Alaska Department of Fish and Game
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Federal Aid in Wildlife Restoration
Research Final Report

INTERPRETATION OF
BEAR HARVEST DATA

by
Sterling D. Miller
and SuzAnne M. Miller
Projects W-22-6 through W-23-3
Study 4.18
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Sterling D. Miller
SuzAnne M. Miller

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State: Alaska

Cooperators: Dr. D.E.N. Tait  
Dr. Robert Fagen  
Mr. Jie Zheng  
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SUMMARY

During this project 2 models were developed. The first model is a deterministic spreadsheet population model that was used to (1) estimate sustainable harvest rates for black bears (Ursus americanus) and brown bears (Ursus arctos) under assumed optimal conditions of productivity and with empirical productivity data derived from bear studies in Southcentral Alaska and (2) evaluate the relationship between sex and age composition of harvest and population trend.

Sustainable harvest levels for black and brown bear populations under optimum conditions of low natural mortality and high productivity were estimated using this model. Under these conditions the maximum sustainable hunting rate was 5.7% for brown bears and 14.2% for black bears. These simulations were also used to estimate the period of time it would take for bear populations to recover from overharvests that resulted in a 50% decline in population size. If hunting during the recovery period occurred at 75% of maximum sustainable levels, it took the simulated brown bear population 40 years to recover, compared with 17 years for black bears (Miller 1990a, 1990b). With minor modifications this model was also used as a moose (Alces alces) population model to evaluate impacts of increased spring calf survivorship on fall calf:cow ratios (Miller, In press).

In addition, a brown bear harvest data interpretation model developed by Tait (1983) was acquired, modified, and tested under a contract with R. Fagen (Univ. of Alaska, Southeast), who was assisted by UAS programmer Jie Zheng. A report on these tests is attached as Appendix A to this report. Although this model now executes, additional work is needed to determine whether and under what conditions this approach will be a useful tool for interpretation of real harvest data. The most significant points in this report are as follows:
1. With simulated data sets, the model correctly identified trend for increasing and decreasing populations but misidentified a stable population as declining. Errors in estimating rates of decline or increase were relatively small in the tests conducted.

2. The model's performance as a trend indicator was relatively unaffected when errors in aging, sexing, or reporting were introduced into simulated data sets.

3. The model generated a consistent overestimation bias for population size in the simulated data sets. The consistency of this bias suggested a mathematical flaw somewhere in the model that is likely correctable.

4. Runs on real harvest data were generally unbelievable both in terms of trend and in estimates of population size. There appeared to be a bias toward prediction of decline where independent indicators suggested stability or increases. These tests were conducted on data from all of the 4 GMU's examined, the model might perform better on data from selected subregions that meet model assumptions such as homogeneity of hunter effort.

This study concludes that sex and age composition of bear harvest data are very difficult to interpret. We knew this when we started. In this study we have been more successful at demonstrating the problems in interpreting these data than we have been at developing meaningful new ways of interpretation. Regardless, we believe the sex and age composition of harvest data, if used very cautiously and in combination with other indicators, can provide an indicator of likely trend in bear populations under some circumstances. Given the difficulty and expense of determining population trend in other ways (Harris 1986, Miller 1990b), it would be premature to discontinue collection and inspection of sex and age composition of bear harvests. We recommend continued and more widespread involvement in efforts to interpret harvest composition data and additional tests and modifications of the Tait approach.

Key words: Alaska, brown bear, Ursus arctos, black bear, Ursus americanus, harvest data interpretation, population modeling, harvest levels
INTRODUCTION

Background

Brown-grizzly bear (*Ursus arctos*) managers are faced with the problem of establishing acceptable levels of harvest for a species with a slow growth rate for which no generally accepted techniques for determining changes in population status exist through either direct or indirect monitoring (Harris 1986). In some portions of Alaska, the need for such monitoring techniques
is particularly strong, as managers attempt to lower grizzly bear numbers in order to reduce bear predation on ungulates. Such reductions are difficult to monitor without techniques for evaluating bear population status or population growth potential.

Currently, Alaska’s bear managers judge trends in bear populations largely by interpreting sex and age data derived from mandatory registration of bears harvested by hunters. These judgements of trends, however, are not conclusive, and the same data sets are sometimes interpreted in dramatically different ways. No models are available to evaluate which are the most reasonable or even feasible interpretations. Neither are there models available through which a relationship can be established between bear productivity and sustainable harvest rates. The lack of information in this regard is important because bear productivity can vary widely in different portions of the state.

Better understanding of bear population dynamics is important for interpretation of harvest data and development of methods for directly assessing the status of living populations. The use of simulation models to mimic the dynamics of the possible responses of a population to a variety of introduced variables is a well-established, relatively inexpensive, and occasionally misused tool of modern game managers who seek to better understand these dynamics (Pojar 1981). For bears, the modeling approach has been most extensively used by Bunnell and Tait (1980, 1981) to model, among other things, sustainable mortality rates (from all causes) as a function of reproductive parameters. Sidorowicz and Gilbert (1981) used a similar model to predict sustainable hunting levels of 2-3%/year for grizzlies in the Yukon Territory.

Harris (1984) and Harris and Metzgar (1987) used the sex and age composition of simulated harvest data to examine the sensitivity of such data to changes in bear population status or trend and concluded that such data are not very revealing. The bear harvest data analysis approach developed by Fraser et al. (1982) is unlikely to work on Alaska data derived from sealing documents because there is an absence of effort data from unsuccessful hunters in Alaska and because females with newborn cubs are protected by law. This protection results in an augmented proportion of males in the adult age classes of harvested bears.

Tait (1983) presented a mathematical approach to the analysis of harvest data. This worked well on Monte-Carlo simulations of bear populations, but it has yet to be tested on real data. Tait’s model uses as input exactly the kind of information on bears available in Alaska as a result of a 20-year history of sealing and aging bears. Meetings between Tait and ADF&G biologists have established that his model has promise as a management tool.

No population or harvest simulation models have been developed for Alaska’s managers to use in helping to manage grizzly-brown bears, although sufficient data are available in numerous areas
to begin to use such models. These areas include Units 4, 8, 9, 13, 20, 23, and 26 (Schoen and Beier 1990, Smith and Van Daele 1987, Miller and Sellers 1989, Miller 1990a, Reynolds 1990, Ballard et al. 1990, and Reynolds and Hechtel 1984, respectively).

Objectives

Improved understanding of the relationship between data on composition of bears harvested in Alaska and trends in the population from which they were taken is the general objective of this study. The specific objectives are as follows:

1. To identify or construct a bear population simulation model or models useful to bear managers for improving understanding of the relative importance of various reproductive parameters, harvest rates, and bear vulnerabilities in regard to population growth rates and sustainable harvest rates and to examine the utility of sex and age composition data derived from harvest records in making conventional interpretations of bear population status.

2. To evaluate Tait's harvest data model (Tait 1983) and, to the extent practical, adapt it as a management tool for use in interpretation of bear harvest data in Alaska.

3. To evaluate methods used to manage bear populations elsewhere in the U.S. and Canada.

Procedures

Objective 1--Obtain, Develop, and Use Population Models:

Two population models were acquired and one was developed in order to evaluate bear population dynamics. The first model was the Generalized Animal Population Projection System (GAPPS) (Harris et al. 1986). This is a sophisticated framework for developing stochastic population models for small populations of any species. As part of this project we contracted with the Harris and the programmer who wrote GAPPS (C. D. Bevins) to develop a version compatible with DBASE III. The original version was based in DBASE II. The second model was 3 versions of ANURSUS (Taylor et al. 1987b) for modeling polar bears, black bears (Ursus maritimus), and grizzly bears that were obtained from M. Taylor. ANURSUS is a deterministic model with optional stochastic features. The model appears to include all parameters needed to mimic bear population dynamics. Little testing was done of this model, because documentation is still being developed. A third model was developed for this project by S. D. Miller. This is a simple deterministic model based in LOTUS 1-2-3. Results of altering any of the input parameters can be viewed using graphs built into the model. This model and the uses made of it were described by Miller and Miller (1988).
Using this LOTUS model, 4 scenarios were examined in simulation studies designed to evaluate the relationship between population trend and harvest statistics (Miller and Miller 1988). In the first, a population was allowed to grow under a regime of light exploitation. In the other 3 scenarios, this increasing population was overharvested (population declines of 1.6-2.6%/year) under circumstances where different age and sex classes had different relative vulnerabilities to hunters. In all scenarios males were more vulnerable to hunters than females. The model was also used to estimate sustainable harvest rates for both black and brown bear populations (Miller and Miller 1988, Miller 1988). In this application the vulnerabilities of different sex and age classes were altered until a stable population with a stable sex-age composition was achieved. The corresponding harvest percentage rate was calculated directly from the number harvested divided by the population size under these stable conditions.

The LOTUS model used to conduct these simulation exercises was also used to estimate sustainable rates of harvest in the GMU 13 brown bear population in Unit 13 and black bear populations in Units 13 and the Kenai Peninsula (Miller 1988, Miller and Miller 1988). Reproductive data used were based on telemetry studies (Miller 1987, Schwartz and Franzmann 1991) and varied between the 2 areas; population structure and relative vulnerabilities to hunting and natural mortality were held constant in each area. Sustainable harvest rate for each area was estimated to be exploitation rate as calculated by the model plus population growth rate as calculated by the model.

Simulation studies using a DBASE III simulation program were conducted to estimated length of study period and sample size required to estimate reproductive parameters (i.e., reproductive interval, litter size, age at first reproduction). Simulations were analogous to investigations where a number of female bears are radio-marked in the first year of study and subsequently followed for many years to determine reproductive rates. For each parameter, complex (heterogeneous) and simple (homogeneous) scenarios that were thought to bound the range biologically feasible for brown bears were modeled. Simulations were conducted as if 10, 25, 50, and 75 radio-marked females were available for each scenario. Samples sizes and periods of study were classified as adequate when 90% of the samples drawn from the population correctly estimated the parameter within ±5% of the true value (Miller 1990a). The results reported by Miller (1990a) are preliminary; additional simulations need to be done to make the test scenarios more realistic of the extremes for complex and simple bear populations. Also, the analysis needs to be expanded to include black bear reproductive parameters, and more appropriate sensitivity analysis techniques need to be applied to the results.

4
Objective 2--Develop and Test the Tait Model:

A version of the harvest data interpretation model described by Tait (1983) was obtained, and preliminary modifications were accomplished by S. M. Miller. Other priorities prevented additional progress on evaluating this model until 1990, when R. Fagen of the University of Alaska, Southeast, was contracted to modify and test this model.

Objective 3--Survey of Management Approaches Elsewhere:

In 1986 states and provinces were contacted to describe their procedures for evaluating trends in exploited bear populations. These results were reported by Miller (1990b). A similar but more detailed analysis of black bear management in different states and provinces was prepared by Garshelis (In press).

RESULTS AND DISCUSSION

Objective 1--Bear Population Models and Analyses

Population Models:

Little use was made of GAPPS or ANURSUS, besides acquiring the software and establishing that it worked and was available to use when needed. Most results were accomplished using the LOTUS population model. These results are summarized below; more details are provided in Miller and Miller (1988).

In all three of the overharvest scenarios examined with the LOTUS model, the percentage of females in the harvest at first increased and then stabilized, mean age of harvested males declined and then stabilized, and mean age of harvested females sustained little change (Miller and Miller 1988). We concluded that harvest age or sex composition will tend to stabilize in situations where relative vulnerabilities by sex or age remain unchanged, regardless of whether the population is increasing or decreasing. Changes in these values result from changes in the relative vulnerability by sex and age; within a period of less than one life-span following such a change, these statistics will stabilize. Managers should not interpret stability in these harvest statistics as indicating a lack of trend in the population (Miller and Miller 1990a).

A regression of the percentage of males in each age class on age class was proposed as a method of estimating harvest rate of bears by Fraser et al. (1982) (see also Harris and Metzgar 1987). Our LOTUS model was adapted to conduct these analyses. This approach was examined for the 3 overharvest scenarios examined in the above simulation studies, and it correctly estimated harvest rate in some cases. When harvest rates stabilized, generally about 10 years following a change when the age structure stabilized to the new vulnerabilities, the Fraser approach was
unable to detect continued declines in the simulated populations (Miller and Miller 1988).

The LOTUS model was used to estimate maximum sustainable harvest levels for black and brown bear populations under optimum conditions of low natural mortality and high productivity (Miller 1990a, 1990b). Under these conditions the maximum sustainable hunting rate was 5.7% for grizzly bears and 14.2% for black bears. For grizzly bears older than 2.0 years and black bears older than 1.0 year, maximum harvest rates were 7.8% and 15.9%, respectively (Miller 1990a, 1990b). These simulations were also used to estimate the period of time it would take for bear populations to recover from overharvests that resulted in a 50% decline in population size. With no hunting during the recovery period, maximally productive grizzly bear populations could recover in 10 years, compared with 6 years for black bears. If hunting during the recovery period occurred at 75% of maximum sustainable levels (i.e., 25% of recruitment is applied to population growth), the simulated populations recovered in 40 years for grizzly bears and 17 years for black bears (Miller 1990a, 1990b).

In addition to these simulated results, actual estimates of sustainable harvest rates were derived for the brown bear population in Unit 13 (Miller 1988). In this analysis, the number of bears harvested in Unit 13 was found to exceed the sustainable level of harvest that was estimated using the LOTUS model (Miller 1988, 1990b). Similar procedures were followed to estimate sustainable harvest rates for Kenai Peninsula and Unit 13 black bear populations (Miller 1990a). Using extrapolated density estimates to derive population estimates, these rates were used to derive estimates of sustainable number of bears that could be harvested.

One objective of this and a related project (Miller 1988, 1990a) was to examine the relationship of an independently documented downward trend in a brown bear population to harvest data derived from that population. In Unit 13 capture-recapture techniques were used to document a decline in brown bear density, and harvest data from that area was correlated with the decline (Miller 1988). Sex ratio of bears harvested in fall seasons and increasing numbers of subadults harvested best reflected the declining population (Miller 1988). Harris (1984) also noted that in his simulations, sex ratio in harvest best reflected altered population status. In Unit 13 mean age of harvested males also declined, and the number of subadults harvested increased (Miller 1988). Although these trends were present in sex and age composition of the Unit 13 harvest data, they were difficult to detect because these data were noisy. Also, these data are subject to alternative interpretations (Miller 1988, 1990b).
Estimating Reproductive Rates:

The relative importance of different reproductive and mortality factors on polar bear growth rates was examined using ANURSUS by Taylor et al. (1987b). These authors concluded that the single most significant parameter was survivorship of adult females. Similar conclusions for brown bears were reached by Knight and Eberhardt (1984, 1985).

Periods of time and sample sizes required to estimate reproductive parameters were estimated with simulation studies, where the parameters were both complex and simple (Miller 1990a). The complex scenarios would require longer periods and larger samples than the simple scenarios. These studies indicated that 10 marked females were not adequate to estimate any reproductive parameters to the point where 90% of the samples drawn from the same population correctly estimated (within ±5%) the true value of the reproductive parameter in the complex scenarios. This sample size was also inadequate to estimate litter size or age at first reproduction, even for simple scenarios regardless of length of study; it did estimate reproductive interval for the simple scenario after 7 years of study. For sample sizes >25 females, age at first reproduction was correctly estimated within ±5% of the true value in >90% of the samples in year 3 of the study for the simple scenario and in year 5 for the complex scenario. For estimation of litter size this level of precision was reached for samples > 50 in year 11 of the complex scenario and in year 6 of the simple scenario.

Objective 2--Development and Testing of Tait’s Harvest Data Interpretation Model

The components of the model delivered by D. Tait would not work without significant reprogramming; some components appeared to come from a preliminary version of Tait’s model. Portions of the model were rewritten (Appendix A3), and an executable version of the program was obtained through a contract with R. Fagen (University of Alaska, Southeast). This rewritten version does not have all the capabilities described by Tait (1983). The code for the revised version of the model is presented in Appendix B. Fagen also did preliminary testing using simulated data sets, simulated data sets with introduced errors, and real harvest data from Units 4, 8, 9, and 13. Results of the tests on simulated data are presented in Appendix A; results of the tests on real data are in Appendix A1. Results with real data sets were not as successful as with the simulated data sets for reasons which remain unclear. Regardless, it is encouraging that the revised version of the model ran and did not find fatal errors with the real data. Instructions for running the revised Tait model are in Appendix A2.

Additional testing of Tait’s model is necessary to evaluate its utility as an indicator of trend in real bear populations. At
present it appears that the best that can be hoped for is that the model will generate predictions that may provide an additional indicator of population trend under some circumstances. We recommend additional testing and refinement of the model to see if it has this potential. This testing could not be completed in time to be included in this report.

Objective 3. Survey of Bear Management Approaches in North America

States and provinces with significant populations of any of the 3 species of bears in North American were contacted to determine the basis for their management programs. In this survey information was requested on how quotas were set and trends in numbers were determined. No detailed compilation of responses to these queries was done; however, these responses, as well as other results obtained in this study, were used in preparation of a paper on population management of bears (Miller 1990b). Garshelis (In press) compiled results of a similar survey for black bears.

CONCLUSIONS

Sex and age composition of bear harvest data is very difficult to interpret. This study has been more successful at demonstrating this difficulty than at developing meaningful new ways to interpret these data. Reliance on sex and age composition of harvest data to indicate trends in bear populations is extremely risky. Such reliance should be done only when managers are willing to accept high risks of missing trends until such trends are very far advanced. A more thorough discussion of these points is provided in Appendix C.

Even though age composition of harvest data is expensive to collect for bear populations, the insights into population trend that can potentially be gained from a thorough and open-minded examination of these data may be worth the expense. Although reliance on these data is inadvisable in most circumstances, they may be useful as an additional indicator of trend in helping to select between conflicting interpretations. Additional study is necessary to more completely evaluate the usefulness of this age data; at present it would be premature to stop collecting age data. This is especially true for bear populations for which there are few techniques available to directly measure numbers or trends (Harris 1986) and where the techniques that are available are usually very expensive, typically imprecise, and also commonly apply only to areas that are small, compared with the size of the areas for which managers are responsible. For these same reasons it is necessary to continue to experiment with the harvest data model described by Tait (1983) to see whether it can be developed into a useful tool. At present, a reasonable way to set harvest quotas appears to require a population estimate (sometimes obtained by extrapolation from density estimates), an
estimate of sustainable harvest rate (requires data on reproductive rates and natural mortality rates), and accurate data on number of male and female bears killed (Miller 1990b). In some areas, these data may be usefully supplemented by trend surveys (Sellers and McNay 1984, Schoen and Beier 1990). Techniques available to detect trends in bear populations are inadequate to detect small-to-moderate changes in bear numbers in short periods of time. This means that in circumstances where managers desire to avoid large reductions in bear populations, conservative quotas must be established (Miller 1990b).

LITERATURE CITED


PREPARED BY:

Sterling D. Miller
Game Biologist III

SuzAnne M. Miller
Biometrician III

Karl B. Schneider
Regional Research Coordinator

APPROVED BY:

W. Lewis Pamplin, Jr., Director
Division of Wildlife Conservation

Wayne L. Regelin, Deputy Director
Division of Wildlife Conservation
Appendix A. INTERPRETATION OF SIMULATED BROWN BEAR HARVESTS USING TAIT’S POPULATION MODEL

by
Robert Fagen
University of Alaska, Southeast
June 1990

BACKGROUND AND OBJECTIVES

Tait (1983) applied a mathematical population model to the problem of estimating brown bear population trends and demographic parameters from harvest data. Tait’s original running programs seem not to have been preserved, but Tait delivered a later implementation in FORTRAN code to ADF&G (Miller and Miller 1987). The format of this later program did not permit testing under an adequate range of simulated conditions, much less on real harvest data.

There is need to improve estimates of brown bear population trends, and interpretation of harvest data using Tait’s or other computer models is one possible approach. Miller and Miller (1988) discuss the issues in depth and present simulation results that directly address feasibility of such interpretations.

This study evaluated the Tait program as received from the Division of Wildlife Conservation, made extensive changes to the code to enable testing on simulated data, and carried out a specified series of tests. The objective of the study was to evaluate the performance of the Tait program in terms that would allow biometricians and managers in the Division to decide on its possible applicability and potential usefulness for analyzing brown bear population trends.

Results of Initial Testing

The Tait program was initially tested on representative datasets from Tait’s thesis, two simulated datasets furnished by Sterling Miller, and one dataset supplied with the code itself. The program would not execute on any of these datasets except for the one supplied with the code. Fatal arithmetic errors (exponential overflow) occurred in two subroutines of the program that calculate coefficients linking female to male population estimates through a recruitment model. The following steps were taken to analyze this situation.

1. The equations in Tait’s thesis were rederived.
2. The FORTRAN code was checked line-by-line and all numerical calculations verified by hand.

Results of these two analyses identified modelling approximations and/or assumptions that need to be examined. An obvious programming error was detected and corrected.
Tait's thesis and program assume that recruits in a given year are produced by the females alive that year. This would only be the case if all cubs born in a given year became vulnerable to hunting in that same year. This assumption has been replaced by introducing the correct time lag between birth and recruitment. When the program estimated a demographic parameter such as natural mortality or recruitment, it stored its estimates in a scratch variable. Because of a programming error, these values were never copied into the parameter vector actually used in population estimation. This error has been corrected. The recruitment coupling terms used for feeding back information from one sex to the other were approximations rather than full implementations of the likelihood function. These terms seemed to cause numerical problems. They were truncated to avoid these problems in the hopes of producing code that would generate population and parameter estimates rather than fatal arithmetic errors. The question of how best to model and implement brown bear recruitment for estimation purposes remains open, both in the context of Tait's program and in general.

Since parameter estimation appeared to be a problem for the original program, an alternative parameter estimation method known as systematic search was coded in addition to Tait's original likelihood approach. A user can select either of these two approaches, parameter-by-parameter, when running the code. Systematic search is a structured version of likelihood estimation in which many different starting values are used in the hopes of finding multiple local maxima, then selecting the most probable of these local solutions. In most cases, Tait's original likelihood approach performs as well (or as poorly) as systematic search. In some cases, systematic search works better, but it is not yet possible to predict just what circumstances would favor this method over Tait's likelihood equations.

Several other changes to the program were necessary to make it easier to run and test (e.g., free-format input). The job of preparing the Tait program for testing was finally completed in mid-May 1990. Although the program has been extensively reworked, the code was developed solely in order to make it possible to test Tait's approach on simulated data. It was not the goal of the project to develop a production-style program or to optimize code. Some of the redundancies and flaws in Tait's original program remain in the code we tested, but they did not interfere with the actual testing or influence the interpretation of the results. The program that we tested retains the following limitations of Tait's original program:

1. The four parameters estimated are sex-independent natural mortality, age-independent male and female hunting mortality, and recruitment, as defined in Tait's thesis. If these quantities are assumed to vary over age and year, the user would need to modify the code, either
a. to estimate age, sex and year-specific values (probably impractical), or preferably
b. to assume that the ratios of parameters are known by age, sex, year, etc. so that any age, sex, or year-specific parameter could be calculated from the estimate. For example, suppose that we knew that hunting effort in years 1-10 was about half that of years 11-20, but we did not know the absolute values. It would then be possible with minimal work to reprogram the code so that what was actually estimated was the year 1-10 mortality. The year 11-20 mortality would simply be calculated from the year 1-10 mortality estimate by doubling its value. If it is possible to specify in advance the most general case to be considered (e.g. the full model in Tait's thesis, in which all parameters are age-, sex-, and year-specific), a more flexible program could then be written to accommodate this full generality, with user-friendly input options to specify particular subsets of assumptions. This was not actually done because it took so much time just to get the program running at all.

Recruitment Model

The recruitment model assumes that recruitment rates are independent across year, mother’s age, and sex. Is this assumption valid? In a good year, all mothers of all ages are likely to produce more cubs of both sexes. There may be some statistical dependence that is important to good estimation but that the model neglects. We also know from Mitch Taylor’s simulations that it can be risky to assume an equal probability of birth per female per year when females with dependent young have probability 0 of producing more offspring before weaning their current litter. And Tait’s ad hoc method for computing recruitment variance is formally equivalent to a binomial variance, but the quantity a in Tait’s formula

$$\frac{1}{2} \left( Na(1-a) \right)$$

is a recruitment rate, not a probability, and could actually be greater than 1. The recruitment model also does not acknowledge factors important to reproduction such as individual innovativeness, the quality of mother-young relationships, etc. which are much more apparent when bear families are observed in the field than when they appear as harvest statistics.

Results of Simulation Runs

There were three kinds of simulation runs: deterministic in which all assumptions were obeyed; stochastic in which all assumptions were obeyed; and stochastic in which errors of certain kinds were introduced. In general, our version of the Tait program correctly detects population trends in all three cases. However, it frequently mis-estimates absolute population sizes. Also, the errors in its estimate of annual rates of population increase or decrease may be unacceptably high in some cases and for some purposes.
A tabulation and discussion of the specific experiments follows.

Test Data

Three test datasets were used to evaluate the program. These datasets were chosen to best demonstrate the strengths and weaknesses of Tait's approach, not to mimic actual bear populations in detail.

Each dataset assumed a maximum age of 30 years. 20 years of data were generated from an initial age distribution vector. Bears were assumed to be vulnerable to hunting beginning at age 2. Female bears were assumed to begin producing young at age 5. The first and second datasets both had an initial age distribution vector identical to that used by Tait (1983, Table I, page 51).

The three datasets differed in order to simulate increasing, decreasing, and near-constant populations. Table I gives the parameter values defining each dataset. All rates are on an annual basis and are defined as probabilities (fractions), not percentages. At and following the age of first reproduction, all females were assumed equally likely to produce surviving offspring. Sex ratio of recruits was assumed to be 1:1. Except in the specific cases cited above, parameters were assumed constant over age, sex and year class.

Deterministic Simulations

The three populations were simulated deterministically and the modified Tait program run with parameter estimation. True parameter values were given to the program as initial conditions. The program estimated all four parameters, given these initial conditions and the harvest data. If the results of this test warranted further investigation, a second run was made in which the program was given the true parameter values and no estimation was done. Experiments in which inaccurate starting values were supplied as initial conditions for parameter estimation were not performed.

TABLE I

<table>
<thead>
<tr>
<th>Data Set Parameter Values</th>
<th>Data Set 1 (Increasing)</th>
<th>Data Set 2 (Decreasing)</th>
<th>Data Set 3 (Near Constant)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rate of Population Growth</td>
<td>0.03</td>
<td>-0.08</td>
<td>0.001</td>
</tr>
<tr>
<td>Natural Survival</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
</tr>
</tbody>
</table>
Male 0.1 0.3 0.1
Death Rate (hunting)

Female 0.03 0.09 0.03
Death Rate (hunting)

Recruitment 0.2 0.1 0.1476
(female recruits/adult female)

The increasing population (Data Set 1) was reconstructed accurately (Fig. 1) with all parameter estimates within less than 1% of their true values (.929 for survival, .099 for male hunting mortality, .03 for female hunting mortality, .194 for recruitment). The trend of the decreasing population (Data Set 2) was correctly indicated by the estimates, with some bias apparent (Fig. 2 for estimates, Fig. 3 for true). Is the difference between the deterministic results for Data Set 1 and Data Set 2 due to deviations from the stable age distribution in the initial age distribution vector? The same initial population was used for both data sets, and one vector cannot be the stable age distribution for two sets of vital rates, but the true population seems to be changing exponentially in both cases with no signs of transient behavior.

Transients were apparent in the Data Set 3 population, which stabilized after about 15 years. Data Set 3 was analyzed from years 5-25 (Figure 4) and 15-35 (Figure 5). The true population was tracked in both cases, with population size estimates that were biased slightly (less than 2%) upwards and good parameter estimation given the true values as initial conditions (.93 survival, .098 male hunting, .029 female hunting, .143 recruitment).

Stochastic Simulations

Random noise was added to the population model as in Tait (1983 p. 23-30), assuming independent binomial distributions for each sex, age, and year class and for each population process (hunting, natural mortality, recruitment). In general, performance was considerably poorer for the stochastic case, and a bias in population reconstruction was evident (Figs. 6-8 for Data Sets 1-3). There were few noticeable differences between replicates (Figs. 7, 9.) When recruitment was fixed at its true value for Data Set 2, the bias appeared to be slighter (Fig. 10). Tait (1983, pp. 52-77) concluded that when his population reconstruction is based on true parameter values, it is nearly unbiased. However, with all parameters fixed at their true values, the experiment with Data Set 3 (Figure 8) indicates a
failure to track a near-constant population. Without numerous replicates, it is impossible to say whether this error is a chance deviation or represents a true bias of the population reconstruction method.

Ageing Errors

For Data Sets 1 and 2, ageing errors were simulated by assuming that 10% of the sample was incorrectly assigned to age classes 2 years older than true (Fig. 11 for Data Set 1, Fig. 12 for Data Set 2) or 2 years younger than true (Fig. 13 for Data Set 1, Fig. 14 for Data Set 2). Comparing with Figs. 6-7, the error introduced by mis-ageing appears to be considerably less than the errors introduced by population reconstruction and parameter estimation when all ages are correct. The sign of the overall population trend is correctly estimated in all cases.

Females Wrongly Sexed as Males

For Data Sets 1 and 2, when 10% of females were wrongly sexed as males (Fig. 15 for Data Set 1, Fig. 16 for Data set 2), the error is smaller for Data Set 1 than in the unperturbed case and larger for Data Set 2. The sign of the estimated population trend is correct in all cases.

Unreported Kills

When 20% of the harvest is randomly selected as not reported (Fig. 17 for Data Set 1, Fig. 18 for Data Set 2), the estimates of population sizes are affected, but the trends remain correct.

Analysis of Miller and Miller Scenarios 1-4

Miller and Miller scenarios 1-4 were analyzed using the modified Tait program. These scenarios included parameters that varied over age and/or time. The Tait program assumed these parameters to be constant. Also, random noise was added. These two conditions represent a stronger test of the program, more demanding than the previous simulations because of the combination of unmodelled parameter trends plus random noise. Results of the runs are presented in Figures 19-22 (comments in brackets were added by SDM).

The Scenario 1 population is tracked correctly with the usual bias error (Figure 19). [This scenario represented an increasing population with 10% harvest of males and 5% harvest of females in each age class and low natural mortality (growth rate = 2.86%/year)].

The true Scenario 2 population is declining very slowly. The program estimates a slight increase over 20 years, again with the usual bias (Figure 20). [In this scenario older animals of both sexes were less vulnerable than younger ones. As in Scenario 1, males were twice as vulnerable as females in each age class.
This scenario simulates opportunistic hunting where older experienced animals are better at avoiding hunters.

The true Scenario 3 population is declining very slowly, but the program estimates an increase of about 1%/year over 20 years with the usual bias error. This experiment was one of the few cases in which the sign of a population trend was estimated incorrectly over the entire simulation period of 20 years. The absolute magnitude of the error, however, is relatively small (Figure 21). [In this scenario, older bears of both sexes were more vulnerable than younger ones in each age class, males were still twice as vulnerable as females in each age class. This scenario simulates trophy hunting].

The true Scenario 4 population is declining very slowly. The program estimates a more rapid decrease (Figure 22). (Is this result comparable with the Data Set 3 result, Figure 8?). [In this scenario older females are less vulnerable than younger ones and older males are more vulnerable than younger ones. This scenario simulates trophy hunting of males and protection of females with cubs].

Analyses of Actual Data (see Appendix A1)

Experimental analyses of real data using the modified Tait program were reported to the Division. The program ran normally and produced numerical output using Tait’s likelihood method for parameter estimation, but failed in two instances when using systematic search. Division staff had previously determined that analysis of real data was a problem for the original Tait program, in contradiction to the results in Tait (1983, p. 107-122). The approach taken to analyze real data was to run the program with parameter estimation, and in addition to conduct separate runs assuming a priori lower and upper bounds for the parameters. These bounds were given to the program as fixed inputs and no parameter estimation was conducted.

Conclusions and Recommendations

1. The original Tait program as received from Tait by the Division should not be used at all except for archival purposes.
2. The modified Tait program developed on this project is an appropriate research tool that could be used in management as an aid to intuition by an experienced manager in conjunction with appropriate additional indicators of population trends. It should not be used alone or by individuals unfamiliar with its assumptions and simplifications. It should not be used at all by individuals unfamiliar with brown bear biology and management. In its current form and with its current performance characteristics, it should not now be adopted by the Division as the method of choice for interpreting brown bear harvest data. This is not to say that it is useless. In fact, it consistently distinguished moderately strong "up" trends from strong "down"
trends, even when realistic errors were introduced in the simulations.

3. The program's estimates on simulated stochastic data are virtually always higher than the true values. This is a true bias and has the same sign and about the same magnitude on multiple Monte Carlo replicates. Why does this bias occur? Tait reported no bias in his numerical experiments and stated that the program's estimates were unbiased.

4. With the stochastic Data Set 3, true parameter values were given to the program, but the reconstruction did not track a constant population. This population should have been reconstructed with more accuracy than Figure 8 indicates.

5. It would be feasible to further improve the modified Tait program, and these improvements could be expected to yield considerable benefits in terms of performance, both in research and as a management tool. Specific recommendations for future work are as follows.

   a. Find the reason for the bias error (3. above) and remove the error.

   b. Find the reason for poor tracking of a constant population (4. above) and correct this error.

   c. Redo the recruitment model to obtain better coupling, and therefore better estimation, using better natural history and demographic information.

   d. Investigate the use of auxiliary data -- demographic parameters from telemetry studies, effort estimates, theoretical calculations, and possible additional data sources.

6. There is already enough information available on brown bear population dynamics in general, and Alaska brown bears in particular, to convincingly demonstrate the sensitivity of brown bear populations in the abstract to development and overharvesting. Whether this information alone will be sufficient to demonstrate specific threats to specific Alaskan populations is not clear. It would pay to know just what sort of information would be convincing enough to effect changes where changes are needed now and in the immediate future to ensure healthy brown bear populations in the long term.

7. As experience over the past decade with Tait's program should clearly indicate, development of complex numerical computer programs is slow, expensive and frustrating. Tait's modified program has 840 lines of FORTRAN code. In the 6 years since 1984 -- an overall rate of progress less than one FORTRAN statement every three days -- this program has still not developed into a practical tool for wildlife managers. Its behavior continues to puzzle experienced technical analysts. The key difficulty
appears to be the model's (and program's) approach to recruitment. This approach is both too simple to be realistic and too complex to implement in functional code in a reasonable amount of time. There is need for quantitative studies to better understand the social and reproductive behavior of bears and its population consequences. These studies would lead to development of a formal recruitment model incorporating breeding by females, rearing of young to independence, litter size, interbirth intervals, and natural mortality of adult females. This goal can only be attained by conducting long-term studies of known individuals whose behavior can be monitored both intensively, as individuals, and extensively, as members of populations, over time periods of a generation or more.

8. The Tait program is the best available quantitative method for analyzing age-structured brown and grizzly bear harvest data in the absence of auxiliary information. Additional work is needed, but prospects for developing the program into a powerful research tool are excellent. Used in conjunction with auxiliary information, it also has potential for contributing to quantitative management. National and international interest groups, including some with in-house research capabilities and strong extramural funding programs, may seek to declare grizzly and brown bears threatened or endangered during the next decade. Tait's method could become a quantitative research technique that would positively support the Division's activities in bear biometrics in a scientifically visible manner on the national and international levels.

LITERATURE CITED


Appendix A. List of Figures

Figure 1. Predicted and actual trend for a deterministic test dataset of a growing population.

Figure 2. Predicted and actual trend for a deterministic test dataset of a declining population with parameter estimation.

Figure 3. Predicted and actual trend for a deterministic test dataset of a declining population without parameter estimation.

Figure 4. Predicted and actual trend for a deterministic test dataset of a stable population during simulation years 5-25.

Figure 5. Predicted and actual trend for a deterministic test dataset of a stable population during simulation years 15-35.

Figure 6. Predicted and actual trend for a stochastic test dataset of a growing population.

Figure 7. Predicted and actual trend for a stochastic test dataset of a declining population with parameter estimation.

Figure 8. Predicted and actual trend for a stochastic test dataset of a stable population without parameter estimation.

Figure 9. Predicted and actual trend for a stochastic test dataset of a declining population with parameter estimation.

Figure 10. Predicted and actual trend for a stochastic test dataset of a declining population without parameter estimation.

Figure 11. Results of introducing aging error (10% of harvest overaged by 2 years) for a deterministic test dataset of a growing population.

Figure 12. Results of introducing aging error (10% of harvest overaged by 2 years) for a deterministic test dataset of a declining population.

Figure 13. Results of introducing aging error (10% of harvest underaged by 2 years) for a deterministic test dataset of a growing population.

Figure 14. Results of introducing aging error (10% of harvest underaged by 2 years) for a deterministic test dataset of a declining population.

Figure 15. Results of introducing sexing error (10% of female harvest missexed as male) for a deterministic test dataset of a growing population.
Figure 16. Results of introducing sexing error (10% of female harvest missexed as male) for a deterministic test dataset of a declining population.

Figure 17. Results of introducing underreporting error (20% of harvest randomly selected as not reported) for a deterministic test dataset of a growing population.

Figure 18. Results of introducing underreporting (20% of harvest randomly selected as not reported) for a deterministic test dataset of a declining population.

Figure 19. Results of data generated by Scenario 1 of Miller and Miller 1988 (increasing population with 10% harvest of males and 5% harvest of females in each age class and low natural mortality; growth rate = 2.86%/year).

Figure 20. Results of data generated by Scenario 2 of Miller and Miller 1988 (decreasing population with older animals of both sexes less vulnerable than younger ones, but males twice as vulnerable to females in each age class; growth rate = negative 2.6%/year).

Figure 21. Results of data generated by Scenario 3 of Miller and Miller 1988 (decreasing population with older animals of both sexes more vulnerable than younger ones, but males twice as vulnerable to females in each age class; growth rate = negative 1.6%/year).

Figure 22. Results of data generated by Scenario 4 of Miller and Miller 1988 (decreasing population with older females less vulnerable than younger ones and older males more vulnerable than younger ones; growth rate = negative 1.6%/year).
True (---) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Females Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year

Fig. 5

Total Population

1375 1380 1385 1390 1395 1400 1405 1410 1415

0 5 10 15 20

Year
True (--) and Estimated (*) Totals Vs. Year
True (- -) and Estimated (*) Totals Vs. Year

Fig. 7

Total Population

0  200  400  600  800  1000  1200  1400  1600

0  5  10  15  20

Year
True (--) and Estimated (*) Totals Vs. Year

FIG. 8

Year

1300 1400 1500 1600 1700 1800 1900

Total Population
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year

Fig. 10

Total Population

Year

0 5 10 15 20
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year
True (--) and Estimated (*) Totals Vs. Year

Year

Total Population

0 1500 2000 2500 3000 3500 4000 4500 5000 5500

20
True (--) and Estimated (X) Totals Vs. Year

Fig. 21

Total Population

2000 3000 4000 5000 6000 7000

Year

0 5 10 15 20
APPENDIX A1. TEST ANALYSES WITH ACTUAL HARVEST DATA

[CAUTIONARY NOTE FROM S.D. MILLER: Our instructions to Dr. Fagen were to prepare a separate report describing results of his preliminary tests on actual data sets. Our intention was not to print these analyses in this report because of concerns that such analyses could be misapplied to a management program. However, we have decided to include these analyses as the report is incomplete without them; these analyses clearly indicate remaining problems with using the Tait approach to interpret real data sets. In Unit 9, for example, we have independent evidence that the population has increased during the late 1970s and 1980s (Sellers and McNay 1984: Board report; and Miller and Sellers Black Lake Progress report, 1990), rather than decreased as illustrated in these tests. Bear hunting has been very conservative on in GMU 8 (Kodiak) and we are quite sure the population there is stable rather than declining as indicated in these preliminary runs. Perhaps this indicates a similar problems as indicated, above, with the misidentification as declining of a simulated stable population. The predicted trend in GMU 13, on the other hand, generally corresponds with independent analyses of trend in that area (Miller 1990). In GMU 4 we know that assumptions of geographic homogeneity of kill is incorrect, most hunters kill bears along the beach leaving interior subpopulations relatively unhunted. These analyses of these real datasets from these 4 areas should not be utilized in any management context, they are included only for the purposes of better understanding the strengths and weaknesses of the model as it is currently configured.]--SDM.

ACTUAL HARVEST DATA

I received real harvest data from the Division and conducted exploratory analyses of the data from Units 4, 8, 9, and 13. In each case I analyzed the total (spring + fall) dataset for each year. I analyzed all of each unit and did not do any analyses of individual subunits. The program assumed that natural mortality was constant over age, sex, and year; male harvest rate was constant over age and year; female harvest rate was constant over age and year; and recruitment rate was constant over year.

For the first 4 runs (Figures A, B, C, D) I assumed a fixed annual natural mortality of 0.01 (1%) of each age-class, annual recruitment rates (females/adult female) of .115 for Units 4, 9, and 13 and .135 for Unit 8. The program estimated male and female harvest rates using maximum likelihood. In these runs, we get:

<table>
<thead>
<tr>
<th>Figure</th>
<th>Unit</th>
<th>Average population</th>
<th>Overall trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>4</td>
<td>300</td>
<td>Accelerating Decrease</td>
</tr>
<tr>
<td>B</td>
<td>8</td>
<td>500</td>
<td>Accelerating Decrease</td>
</tr>
</tbody>
</table>

45
For the next 8 runs (Figures E, F, G, H, I, J, K, L) I bounded the possible trends in the population using fixed parameter values rather than parameter estimation. Low-productivity and higher-productivity options were used. The recruitment values were fixed and unchanged from the previous 4 runs.

<table>
<thead>
<tr>
<th>Fig.</th>
<th>Area</th>
<th>Productivity</th>
<th>Avg. pop.</th>
<th>Overall trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>E</td>
<td>4</td>
<td>Low</td>
<td>300</td>
<td>Accelerating Decrease</td>
</tr>
<tr>
<td>F</td>
<td>4</td>
<td>High</td>
<td>12000</td>
<td>Increase</td>
</tr>
<tr>
<td>G</td>
<td>8</td>
<td>Low</td>
<td>500</td>
<td>Constant -&gt; Decrease</td>
</tr>
<tr>
<td>H</td>
<td>8</td>
<td>High</td>
<td>4500</td>
<td>Increase</td>
</tr>
<tr>
<td>I</td>
<td>9</td>
<td>Low</td>
<td>200</td>
<td>Constant -&gt; Decrease</td>
</tr>
<tr>
<td>J</td>
<td>9</td>
<td>High</td>
<td>1100</td>
<td>Constant -&gt; Decrease</td>
</tr>
<tr>
<td>K</td>
<td>13</td>
<td>Low</td>
<td>100</td>
<td>Increase -&gt; Decrease</td>
</tr>
<tr>
<td>L</td>
<td>13</td>
<td>High</td>
<td>200</td>
<td>Increase -&gt; Decrease</td>
</tr>
</tbody>
</table>

For Units 9 and 13, results of all experiments are consistent and indicate populations currently decreasing. For Units 4 and 8, conclusions are sensitive to assumed parameter values.

My results are not conclusive. However, in view of the overall good performance of the modified Tait program in detecting trends in simulated bear populations, I feel it would be unwise to ignore the suggestive evidence of bear populations at great risk.
that these experiments appear to furnish for widely separated areas of Alaska.
Appendix A1. List of Figures

Figure A. Predicted trend in GMU 4 a higher using fixed annual natural mortality rate of 1% of each age class, and fixed annual recruitment rate (0.115 females produced/adult female).

Figure B. Predicted trend in GMU 8 using fixed annual natural mortality rate of 1% of each age class, and a higher fixed annual recruitment rate (0.135 females produced/adult female).

Figure C. Predicted trend in GMU 9 using fixed annual natural mortality rate of 1% of each age class, and fixed annual recruitment rate (0.115 females produced/adult female).

Figure D. Predicted trend in GMU 13 using fixed annual natural mortality rate of 1% of each age class, and fixed annual recruitment rate (0.115 females produced/adult female).

Figure E. Predicted trend in GMU 4 using fixed parameter values for low-productivity.

Figure F. Predicted trend in GMU 4 using fixed parameter values for high-productivity.

Figure G. Predicted trend in GMU 8 using fixed parameter values for low-productivity.

Figure H. Predicted trend in GMU 8 a higher using fixed parameter values for high-productivity.

Figure I. Predicted trend in GMU 9 using fixed parameter values for low-productivity.

Figure J. Predicted trend in GMU 9 using fixed parameter values for high-productivity.

Figure K. Predicted trend in GMU 13 using fixed parameter values for low-productivity.

Figure L. Predicted trend in GMU 13 a higher using fixed parameter values for high-productivity.
GMU 4
APPENDIX A2. INSTRUCTIONS FOR RUNNING THE TAIT PROGRAM

These instructions refer to the microcomputer version of the Tait program delivered to the Division in June 1990.

Inputs for harvest data are unchanged from the original Tait program except that the format is now free rather than fixed.

The program (subroutine GETDAT) reads male, then female harvest from file 9.

First Year  Male Harvest (ages...)
            Female Harvest (ages...)

Second Year Male Harvest (ages...)

There are two output files, one for the population reconstruction by age and a second for data (male, female, total) to be graphed.

To actually run the program, select input and output files from the keyboard and then specify a parameter option. Systematic search is not recommended at this stage, so when the program (subroutine CHANGE) asks for parameter selection for systematic search, type 0 (zero). Then enter the total number of parameters to be estimated (up to 4) as an integer. The program will then ask for the ID's. For instance, if you wanted to estimate male and female harvest rates, leaving natural mortality and recruitment as fixed inputs, you would have specified the fixed parameter values in the last line of your input file, typed 2 for the number of parameters to be estimated, and then at the prompt "Enter ID of the parameters being estimated", typed 2 3 for male and female hunting mortality. If estimating all 4 parameters, the inputs are:

Parameter Selection for Systematic Search
0

Enter # of parameters being estimated:
4

Enter ID of the parameters being estimated:
1 2 3 4

These inputs are also free-format -- see subroutine CHANGE.

The units of the parameters are:

Adult survivorship rate, fraction surviving per year (input 1 minus natural mortality)
Harvest rates, fraction killed per year

Recruitment, number of females recruited per year/number of adult females NR years ago where NR is age at which bears become vulnerable to hunting.

Disregard the comments on harvest effort and relative vulnerability in the main program header -- male and female harvest rates are input, not effort and relative vulnerability.
APPENDIX A3. Description of general changes from original to modified versions of Tait's program.

Main Differences Between Programs TAIT and TAITBEAR

The computer program from Tait (called TAIT) has completely been re-organized as a new program TAITBEAR. The following documents the main changes and differences between these two programs.

Main Differences of the Common Subroutines of two Programs

1. Dimension declaration and common statements has been organized in file TAITB.CMN for program TAITBEAR. TAITB.CMN is included in the main program and subroutines of TAITBEAR. Such changes are necessary so that the program is easily modified for large data sets, and the codes are more concise and clean.

2. Main program has been modified to perform systematic search.

The tasks in the old main program have been moved to subroutine ESTIMATE.

3. Subroutine OUTPUT (in old program as PTOUT) outputs only the best reconstructed population and associated parameters in program TAITBEAR. The old program outputs the results at each iteration. When the iteration number is large, it is impossible for a hard disk to contain the output for each iteration. Outputting all the results also waste users' time for finding the best solution and separating the best solution from the rest of garbages.

4. Subroutine GETDATA: change the format-input as free-format input. Free-format input can save users' time to prepare the input data sets. Birth rate parameter PN(4) is re-defined as recruitment rate for relaxing assumptions of constant survival rate from the time born to the time of recruiting. PN(4) and PN(5) have been generalized for different data sets.

5. Subroutine XDFUN: Delete statements which re-assign values to PN(). Such re-assignment is an error of the old program. With the re-assignment statements, no new estimated parameters can be used. Subroutine XDFUN has been changed into a part of subroutine ESTIMATE.

6. Subroutine BT: See the previous notes. The BT term has been re-derived and implemented.

7. Subroutine BTSUM: the new program has implemented the time lag of recruitment. In the old program, females in current years producing recruitment in current year was assumed. This assumption is not very realistic and has been relaxed in the new program.

8. Subroutine XIT: Some useless statements in the old program has been cleared up for efficiency and conciseness.

9. Subroutine GEST: Add algorithms to estimate male harvest rate, female harvest rate and recruitment rate, which are not available in the old program.

10. Subroutine INIT: Clear up useless statements in the old program.
Unchanged Subroutines and Functions
ADJ, DBYDX, EQ, INDOF, REDIST, SETX, SGTSL, and TRISUP.

New Subroutines
1. Subroutine CHANGE: Specify parameters for systematic search, input new parameter values, and indicate parameters for estimation. This subroutine is essential to make the program general.

2. Subroutine ESTIMATE: Basically perform the same tasks as the main program and subroutine XDFUN in the old program. The tasks are to call different subroutines to reconstruct abundances and estimate parameters. The reconstruction and estimation process will be iterated until the maximum change in the reconstructed population is less than 0.1 or the iteration number exceeds 200.

   The final results are the reconstructed population and associated parameters under which the log-likelihood function value is maximized.

3. Subroutine LIKELI: Calculate the likelihood function value for a set of reconstructed abundances and estimated parameters, i.e. evaluating equation 3.4 at p29 of the Tait's thesis.

4. Subroutine INOUT: Get input and output file names.

Programs
$ diff newtait.for taitbear.for
**********
Appendix B. Source language for modified version of Tait's model.

PROGRAM TaitBear
C=======================================================================C 
C This program reconstructs bear population through maximum 
C likelihood method. The old version of this program is TAIT, which 
C implemented the Tait's model. Systematic search with maximum likelihood as 
C objective function for population parameter estimation has been 
C to this new version. Tait's thesis (1983, UBC) contains the 
C information on the model. ---Jie Zheng, UAF, AK, May 31, 
C 1990. C
C
\begin{verbatim}
C
C br(,) are recruitment rates by year and age.
C bv(,) are variances of recruitment by year and age.
C Harv(,,) are hunting data by year, age and sex.
C hp(,,) are hunting mortality rates by year, age and sex.
IA IS THE AGE OF THE FIRST HARVESTABLE AGE CLASS.
ijk(,) are index function (3D <-> 2D).
NA IS THE NUMBER OF HARVESTED AGE CLASS.
NP is NUMBER OF PARAMETERS.
NR IS THE AGE OF THE FIRST REPRODUCTIVE AGE CLASS.
NY IS THE NUMBER OF YEARS.
PN(1) IS THE ADULT SURVIVORSHIP RATE.
PN(2) IS THE HARVEST EFFORT (MALE HARVEST RATE)
PN(3) IS THE RELATIVE VULNERABILITY (FEMALE HARVEST RATE)
PN(4) IS THE RECRUITMENT RATE.
PN(5) IS THE RECRUITMENT VARIANCE.
pp() are the same as PN(), but contains the best estimated 
C
\end{verbatim}


ps is step size for Newton correction.

sb() are expected recruitment by year.

sn() = rhs2() are the estimated abundances by year, age and sex.

sp(,,) are survival rates by year, age and sex.

sv() are variances of recruitment by year.

x(,,) are the estimated abundance-by-age-by-sex.

xx(,,) are the best estimated abundance-by-age-by-sex.

C=======================================================================C
 inclusive: ’taitb.cmn’

dimension pl(np-l),pm(np-l),si(np-l),id(np-l),inv(np-l)
data si/0.05,0.02,0.02,0.02/
call inout
call getdat
do 5 i = 1, np-1
   pl(i) = pn(i)
5 pm(i) = -1.0
   call change(np-1,pl,pm,si,iy,iid)
   j = 0
do 10 i = 1, np-1
   j = j + 1
   if (pm(i).lt.0.0) then
      pn(i) = pl(i)
      j = j - 1
   else
      id(j) = i
      inv(j) = int((pm(i)-pl(i))/si(i))
   endif
10 continue
if (j.lt.1) then
   call estimate
   goto 71
endif

do 60 i = 1, inv(1)
   pn(id(1)) = pl(id(1))+(i-1)*si(id(1))
   if (j.lt.2) then
      call estimate
   else
      do 50 i1 = 1, inv(2)
         pn(id(2)) = pl(id(2))+(i1-1)*si(id(2))
         if (j.lt.3) then
            call estimate
         else
            do 40 i2 = 1, inv(3)
               pn(id(3)) = pl(id(3))+(i2-1)*si(id(3))
         endif
      endif
   endif
60 continue

if (j.lt.4) then
  call estimate
else
  do 30 i3 = 1, inv(4)
   pn(id(4)) = pl(id(4))+(i3-1)*si(id(4))
  call estimate
end if
endif
continue
endif
continue
endif
continue
71 call output
stop
END

SUBROUTINE ADJ(IJK, NY, NA,N)
C ROUTINE ADVANCES THRU THE IJK INDEXES TO SPAN
C THE TOTAL MALE AND FEMALE POPULATION
C I J K ARE THE POPULATION SUBSCRIPTS
C I1 J1 K1 ARE THE COHORT POINTERS THE SUBSCRIPTS OF THE AGE
C SEX CLASS LEADING THE I J K COHORT
C
C START BY UPDATING I AND J THEN CHECK IF FEASIBLE
INTEGER IJK(3,N)
K = 1
I1 = NY
J1 = 1
I = I1
J = J1
IJK(1,1)=I
IJK(2,1)=J
IJK(3,1)=K
DO 10 ID=2,N
  I=I+1
  J=J+1
  IF (I .LE. NY .AND. J .LE. NA) GOTO 5
  I1 = I1 - 1
  J1 = 1
  IF (I1 .LT. 1) J1 = 2 - I1
  I=I1
  IF (I1 .LT. 1)I= 1
  J= J1
  IF (J1 .LE. NA) GOTO 5
C NA*NY ELEMENTS COMPLETED UPDATE K
  K = K + 1
  I1 = NY
  J1 = 1
  I=I1
  J=J1
5  IJK(1,ID)=I
  IJK(2,ID)=J
10  IJK(3,ID)=K

67
SUBROUTINE BT

$include: 'taitb.cmn'

DO 100 IN=1,N
   HBT(IN) = 1.0
   I=IJK(1,IN)
   J=IJK(2,IN)
   K=IJK(3,IN)
C LOOK FOR A RECRUITED AGE SEX CLASS
   IF(J.eq.1 .and. I.gt.ia) hbt(in)=exp((sb(i)-
      x(i,1,k))/sv(i))
100 continue
return
END

SUBROUTINE BTSUMS

$include: 'taitb.cmn'

C BTSUMS ESTIMATES THE EXPECTED NUMBER OF RECRUITS IN YEAR I
C SB(I) THAT WOULD BE PRODUCED BY FEMALES THAT
C WOULD RECRUIT TO THE FIRST HARVESTABLE AGE CLASS
C AND THE EXPECTED VARIANCE OF RECRUITES SV(I)
c include time lag for recruitment and adopt the following approximate
C approach: sb(1) to sb(ia) equal to the average of male &
female
C recruitments, and sv(1) to sv(ia) equal to sv(ia+1).
C SUM UP THE BIRTH RATES AND VARIANCES FOR EACH YEAR
   DO 10 I = ia+1, NY
      SB(I) = 0.
      SV(I) = 0.
   C
      DO 10 J = 1, NA
         SB(I) = SB(I) + X(I-ia,J,1) * BR(I-ia,J)
      10 SV(I) = SV(I) + X(I-ia,J,1) * BV(I-ia,J)
   if (ia.ge.1) then
      do 5 i = 1, ia
         sb(i) = (x(i,1,1)+x(i,1,2))/2.0
      5 sv(i) = sv(ia+1)
   endif
RETURN
END

subroutine change(np,pl,pm,si,iy,iid)
real*8 pl(np),pm(np),si(np)
integer iid(np)
1 write(*,100)
   read(*,*) i
   if (i.eq.0) then
      write(*,'(a)') ' Enter # of parameters being estimated:'
      read(*,*) iy
   endif
write(*, '(a)') ' Enter ID of the parameters being estimated:
      read(*, *) (iid(i), i=1, IY)
      endif
      else if (i.gt.np) then
        print *, 'Wrong choose! Try again please...'
        goto 1
      else
        write(*,110)
        read(*,*) pl(i), pm(i), si(i)
        goto 1
      endif
      100 format('$'//' Parameter Selection for Systematic Search:'//
       + ' 0 --- quit'
       + ' 1 --- adult natural survival rate'
       + ' 2 --- male hunting mortality rate'
       + ' 3 --- female hunting mortality rate'
       + ' 4 --- recruitment rate'
       + ' Which parameter for systematic search: ')
      110 format(' If fixing a parameter, enter NEW VALUE, -1, 0'
       + ' Minimum value, Maximum value, Step size...')
      return
end

SUBROUTINE DBYDX(R)
$include:'taitb.cmn'
dimension R(NN)
C ROUTINE MODIFIES THE DIAGONAL OF D (SD) BY THE DERIVATIVE
C OF D WITH RESPECT TO X TIMES THE RHS2
C ONLY THE RECRUITING AGE CLASSES ARE RELEVANT
NY1=NY-1
DO 20 K=1,2
  DO 10 I=1,NY1
    IN=INDOF(I,K,NY,NA)
    SD(IN)=SD(IN)-R(IN)*(1.-SP(I,1,K))*(1.-HP(I,1,K))*HBT(IN)/SV(I)
  10 CONTINUE
C HANDLE THE CORNER RECRUITING AGE CLASS
  IN=INDOF(NY,K,NY,NA)
  SD(IN)=SD(IN)-R(IN)*(1.-HP(NY,1,K))*HBT(IN)/SV(NY)
C TRY OUT INCLUDING A FACTOR FOR THE FIRST YEAR TERMS
  IN=INDOF(1,1,NY,NA)
  JM=NA-NY+1
  DO 30 J=2,JM
    I=IN+NY*(J-1)
    JJ=IJK(2, I)
    SD(I)=SD(I)-R(I)*(1.-HP(1,JJ,1))*(1.-SP(1,JJ,1))*HBT(I)*2.*BR(1,JJ)/SB(1)
  30 CONTINUE
  JM=NY-2
  DO 40 J=1,JM
    I=I+NY-J+1
    JJ=IJK(2, I)
\[ SD(I) = SD(I) - R(I) \times (1 - HP(1, JJ, I)) \times (1 - \text{BR}(1, JJ)/SB(1)) \times \text{SP}(I, JJ, I) \times \text{HBT}(I) \times 2 \times \text{BR}(1, JJ)/SB(1) \]

\[ \text{CONTINUE} \]
\[ \text{RETURN} \]
\[ \text{END} \]

---

```
subroutine estimate
$include: 'taitb.cmn'
c estimate population abundance by age by sex, and parameters.
\[ \text{pn}(\text{np}) = \text{pn}(\text{np}-1) \times (1.0 - \text{pn}(\text{np}-1)) \]
C SET UP THE INITIAL GUESS AND INITIAL RECONSTRUCTION
CALL \text{INIT}
iter = 0
1 if (iy.ge.1) then
do 10 i = 1, iy
10 call \text{gest}(iid(i))
call \text{redist}
call \text{xit}(\text{chmx})
iter = iter + 1
if (\text{chmx.gt.0.1} \quad \text{and. iter.le.200}) goto 1
call \text{likeli(value)}
c if the estimation is better, then record the parameters.
if (\text{value.gt.hood}) then
hood = value
do 20 i = 1, np
20 \text{pp}(i) = \text{pn}(i)
do 30 i = 1, ny
do 30 j = 1, na
do 30 k = 1, 2
30 \text{xx}(i,j,k) = \text{x}(i,j,k)
endif
return
end
```

---

```
SUBROUTINE GEST(kk)
$include: 'taitb.cmn'
dimension TF(mny), TFH(mny), TM(mny), TMH(mny), TRF(mny)
C ROUTINE IS USED TO ESTIMATE THE VALUES OF THE PARAMETERS
C GIVEN THE CURRENT ESTIMATE OF THE POPULATION
goto (1, 31, 51, 71) kk
1 continue
C TFS IS TOTAL FEMALES
TFS = 0.
```
C TMS TOTAL MALES  
TMS = 0.  
C TFHS TOTAL FEMALE HARVEST  
TFHS = 0.  
C TMHS TOTAL MALE HARVEST  
TMHS = 0.  
C THR TOTAL HARVEST OF RECRUITS  
THR = 0.  
C THF TOTAL HARVEST OF FINAL AGE CLASS  
THF = 0.  
C TR TOTAL RECRUITS  
TR = 0.0  
C TFIN TOTAL FINAL AGE CLASSES  
TFIN = 0.0  
DO 20 I = 1, NY  
C TF(I) TOTAL YEAR CLASS I FEMALES  
TF(I) = 0.  
TRF(I)=0.0  
C TM(I) TOTAL YEAR CLASS I MALES  
TM(I) = 0.  
C TPH(I) TOTAL FEMALE HARVEST YEAR I  
TPH(I) = 0.  
C TMH(I) TOTAL MALE HARVEST YEAR I  
TMH(I) = 0.  
TR = TR + X(I,1,1) + X(I,1,2)  
TFIN = TFIN + X(I,NA,1) + X(I,NA,2)  
THR = THR + HARV(I,1,1) + HARV(I,1,2)  
THF = THF + HARV(I,NA,1) + HARV(I,NA,2)  
DO 10 J = 1, NA  
IF(J-1+IA.GE.NR)TRF(I)=TRF(I)+X(I,J,1)  
TF(I) = TF(I) + X(I,J,1)  
TM(I) = TM(I) + X(I,J,2)  
THF(I) = THF(I) + HARV(I,J,1)  
TMH(I) = TMH(I) + HARV(I,J,2)  
10 CONTINUE  
C TOTP(I)=TF(I)+TM(I)  
TFS = TFS + TF(I)  
TMS = TMS + TM(I)  
TFHS = TFHS + TPH(I)  
TMHS = TMHS + TMH(I)  
20 CONTINUE  
C TPOP TOTAL POPULATION  
THARV TOTAL HARVEST  
TPOP = TFS + TMS  
THARV = TFHS + TMHS  
C ESTIMATE AVERAGE NATURAL SURVIVORSHIP  
S = (TPOP - TM(1) - TF(1) - TR + X(1,1,1) + X(1,1,2))  
SDOM = TPOP - TM(NY) - TF(NY) - TFIN + X(NY,NA,1) + X(NY,NA,2)  
THF+HARV(NY,NA,1)+HARV(NY,NA,2))  
S = S / SDOM  
IF (S .GT. .99) S = .99  
PN(1)=S  
71
31  continue

c estimate male harvest rate.
  tem = 0.0
  temx = 0.0
  do 40 i = 1, ny
      do 40 j = 1, na
          tem = tem + harv(i,j,2)
          temx = temx + x(i,j,2)
  40  continue

  pn(2) = tem/temx
  if (pn(2).gt.0.99) pn(2) = 0.99
  return

51  continue

c estimate female harvest rate.
  tem = 0.0
  temx = 0.0
  do 60 i = 1, ny
      do 60 j = 1, na
          tem = tem + harv(i,j,1)
          temx = temx + x(i,j,1)
  60  continue

  pn(3) = tem/temx
  if (pn(3).gt.0.99) pn(3) = 0.99
  return

71  continue

c estimate recruitment rate.
  tem = 0.0
  temx = 0.0
  do 80 i = ia+1, ny
      tem = tem + x(i,1,1) + x(i,1,2)
      do 90 i = 1, ny-ia
          do 90 j = nr-ia+1, na
              temx = temx + x(i,j,1)
      90  temx = temx/(2.0*temx)

  pn(4) = tem/(2.0*temx)
  if (pn(4).gt.0.99) pn(4) = 0.99
  pn(5) = pn(4)*(1.0-pn(4))
  return

END

C-------------------------------------------------------------

SUBROUTINE GETDAT
$include: 'taitb.cmn'
C GETDAT IS USED WITHIN THE NONLINEAR MONITOR TO READ IN THE
HARVEST DATA
C GENERATED BY THE SIMULATOR MONTE.S. IT IS INVOKED WITHIN
THE MONITOR
C BY A CALL GETDAT COMMAND. IT WILL READ THE SIMULATED
HARVEST DATA
C SET FROM UNIT 9
print *, '----->>>Reading in Hunting Data...'
REWIND 9
READ(9,*) NA
READ(9,*) NY
DO 30 I=1, NY
READ(9,*) (HARV(I,J,2), J=1,NA)
READ(9,*) (HARV(I,J,1), J=1,NA)

30 CONTINUE
READ(9,*) (PAS(I), I=1,6)
C FIRST SET UP THE PARAMETERS
PN(1)=PAS(1)
PN(2)=PAS(4)
PN(3)=PAS(3)
C PN(4)=RECRUITMENT RATE
pn(4) = pas(6)
PN(5)=pn(4)*(1.0-pn(4))
do 40 i = 1, np
40 pp(i) = pn(i)
hoed = -1.0e+20
NR=PAS(5)
IA=PAS(2)
N=NY*NA*2
ISTART=NY+1
IEND=NY+2
DO 50 I=ISTART,IEND
DO 50 K=1,2
DO 50 J=1,NA
50 HARV(I,J,K)=0.
C SET UP THE SUBSCRIPT TRANSFORMATION FROM BLOCK NOTATION TO VECTOR
CALL ADJ(IJK,NY,NA,N)
RETURN
END
C---------------------------------------------------------------
FUNCTION INDOF(I,K,NY,NA)
C FUNCTION RETURNS THE VECTOR INDEX OF SUBSCRIPT I,1,K
IF((NY-I).LE.NA)INDOF=NY*NA*(K-1)+(NY-I)*(NY+1-I)/2+1
IF((NY-I).GT.NA)INDOF=NY*NA*(K-1)+(NY-NA)*(NY-NA+1)/2+(NY-NA-I)*
1 NA+1
RETURN
END
C---------------------------------------------------------------

SUBROUTINE INIT
$include: 'taitb.cmn'
print *, 'Initial estimation...'
C ROUTINE IS TO SET UP THE INITIAL VALUES AND ESTABLISH
C COMMUNICATION
C INITIALIZE ALL ELEMENTS OF HBT TO 1
DO 25 IN=1,N
25 HBT(IN)=1.
C
C INITIALIZE X
CALL REDIST
CALL SETX
RETURN
END
subroutine inout
CHARACTER*25 INFIL,outfil
LOGICAL ISFILE
print *, ' ::::: BEAR POPULATION RECONSTRUCTION :::::'
10 WRITE(*,'(a)') ' ENTER THE NAME OF THE INPUT FILE: '
READ(*,'(A)') INFIL
INQUIRE(FILE=INFIL,EXIST=ISFILE)
IF(ISFILE) THEN
   OPEN(9,FILE=INFIL,status='old')
ELSE
   WRITE(*,110)
   110 FORMAT('***THAT FILE DOES NOT EXIST***TRY AGAIN'/)
   GO TO 10
ENDIF
WRITE(*,'(a)') ' ENTER THE NAME OF THE OUTPUT FILE: '
READ(*,'(A)') OUTFIL
OPEN(6,FILE=OUTFIL,status='UNKNOWN')
WRITE(*,'(a)') ' ENTER THE NAME OF THE GRAPH OUTPUT FILE: '
READ(*,'(A)') OUTFIL
OPEN(7,FILE=OUTFIL,status='UNKNOWN')
return
end

subroutine likeli(value)
$include: 'taitb.cmn'
c compute likelihood function.
value = 0.0
DO 30 i = 1, ny-1
   DO 30 j = 1, na-1
   DO 30 k = 1, 2
      tem1 = 0.0
      n1 = x(i,j,k) - harv(i,j,k)
      IF (n1 .LT. 0) n1 = 0
      IF (x(i,j,k) .GE. 1.5) THEN
         DO 10 m = n1+1, INT(0.5+x(i,j,k))
            tem1 = tem1 + ALOG(FLOAT(m))
         END IF
         tem2 = 0.0
         n2 = x(i,j,k) - harv(i,j,k) - x(i+1,j+1,k)
         IF (n2 .LT. 0) n2 = 0
         n21 = INT(x(i,j,k)-harv(i,j,k)+0.5)
         IF (n21 .GE. 2 .AND. n21.LE.n2+1) THEN
            DO 15 m = n2+1, n21
            tem2 = tem2 + ALOG(FLOAT(m))
         END IF
         tem3 = 0.0
         n3 = INT(harv(i,j,k)+0.5)
         IF (n3 .GE. 2) THEN
            DO 20 m = 2, n3
            END IF
            20 CONTINUE
         END IF
         15 CONTINUE
      END IF
      10 CONTINUE
   END IF
   30 CONTINUE
END
tem3 = tem3 + alog(float(m))
endif

if (n4 .ge. 2) then
doi m = 2, n4
endif

value = value + tem1 + tem2 - tem3 - tem4
value = value + harv(i,j,k)*dlog(hp(i,j,k))
+ (x(i,j,k)-harv(i,j,k))*dlog(1.0-hp(i,j,k))
value = value + x(i+1,j+1,k)*dlog(sp(i,j,k))
+ (x(i,j,k)-harv(i,j,k)-x(i+1,j+1,k))*dlog(1.0-
sp(i,j,k))
continue
i = ny
j = na
do 50 k = 1, 2
tem1 = 0.0
n1 = x(i,j,k) - harv(i,j,k)
if (n1 .lt. 0) n1 = 0
if (x(i,j,k) .ge. 1.5) then
do 35 m = n1+1, int(0.5+x(i,j,k))
endif
tem3 = 0.0
n3 = int(harv(i,j,k)+0.5)
if (n3 .ge. 2) then
do 40 m = 2, n3
endif
value = value + tem1 - tem3
value = value + harv(i,j,k)*dlog(hp(i,j,k))
+ (x(i,j,k)-harv(i,j,k))*dlog(1.0-hp(i,j,k))
continue
doi 60 i = 1, ny
do 60 k = 1, 2
value = value -0.5*dlog(2.0*3.14158*sv(i))
+ - 0.5*(x(i,1,k)-sb(i))**2/sv(i)
return
end

SUBROUTINE output
$include: 'taitb.cmn'
WRITE(6,100) (pp(I),I=1,np-1),hood
100 FORMAT(1H '******ESTIMATED PARAMETERS******'//
& 1H 'ADULT NATURAL SURVIVAL RATE=',F7.3/
& 1H 'MALE HARVEST RATE=',F7.3/
& 1H 'FEMALE HARVEST RATE=',F7.3/
& 1H 'RECRUITMENT RATE=',F7.3/
& 1H 'Log-likelihood value = ',g12.4//)
WRITE(6,110)
110 FORMAT(/1x 'ESTIMATED POPULATION------MALES------'//
& 1x , 'AGE', 20X , 'YEARS')
  DO 10 J=1,NA
10 WRITE(6,120) (xx(I,J,2),I=1,NY)
120 FORMAT(1x,25(F7.2,1X))
WRITE(6,130)
130 FORMAT(/1x , 'ESTIMATED POPULATION------FEMALES------'/
& 1x , 'AGE', 20X , 'YEARS')
  DO 20 J=1,NA
20 WRITE(6,120) (xx(I,J,1),I=1,NY)
  DO 40
     i = 1, ny
     tmale = 0.0
     tfemale = 0.0
     do 30 j = 1, na
     tmale = tmale + xx(i,j,2)
30     tfemale = tfemale + xx(i,j,1)
     write(7,140) tmale, tfemale; tmale+tfemale
40 continue
140 format(1x,J(f10.2,2x))
RETURN
END

C---------------------------------------------------------------

SUBROUTINE REDIST
$include: 'taitb.cmn'
C ROUTINE REDISTRIBUTS THE AGGREGATED PARAMETERS IN PN
C INTO THE BASE PARAMETERS REPRESENTING HARVEST DEATH AND
BIRTH
C J1 AND J2 PARTITION THE AGE CLASSES BETWEEN THE
REPRODUCTIVE
C AND THE NON REPRODUCTIVE CLASSES
J1=NR-IA+1
J2=J1-1
  do 5 k = 1, np
     if (pn(k).gt.0.999) pn(k) = 0.999
     if (pn(k) .lt. 0.001) pn(k) = 0.001
5 continue
  DO 20 I=1,NY
     DO 10 J=1,NA
     HP(I,J,1) = PN(3)
     HP(I,J,2) = PN(2)
     SP(I,J,1) = PN(1)
10     SP(I,J,2) = PN(1)
     DO 15 J=J1,NA
     BR(I,J) = PN(4)
15     BR(I,J) = PN(5)
     IF(J1.LE.1)GOTO 20
     DO 18 J=1,J2
     BR(I,J) = 0.
18     BV(I,J) = 0.
20 continue
RETURN
END

C---------------------------------------------------------------

SUBROUTINE SETX
C ROUTINE IS USED TO INITIALIZE X
CALL TRISUP
CALL SGTSUP(N,SL,SD,SU,RHS,IERROR)
IF (IERROR.NE.0) GO TO 100
DO 40 IN=1,N
   I=IJK(1,IN)
   J=IJK(2,IN)
   K=IJK(3,IN)
   X(I,J,K)=RHS(IN)
40   XN(IN)=RHS(IN)
CALL BTSUMS
CALL BT
RETURN
100 WRITE(6,101)
101 FORMAT(1H , 'SETX-------ERROR RETURN FROM SGTSUP')
STOP
END

SUBROUTINE SGTSUP(N,C,D,E,B,INFO)
INTEGER N,INFO
REAL*8 C(1),D(1),E(1),B(1), T
INTEGER K,KB,KP1,NM1,NM2
SGTSUP GIVEN A GENERAL TRIDIAGONAL MATRIX AND A RIGHT HAND SIDE WILL FIND THE SOLUTION.
ON ENTRY
N INTEGER
C IS THE ORDER OF THE TRIDIAGONAL MATRIX.
C REAL(N) IS THE SUBDIAGONAL OF THE TRIDIAGONAL MATRIX.
C SUBDIAGONAL.
C C(2) THROUGH C(N) SHOULD CONTAIN THE ON OUTPUT C IS DESTROYED.
C C D REAL(N)
C IS THE DIAGONAL OF THE TRIDIAGONAL MATRIX.
C ON OUTPUT D IS DESTROYED.
C C E REAL(N)
C IS THE SUPERDIAGONAL OF THE TRIDIAGONAL MATRIX.
C SUPERDIAGONAL.
C E(1) THROUGH E(N-1) SHOULD CONTAIN THE ON OUTPUT E IS DESTROYED.
C C B REAL(N)
C IS THE RIGHT HAND SIDE VECTOR.
C ON RETURN
C C B IS THE SOLUTION VECTOR.
C C INFO INTEGER
= 0 NORMAL VALUE.
= K IF THE K-TH ELEMENT OF THE DIAGONAL BECOMES
EXACTLY ZERO. THE SUBROUTINE RETURNS WHEN
THIS IS DETECTED.

LINPACK. THIS VERSION DATED 08/14/78.
JACK DONGARRA, ARGONNE NATIONAL LABORATORY.

NO EXTERNALS
FORTRAN ABS

INTERNAL VARIABLES

BEGIN BLOCK PERMITTING ... EXITS TO 100

INFO = 0
C(1) = D(1)
NM1 = N - 1
IF (NM1 .LT. 1) GO TO 40
D(1) = E(1)
E(1) = 0.0E0
E(N) = 0.0E0

DO 30 K = 1, NM1
KP1 = K + 1

FIND THE LARGEST OF THE TWO ROWS

IF (ABS(C(KP1)) .LT. ABS(C(K))) GO TO 10

INTERCHANGE ROW

T = C(KP1)
C(KP1) = C(K)
C(K) = T
T = D(KP1)
D(KP1) = D(K)
D(K) = T
T = E(KP1)
E(KP1) = E(K)
E(K) = T
T = B(KP1)
B(KP1) = B(K)
B(K) = T

CONTINUE

ZERO ELEMENTS

IF (C(K) .NE. 0.0E0) GO TO 20
INFO = K

.............. EXIT
GO TO 100

CONTINUE
T = -C(KP1)/C(K)
C(KP1) = D(KP1) + T*D(K)
D(KP1) = E(KP1) + T*E(K)
E(KP1) = 0.0E0
B(KP1) = B(KP1) + T*B(K)

30 CONTINUE
40 CONTINUE
   IF (C(N) .NE. 0.0E0) GO TO 50
      INFO = N
GO TO 90
50 CONTINUE

C
C   BACK SOLVE
C
NM2 = N - 2
B(N) = B(N)/C(N)
   IF (N .EQ. 1) GO TO 80
      B(NM1) = (B(NM1) - D(NM1)*B(N))/C(NM1)
   IF (NM2 .LT. 1) GO TO 70
      DO 60 KB = 1, NM2
         K = NM2 - KB + 1
         B(K) = (B(K) - D(K)*B(K+1) - E(K)*B(K+2))/C(K)
60 CONTINUE
70 CONTINUE
80 CONTINUE
90 CONTINUE
100 CONTINUE
C
RETURN
END

---
---

SUBROUTINE TRISUP
$include: 'taitb.cmn'
C   TRISUP IS USED TO SET UP THE TRI-DIAGONAL MATRIX AND THE
C   RIGHT
C   HAND SIDE IN THE VECTORS SL,SD,SU AND RHS. IT USES AS
C   INPUT
C   HARV THE NUMBER OF HARVESTED ANIMALS AND THE VALUES OF THE
C   PARAMETERS HP, SP BR AND BV. X INDEXED IJK THE CURRENT
C   ESTIMATE
C   OF THE POPULATION IS SAVED AS XN INDEXED IN. TRISUP
C   HANDLES THE IN
C   'TH ROW. A CALL TO BT GETS THE ESTIMATE OF THE BIRTH RATE
C   ADJUSTMENT
C   REMEMBER THE OLD VALUE
   DO 100 IN=1,N
      I=IJK(1,IN)
      J=IJK(2,IN)
      K=IJK(3,IN)
   C GET THE BIRTH RATE ADJUSTMENT
   C RUN THRU THE POSSIBLE EQUATIONS -- A FUNCTION OF SUBSCRIPTS
      IF (I .GE. 2 .AND. J .GE. 2) GO TO 10
      IF (I .EQ. NY .OR. J .EQ. NA) GO TO 30
C WE ARE ON AN EDGE AND NOT A CORNER
79
SD(IN) = (1. - HP(I,J,K)) * (1. - SP(I,J,K)) * HBT(IN) - 1.
SU(IN) = 1.
SL(IN) = 0.
RHS(IN) = -HARV(I,J,K)
GOTO 100
10 IF (I .EQ. NY .OR. J .EQ. NA) GO TO 20
C AN INTERIOR POINT
  XMULT = (1. - HP(I,J,K)) * SP(I - 1,J - 1,K) * (1. - SP(I,J,K)) * HBT(IN)
  XMULT = XMULT / (1. - SP(I-1,J-1,K))
  SD(IN) = XMULT + 1
  SU(IN) = -1.
  SL(IN) = -XMULT
  RHS(IN) = HARV(I,J,K) - XMULT * HARV(I - 1,J - 1,K)
  GOTO 100
20 IF (I .EQ. 1 .OR. J .EQ. 1) GO TO 30
C A BOTTOM OR RIGHT SIDE EDGE
  XMULT=(1.-HP(I,J,K))*SP(I-1,J-1,K)*HBT(IN)/(1.-SP(I-1,J-1,K))
  SD(IN) = -XMULT - 1.
  SL(IN) = XMULT
  SU(IN) = 0.
  RHS(IN) = -HARV(I,J,K) + HARV(I - 1,J - 1,K) * XMULT
  GOTO 100
C A CORNER POINT
  30 SD(IN) = (1. - HP(I,J,K)) * HBT(IN) - 1.
C WATCH OUT FOR OVER SHOOT CREATES A NEGATIVE X --SD0
IF(SD(IN).LE.0.)GOTO 31
HBT(IN)=.5*(HBT(IN)-1.)+1.
GOTO 30
31 SU(IN) = 0.
SL(IN) = 0.
RHS(IN) = -HARV(I,J,K)
100 CONTINUE
RETURN
END

SUBROUTINE XIT(chmx)
$include: 'taitb.cmn'
DO 10 IN=1,N
  XN(IN)=X(IJK(1,IN),IJK(2,IN),IJK(3,IN))
  CALL EQ(RHS2,XN,N)
C SET UP TRISLV VECTORS
  CALL TRISUP
C GENERATE H (XD) FOR NEWTON CORRECTION
  N1=N-1
  XD(1)=SD(1)*XN(1)+SU(1)*XN(2)-RHS(1)
  XD(N)=SL(N)*XN(N-1)+SD(N)*XN(N)-RHS(N)
C DO 30 IN = 2, N1
  XD(IN)=SL(IN)*XN(IN-1)+SD(IN)*XN(IN)+SU(IN)*XN(IN+1)-RHS(IN)
30 CONTINUE
MODIFY THE DIAGONAL OF D TO GENERATE THE NEWTON CORRECTION

CALL DBYDX(XN)

CALL SGTSL(N,SL,SD,SU,XD,IERROR)
IF (IERROR .NE.0) GO TO 60

C UNRAVEL THE SOLUTION
CHMX = 0.
PS=1
DO 45 IN = 1, N
   I=IJK(1,IN)
   J=IJK(2,IN)
   K=IJK(3,IN)
   X(I,J,K)=RHS2(IN)
   X(I,J,K)=X(I,J,K)-PS*XD(IN)
   XN(IN)=X(I,J,K)
45 CONTINUE
CALL BTSUMS
CALL BT

C MEASURE ITS PERFORMANCE
CALL TRISUP
N1=N-1
XH=SD(1)*XN(1)+SU(1)*XN(2)-RHS(1)
CHMX=ABS(XH)
XH=SL(N)*XN(N-1)+SD(N)*XN(N)-RHS(N)
IF(CHMX.LT.ABS(XH))CHMX=ABS(XH)

DO 32 IN = 2, N1
   XH=SL(IN)*XN(IN-1)+SD(IN)*XN(IN)
1   +SU(IN)*XN(IN+1)-RHS(IN)
   IF(CHMX.LT.ABS(XH))CHMX=ABS(XH)
32 CONTINUE
PRINT *, 'Maximum change = ',CHMX
200 RETURN
60 WRITE (6,90)
STOP
90 FORMAT (' NO SOLUTION FOUND BY SGTSL')
END
EXECUTIVE SUMMARY

Brown bear age-at-harvest data are widely misinterpreted by division staff. The most common misinterpretation is that lack of change in mean age of harvested bears indicates a stable population. Additional common misinterpretations are that changes in mean age of harvest mean a change in population trend and that a younger mean age of harvest, especially for males, indicates a population more heavily hunted than where mean harvest age is older. Although these interpretations may, at times, be correct, simulation studies indicate that they are equally likely to be wrong or to lag far behind changes in population status (Harris 1984, Harris and Metzgar 1987a, Miller and Miller 1988). More soundly based models for interpretation of age-and-sex-at-harvest data are available but these also do not provide unambiguous indications of population trend.

Currently, age-at-harvest-data are most useful in selecting between conflicting interpretations of population trend or where changes in population status have been extreme. This may be adequate justification to continue collecting these data.
Alternative methods of rejecting alternative interpretations of population status may require field studies which will be much more costly than cementum aging of harvest age. With available technology, age-at-harvest data should be viewed as an indicator that, when appropriately used and in association with other indicators, can sometimes help evaluate probable trend in bear populations.

A model specifically designed to interpret population trend from the kind of data collected from harvested brown bears in Alaska was developed by Tait (1983). Although Tait has provided this division with workshops on the uses of his model and the framework of the model, other priorities have prevented our development and testing of Tait’s approach. A proposal is in hand to accomplish this development and testing with a $4,500 RSA to R. Fagan of UAA-Juneau.

BACKGROUND

This report was prepared to provide a brief overview on the usefulness of information obtained by aging teeth from harvested brown bears. In Alaska, brown bear teeth have been extracted, sectioned, and aged by counting cementum annuli since 1970. The PRC considered it important to review whether and how these data have helped make better management decisions. This is part of a review on how use of bear harvest age data can be improved and whether these data should continue to be collected. Another report by L. VanDaele is available on the accuracy, economics and alternatives of bear tooth aging.

CURRENT USE

Before looking at what harvest age can be used for, it is worthwhile to briefly discuss how these data can be misused. A review of recent S&I reports suggests that the most common current use of bear harvest age data is to infer that bear population numbers are unaffected by harvest because mean age or sex ratio statistics are not changing over time. This is a misuse of harvest age data. All studies of these statistics indicate that their relationship, if one exists, to population trend, is not so straightforward (Caughley 1974, Harris 1984, Harris and Metzgar 1987a, Miller and Miller 1988, Miller 1988). Where a relationship exists, changes in mean age will lag far behind changes in population status (Harris 1984, Harris and Metzgar 1987a).

It is widely recognized in the Division that harvested animals are not a random selection from the population, hunters are selective for large animals in some instances and are selective for the easiest to get (usually young) animals at other times or places. In spite of this knowledge, the belief persists that the harvest age somehow reflects population age and this is not necessarily correct. Harvest age best reflects relative vulnerability of the different ages to hunters (Miller and Miller 1988). In illustration, area biologists know that spring season harvests will have more older bears and more males than fall seasons in the same area. This is a reflection of hunter
selectivity and different vulnerabilities of bears in these 2 seasons.

Just as stability in mean age statistics does not mean stability in population trend, a shift in hunting intensity, from lightly hunted to overhunted for example, will not necessarily result in a decline or other changes in the mean age of harvest. If the shift results in a change in relative vulnerability of different ages, there will be a change in mean age. This change will reflect the vulnerability change and not necessarily a change in population trend (Miller and Miller 1988). If there is no change in relative vulnerability of different ages the mean age and distribution of ages in the harvest will remain the same regardless of how much hunting intensity is increased (Miller and Miller 1988). When there are no longer any old animals left, the age at harvest may decline but this will happen very late in the process of decline of species like bears that can sustain only a very low rate of harvest. In addition to this problem, an increasing population, with a larger proportion of young animals, could theoretically display the same pattern (more young animals) as an overhunted one (Caughley 1974). Practically, however, this kind of confusion is less likely for bears than for ungulates.

Frequently mean age of harvested bears is lower in more heavily harvested areas. This can result because the population has fewer old individuals or because hunters are less selective for large (old) individuals. In neither case does this statistic indicate whether the population is being harvested at more or less than sustainable rates. The differences in mean age of harvested animals from different areas with different harvest intensities may have led to the expectation that a change from harvest levels at which populations were stable to one where populations were declining would be accompanied by a decline in mean age.

APPROPRIATE USES OF AGE-AT-HARVEST DATA

It is technically easier to debunk statistics based on harvest age data that to convincingly demonstrate the utility of this information. With currently available techniques it is clear that harvest age data alone will seldom provide an unequivocal interpretation of harvest trend. The bear population manager, however, does not operate in a vacuum where this is the only information available on which to base decisions. Usually a manager will have other indicators related to population trend (e.g. increases or decreases in number harvested, estimates of sustainable harvest numbers, sex ratio in kill, success/unit effort, observations of guides, etc.) which will permit exclusion of some alternative explanations as unfeasible. When harvest age data are related to population age data, harvest age can be used as an additional indicator of possible trend that is worth considering in making management decisions.

Two specific models have been proposed as ways in which to use harvest age data to interpret trend in bear populations. Both exploit the difference in vulnerability between sexes which results in relatively fewer males in older age classes of the population.
Fraser Model. The most straightforward of these models was proposed for use on black bears by Fraser et al. (1982). Because males are more vulnerable than females, older age classes of the population will contain a progressively higher proportion of females. At some age class the higher proportion of females remaining will compensate for the higher vulnerability of males. More females than males will be harvested in this and older age classes. Correspondingly, a regression of percent males in the harvest (vertical axis) on age class will have a negative slope. The more heavily harvested the population, the steeper this slope will be or, in other words, the younger will be the age class at which females in the harvest first predominate. When the assumptions of the model are met, the reciprocal of the age at which females first predominate is an estimate of exploitation rate (Fraser et al. 1982).

In order to use this model correctly, information on hunter effort must be available. Appropriate effort data are not available in Alaska. An analysis of this model by Harris and Metzgar (1987b) indicated that this model is not robust to violation of underlying assumptions. Another problem with this approach for Alaska data is that legal protection of females with cubs makes the age at which females first predominate older than would otherwise be the case; this results in an underestimation of harvest rate. Protection of females with cubs also results in a poor fit of the regression to the data as the percent females in the harvest declines in the age class at which females have their first litters. Finally, this approach requires a reasonable sample size of harvested animals otherwise too few female animals will be harvested in the older age classes to calculate a meaningful sex ratio. In such cases age classes or years of data must be combined which can mask trends that might be evident if sample sizes were larger. A special printout of brown bear harvest data in the appropriate format for this type of analysis has been available for about 7 years but has seldom been used.

The Fraser model was used to demonstrate an increase in harvest rate in GMU 13 by showing that recent harvests had a steeper slope for this relationship than earlier harvests (Miller 1988). This was a worthwhile contribution because it refuted the contention that the increased harvests in this area reflected a expanding population base rather than an increase in exploitation rate. In this case the harvest age data were used to eliminate one suggested alternative explanation of population status. A similar approach was used to suggest that grizzly bear harvest rates in the Northern Continental Divide Ecosystem, Montana were higher than in the East Kootenay Region of British Columbia (McLellan and Shackleton 1988).

Tait Model. The second model available to interpret sex and age of harvest data was developed by Tait (1983) and does not have the limitations of the Fraser approach. This approach also exploits the difference in vulnerability of different sexes and, through a complex non-linear optimization procedure, develops maximum likelihood solutions for population size, exploitation rate, recruitment rate, and other parameters. In simulation
studies this model has been demonstrated to converge on correct estimates of these parameters. As part of an ongoing research project (Miller and Miller 1988) the necessary components of this model were obtained during consultations with Tait over 4 years ago but these pieces have not been assembled and the model has not been tested with real data. This is because other tasks have been assigned higher priorities for SuzAnne Miller’s time and SuzAnne is the only ADF&G staff member who has both the programming and mathematical skills to accomplish this work. However, a biometrician/programmer team at the University of Alaska-Juneau (R. Fagan/Jie Zheng) has become interested in this approach as part of a similar program they are developing for interpretation of age at catch data for fish populations. They have proposed a contract with us in which they would convert Tait’s model into a readily-usable internally documented program, test it with simulated and real data sets, and provide us with documentation and technical reports on the results. They seek $4,500 for graduate student (Zheng) support for this work which, if the money is available, could easily be provided under an RSA with the University. Work on the project could begin this winter and be largely completed by the end of summer 1990.

It is hard to predict whether Tait’s model will work on Alaska bear harvest data sets. Violation of underlying assumptions, or, more likely, errors in the data may cripple this approach. Regardless, Tait developed this approach precisely to answer the types of questions we ask of our bear harvest data with precisely the kind of data we collect. It would be peculiar to decide that these data can not be adequately interpreted and to stop collecting them, before his approach was thoroughly tested.

Age Ratio Analyses. Although mean age data is usually unrevealing of population trend, ratios of various age classes may prove to be more sensitive. The ratio of subadult females to adult females killed, for example, may provide an index to the degree that females are being killed prior reaching maturity when they are less vulnerable by virtue of being accompanied by cubs. Use of such ratios as population status indicators has been little investigated so far. Skull size data combined with tooth wear observations could be used as a substitute for cementum ages in making such ratios, but some precision and flexibility would be lost.

As a preliminary step towards examination of such ratios, trends in the number of bears harvested in different age classes ("young, middle-aged, and old" bears) were examined in an area where bear populations were known to be declining as a result of heavy harvests (Miller 1988). These trends were found to be consistent with several hypotheses about how age at harvest indicate overharvest and inconsistent with others (Miller 1988). The clearest trend was evident an initial increase in the number (not ratio) of 2-year old bears harvested followed by a decline. The decline may have resulted from as overharvests and natural mortality from old age began to reduce the number of adult females available to produce recruits.
Intuitive and Political Uses. Although not useful as rigorous indicators of population trend, managers report a number of useful applications of harvest age data (see appendix). On Kodiak Island the age data demonstrates that "trophy" (old) bears are still available and that current management is compatible with refuges goals to maintain "diversity" in the population. Similarly, data on the number of females of reproductive age being killed is the key statistic in evaluating whether harvests levels are sustainable (Knight and Eberhardt 1984). Roger Smith points out (Appendix) that if he were approximating number of adult females killed using skull size data, he'd need to be more conservative in his management because of the relative imprecision of skull size as a measure of age. Providing the age of their kill to hunters who request it generates some good will for the Division.

MODEL ASSUMPTIONS AND PROBLEMS

Homogeneity of effort. All conceptual models for interpretation of age data assume that the population has geographically consistent vulnerability within each age-sex class. This is almost never true in reality as some areas receive heavier hunting pressure than others. The most common result of this bias is that the harvests will tend to mimic overhunted populations more than they should.

Incorrect data. All models assume that the data are correct. The mean age and Fraser models are probably not so sensitive to incomplete data (non-reported kills) if the reported kills are a non-biased sample. Tait's model requires low levels of unreported mortalities to adults (human caused or natural). Incorrect data may result from errors in aging, sexing, non-reporting, geographic bootlegging, etc.

Sample size. Sample size of harvested bears will usually be a small fraction of the total population. This means that the harvest represents a very small and biased window through which to view the population. This sample size problem is illustrated by simulation studies that suggest that the maximum sustainable harvest rate of a brown bear population is less than 6% (Miller in press). In almost all GMUs, most of the harvest is in the youngest age classes (2-4) leaving very few animals in each of the oldest age classes.

There is no easy answer to the question of what is the minimum number of bears required to make a meaningful analysis of harvest age data. Obviously, 2-3 bears killed/year would be inadequate and 1000/year would be nice from an analytical standpoint. Only extreme declines in population number could be evidenced in a "small" sample. With small samples more lumping of age classes, with corresponding loss of precision, would be necessary to use the Fraser et al. (1982) approach. To increase sample size one might try to group together geographic areas with different hunting patterns and this would also result in loss of precision. Limited insights into population status from age at harvest data were obtained from the Kenai Peninsula kill averaging only 10 bears/year (Jacobs 1989, memo from Schwartz in Appendix). Sex-and-age-at-harvest data were used to contrast
impacts of human killing of grizzly bears in 2 areas where kill averaged only 18.4 and 19.1 bears/year (McLellan and Shackleton 1988). Even a casual review of the harvest data from heavily-hunted NE Chicagoff Island reveals a lack of old animals which supports the other available indicators of overharvest. It is true that the smaller the harvest sample the less credence should be placed on harvest age interpretation. However, even with samples as small as 10 year, harvest age data may sometimes be useful as an additional indicator of suspected population status.

Induced biases. Shifts in effort, technology, hunter selectivity, or regulations may alter relative vulnerability of different sexes or age and complicate interpretations.

Closed population. All models assume that the population is closed with no immigration or emigration. This assumption is not critical if residents of adjacent populations providing the immigrants have been subject to same hunting pressures and movements in and out are of equal magnitude.

Constant vulnerability over time. If relative vulnerability by sex or age class is changing over time, changes in harvest age structure may reflect these changes more than population status. In Tait's model this requirement is relaxed but some estimates must be made of the relative changes in vulnerability that occur, by addition of a spring season, for example.

Sufficiently long data series. Tait's model requires that the time sequence of data be sufficiently long so that changes in the adult female population can be observed as changes in the recruitment rates to the harvestable age classes. There is no need to assume a stable age distribution. The Fraser model can work with a single year's data and is not dependent on historical data.

CONCLUSIONS

Using currently available models, the harvest age data are, by themselves, inadequate to unequivocally depict trend in bear populations. A model developed by D.E.N. Tait that may do this is available, but has not been tested. This model requires accurate age data. Another model is reported to be under development in California and it is possible that some fisheries age-at-catch models may be applicable to this problem.

However, no good area biologist expects the harvest age data, by itself, to provide irrefutable evidence of bear population status. These data are used in conjunction with other indicators to deduce population status. For example under conditions where regulations were liberalized and harvest numbers increased dramatically and there was a decline in mean age of males, it would not be wise or parsimonious to conclude the population was increasing. A wise manager would strongly suspect the opposite and adjust his management accordingly. This approach could be called "management by consensus of indicators". Although this approach will seldom provide unambiguous evidence of population trend, a manager has no real alternative except for expensive and long-term research projects. Used appropriately, with a correct understanding of the data's limitations, managers will usually be better off with the additional indicator provided
by age-at-kill data. Recent studies have led to discouragement because they have shown that the age-at-harvest data are not as good at reflecting population status as some had assumed. This does not mean, however, that the data do not have value. With current technology, bear population management is a very difficult and imprecise science (Harris 1986, Miller in press). Eliminating any of the available indicators should be done only if the Division is willing to spend much more money in documentation of population status with field studies or to adopt more conservative management strategies.

RECOMMENDATIONS OF AUTHOR

1. Increase familiarity by area biologists of the limitations of harvest age data to detect population trend.
2. Contract with R. Fagan of UAA to convert and test Tait’s model for interpretation of bear harvest data.
3. Encourage more widespread efforts to develop meaningful indicators of population trend from age-at-harvest data.
4. Continue to obtain estimated ages of harvested brown bears by counting cementum annuli in all areas. If it is decided to eliminate aging in some areas make the decision to exclude areas where reported plus suspected unreported harvests is a small fraction (<30%) of estimated sustainable levels.
5. Continue to collect teeth from harvested black bears and have these teeth sectioned and read in areas where excessive harvest are suspected.
6. Management objectives for bears expressed in terms of mean age of harvested animals should be reexamined to determine whether there is any reasonable and objective basis for setting objectives based on this criterion.

LITERATURE CITED


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