. 1, curves were fitted using a LOWESS smoothing function with tension = 0.6.



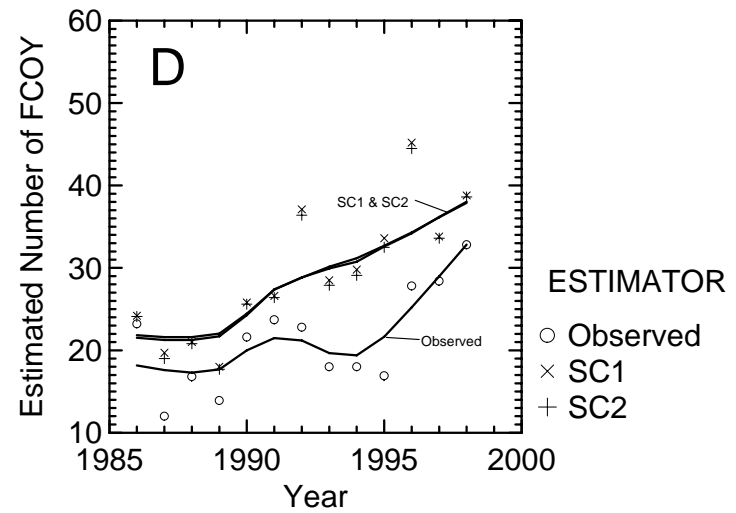
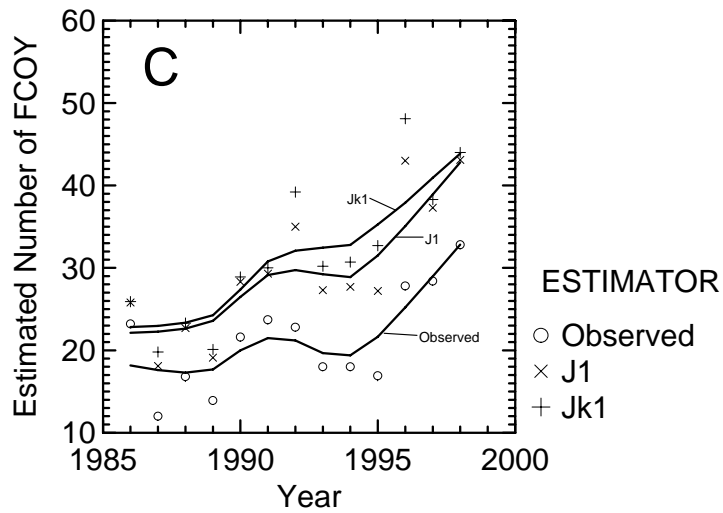
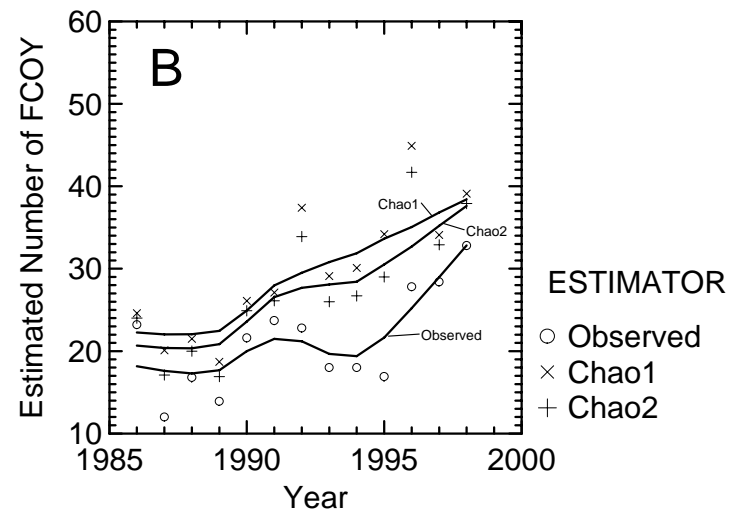
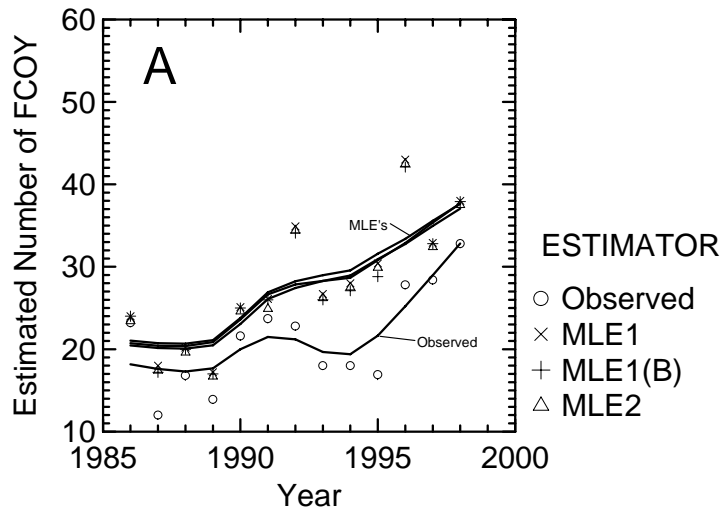


Fig. 2

**Fig. 3.** Numbers of known human-caused mortalities versus calculated mortality limits for 1988-1998, including (A) total mortalities, and (B) female mortalities. All data and limits are for mortalities occurring within the grizzly bear recovery and 10-mile buffer zones. Total mortality limits were calculated as 4.0% of the estimated total population size in year  $t$  ( $\hat{N}_{T,t}$ ), female mortality limits were calculated as 1.2% of  $\hat{N}_{T,t}$ , and  $\hat{N}_{T,t}$  was estimated per Eq. (8), using  $\hat{N}_{MLE2}$  to estimate the number of females with cubs-of-the-year in the population. All calculated mortality limits were rounded to the nearest whole number.

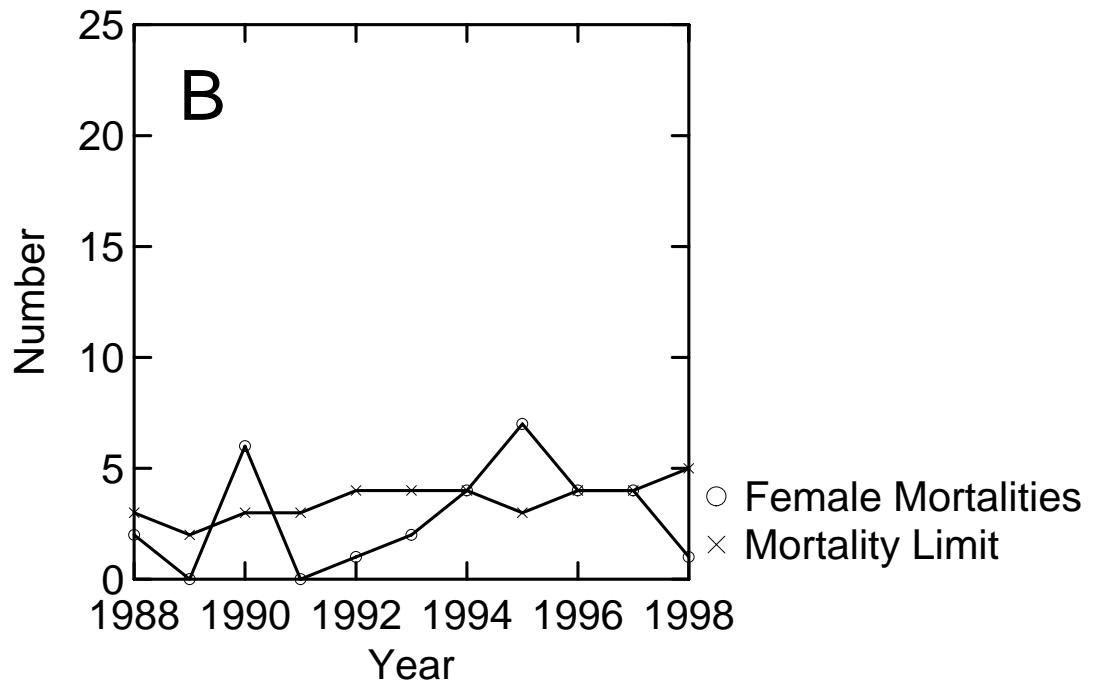
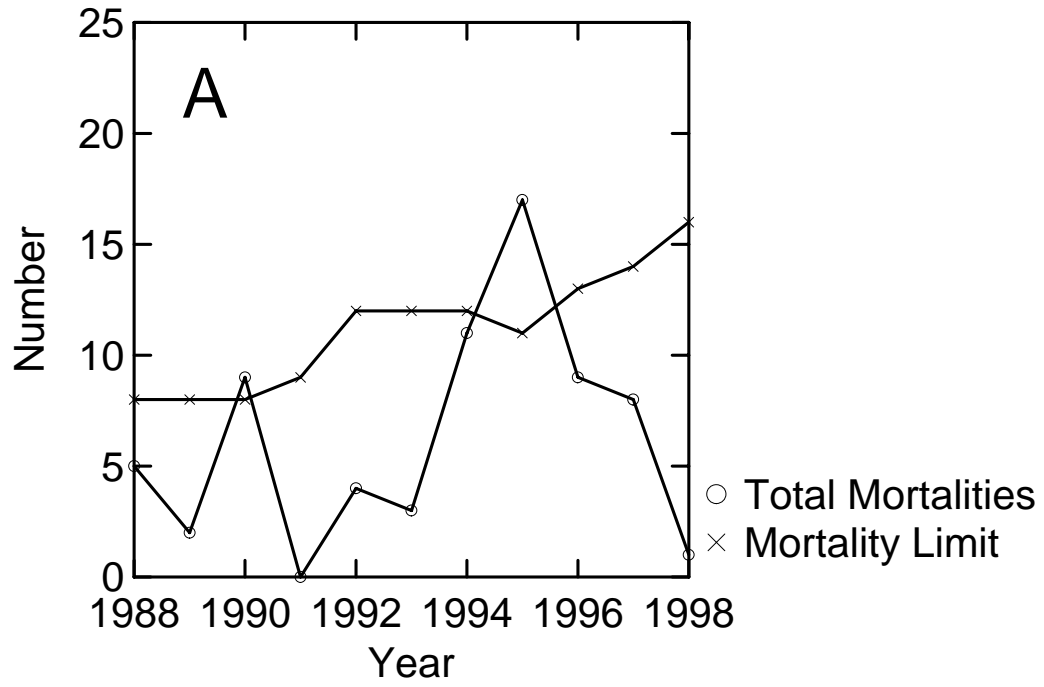


Fig. 3