# HARVEST AGE STRUCTURES AS INDICATORS OF DECLINE IN SMALL POPULATIONS OF GRIZZLY BEARS

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*Abstract:* We used simulated grizzly bear (*Ursus arctos*) harvest data to answer 2 questions: (1) can we use 2-group discriminant function analysis to distinguish harvest age structures from populations that have equilibrated from those beginning to decline from overharvest? and (2) how powerfully can it distinguish with small samples typical of grizzly bear data? Simulated populations were subjected to experimental harvests to determine the harvest level that caused chronic declines. For each run, statistics that described age structures were calculated. We constructed a linear discriminant function equation based on the descriptive statistics that separated declining from equilibrating populations, and estimated the power of the equation using decline as the null hypothesis. Accepting a 10% chance of failing to detect a decline (Type I error), the equation had little power to correctly classify equilibrated populations. With sample sizes from a 3-year period in the range 72–153 animals, estimated power was about 50%. With 3-year sample sizes in the range 24–51, power was roughly 20%–25%. Only when comparing severely overharvested populations with equilibrated populations could power be raised to >60%. We conclude that detecting grizzly bear population declines at their outset will be unreliable when based solely on harvest age structure data.

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By observing changes in the age and sex composition of harvest data, most managers of bear populations can detect a severe population decline without sophisticated analyses. Gilbert et al. (1978) concluded that "If only juvenile males are being killed, it does not take a model to tell managers that their bear population is in trouble." However, it may be desirable to detect gradual population declines at their outset. In this study we addressed the questions (1) can we apply linear discriminant function analysis to kill data from grizzly bear harvests to distinguish populations that are in equilibrium from those beginning to decline from overharvest and (2) how sensitive is the index when used with the small samples typical of grizzly bear harvests? These questions arose out of managers' oft repeated desire to have an "early detection system" of overharvest.

Gilbert et al. (1978) provided general guidelines for interpreting age structures of black bear (*U. americanus*) harvests. They concluded that age of bears and incidence of males in the harvest would decline as harvest intensity increased. Our approach has been to use stochastic simulation models to evaluate indices such as those proposed by Gilbert et al. (1978) empirically and to quantify their power to classify populations as declining from overharvest or equilibrated under sustainable harvest.

We view the dynamics of a harvested grizzly bear population in terms of its sustained yield curve (Fig. 1), which summarizes eventual trajectories under various levels of constant harvest. A population exists either in the stable portion (solid line) and equilibrates under constant harvest or in the unstable portion (dashed line) and declines toward extinction. Sustained yield theory is reviewed by Beddington (1979), May (1977), and McCullough (1979) among others.

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## SIMULATION MODEL

### Model Structure

The simulation model is a stochastic, discrete time, age-structured population projection model that follows the history of individual grizzly bears from birth until death. Unlike Leslie matrix-based models, survival and reproduction of each individual in each year are randomly determined with probabilities given by age-specific rates. This general structure allows demographic stochasticity, in common with other recent simulation models designed for bears (Shaffer 1978, 1983; Knight and Eberhardt 1984, 1985). Each bear is subjected to 5 life history events during the simulation year: breeding, hunting mortality, natural mortality, birth, and family breakup (weaning). Each individual is identified by traits governing its likelihood of dying, breeding, and so forth, including its sex, age, membership in a family group and, if female, whether it is attended by offspring, pregnant, or solitary. Hunting removes individual animals according to relative vulnerability coefficients so that harvest

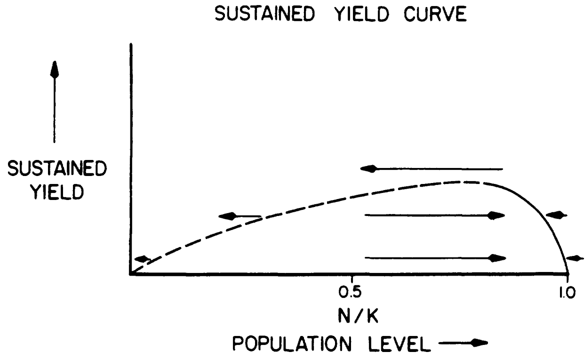


Fig. 1. An idealized sustained yield curve, showing population trajectories at different levels of population relative to carrying capacity ($K$) and constant yield. Solid portion of curve is stable; populations perturbed from this area return to it. Dashed portion is unstable; populations perturbed from this area increase to the stable portion or decline toward extinction.

age structures are biased samples of standing age structures.

With 1 exception, natural survival rates are considered density-dependent functions of $N/K$, where $N$ is the entire population, and $K$ is the equilibrium of an unhunted population and serves to scale the population. The exception is survivorship of subadult males, which is considered a density-dependent function of $N_m/K_m$, where $N_m$ is the number of adult (4+ years old) males and $K_m$ the number of adult males at population equilibrium. This model generally mimics the male-based population regulation theories of Bunnell and Tait (1981) and others (Kemp 1972, 1976; Young and Ruff 1982; Stringham 1980, 1983). We use Michaelis-Menton equations to produce nonlinear responses to density that are characteristic of large mammals (Fowler et al. 1980, Fowler 1981). Natality rates (age at 1st reproduction, litter size, and breeding interval) are considered independent of population density, varying only in response to environmental fluctuations. Population regulation thus follows Bunnell and Tait (1981), who suggested that natality is nutrition-based and that nutritional status is not substantially affected by population density.

All vital rates, whether density-dependent or -independent, are subject to environmental variation. Environmental fluctuations are simulated by allowing $K$ to vary independently and lognormally each year around its expected value with a standard deviation of 13% of the median. We assume equal sex ratios at birth throughout. A detailed description of the model structure appears in Harris (1984).

### Vital Rates Used in Simulations

We generalized vital rates of grizzly bears from southern interior populations, i.e., the area bounded by the national parks of the Canadian Rockies on the north and Yellowstone National Park on the south. The intent was not to mimic the behavior of a particular population, but to create a "representative" population by combining the best available data from similar areas. Data came from unhunted populations in Glacier National Park, B.C. (Mundy and Flook 1973), Glacier National Park, Montana (Martinka 1974), and Yellowstone National Park (Craighead et al. 1967, 1974; Knight et al. 1983; Knight and Eberhardt 1984, 1985); and hunted populations in southeastern British Columbia (McClellan 1983) and northwestern Montana (Jonkel 1982, Aune and Stivers 1983). Additional references were Stirling et al. (1976), Bunnell and Tait (1980, 1981), and McCullough (1981). We modeled hunting as opportunistic rather than trophy oriented, i.e., relative vulnerabilities to hunting were related to behavioral characteristics of bears rather than hunter selection. Vital rates and the coefficients of relative vulnerability to hunting are summarized in Table 1. A more detailed exposition of rates used in these simulations appears in Harris (1984).

## METHODS

### Creation of Harvest Age Structure Samples

We generated 10 independent population age structures at approximate equilibrium ($K$) and termed them "initial populations." These were considered representative of the random variation expected among populations having attained their stable age distribution. Each initial population was then hunted at a level known to be slightly greater than sustainable, causing a slow decline. New age structures were retained when the initial populations reached levels just below that yielding maximum productivity (approximately $0.73K$ in our simulations). These new age structures were considered representative of the random variation among heavily harvested age structures. Each of these 10 was then subjected to 10 different trial harvest levels for 10 years. Under trial harvesting, populations either adjusted toward their new equilibrium (if harvest levels were sustainable) or continued on a downward trajectory (if harvest levels were still higher than sustainable). Trial harvests were chosen to bracket the region where we hypothesized trajectories would change from equilibrium to decline.

The trajectory of each 10-year run was quantified by its instantaneous rate of change, $r$, calculated as the slope of the natural logarithm of population size over time. The run was classified as declining when $r$ was significantly ($P < 0.01$) negative; otherwise it was considered to have adjusted to its new harvested equilibrium. The procedure was repeated at population scales $K = 200$ and $K = 600$ to represent typically sized management units. The 10 trial harvests varied from 8 to 17 animals/year (for $K = 200$ populations) and from 24 to 51 animals/year in increments of 3 (for $K = 600$ populations). The entire procedure was replicated for 4 models incorporating slightly different mechanisms of density-dependence. Age structures among the four were similar (Harris 1984), so all were combined for this analysis, yielding 800 independent strings of 10-year age structures for inclusion into the discriminant function analysis.

## Development of the Discriminant Index and Estimation of its Power

From previous work (Harris 1985), we knew that descriptive statistics of small hunted samples of grizzly bear populations would exhibit considerable variability, largely in response to yearly differences in cohort strength (the model produces large cohorts at roughly 3-year intervals because most adult females give birth every 3 years). Therefore, we first summed the age-class frequencies from each period of 3 con-

**Table 1. A. Natality and survival rates used in the stochastic model to simulate grizzly bear populations.**

A. Natality Rates

| | | | | |
|---|---|---|---|---|
| Age (years) at 1st reproduction: | 5 | 6 | 7 | 8 |
| Percent: | 65% | 26% | 9% | 1% |
| Mean age at 1st reproduction: 5.50 years | | | | |
| Litter size (no. cubs): | 1 | 2 | 3 | |
| Percent: | 19% | 55% | 26% | |
| Mean litter size: 2.07 cubs | | | | |
| Breeding interval (years): | 2 | 3 | 4 | 5 |
| Percent: | 14% | 63% | 20% | 2% |
| Mean breeding interval: 3.09 years | | | | |
| Mean cubs/reproductive female/year: 0.67 | | | | |

B. Survival Rates

B.1. Survival Rates in the Absence of Hunting (%)

| | Maximum survival | | Survival at $K$ | |
|---|---|---|---|---|
| Age | Females | Males | Females | Males |
| 0 | 93 | 93 | 86 | 86 |
| 1 | 88 | 88 | 88 | 86 |
| 2 | 79 | 79 | 73 | 68 |
| 3 | 90 | 90 | 86 | 77 |
| 4 | 95 | 90 | 91 | 77 |
| 5–12 | 95 | 95 | 91 | 89 |
| 13–20 | 90 | 90 | 86 | 84 |
| 21–24 | 75 | 75 | 71 | 69 |

B.2. Hunting Vulnerability

| | Relative vulnerability to hunting | |
|---|---|---|
| | Females | Males |
| Cub with mother | 0.05 | 0.05 |
| Older juvenile with mother | 0.20 | 0.20 |
| Age 0–4 | 2.00 | 7.00 |
| Age 5–24 | 0.80 | 1.00 |
| Female with young | 0.20 | |

secutive simulation years, omitting the 1st year, to create "average" 3-year age structures that we termed "year-groups" (i.e., group 1 = years 2–4, group 2 = years 5–7, and group 3 = years 8–10). The descriptive statistics in Table 2 were then calculated for each of the resulting "year-group" age structures. Arc-sine transformations were applied to all proportions and ratios to stabilize variances. We did not use age-class frequencies directly for analysis because of their nonnormality and large variances. The descriptive statistics for each sample were used as input variables to generate a linear 2-group discriminant function equation. The known groups were "decline" and "equilibrium," and we used SPSS program DISCRIMINANT (Nie et al. 1975) to generate the discriminant function. Variables were entered into the equation in stepwise order as they maximized the Mahalanobis distance and its corresponding partial F value. Variables failing to make a significant ($P < 0.50$) contribution to the separation between group centroids were omitted.

The critical decision point in linear 2-group discriminant function analysis (DFA) is taken as the midpoint between the 2 group means when the objective is to minimize errors in classifying samples into pre-specified groups (Morrison 1976). However, here we considered that the 2 kinds of errors were not of equal consequence. Classifying as a declining population one that has actually equilibrated is a relatively benign error for a manager. At most, the consequences of the erroneous classification will be unnecessarily conservative measures. But classifying as a stable population one that is actually in decline from excessive harvest is a serious error. The decision implies a stable situation when continuation of the status quo leads to serious overexploitation. Therefore, we chose as the critical decision point the value that ensured no greater than a 10% probability of misclassifying populations that were actually declining (Fig. 2).

Power of the index was estimated as follows: new, independent data sets were generated, using the same procedures as for generating the original data. After discriminant function scores were computed for each new year-group, the mean and variance of scores for the (known) declining group were computed. Each sample in the declining group was then coded with its distance from the associated standard $z$-score, giving the mean score for declines in standard deviation units. Because the discriminant scores were approximately normally distributed, the critical score that ensured no greater than approximately 10% misclassification of known decliners was that corresponding to $z = 1.282$. The number of misclassifications of equilibrated populations (Type II error) was then computed empirically by comparing actual vs. predicted group membership and power was taken as (1 - probability of Type II error). Among the new data generated for estimating the discriminant function's power, age structures from adjacent year-groups were not wholly independent. However, because most harvests were relatively small proportions of standing populations, we believe lack of independence was a minor problem (Harris, unpubl. data).

Choosing the critical point in this way explicitly recognized 2 types of errors, analogous to Type I and Type II errors of standard statistical theory. The null hypothesis was that a sample age structure came from an overharvested population, and we tested the power of the discriminant function to disprove this hypothesis with $\alpha = 0.10$. The basic question of DFA was thereby modified from "how accurately can this pro-

**Table 2. Descriptive statistics computed for each harvest age structure sample.**

| Abbreviation | Description |
|---|---|
| MXBAR | Mean age of males |
| FXBAR[a] | Mean age of females |
| MMED | Median age of males |
| FMED[a] | Median age of females |
| MSUBAD | Proportion of males in subadult (0–3) age class |
| FSUBAD | Proportion of females in subadult (0–3) age class |
| M58JUV[a] | Ratio of males age 5–8 to males age 0–1 |
| F58JUV[a] | Ratio of females age 5–8 to females age 0–1 |
| MFALL | Proportion of males among all animals |
| MFAD | Proportion of males among adults (ages 4+) |

[a] Variable not used in the discriminant function.

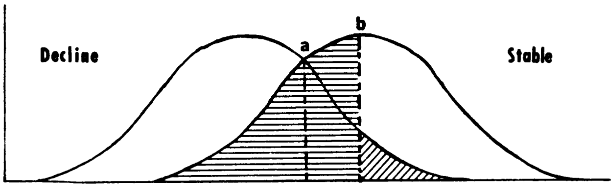


Fig. 2. Two idealized distributions of index scores, showing the procedure used to estimate power of index. Harvest age structures from declining populations (left) received lower scores than those from equilibrated populations (right). Point a would minimize total misclassification probability. We used point b to maintain Type I errors (slanted hatching) at 10% or less. Power was calculated as 1 - $\beta$, where $\beta$ is the probability of a type II error (horizontal hatching on right-hand curve).

cedure predict group membership?" to "given that it will misclassify declining populations with probability 10%, how much power to correctly classify equilibrated populations does this procedure have?"

## RESULTS

### Index to Population Decline from Harvest Data

Discriminant functions were originally developed using data from each of the 3 year-groups (i.e., years 2–4, 5–7, and 8–10). The function using the 1st year-group was the most powerful and is the only one discussed further. This discriminant function used 7 of the 10 input variables from Table 2, listed in decreasing order of their relative contribution to the discrimination in Table 3. Overharvested populations were given lower scores and assigned to group 1; equilibrated populations received higher scores and were placed in group 2. Age structures from the 2 groups were significantly different (Wilks $\lambda = 0.724$, $\chi^2 = 242.56$, df = 7, $P < 0.0001$), but the canonical correlation was only 0.526, indicating that only about 28% of the total variation among age structures was explained by the groupings.

Two of the 3 most powerful discriminating variables were measures of sex ratio: proportion males and proportion males among adults. The remaining discrimination power was added by measures of the relative age of the animals in the sample. Surprisingly, mean age of males made only a minor contribution. With 1 exception (variable FSUBAD), measures of the relative age of females in the sample did not contribute.

The resulting linear discriminant index reflected the general behavior of harvest age structures of bears under light and heavy harvests. We found, as did Gilbert et al. (1978), that:

1. Sex ratios, especially among adults, increasingly favored females as harvest intensity increased. Thus as the proportion males among adults (MFAD) declined, so did the index, resulting in classification into group 1, overharvest.
2. The male component of the sample contained progressively fewer old individuals as harvest intensity increased. Thus the index declined along with median male age (MMED), again leading to classification as an overharvested population.

However, the relative ages of males in our simulated age structures did not decrease uniformly with increasing harvest pressure. Because our modeled harvests simulated opportunistic rather than trophy hunts, lone subadult males (age 2–4) were considered far more vulnerable than other bears (Table 1) and dominated harvest age structures even when older male bears were present in the population. Thus, our harvest samples had relatively youthful male age structures in both lightly and heavily harvested populations. With heavy harvest, subadult males became

Table 3. Coefficients for the discriminant function listed in decreasing order of their contribution.[a]

| Variable | Standardized coefficient | Unstandardized coefficient |
|---|---|---|
| MFAD | 4.70778 | 0.69170 |
| MSUBAD | 3.02743 | 0.48955 |
| MFALL | −2.07158 | −0.54121 |
| FSUBAD | −1.76279 | −0.34306 |
| MMED | 1.10874 | 2.62271 |
| MXBAR | −0.81701 | −1.57841 |
| M58JUV | −0.65659 | −0.06682 |
| Constant | | −13.53516 |

[a] Standardized coefficients give the relative contribution of each variable; unstandardized coefficients are those used in computations.

less available, causing the harvest to intensify on less vulnerable older males. Only after harvest pressure became so heavy that older males were depleted did the average age again become very young, i.e., subadults predominated among males despite being substantially depleted because they were the only males left.

## Estimated Power of the Index

Although the index reflected the expected patterns of harvest age structure changes, its ability to correctly classify individual samples was generally poor. Allowing a 10% chance of misclassifying age structures from overharvested populations, its power to correctly classify equilibrated populations varied from less than 25% with small sample sizes to about 58% with the largest sample sizes tested (Table 4).

Power of the index was greater when only the most divergent age structures were compared. Power was estimated at 63.9% (with a Type I error rate of 0.083) when only age structures from the last 3 years of each 10-year run were compared, a process in which independence of samples was not violated. During the 1st 7 years, declining populations moved closer to extinction and farther from equilibrated populations, allowing fuller expression of the differences in age structures. Similarly, if only age structures from runs using the highest and lowest harvest levels were compared, power was increased above that estimated when using all data. For example, when age structures from hunts that always caused declines were compared with age structures from hunts that never caused declines, power was estimated at 64.1% (with Type I error of 0.108).

The relationship between the index and harvest rate was not linear, more nearly resembling a hyperbola

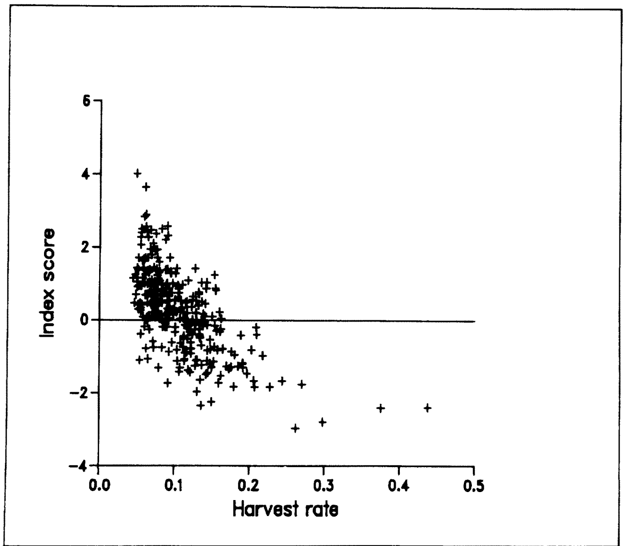


Fig. 3. Scores of the index to decline graphed against harvest rate (hunt/population) applying during years the sample was taken. Data are 3-consecutive-year sums from large ($K$ = 600) populations.

(Fig. 3). Only at the very highest harvest rates (>20%) were declining scores guaranteed. At harvest rates near maximum sustained yield (roughly 5%–7%, Harris and Metzgar, unpubl. data) the index was variable and relatively insensitive.

Despite its weaknesses, the index was a more reliable discriminator than any 1 of the age-structure statistics when taken alone (Table 5). Using the largest sample sizes (for which the estimated power of the index was 58%), the highest power (maintaining a Type I error of 10% or less) using a single variable (MFALL) was 42%, and 5 of the remaining 6 had power of less than 20%.

Table 4. Estimated power of the index to population decline from harvest samples from small (K = 200) and large (K = 600) samples sizes.[a]

| $K$ | Size of harvest sample | Type I error | Power (%) | $N$ |
|---|---|---|---|---|
| A. | | | | |
| 200 | 8–17 | 0.128 | 23.0 | 1,746 |
| 600 | 24–51 | 0.062 | 22.2 | 1,817 |
| B. | | | | |
| 200 | 24–51 | 0.074 | 25.8 | 534 |
| 600 | 72–153 | 0.101 | 58.3 | 554 |

[a] Type I errors are probabilities of failing to detect a population decline (expected probability = 0.10); power estimates are the ability of the test to correctly identify nondeclining populations. Sample sizes are the number of harvest age structures to which the index was applied. A, Samples are yearly harvest age structures. B, Samples are age structures created by summing frequencies from 3 consecutive simulation years.

**Table 5. Estimated power of individual discriminating variables.**[a]

| Variable | Type I error | Power (%) |
|---|---|---|
| MFALL | 0.068 | 41.7 |
| MFAD | 0.098 | 38.9 |
| FSUBAD | 0.092 | 15.3 |
| MMED | 0.092 | 14.4 |
| M58JUV | 0.157 | 10.2 |
| MXBAR | 0.095 | 4.2 |
| MSUBAD | 0.095 | 0.0 |

[a] All samples ($N$ = 554) were created by summing age-class frequencies from 3 consecutive simulation years of the large ($K$ = 600) populations; harvest age structures consisted of 72–153 individuals. Type I errors and power are as in Table 4.

## DISCUSSION

Our results are in general agreement with Gilbert et al. (1978): as hunting intensity increases, harvest age structures increasingly favor females over males and younger males over older males. However, confirming this general pattern does not answer the critical question: when is hunting intensity too great? Our initial objective was to develop an index based on age and sex structures of harvested samples that could serve as a "red flag," warning managers of bear populations when sustainable yields had been surpassed. The analysis failed to produce such an early warning system but instead illuminated the highly variable nature of harvest age structures from small grizzly bear populations.

The linear discriminant index developed here provides a tool that can be applied to an age-structured harvest sample to detect overharvest. However, we estimate that, depending on sample size, the index must misclassify 50%–75% of nondeclining populations to maintain <10% probability of failing to detect overharvest. In practical terms, one must classify so many equilibrated populations as declining to avoid missing a true decline that the index has little management value.

The similarity of harvest age structures from grizzly bear populations with opposite trajectories stems largely from the limited ability of grizzly bears to withstand harvest. Harvest age structures show characteristic responses to increasing kill rates, but grizzly bear populations decline at such low rates that even maximum sustainable harvests are relatively small. Thus a decline may be induced by a harvest that barely perturbs the underlying age structure, while providing such a small sample for analysis that random variations exert a major influence. Heavier harvests would produce greater perturbations to standing age structures and provide larger samples, but generating a large enough harvest sample to eliminate ambiguity may come only at the cost of ensuring overharvest. Sample sizes might be increased by combining data from larger areas (e.g., multiple management units), but we suspect this procedure will mask any differences among differentially harvested populations. The small size of the populations we simulated ($K$ = 200, 600; hunts 8–51/year) reflects our view that larger assemblages are rarely demographically homogeneous.

These conclusions must be viewed with the limitations of our simulation model and linear discriminant analysis procedure in mind. In particular, the predominance of young males in both lightly and heavily harvested populations is likely caused by the "opportunistic" hunt we modeled. Male age structures may behave differently if hunters take older males preferentially when they are available (e.g., Kodiak Island). The model assumes that relative vulnerabilities to harvest among age-classes are constant and therefore independent of relative abundances among age-classes. In nature, vulnerabilities may vary in response to relative availabilities of each age-class. The linear discriminant function may not have been the most powerful discriminator possible, or we may not have chosen the most diagnostic statistics for analysis. Finally, this analysis suffers from the familiar limitation of any single-population model that fails to account for heterogeneity within the population. We have implicitly assumed equal harvest pressure throughout the population (or management unit), but bear populations may be harvested intensively in accessible areas and lightly in remote areas. If animals from lightly harvested areas subsidize an otherwise overexploited population, an analysis that uses the combined harvest age structure to represent the entire area will be unreliable.

However, we suspect that none of the preceding qualifiers will alter our basic finding that grizzly bear harvest age structures are relatively insensitive barometers of the stability of the population they represent. Novel approaches to age structure analysis (e.g., Tait 1983) may increase the level of resolution possible in the future. For the present, we caution against harvesting small grizzly bear populations when the sole purpose is to gain age structure data. Where harvesting already takes place, age structures may be usefully examined for symptoms of overexploitation but should not be solely relied upon to provide unambiguous indicators of any but the most dramatic population decline.

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