

Summary and explanation of methods to estimate population size and sustainable mortality of Yellowstone grizzly bears

January 30, 2007

Participants in analyses and discussions (alphabetical):

Charles R. Anderson, Jr., Trophy Game Section, Wyoming Game and Fish Department, Lander, WY 82520, USA

Keith Aune, Research and Technical Services, Montana Fish, Wildlife and Parks, Helena, MT 59620, USA

Kim Barber, U.S. Department of Agriculture, Forest Service, Shoshone National Forest, Cody, WY 82414, USA

Dan Bjornlie, Trophy Game Section, Wyoming Game and Fish Department, Lander, WY 82520, USA

Steve Cherry, Department of Mathematical Sciences, Montana State University, Bozeman, MT 59717, USA

Kevin Frey, Wildlife Management Specialist, Montana Fish, Wildlife and Parks, Bozeman, MT 59717, USA

Kerry Gunther, Bear Management Office, Yellowstone National Park, WY 82190, USA

Lauri Hanauska-Brown, Idaho Department of Fish and Game, Idaho Falls, ID 83401, USA

Mark A. Haroldson, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study team, Montana State University, Bozeman, MT 59717, USA

Richard B. Harris, Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA

Kim A. Keating, U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, MT 59717, USA

Dave Moody, Trophy Game Section, Wyoming Game and Fish Department, Lander, WY 82520, USA

Charles C. Schwartz, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study team, Montana State University, Bozeman, MT 59717, USA

Christopher Servheen, U.S. Fish and Wildlife Service, University of Montana, Missoula, MT 59812, USA

Gary C. White, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA

Compiler: Richard B. Harris, Montana Cooperative Wildlife Research Unit

This document is the product of team work. All participants contributed to its production. Please cite as follows: Interagency Grizzly Bear Study team. 2007. Summary and explanation of methods to estimate population size and sustainable mortality limits of Yellowstone grizzly bears. Interagency Grizzly Bear Study team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana, USA.

Table of Contents

[What this document is](#)

[Summary and management recommendations](#)

[Background](#)

[The original \(1993\) protocol: a closer look](#)

[Counting females with cubs of the year \(\$F_{\text{cubs}}\$ \)](#)

[From \$F_{\text{cubs}}\$ to total population](#)

[Mortality limits](#)

[Advantages of the original \(1993\) protocol](#)

[Weaknesses of the original \(1993\) protocol](#)

[New protocols](#)

[Method for estimating population size](#)

[New estimate of yearly \$F_{\text{cubs}}\$](#)

[Using all data to estimate yearly \$F_{\text{cubs}}\$](#)

[Estimating the number of adult females from \$F_{\text{cubs}}\$](#)

[Estimating the number of sub-adult females from adult females](#)

[Estimating the number of cubs and yearlings](#)

[Estimating the number of subadult and adult males](#)

[New guidelines for limiting mortality](#)

[Estimating unknown and/or unreported mortality](#)

[Advantages of the new protocol](#)

[Limitations of the new protocol](#)

[An example worked out: 2004 data](#)

[Population monitoring](#)

[How might methods, analyses, or data err?](#)

[Glossary](#)

[Literature cited](#)

What this document is

[◀ Back to contents](#)

This document explains proposed methods for monitoring the Greater Yellowstone Ecosystem (GYE) grizzly bear population, and methods used to establish and monitor mortality limits. It is intended for land and wildlife managers, biologists, and members of the public who wish to understand both deliberations and proposals regarding past, present, and future monitoring of GYE grizzly bears. This document is a product of the Interagency Grizzly Bear Study team (Study team, hereafter). Funding for its production came from the USFWS, Grizzly Bear Recovery Office.

Why this document exists

In 2001, funding was obtained by the Study team to re-examine data and assumptions underlying existing protocols for i) estimating population size and trend for grizzly bears in the GYE, and ii) determining a sustainable mortality limit that federal and state agencies cannot exceed. This initiative resulted in a group of closely-related studies, and many have already been published in the peer-reviewed literature (e.g., Schwartz et al. 2006a), while others are ongoing as of this writing.

The Study team did not, however, publish recommendations for revision of specific management protocols, because the

process required both documentation and consideration by agency managers, politicians, and the general public. Instead, a group of biologists involved with data analysis and familiar with the requests from managing agencies for data and rule-sets, embarked on additional, post-publication analyses and discussions. The result of these considerations, which occupied various times during 2004 and 2005, was a public document entitled “Reassessing methods to estimate population size and sustainable mortality limits for the Yellowstone grizzly bear” which was completed on August 31, 2005 (“Reassessing” hereafter). Public comments were requested on this “Reassessing” document. In response to public comments on this document and to comments on the proposal to delist the Yellowstone grizzly population from protections under the Endangered Species Act in November, 2005, which in part relied on this “Reassessing” document, a Supplement to the “Reassessing” document was completed in December 2006.

A number of comments, from agencies, from scientists, and from the general public, were received that were related to the “Reassessing” document. Among those most relevant here is


The highly complex scientific nature of the Reassessing Methods Document frustrates public comment and masks the significance of the proposed changes. If an agency seeks meaningful public comment, it must produce a document that the average person can understand.

The “[Reassessing](#)” document and its [Supplement](#) were written to be scientifically precise; in order to avoid excessive length, they were written assuming some background in wildlife ecology (and population dynamics and accompanying biometric methods in particular). The [Study team](#) believed (and continues to believe) that this was appropriate. However, we acknowledge that both documents contain highly technical language and can be difficult to follow. We would like to improve the understanding of our considerations and recommendations as much as possible. Thus, we believe the concern expressed above is legitimate and deserves some effort to resolve. Acknowledging that it may be difficult to know exactly what an “average person” can understand, this document is an attempt to provide a more easily read and understood document that still provides the important information.

How this document works

There is a danger that as soon as one begins to simplify science or complex considerations, something will be lost (or worse yet, mis-stated). If the concern is that the significance of changes be masked, that would pale in significance to the potential that an overly simplified version might, inadvertently or not, focus on some aspects to the exclusion of others, and thus mislead rather than edify.

Our solution to that dilemma is to provide as objective as possible an overview of the various components of the “[Reassessing](#)” report in simple prose that assumes an intelligent and educated reader — but not necessarily one with a recent graduate education in wildlife population dynamics. To enhance readability, we’ve attempted to keep this part of the document simple and flowing. Necessarily then, details are

omitted. To rectify that, we provide additional details in various sections which are accessible via [links](#). Clicking on a link will move you directly to the part of the document with more detail. To move back to the original place in the main document, click on the [◀ Back](#) icon (if the link is to another location within the document), or on the  icon in your web browser or use View-GoTo-Previous View (if the link is to a separate pdf document) in Reader 7.0 . Some sections are, in turn, provided with additional [links](#) which, when clicked, move the reader directly to source documentation (at which point, the reader is faced again with “highly complex scientific” writing). Terms defined in the glossary appear in [green](#). Of course, you can also scroll back and forth as needed, or dispense with all the clicking and linking entirely and simply read the entire document. If really desperate, you can even print it out and read it the old-fashioned way, on paper!

It is also important to note that, while every attempt has been made here to include and reference the latest publications and thinking in regard to the important issue of monitoring the [GYE](#) grizzly bear populations and providing management recommendations regarding acceptable mortality, some research work is ongoing. The point is not to create an ever-receding target, but rather to continually respond to deficiencies in data and analysis when that is possible, and to provide the best analyses and documentation we can.

While we recognize that most readers of this document will be doing so in the context of the proposal by [USFWS](#) in November 2005 to classify grizzly bears in the [GYE](#) as a distinct population segment and remove them from protection under the US Endangered Species Act, we emphasize that the monitoring protocols

we've considered and propose here are independent of that effort. Analyses and recommendations herein are relevant regardless of the administrative status of the grizzly bear in the GYE.

Summary and Management Recommendations

[◀ Back to contents](#)

1. There is no single best way to estimate the population size of grizzly bears in the Greater Yellowstone Ecosystem (GYE), and certainly no inexpensive way to produce precise estimates. There will thus be some uncertainty attending any population monitoring and any attempt to develop mortality limits.

2. Our proposals here assume that continued demographic study of the GYE grizzly population (employing a sample of radio-collared animals) will continue. These studies provide crucial background and support for the monitoring protocols we recommend.

3. Much of the basis for our new protocols for estimating the number of grizzly bears in the GYE, and how much mortality they can absorb before declining, remains as identified in the 1993 Grizzly Bear Recovery Plan. In particular, field observations of females with cubs of the year, subjected to objective criteria to best estimate how many unique individuals those observation represent, remain a core data requirement. In addition, demographic modeling provides the basis for estimates of sustainable mortality.

4. However, our new recommended protocols differ from that outlined in the 1993 Recovery Plan in a number of ways that reflect increased understanding, new data, better analyses, and criticisms and suggestions from other scientists and the general public. Although we acknowledge that they contain weaknesses and cannot be equipped with a guarantee, we believe these new protocols are built on better science and represent a substantial improvement over the older ones.

5. Principal changes from the older protocols to the new ones are:

a. They use a well-explored frequency-of-capture model to estimate the total number of females with cubs present in the GYE each year, rather than simply using an unadjusted “minimum” count.

b. Rather than the *ad-hoc* method of summing these values over a 3-year period (to emulate the roughly 3-year cycle of reproduction in GYE grizzly bears), they use each year's estimate of females with cubs. However, they use historical as well as current data as well as several statistical approaches (regression, information-theoretic techniques, and model averaging) to refine the estimate of the number of females with cubs present in each year.

c. They use unbiased data from marked Yellowstone females to estimate the mean probability that an adult female will have cubs in any given year, and thus a new multiplier to estimate the total number of adult females.

d. They use newer demographic data to project the total number of bears of both sexes and all age-classes from these estimates of adult females.

e. Rather than mortality limits being applied only to human-caused mortality (which

often required determination of the cause of death), new mortality limits apply to all mortalities.

f. Like the older protocols, they assume that not all dead bears become known to agency personnel. However, rather than an *ad-hoc*, assumed number of unknown mortalities, the new protocols use Bayesian methods and data from radio-marked grizzly bears in the GYE to estimate the number of unknown and reported mortalities that occur yearly.

g. Mortality limits are based on newer, published demographic modeling which used GYE-specific data, and which avoided making critical assumptions that the previous model did.

h. A new protocol for interpreting trends and fluctuations in the resultant population estimations is provided, which uses information-theoretic methods to distinguish between short-term, inconsequential fluctuations, and a true change in the underlying population trajectory.

i. All values used in the new protocols have some type of standard error or confidence interval, allowing users some sense of their precision and reliability.

[◀ Back to contents](#)

Background

[◀ Back to contents](#)

This project began in 2000, following a review of the current methods used to estimate sustainable mortality and issues facing management of the GYE grizzly bear. The Study team, in cooperation with the USFWS, prepared a series of proposals soliciting funding to address the following objectives: (1) evaluate the unduplicated female rule set established by

Knight et al. (1995), (2) explore and evaluate techniques to generate an annual estimate of adult females (>3 years of age) incorporating uncertainty, (3) explore and evaluate techniques to generate an annual estimate of total population size incorporating uncertainty, and (4) establish sustainable mortality limits based on recent demographic information from the GYE.

Funding was obtained in fiscal year 2001. We established a demographics working group and began to address these issues. Much of the demographics work identified was completed in 2003 and published as Schwartz et al. 2006a. Further discussions were held February 1-4, 2005 in Fort Collins, Colorado, March 23-25 and May 11, 2005 in Bozeman, Montana, and June 19-21, 2006 in Grand Teton National Park.

The original Grizzly Bear Recovery Plan of 1982 recommended the development of population monitoring methods and the establishment of mortality thresholds for all bears in all “ecosystems” (USFWS 1982). The 1993 revision of the Recovery Plan (USFWS 1993) adopted specific monitoring methods and population criteria specifically for the GYE:

- A central repository for all observations of females with cubs of the year (F_{cubs} , hereafter) would be established, and standardized methods would be developed for distinguishing unique F_{cubs} from duplicate observations of a F_{cubs} already observed and recorded. The Recovery Plan then required that a minimum of 15 F_{cubs} be documented over a running 6-year average from the area including

the Recovery Zone and a buffer of 10-miles immediately surrounding it;

- To ensure adequate geographic distribution of the population (that is, to prevent a situation in which 15 F_{cubs} could be documented — and thus the criterion seemingly met — while large sections of the GYE were without reproductive females), 16 of the 18 bear management units (BMUs, geographical units that had earlier been delineated) within the GYE had to be occupied by females with young (cubs, yearlings, or 2-year-olds) over a running 6-year sum of observations, and no 2 adjacent BMUs could be unoccupied;
- A “minimum population estimate” would be developed, based on the most recent 3-year sum of unduplicated F_{cubs} . *Known* human-caused mortality could not exceed 4% of this minimum population estimate. (This rule was amended in 2000 to include *probable* human-caused

mortalities, and cubs accompanying both known and probable human-caused female deaths as part of the tally of mortalities);

- No more than 30% of these deaths (i.e., the 4% above) could be females;
- These mortality limits could not be exceeded during any 2 consecutive years.

Although formalized in the 1993 Recovery Plan revision, science and knowledge continued to move along. There are points in time where it is appropriate to use newer data and analytical techniques to re-assess what had earlier been agreed, and by the early 2000s, it seemed that such a point had indeed been reached. Thus, the *Study team* began reviewing all the available demographic data, with the intent of determining if these criteria remained the best that could be produced, or if alternatively, there were better ones. The “*Reassessing*” document, [Schwartz et al. 2006](#), and this document, are products of that effort.

The original (1993) protocols: a closer look

◀ [Back to contents](#)

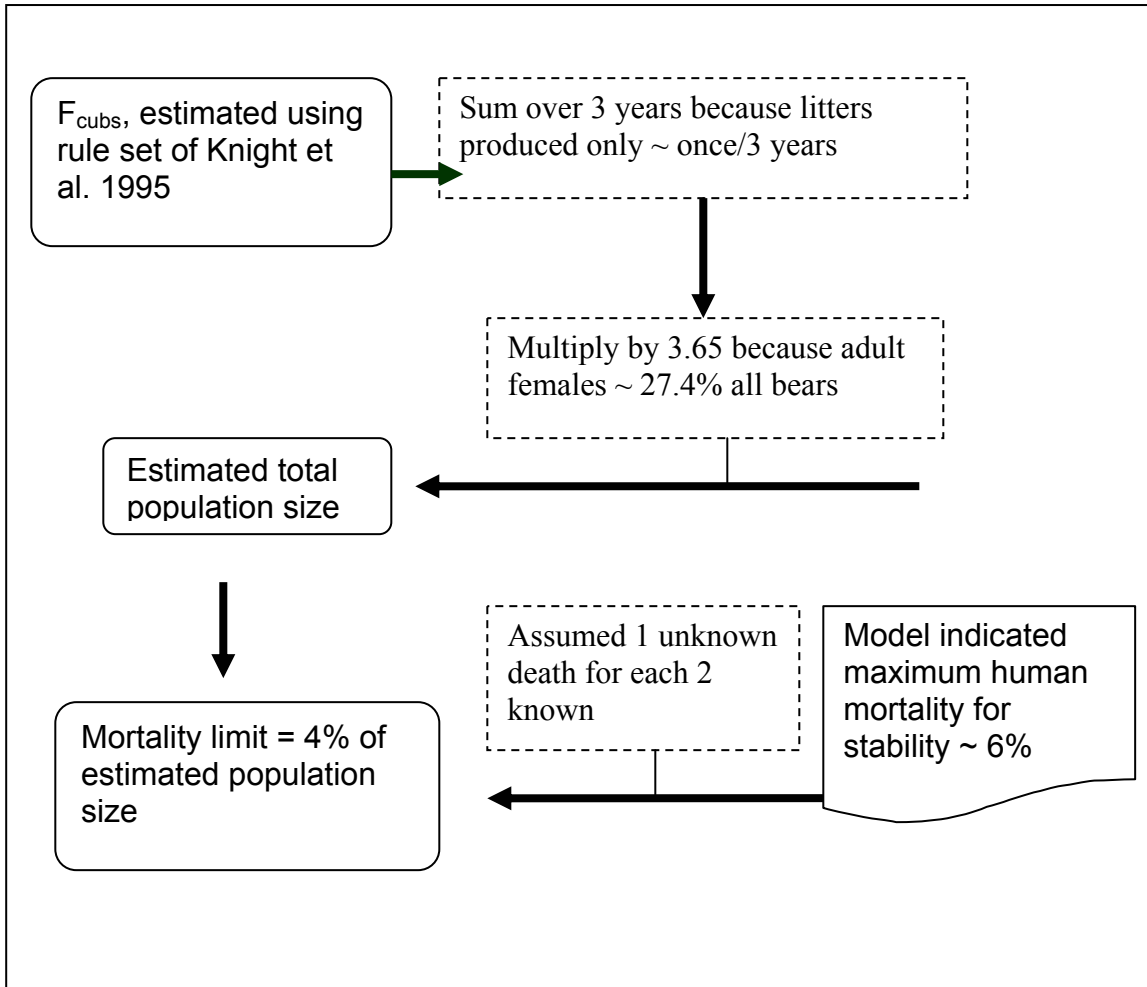


Illustration 1. Flow chart of the original (1993) protocol for estimating the number of grizzly bears in the GYE and limits to mortality. F_{cubs} = females with cubs of the year.

◀ [Back to contents](#)

Counting females with cubs of the year (F_{cubs})

[◀ Back to](#)

It has long been recognized that any kind of population estimation for grizzly bears is very difficult to obtain. In earlier years of the Yellowstone research and monitoring effort, it had, however, been noted that bears were occasionally observed, and that by careful parsing of *some* of these observations, it might be possible to estimate which observations represented the same individuals and which not. Bears are not individually recognizable in general, but adult females possess one characteristic that other bears do not: they sometimes have cubs, sometimes yearlings, sometimes older offspring, and sometimes no offspring at all. Further, litter sizes vary from 1 to 3. These characteristics, combined with dates and locations, allowed the beginnings of a rule set to differentiate duplicate observations of a particular animal from observations of unique animals. From this protocol, an estimate of the number of females with cubs of the year (F_{cubs}) could be generated each year.

The rule set ultimately developed acknowledged that there could be two kinds of error in categorizing such observations: 1) observations that were really of the same animal could erroneously be considered those of 2 or more animals, and 2) observations of 2 or more animals could erroneously be considered the same animal. The rule set developed was designed to make errors of the 1st kind rare, even if it made errors of the 2nd kind more common. It is in this sense that members of the [Study team](#) considered it “conservative” (i.e., more likely to

undercount than to overcount; it is probably not accurate, however, to call it a “minimum”). More details on how this was ultimately formalized can be found by clicking [here](#). Note that it was never claimed or believed that every single female with cubs in that year would be observed or reported.

Adult female grizzly bears do not produce cubs every year; in fact, in the [GYE](#), most females give birth to a new litter about every 3 years. Thus, counting only F_{cubs} was not a count of *all* the adult females. (The technique was not used to estimate females with yearlings and 2-year olds, because it is more difficult to determine the age of larger offspring. Some yearlings that grow quickly can be as large as 2-year-olds that grow slowly. Lone females cannot be distinguished from young males because both are about the same size. Consequently, the only easily distinguished group of bears is females with cubs of the year.) Thus a simple rule of summing all the F_{cubs} seen over a 3-year period was developed. Since on average adult females give birth about every 3 years, this 3-year sum was assumed to represent the adult female segment of the population. (Summing over 3 years also has the effect of dampening yearly fluctuations).

From F_{cubs} to total population

[◀ Back to contents](#)

How to move from an estimate of the number of adult females to an estimate of the total population? Direct observations from the field would never be useful for this task. Instead, models of how the population likely operates were developed in the mid 1980s (by Lee

Eberhardt, among others) that suggested that, on balance, a population with birth and death rates as the GYE seemed to have at the time would consist of approximately 27.4% adult females (“adult” was defined as age 5 and older). Thus, dividing by the proportion 0.274 (or equivalently, multiplying by $(1/0.274 = 3.65)$ provided an estimate of the total number of bears. Further if any adult females were known to have died, these first would be subtracted from the total before the total population size was estimated.

So, in a nutshell, this method of estimating population size was:

1) Use the Knight et al. 1995 rule set to separate all observations of F_{cubs} seen in any given year into unique F_{cubs} or repeat observations of the same F_{cubs} , subtract any known deaths;

2) Add the minimum counts from for the 2 previous years to the current year (i.e., for 3 consecutive years), on the assumption that this total is a reasonable estimate of adult females in the population in any given year (because females only produce cubs, on average, once every 3 years); and

3) Multiply that number by 3.65, on the assumption that adult females are only 27.4% of all bears.

[◀ Back to contents](#)

Mortality limits

Having some kind of population estimate is good, but it is also necessary to know if too many bears are being killed to maintain a healthy population. Here, the 1993 protocol used two, complementary figures: 1) It set a criteria that known and probable human-caused mortalities be no more than 4% of the total estimated population, and 2) It set an additional criteria that of this 4%,

no more than 30% could be females (i.e., female deaths could not exceed $[30\% \times 4\% = 1.2\%]$ of the total number of bears, as estimated using the F_{cub} protocol summarized above.

How was the 4% limit derived? And where did the 30% of that 4% come from? They were derived using a population model from 1985 that compared birth rates to death rates (Harris 1986). By comparing births to deaths, it is possible to estimate how many bears can die each year yet maintain a healthy population. It is difficult to know precisely how any given grizzly bear population responds to any given number of human-caused deaths. But we can say with certainty that grizzlies reproduce much more slowly than do most other mammal species. Consequently, mortality thresholds are low when compared to deer, elk, or even black bears. We also know that once grizzly bears are independent of their mother, nearly all deaths are directly or indirectly caused by humans. Unfortunately, back in 1985 when Harris constructed these models and established mortality thresholds, detailed information on reproduction and survival for the GYE were not available, so Harris used general estimates from grizzly bear populations elsewhere.

That model, which incorporated as much information and state-of-the-art theory as was available at the time, estimated that, to be 90% confident that human-caused mortality would not be more than a grizzly bear population could handle, such deaths could not exceed about 6% of the total number of live bears. In this model, human-caused deaths were allotted among sex and ages such that 70% of dead bears were males and 30% were females. The 6% “maximum sustainable harvest” from this model population was then reduced to 4%, on the assumption that not all dead bears would become known to

managers, and that roughly 1 additional bear died for every 2 that were known to have died. Thus, the “4% + 30%” rules came from the assumptions that:

1) The model of [Harris \(1986\)](#) was a reasonable caricature of real grizzly bear populations;

2) That the specific algorithms used to estimate sustainable mortality were reasonable;

3) That 1 unknown bear died for each 2 that could be accounted for (thus lowering the 6% from the model to 4%); and

4) That because the model assumed that human-caused mortality was strongly male-biased (such that 70% of deaths were males), the above protocol would also require that female deaths be limited to 30%.

For more information on this model, click [here](#).

[◀ Back to contents](#)

Advantages of the original (1993) protocols

- While one can never be sure, all indications are that population estimates produced by the protocol outlined above are lower than true population sizes (i.e., are conservative). There are two primary reasons for this: 1) the rule-set for identifying individual F_{cubs} tends to lump rather than split (see above), and 2) it moves forward on the rather naïve assumption that all F_{cubs} in any given year are actually seen and recorded (the notion that a survey can detect 100% of animals is almost never true; wildlife population estimation is largely an exercise in various ways to figure out what was never seen).

- Similarly, while the “4% and 30% rule” is based on some very coarse approximations, living within those mortality limitations seems to

have had some benefits. At the least, it has not prevented the GYE grizzly bear population from increasing during the time it’s been in place.

- Given the difficulties of estimating population size and of developing mortality limits, it is relatively simple.

[◀ Back to contents](#)

Weaknesses/limitations of the original (1993) protocols

- The estimate of the number of unique F_{cubs} does not deal with the likelihood that not *all* females with cubs actually present are likely to be documented in any given year. In the parlance of quantitative biology, it is not an estimate at all, but rather an index. Although it no doubt bears some relationship to the true number, it’s impossible to know what that relationship is. Although the index is almost certainly lower than the true number (because we almost never observe 100% of any animal population), it’s impossible to know how *much* lower.

- The calculations to produce an estimate of the total population from the estimate of F_{cubs} are approximate, and may have biases:

1) First, summing over a 3-year interval is only an approximate way to move from “females with cubs in any given year” to “total number of adult females” (defined here as females aged 5 and above). In fact, updated calculations have suggested that the mean interval between successive litters of adult females is 3.2, not 3.0 as assumed by summing over 3 years. Further, the true interval between successive litters varies yearly, and ignoring this variability can result in underestimating the number of adult females in some years and overestimating in others. In fact, the variability in the number of F_{cubs} observed yearly – a variability which persists under any

reasonable alternative way of generating this number – is a problem that bedevils all of the possible protocols considered.

2) The denominator 0.274, used to project from the number of adult females to total population size (i.e., including younger females and all males) is not only approximate and unaccompanied by confidence limits, but, strictly speaking, refers only to age-classes. But recall that the data going into this calculation are number of reproductive females, which is close to, but not exactly that same as, the number of females aged 5 and above.

- The model underlying estimates of sustainable mortality was an approximation, and did not use information specifically from the GYE.

- The protocol for estimating the total number of bears killed by people from the number that were *known* to have been killed (i.e., assuming 1 unknown death for every 2 known deaths) was approximate, not based on GYE-specific data, and not accompanied by an indication of its precision.

- Values used in the protocol were not accompanied by error terms (e.g., standard errors). Thus there was no way to know how reliable or precise they were.

[◀ Back to contents](#)

New protocols

[◀ Back to contents](#)

Here we outline what we believe are superior protocols for monitoring GYE grizzly bears. We divide this into 4 sections: 1) estimating population size, 2) developing mortality limits, 3) estimating how many bears

die, and 4) monitoring. Here is a step-down listing of the entire protocol:

1. Raw observations of sightings of females with cubs of the year are separated into observations of unique females and repeat observations of the same female using the methods of Knight et al. (1995).
2. The Chao2 estimator is applied to sighting frequencies of unique females to obtain an estimate of the total number of females with cubs of the year in the population.
3. The number of unique females obtained from the Chao2 estimator each year is added to the existing dataset, and a model averaging process applied.
4. The predicted number of females with cubs obtained from the model fit is then used as the best estimate of the total number of independent females in the population accompanied by cubs of the year for that year.
5. Recognizing that with each iteration, some change in number of females predicted for earlier years is expected, we recommend against retrospectively adjusting estimates from previous years.
6. The predicted number of females with cubs is then divided by the proportion of females ≥ 4 years old estimated to be accompanied by cubs of the year (transition probability = 0.289) to estimate the total number of females in the population ≥ 4 years old.
7. The number of females ≥ 4 years old is then divided by the estimated proportion of females ≥ 4 years old in the population of females ≥ 2 years old (0.77699) to estimate the number of independent

- females (≥ 2 years old) in the population that year.
8. The sustainable mortality limit for independent females is 9% of the population estimate of independent females. This includes all sources of mortality – natural, human-caused, and unknown and unreported deaths. We define sustainability as a mortality level low enough that there is a 5% or lower chance that it would lead to a population decline.
 9. Unknown and unreported mortality is estimated based on the methods of [Cherry et al. \(2002\)](#) as described in the [Reassessing Methods Document](#).
 10. The number of independent males in the population is based on the estimated ratio of independent males:independent females (0.63513) to estimate the number of independent males that year.
 11. The sustainable mortality limit for independent males is set at 15% of the population estimate of independent males. This includes all sources of mortality – natural, human-caused, and unknown and unreported deaths.
 12. The number of cubs in the annual population estimate is calculated directly from the model-predicted estimate of females with cubs of the year by multiplying by the mean litter size (2.04) observed from 1983–2002.
 13. The number of yearlings is estimated by multiplying the estimated number of cubs from the previous year by the mean survival rate for cubs (0.638) observed from 1983–2001.
 14. The sustainable mortality limit for dependent young (cubs and yearlings) is set at 9% of the annual estimate of dependent young. Only human-caused deaths (reported known and probable) are tallied against this threshold.
 15. Natural, and unknown and unreported mortalities are not estimated for dependent young.
 16. Because this protocol smoothes variability, we no longer base annual limits on a 3–year running average as originally proposed in the [Reassessing Methods Document \(Interagency Grizzly Bear Study Team 2005\)](#). Rather, we recommend annual mortality limits based on data and calculations from the current year only.
 17. All values have estimates of uncertainty.
 18. We recommend the demographic objective originally proposed in the [Reassessing Methods Document \(Interagency Grizzly Bear Study Team 2005:44–45\)](#) of $48 F_{\text{CubChao2}}$ remains the same, however we recommend using the predicted number based on model averaging.
 19. We recommend a biology and monitoring review should this predicted estimate of F_{Cub} decline below 48 for any 2 consecutive years.
 20. We also recommend the management agencies direct management action to limit female mortality if the model predicted estimate of Chao2 drops below 48 in any given year.
 21. We recommend a biological and monitoring review as per the [Yellowstone Conservation Strategy](#) if independent female mortality exceeds the 9% limit in any 2 consecutive years.

22. We recommend a biological and monitoring review if independent male mortality exceeds the 15% limit in any 3 consecutive years.
23. We recommend a biological and monitoring review if dependent young mortality exceeds the 9% limit in any 3 consecutive years.
24. We recommend that if the AIC_c weight favors the quadratic term (i.e., > 0.5) in modeling the rate of change of females with cubs, a full review of the population's demographics be undertaken

- to better understand its status. (See below for descriptions of what this means).
25. We recommend that dead bears reported in years subsequent to actual year of mortality be tallied against year of death and mortality total be recalculated. If mortality exceeds the threshold for that year, the difference (total mortality minus threshold) be counted against the current year's threshold.

Below is a diagram illustrating the important components of the new protocols:

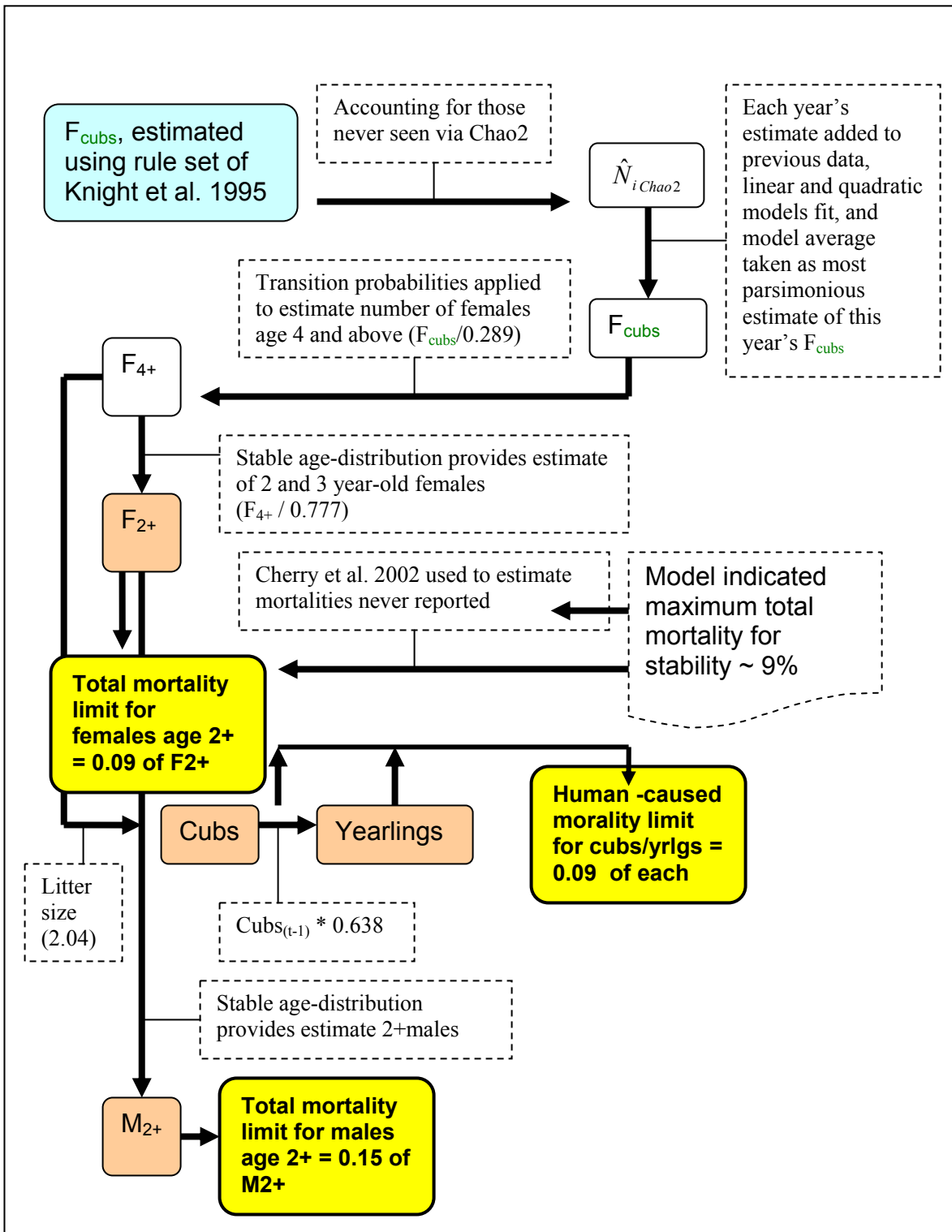


Illustration 2. Flow chart of the proposed protocol for estimating the number of grizzly bears in the GYE and limits to mortality. \hat{N}_{iChao2} = estimated number of females with cubs in year i using the Chao2 estimator; F_{2+} = females aged 2 and older F_{4+} = females aged 4 and older; M_{2+} = males aged 2 and older

[◀ Back to contents](#)

Method for estimating population size

[◀ Back to contents](#)

Motivation

Despite all the work that has gone into understanding the GYE grizzly bear population, figuring out how many bears there are is, alas, not much easier than it has ever been. Although cognizant of its problems and limitations (click [here](#) for information on alternative methods to estimate population size that have been considered but are not recommended), we recommend that population estimates – needed so that mortality limits can be set in context – be based on estimates of the number of adult females, which, in turn, are derived from estimates of the number of F_{cubs} observed yearly. However, a number of changes from the original 1993 protocol are recommended, all of which have the effect of minimizing bias and considering and disclosing uncertainty.

Both the current and proposed protocols for estimating F_{cubs} depend on the same rule set for identifying individual F_{cubs} from the totality of observations (many of which represent duplicate observations of the same animals) each year. But whereas the original 1993 protocol does nothing about F_{cubs} present but never documented, the new protocol uses mark-resighting theory to estimate that number. Rather than F_{cubs} being some poorly understood “index” of the true number of females with cubs in the GYE during that year (a number that is probably lower than the true number, but for which there is no way to determine by how much), the proposed F_{cubs} is an actual statistical estimate, premised on well-

understood statistical theory, and accompanied by an indication of its level of precision.

Next, the proposed protocol deals with the variability in the yearly estimates of F_{cubs} and the fact that females don’t produce litters each year in a different (and we believe, better) way than the original 1993 protocol. We use all the yearly estimates of F_{cubs} , up to and including the current year’s, to derive a regression equation that best fits all the data (and even accounts for uncertainty about the shape of the regression slope) to model the number of F_{cubs} in the current year. And rather than using a proportion from a modeled age-structure to estimate the number of adult females from the number of reproductive females, we estimated a series of transition probabilities directly from GYE grizzly bear data (1983-2001), that can be used to answer the question “Given that there is a female aged 4 or older, what is the probability that she will have cubs in any given year?”

Rather than use the old “4% and 30% rule” from a generic model, this new protocol makes use of estimates of mortality that produce a non-declining population based directly on Yellowstone grizzly bear data. The newer modeling (Harris et al. 2006) makes fewer and milder assumptions than the earlier modeling effort (Harris 1986). We also use more formal methods to incorporate the number of grizzly bear mortalities that are never discovered or reported (Cherry et al. 2002). A higher mortality threshold is allowed for males.

Finally, we make more explicit recommendations for interpreting trends from these population estimates, and of initiating more formal demographic analyses (using information from radio-marked bears).

[◀ Back to contents](#)

New estimate of yearly F_{cubs}

Keating et al. (2002) explored a number of ways to use the frequency with which individual animals were observed to estimate the number of animals *never* observed. On the basis of a number of simulations, they concluded that an estimator that they termed the “second-order sample coverage” (\hat{N}_{SC2} in their paper; the “hat” over the N signifying that it’s an estimate, not necessarily the true number) estimator performed best. However, subsequent to that work, it was discovered that the simulations conducted for that paper were not as representative of the GYE observational data as originally believed. Thus, a new series of simulations were conducted that better captured the variability and sample sizes of field observations. As a result of this reconsideration, the best method for using the observations to estimate F_{cubs} was concluded to be one of the estimators that Keating et al (2002) termed \hat{N}_{Chao2} (after Dr. Elaine Chao, a Taiwanese biometrician who developed it). For example, in 2004 a total of 48 unique F_{cubs} were identified using the Knight et al. (1995) protocol (from some 202 accumulated observations), and the \hat{N}_{Chao2} procedure estimated that true number present was 57.55. For more details on these considerations, click [here](#). We recommend using this mark-resight estimator as the best available way to move from a non-statistical index of the number of F_{cubs} to an actual estimate of the number of F_{cubs} .

[◀ Back to contents](#)

Using all data to estimate yearly F_{cubs}

Although the [Chao2](#) estimator does a good job of accounting for F_{cubs} never seen, there

will remain considerable fluctuations in the estimated number of F_{cubs} under any conceivable observation system. Some of this fluctuation reflects true variation in the population (for example, in a very poor food year, females may fail to breed or later resorb their fetuses; if this occurs, there tends to be a surge in litters produced the following year). Some of this fluctuation reflects sampling variation (i.e., despite using the [Chao2](#) estimator, we are still *sampling*, and thus the data are noisy). Any estimation of the total population based on such fluctuating numbers will fluctuate accordingly. Thus the population will seemingly lurch up and down, but this will be a reflection more of our sampling limitations than anything biologically meaningful. In turn, mortality limits based on this fluctuating population estimate would have to change dramatically from year to year, causing confusion and making planning difficult (all while failing to make management any better). Thus, some sort of smoothing of yearly population estimates is desirable.

In the original protocol, this smoothing was accomplished via summing the F_{cubs} estimates over 3 years, but this method has problems. The new protocol takes advantage of the fact that we not only have a F_{cubs} estimate for the current year, but in fact have a series of such estimates from previous years. We can incorporate this historical data with the data for the present year to improve the estimate of the present year’s F_{cubs} . The easiest way to do this is to derive a linear regression using all the data (including the present year’s), and “predict” the current year’s F_{cubs} (Fig. 1).

However, using only a linear regression would unduly (and possibly erroneously) constrain the current year’s estimate to conform to recent trends. What if the trend has truly

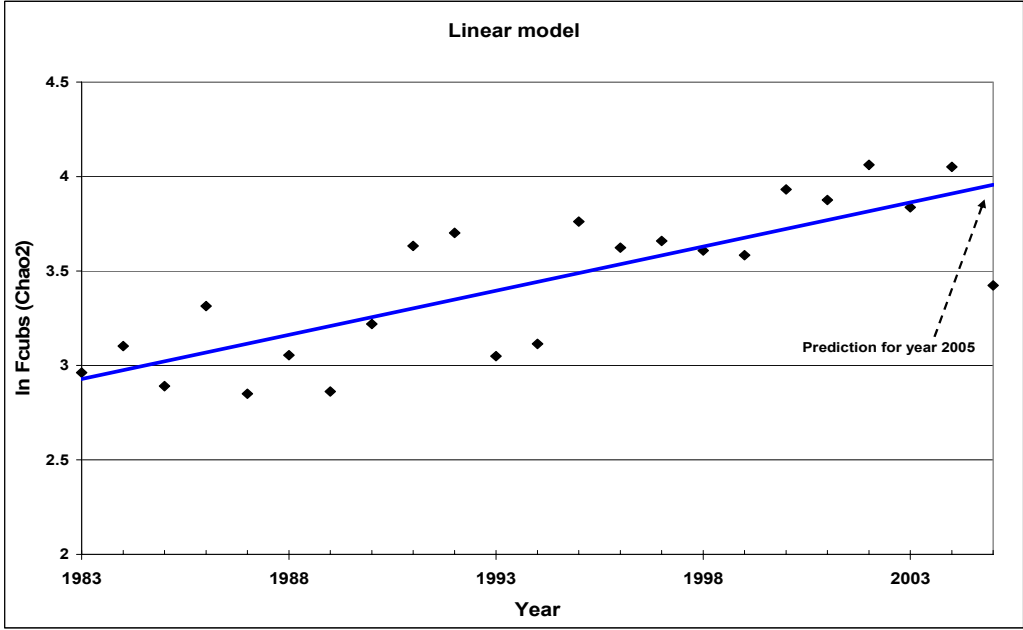


Figure 1 Linear regression of F_{cubs}

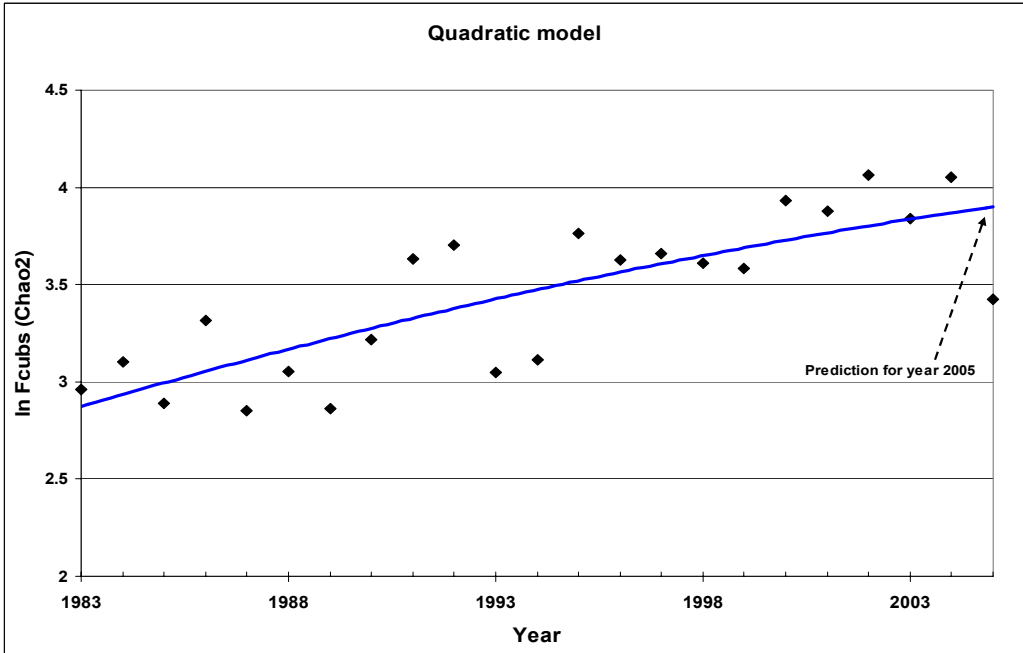


Figure 2 Quadratic regression of F_{cubs}

changed? If so, we need a smoothing technique with the flexibility to reflect that fact. One option is to model the entire data series using a quadratic (i.e., squared) term, which allows the fitted line to curve (Fig 2).

But now we have 2 possible ways to smooth the fluctuations in population estimates, and although both use all the data, they produce slightly differing estimates of the current population size. How do we decide between them?

Here, we can use recent advances in the field of information-theory to avoid *deciding* entirely, but instead to quantify the evidence for both models, and then calculate a weighted average. This provides the best possible combination of using all the available data, smoothing erratic swings in estimation that result from factors unrelated to

true population changes, while still preserving the flexibility needed to capture true changes. For example, from the \hat{N}_{Chao2} estimate of 57.55 for year 2004, the model-averaging procedure used the accumulated data to predict 49.48 females with cubs. Estimates from 1984-2005 are shown in Fig. 3.

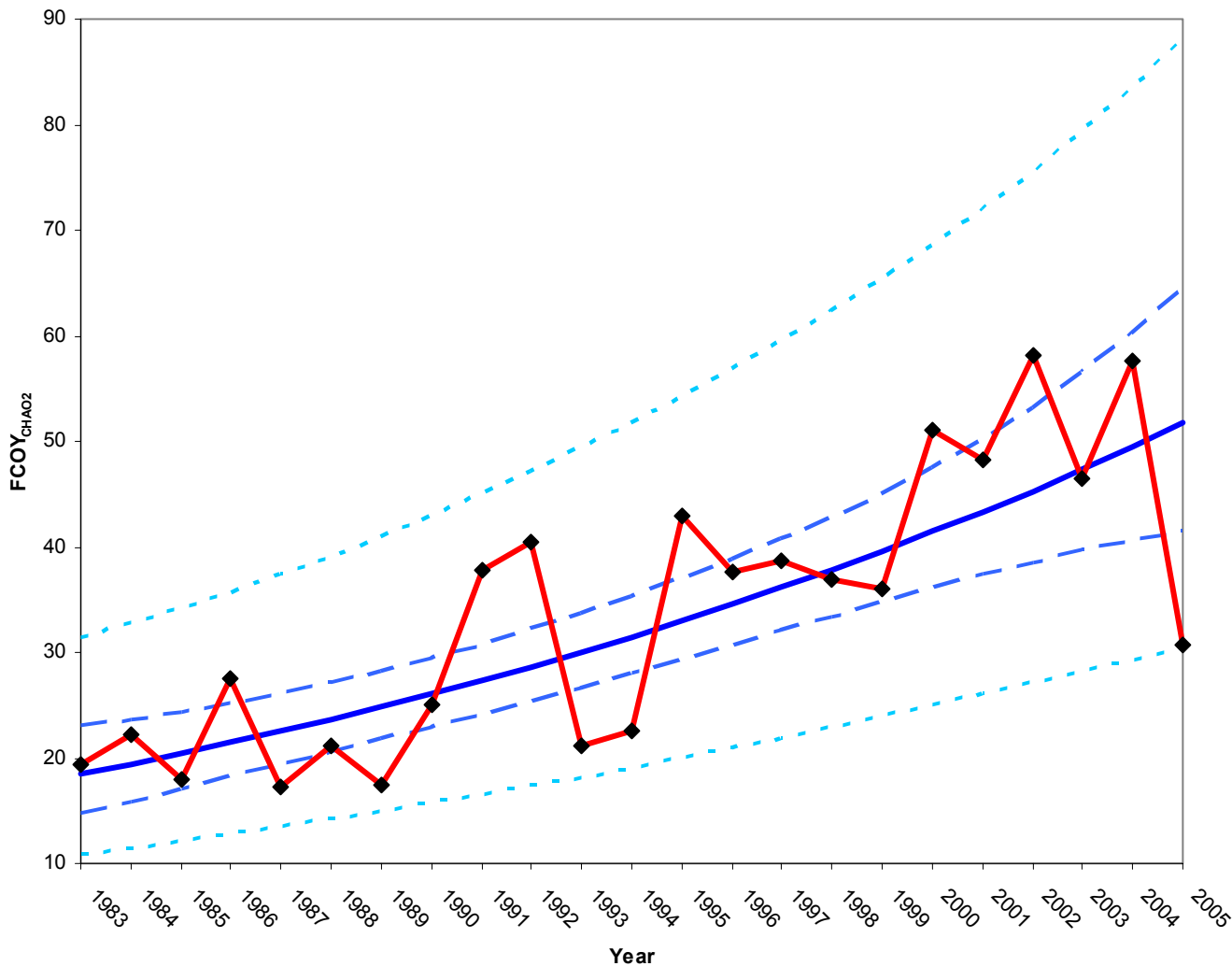


Figure 3. Trend of the F_{cub} index as predicted using the Chao2 estimator (red line) and predicted fit using the weighted model average of the linear and quadratic models (solid blue line). Dashed blue lines above and below the fitted line represent 95% confidence intervals of the model average fitted line; dotted lines above and below represent 95% prediction intervals for any given year's index. In contrast to Figures 1 and 2, this figure plots counts on an arithmetic scale.

[◀ Back to contents](#)

Estimating number of adult females from F_{cubs}

Even with this smoothing, there is still the problem that what one is estimating is merely the number of females accompanied by cubs in any given year; we know that most adult females don't have cubs at any given time (because some have no offspring, others are accompanied by yearlings, yet others by 2-year offspring). What we really wish to know is how many adult females are in the population, not merely how many females have cubs in any given year. In contrast to the rather ugly "summing over 3-year" solution in the original protocol, the new protocol uses 1983-2001 data from captured females in the GYE to estimate the proportion of females aged 4+ that can be expected to be accompanied by cubs in any given year, and divides the yearly F_{cub} estimate by this proportion to yield the total number of 4-year old and older females.

A naïve way to do this would simply be to tally the number of marked adult females in the various categories (e.g., with cubs, with yearlings, etc.). If animals were marked exactly in proportion to their presence in the population, this would produce an unbiased estimate of the proportion of adult females expected to have cubs.

However, our analyses strongly suggested that capture and marking of females was *not* independent of their reproductive status at the time: females without offspring were more likely than expected to be captured, whereas females with cubs were less likely than expected to be captured. With collars only lasting a few years, this meant that the proportion of marked females with cubs was not a representative picture of the true proportion of females with cubs.

Instead, we developed an analysis that used only females already captured and marked, and asked: "Given that an adult female was in a specified reproductive state (e.g., without offspring), what was the probability she would be in another reproductive state (e.g., with cubs) the next year?" We called this a "multi-state" model, and the object was to use GYE grizzly bear data to estimate "transition probabilities" from one reproductive state to another (including the same state). Of course, some of these transition probabilities must be zero because they are logical impossibilities (e.g., from being unaccompanied in one year to having yearlings the next, or having yearlings in 2 consecutive years). Here, below, is the total array of possible states and transitions (the analysis was used to fill in those labeled "estimated"):

	Transfer to state			
Current State	No offspring	Cubs	Yearlings	2-year olds
No offspring	<i>Subtraction</i>	<i>Estimated</i>	<i>Zero</i>	<i>Zero</i>
Cubs	<i>Subtraction</i>	<i>Estimated</i>	<i>Estimated</i>	<i>Zero</i>
Yearlings	<i>Subtraction</i>	<i>Estimated</i>	<i>Zero</i>	<i>Estimated</i>
2-year olds	<i>Subtraction</i>	<i>Estimated</i>	<i>Zero</i>	<i>Zero</i>

(Note that it is possible for a female to transition from having cubs in one year to *again* having cubs the next year, if she loses her entire litter sometime after she is observed but mates again and produces a new litter the next year. It is also possible to transition from having no offspring in one year to the same state the next year, if the female simply fails to breed or cubs are lost so early that they are never observed).

Our analysis of these transition probabilities showed that 0.289 (SE = 0.023) females aged 4 and older were in the “with cubs” state each year. Thus, this inverse of 0.289 (i.e., 3.46) became the multiplier we use to estimate adult (age 4+) females from yearly F_{cubs} . For example, from the year 2004 estimate of 49.48 F_{cubs} , we estimate $(49.48/0.289) = 171.2$ females age 4 and above. For more details on the transition probabilities, click [here](#).

[◀ Back to contents](#)

Estimating number of sub-adult females (aged 2 and 3) from adult females

We had no analogous way to estimate the number of females aged 2 and 3 in the population. Thus, we used our existing data on survival and reproductive rates in the GYE during 1983-2001 to estimate the number of 2- and 3-year olds that would be expected to occur. This was a simple modeling exercise using what wildlife demographers call the “stable age distribution”. These calculations showed that, on average, 0.777 of female bears aged 2 and above would be aged 4 and above (the number we already had to this point). Thus, multiplying the number of 4+

females by $(1/0.777) = 1.294$ provides an estimate of the number of 2+ year olds. For example, from our 2004 estimate of 171.2 females age 4+, we calculate $(171.2/0.777) = 220$ (95% confidence interval = 182-258) females age 2+. For more detail on the calculations of the stable age distribution underlying this, click [here](#).

[◀ Back to contents](#)

Estimating number of cubs and yearlings

To fill out the age-structure, we still need to estimate the number of cubs and yearlings each year. Here, we simply use the mean litter size documented in the GYE during 1983-2001 (i.e., 2.04) and apply it to our yearly F_{cub} number. For example, from the 49.48 F_{cubs} estimated present in 2004, we estimate $(49.48 * 2.04) \approx 100$ cubs present.

To estimate the number of yearlings present, we apply the 1983-2001 GYE estimate of mean cub survival (0.638). However, since we are estimating how many cubs survived to become yearlings, we use the estimate of cubs alive in 2003 and estimate their survival to 2004. Thus, for our 2003 estimate of 96.6 cubs, we would estimate an additional $(96.6 * 0.638) \approx 62$ yearlings in 2004. Of these 162 (95% confidence

interval = 145-181) offspring, half are assumed to be females and half males. (Data from marked animals since 1983 provided no reason to assume otherwise).

[◀ Back to contents](#)

Estimating number of subadult and adult males

All our demographic analyses confirmed that females really control the population growth and trajectory of grizzly bears. But that doesn't mean the males are unimportant, for obvious reasons. We still need a mortality limit for males, which means we need to estimate the number of males in the standing population as well. Unlike females which provide some basis for differentiating among individuals (by virtue of having cubs), unmarked males all basically look alike. Thus, we have no option but to again use our estimates of the stable age distribution, in this case by applying our estimates of the mortality rates among males and females. This then suggests how many males would be expected to exist, given an estimate of the number of females. Our calculations indicated that the number of 2+ year old males is expected to be 63.6% the number of 2+ year old females. (Once past the yearling age, male mortality rates are higher than females, thus there are fewer of them). Thus, for example, from our estimate of 220 2+ old females in year 2004, we estimate an additional 140 males (95% confidence interval 108-172).

[◀ Back to contents](#)

New guidelines for limiting mortality

[◀ Back to contents](#)

Motivation

The “4% and 30%” rule was based on an unpublished, generic model, which made some important assumptions in order to produce an estimate of sustainable mortality. New data and techniques had become available since the time this “old rule” was established. It was time to update this method, and base sustainable mortality limits on Yellowstone-specific data. This modeling effort is detailed in [Harris et al. \(2006\)](#).

Sustainable mortality for females

In short, these analyses suggested that, given prevailing reproductive rates and the level of yearly variation in all survival and reproductive rates we can expect from Yellowstone grizzly bears, mortality *from all causes* of 9% of females aged 2 and older produces a negligible probability (~5%) of a population decline. That is to say, if one knew for sure that one had 100 females aged 2 and older, and one could account for all the deaths, then the overall population would almost certainly stay stable or increase if 9 or fewer of them died annually. Note that this differs importantly from the earlier “4% and 30% rule”:

- It considers all mortality, not just mortality resulting from humans
- It is restricted to females, thus there is no need for a both a total limit of bears and a sub-limit for females.
- It is higher than the previous limit because the previous limit only included human caused deaths.

The last difference (that is, 9% instead of 4%) would appear to be most surprising. However, our analyses have shown that this difference implies nothing dramatic about grizzly bear populations or, for that matter, about the 2 models. Rather, the difference stems largely from the earlier assumption that many females would die of natural causes even in the presence of human-caused mortality. However, GYE data from 1983-2005 showed that very few females 2+ years old are likely to die of natural causes thus making that assumption a tenuous one at best. For the 323 bears radio-tagged during 1983-2001, the Study team documented the cause of death for 64 of the 69 mortalities that occurred while the bears were being monitored (causes for 5 deaths could not be determined). Only 5 of the 64 were *not* human caused, and *none* of the 26 deaths of 171 females were from natural causes; Haroldson et al. 2006:35. Whereas Harris (1986) considered natural and human-caused mortality separate processes, the Harris et al. (2006) work did not separate the two. In both cases, total mortality of about 9% of adult females was unlikely to cause population decline. For more on this difference between the “9% rule” and the “4% + 30% rule”, click [here](#).

“Sustainable mortality” for males

There really are no quantitative methods for estimating a “sustainable mortality rate” for males. We use quotation marks here, because the very meaning of “sustainable mortality” must be specified in the case of males: it is the female side of things that controls the growth rate of the population. Unless the presence of males in some way affects the survival or reproductive rate of females, or there is a chance that too few males will be present to mate with all available females,

the mortality rate for males is immaterial to the overall population trend. Instead, the mortality rate for males affects the *ratio* of females to males in the adult segment, which in turn affects mating structure, genetics, and long-term viability. So males *are* important, but there simply is not a clear analytical (or simulation-based) way of estimating a “sustainable” mortality rate for them.

Given this, we recommend that limits for male mortality be set at approximately our estimate of the rate that pertained during 1983-2001, a time period during which the GYE grizzly bear population increased. Haroldson et al. (2006) estimated survival of males age 2+ to be 0.823 or 0.874 (depending on assumptions about bears whose fate was unresolved). A mid-point between these 2 estimates is about 0.85, thus suggesting that about 15% of males aged 2+ were dying yearly during this period.

[◀ Back to contents](#)

Estimating unknown and/or unreported mortality

We know that it is impossible to find and record all dead bears across the thousands of square miles of wild county in the Yellowstone Ecosystem. The original (1993) protocol simply assumed that 1 additional bear died for every 2 deaths that became known. More recent work by Cherry et al. (2002) used GYE grizzly bear data to estimate the probability of there being unknown deaths given some number of known deaths, as well as to provide error terms on these probabilities. The point estimate of the ratio of reported to unreported deaths was 0.37:0.63. This method assumes that all deaths associated with management removals (sanctioned agency

euthanasia or removal to zoos) and deaths of radiomarked bears are known. It calculates the number of reported and unreported mortalities based on counts of reported deaths from all other causes. For example, in the year 2004, 5 deaths of unmarked grizzly bears from other causes than management removals became known to the [Study team](#), but [Cherry et al. \(2002\)](#), estimated that 13 actually died (the 5 reported deaths plus 8 unknown and unreported). So for 2004, we add to this estimate bears that died as a result of agency removal (4) and deaths of radiomarked bears that were not sanctioned removals (0), to estimate total mortality from all causes = 17 (4 + 0 + 13 = 17). Details of the method and application can be found in [Cherry et al. \(2002\)](#).

Advantages of the new protocols over the original (1993) protocol

- It is based on empirical data from the [GYE](#) grizzly bear population, whereas some components of the 1993 protocol were not.
- To the best of our knowledge, it provides an unbiased way to estimate population size;
- It employs a rigorous method to help interpret the resulting trend

[◀ Back to contents](#)

Limitations/disadvantages of the new protocol

- It is more complex than the original 1993 protocol;

- It depends on the system for identifying unique females with cubs originally developed by Knight et al. (1995); although considerable work has gone into standardizing this system, it is not possible to guarantee that errors are not made. However, as stated earlier, most errors result from classifying sightings of different bears as the same bear rather than splitting multiple sightings of the same bear into different bears (it thus tends to produce conservative population estimates);
- As in the original 1993 protocol, it uses a constant term to project from the number of F_{cubs} in any given year to the total number of adult females. Using a constant means that if reproductive rate changes with time (e.g., goes progressively down, or progressively up from the assumed value), the estimate of the total number of females will be biased. If such a change takes place, the estimate of the number of adult females (and, for that matter, all other sex/age classes) would be biased. To deal with such a possibility, we recommend that these numbers be updated every 8-10 years using recent information from a sample of radio collared females;
- It uses values from a stable age distribution to project from the number of adult females to other segments of the population; to the degree that age-structures vary, some inaccuracy in the projection will result;
- As with any plausible sampling regime, it is subject to sampling error,

and as a result, cannot provide managers or the public with an unambiguous determination of the population trend right up to the moment; a few years must pass before one can be confident that a change in trend has occurred.

[◀ Back to contents](#)

The next page shows an example of the entire set of protocols, worked out for the year 2004.

An example worked out: data from 2004

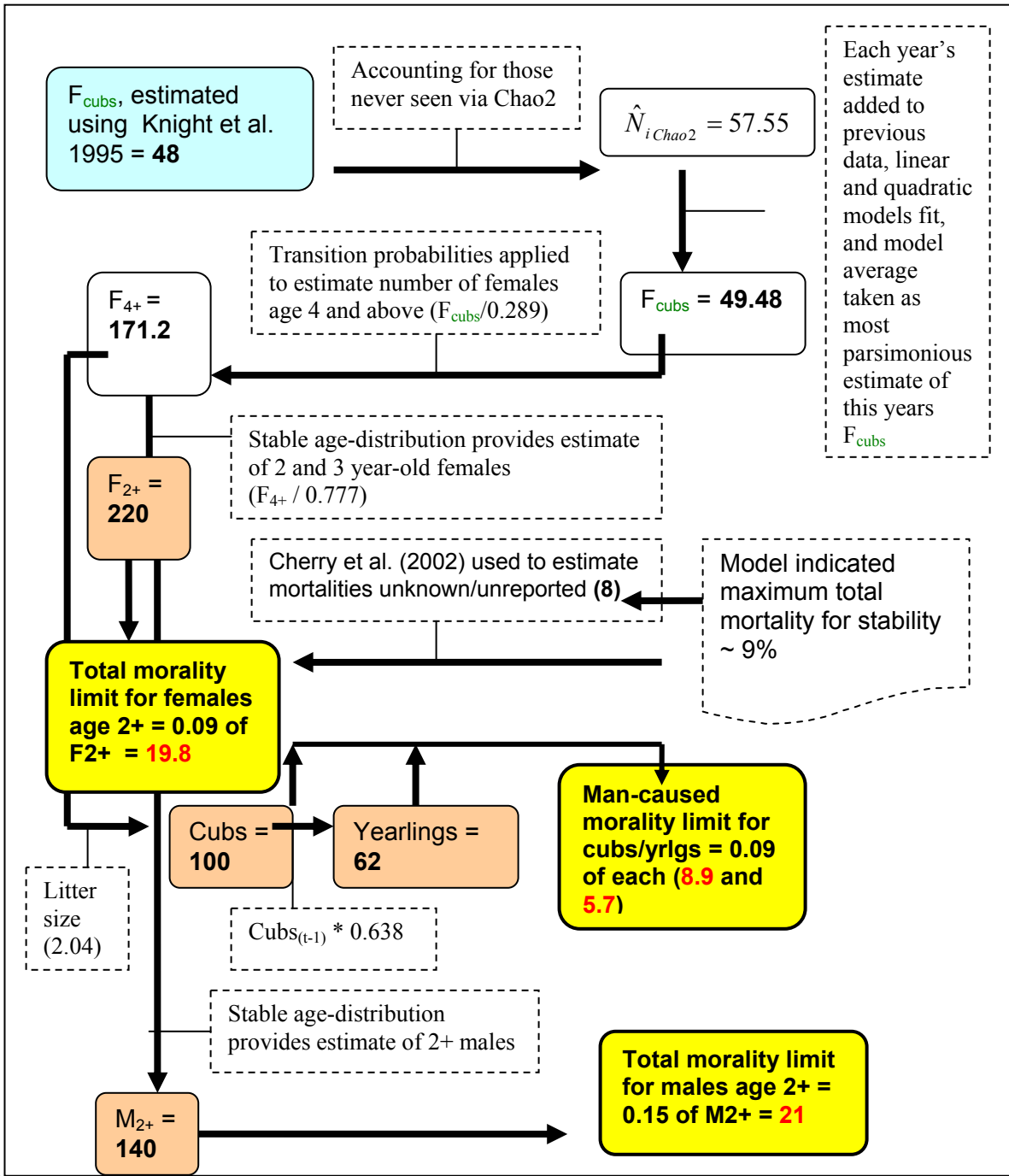


Illustration 3. An example, applying the proposed protocol for estimating the number of grizzly bears in the GYE and limits to mortality for year 2004. The total population size is estimated as $(220 + 140 + 62 + 100 = 522)$. Abbreviations as in Illustration 2.

[◀ Back to contents](#)

Population trend monitoring

[◀ Back to contents](#)

Our recommendation is that the field and analytical procedures detailed here be conducted yearly. In one sense then, trend monitoring is automatic: one simply looks at each year's data and has a "trend". However, there remains the issue of interpreting the inevitable ups and downs. Clearly we cannot banish sampling variation, so there will be noise in our data caused by our own sampling limitations. There may also be true, short-term, and minor fluctuations in population size that don't necessarily indicate a fundamental shift in trajectory. We know that a population whose fundamental trajectory is an increase can display short-term, small-scale declines (because of temporary food shortages, for example), just as one whose fundamental trajectory is decline can display short-term, small-scale increases (say, because of an unexpected nutritional bonanza). We recommend that management aim to keep these short-term, ultimately inconsequential fluctuations in perspective. At the same time, managers need to know if and when a true change in the trajectory has occurred, so that they can take appropriate actions. A monitoring system that has too much inertia by calculating trajectory change over a long period of years will fail to detect a true change unless it is dramatic (or, with such a time lag that dramatic changes in management would be then needed).

How do we find the best balance between correctly detecting real changes in trend, on the one hand, and avoiding responding to every small fluctuation ("...*the population is growing this year*", "*well, in this next year, it seem to be declining...*", "*never mind, in the 3rd year it's going back up again...*") on the other?

Without doubt, the trend of the F_{cub} counts has been up for the past 2 decades or so. Now in

all of our writing we have steadfastly refused to *predict* the future trend of the GYE grizzly bear population (although some readers have naively interpreted population *projections* — which necessarily move things forward in time based on conditions that exist at the moment of projection — as predictions). That said, it seems likely to us that the GYE grizzly bear population will, at some point, stop growing. The critical issue, it seems to us, is determining when that has occurred, and how dramatic the slow-down (or cessation, or even reversal) of population growth has been.

We have considered the possibility of measuring trend along some sort of moving time-frame, but concluded 1) that there is no objective method for deciding what the time-frame should be, and 2) that evaluating trend over short time spans would inevitably yield estimates with such high variability (because of the small number of data points included) that they would encompass all the possibilities from serious decline to dramatic increase.

Instead, our recommended protocol for interpreting the series of counts is to:

- 1) Fit both linear and quadratic regressions to the *entire series* of F_{cub} estimates (as generated by the Chao2 estimator);
- 2) Calculate [Akaike's Information Criterion \(\$AIC_c\$ \)](#) for both models;
- 3) Evaluate the AIC_c weights of both models.

Weight favoring the quadratic term is evidence that population growth has slowed or reversed, but we caution that lack of such evidence is not necessarily proof that change hasn't yet taken place. Gradually increasing evidence for the quadratic model over a few years (assuming a negative quadratic slope, i.e., that growth appears to be slowing) should serve to

keep biologists and managers alert to a possible change in system state. If the AIC_c weight favors the quadratic term (i.e., > 0.5) in modeling the rate of change of females with cubs, we recommend that a full review of the population's demographics be undertaken by the **Study team** to better understand its status. Under the best of circumstances, this monitoring protocol leaves uncertainty about the system state during the most recent few years. We find this a compelling reason to couple the model fitting described above with continued monitoring of demographic rates from a sample of radio-marked females (as well as their unmarked offspring). Although also characterized by variability and time-lags, such monitoring provides an independent measure of population vigor, and is likely to be helpful in explaining any observed changes in numbers of females with cubs. Thus, we re-emphasize that continued demographic studies (i.e., capturing animals and fitting them with radio collars to monitor reproduction and survival) is critical.

Our investigation into the power of this model fitting to correctly detect a leveling-off or a modest (e.g., 5%) decline, given the variability that has thus far characterized the system, suggests that there will be an inevitable delay before one can be certain of a change in system state from its recent increase. For example, if the population were to suddenly begin declining at 5% yearly, it would require roughly 5 years before one would be confident that a decline observed in the F_{cub} estimates reflected a true decline and not merely short-term fluctuations or sampling error (Fig. 4).

Unfortunately, the number of females with cubs can only be estimated, and even our best field and analytic procedures can only do so much to reduce variation in yearly estimates (although any improvements in sampling efforts

that would limit influence of sampling variance would increase statistical power to detect trends). We do not doubt that these estimates track true population change generally, but they have limited statistical power to reliably detect subtle (yet potentially important) changes in λ within the time-frame of a few years. Although our suggestion of fitting linear and quadratic models to the time series and using AIC_c weights to evaluate their relative appropriateness remains sound, we caution that, given realistic projections under variability, a delay of some years is inevitable before one can be reasonably confident that an *apparent* change is a *real* change. (Needless to add, a more dramatic change would be more easily detected). This degree of uncertainty reflects not so much a poor choice of index or analytical technique, as it does the inevitable characteristics of field work on grizzly bears and the mathematically (if not biologically) subtle distinction between growth at roughly 5% annually and no (or slightly negative) growth.

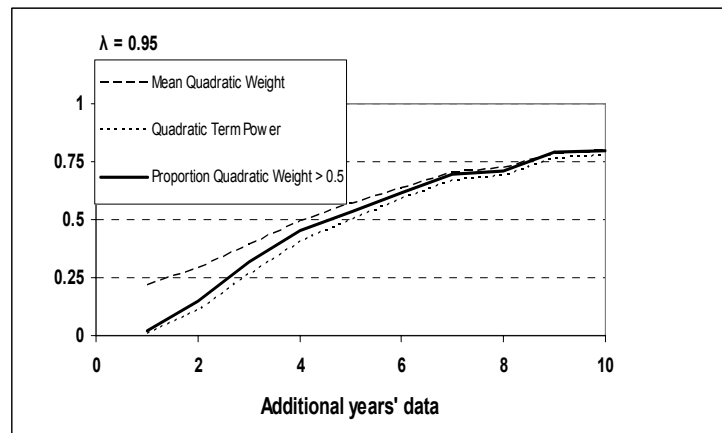


Figure 4. Power of the index to detect a true change in system state when the population begins to decline at 5% yearly in year 0.

For more details on trend monitoring using the F_{cub} estimates, click [here](#).

[◀ Back to contents](#)

How might methods, analyses, or data err?

[◀ Back to contents](#)

Wildlife conservation and management is an imprecise science; decisions are always made under some level of uncertainty. If perfect knowledge was required before decisions could be made, the result would be complete paralysis. To deal with ever-present uncertainty, wildlife managers typically adopt one or both of the following general strategies: a) developing and monitoring on numerous indicators of population status, which — acknowledging that all are imprecise — together allow for information feedback, and b) managing conservatively, so that any errors not detected until later can be corrected before undesired consequences are irreversible.

In obtaining and analyzing data, and proposing protocols for monitoring and limiting mortality of Yellowstone grizzly bears, the [Study team](#) has focused primarily on objective and unbiased estimates, and on understanding our level of uncertainty around those estimates. However, in some cases, limitations of data or the lack of clearly preferred direction required “filling-in” gaps with assumptions. To the degree that any of these are not true, they may cause biases, either positive or negative, in estimates of how much mortality the population can absorb before declining, and/or how a future population responds to such mortality. If our estimate of how the population responds to mortality is biased low, or of how much mortality actually occurs is biased high, our estimates of population response will be “conservative” (i.e., the population will be doing better than we think). Conversely, if our estimates of how the population responds to mortality is biased high, or of how much

mortality actually occurs is biased low, our estimates of population response will be “risky” (i.e., the population will be doing worse than we think).

Here we lay out all of those places where data, analyses, or other factors limited our ability to use hard data to map out every step of the way (and thus where such biases might have crept in), and our best estimates of the direction and magnitude of such biases.

I. Field data

Geographic sampling – large scale.

Sampling of bears for radio-collaring may have lagged behind an expanding geographic front ([Schwartz et al. 2002, 2006e](#)), thus over-sampling bears in relatively high survival areas and under-sampling bears in low survival areas. Our analysis ([Schwartz et al. 2006d](#)) strongly suggested that demographic vigor was strongest within the Recovery Zone where security is high and private land low. At the same time, other analyses suggested that the geographic area occupied by the population has expanded to include an increasing proportion on and near private lands and public lands outside the Recovery Zone. On the other hand, some large wilderness areas in the periphery of the geographic distribution where grizzly survival is high may have been under-sampled. There is reasonable information suggesting our sample was representative of the population at large—[Schwartz et al. \(2006a:12\)](#) — but if biased it may have resulted in either a “conservative” or a “risky” outcome; one we cannot quantify either one.

Non-random sampling on a smaller scale. Within each identified area of relative risk, there may be smaller-scale lack of randomness in the radio-collared sample (despite the efforts of field staff to obtain a random sample). For example, it may have been more difficult to capture bears in remote settings than close to roads. There may also be bears that, for behavioral reasons, are less likely to respond to baits or are more cautious around traps. By their nature, these possible biases are impossible to quantify. That said, all of the likely reasons for a non-random sample within the area trapped generally suggest that sampled bears would have lower survival than unsampled bears. Bears evading research capture because of remoteness, wariness, or cautious behavior are likely to live longer than bears that are easily captured. Thus, we believe any biases here would lead to conservative management.

II. Analyses and Modeling

Reproductive rate. The reproductive rate used for modeling population trajectory (Harris et al. 2006) was probably a little lower than was truly the case. In estimating survival of cubs during their first non-denning season, daily survival was calculated for all cubs assuming a beginning date of April 22 (Schwartz et al. 2006b:20). However, some litters were not observed until after this date; on April 22, litter size may have been larger than ever observed (or some litters may have been lost entirely). Assuming constant survival during the period, Schwartz et al. (2006b: 20) estimated cub recruitment could have been underestimated by about 13% (i.e., if cubs died prior to being observed, true reproductive rate (female cubs/adult female/year) would have been 0.362

rather than the 0.318 used in population projections). However in demographic models, we declined to use the higher reproductive rate figure because doing so would have required us to “assume” bears into existence that were never documented. Given that other analyses we conducted suggested that reproductive rate (termed “ m_x ” in Harris et al. 2006) contributes roughly 9% to population growth rate (Harris et al. 2006:48), our use of 0.318 could have biased population growth rate (and thus our estimate of sustainable mortality) downward (i.e., been “conservative”) by up to 1%.

Survival of orphaned yearlings. The survival rate of yearlings used for modeling population trajectory could have been biased low. In the field, yearlings were not marked; instead, they were assumed to have died if observations of the family group suggested they were no longer associated with their mother. According to Schwartz et al. (2006:26c), “This assumption ... [a decline in litter size denoting death of offspring]...may not have been correct for...yearlings. We know that some females wean offspring as yearlings...but we do not know the fate of these weaned individuals. We lack data to make any objective decision on the proportion that might survive. Hence, we assumed all yearlings that disappeared from their mother died”. This assumption was carried though all subsequent demographic modeling, such that if we projected a future with decreased survival of adult females, yearling survival was assumed to decrease in tandem. We do not know the percentage of weaned or orphaned yearlings that survive to become 2-year olds, but if it was truly higher than zero, our projections were biased low (i.e., “conservative”). Because yearling survival also contributed about 9% to population growth

rate, the conservative bias would be roughly an order of magnitude less than the percentage of yearlings that actually survived (e.g., a conservative bias of 1.8% if 20% of yearlings actually survived).

Correlation of vital rates within years. In “stochastic” modeling of population growth rates, our objective was to capture the full magnitude of yearly variation in vital rates. (By definition, variation is ignored in **Deterministic** estimates of the yearly growth rate, which we typically symbolize using “ λ ”). However, because we had no way to directly estimate correlation among yearly rates, and because we believed that modeling yearly rates from our temporal covariates would fail to encompass the full range of variability, [Harris et al. \(2006\)](#) assumed independence among yearly rates. In fact, any positive correlation among yearly vital rates would tend to push the resultant population trajectory downward. Thus, we biased population projections upward (i.e., ‘risky’) by ignoring such correlation structure.

In a subsequent analysis, we have estimated that yearly survival rates of juveniles (cubs and yearlings) and adults were positively correlated ($r = 0.16$ to 0.68 , depending on models used), but that reproductive rate was weakly negatively correlated with adult survival ($r = -0.15$) and its correlation with juvenile survival ambiguous (r varied from -0.20 to 0.57 , depending on models used). In a Monte Carlo re-sampling exercise, we determined that estimates of mean λ during 1983-2002 were essentially unaffected by ignoring the yearly correlation structure implied by our best models, but that the confidence intervals we estimated would attend any λ generated using our estimated level of yearly variation were insufficiently broad to account for yearly correlation. Given a fixed level

of yearly variation but our best estimate of the magnitude of yearly covariance, we estimate that the lower bounds (but not the means) reported by [Harris et al. \(2006\)](#) were biased high by roughly 1-2%. For example, whereas [Harris \(2006:50, Table 20, 5th row\)](#) estimated that a population with mean adult female survival of 0.91 would have a 5% probability of having $\lambda < 1.015$ or lower, this estimate assumed complete independence among yearly rates. Using our best estimate of the underlying correlation structure observed during 1983-2002, this lower 5% tail of the distribution would lie at approximately $\lambda = 1.005$ (the mean, [i.e., expected λ would remain at 1.029 in either case]). For more details on this, click [here](#).

III. Protocol for ensuring that mortality is sustainable

F_{cubs}. In estimating population size, a number of parameters are estimated from field data of females with cubs of the year. The best estimate of females with cubs of the year may be biased in at least 3 ways:

a) The number determined to be “unique” is very likely lower than the true number, due to inherent limitations of the observational technique. This underestimation is minor when there are few animals (and many observations), but becomes larger — perhaps up to 50% — when population size is larger (regardless of the effort made in observing them). This is because there are only a small number of ways that 2 similar-looking bears can be known to be unique; the more similar bears the live in any given area, the more likely that it will be impossible to reject the possibility that all observations came from a single bear. The burden of proof within the protocol used to decide how many bears actually exist in any given year rests with the argument

that multiple sightings represented multiple bears; lacking strong evidence, the “default” decision is always that a single bear was seen multiple times.

b) Because not all females with cubs are observed in any given year, the protocol uses a statistical method (Chao2) to estimate the actual number of females with cubs in each year. (Perfect detection of anything is very rare in wildlife work). There is, of course, no way to be absolutely certain how many females with cubs went undetected in any given year, and considerable work went into selecting the most unbiased and robust statistical method available. However, even the best method was shown by [Cherry et al. \(2007\)](#) to underestimate the true number under a number of plausible scenarios, from 5% to as much as 25% (it produced no overestimations, and had negligible bias when sampling effort was high).

c) The statistical method to estimate the number of undetected females with cubs is also influenced by sampling effort. As pointed out by some commentators on the draft protocol, the estimate tends to rise when sampling effort is higher and fall when it is lower. In recent years, effort has generally been higher than earlier; thus, the population increase suggested by this statistical model may be an overestimate of the true population increase. Similarly, reduced effort would tend to suggest a population decline even if none had actually occurred; however, as noted

above, the Chao2 estimator did not overestimate the true population in any simulations conducted.

Sustainable mortality. In proposing a limit for sustainable mortality, we chose that level that our best models suggested would lead to a declining population less than 5% of the time. We deliberately avoided choosing a mortality level at which, on average, the population would be exactly stable, because this would have meant roughly a 50% chance that the population would actually decline. If our proposed total limits of 9% total mortality (i.e., from all causes) of adult females yearly are not exceeded, we believe it highly unlikely that the greater Yellowstone grizzly bear population would decline. In one sense, however, this limit is biased low, because our best *expectation* (i.e., the mean of population growth rates given this mortality rates and other parameters as observed during 1982-2002) is that the population would increase at almost 3% yearly under 9% yearly mortality. We believe that this type of “conservative bias” is appropriate management; even if mortality assumed to keep the population stationary results in a 3% (or even greater) yearly increase, this is acceptable (or, from the perspective of increased assurance of ultimate population persistence, welcome) as part and parcel of keeping the probability of decline acceptably low.

[◀ Back to contents](#)

Glossary

AIC – Akaike’s Information Criterion

ESA – Endangered Species Act

Deterministic – fixed, certain. In a **Deterministic** population model, the result (e.g., growth rate) is fixed once the model structure and parameters (e.g., birth and death rates) are fixed.

F_{cubs} – Female grizzly bear accompanied by cubs born that year

FY – Fiscal year

m_x – mean reproductive rate; formally: number of female cubs/adult females/year, measured as soon as possible after birth pulse (for bears, early spring)

GYE – Greater Yellowstone Ecosystem

Stochastic – uncertain, containing an element of randomness. A **stochastic** population model is one in which birth and death rates are allowed to vary around some mean value with each animal, each year,

or each iteration (or some combination of these), and thus each run produces a different outcome. By running numerous iterations, a mean population growth rate can be estimated, as can the probability that a population will grow at a slower or faster rate than the mean.

Study team – Interagency Grizzly Bear **Study team**

λ – the yearly growth rate of a population in multiplicative terms (e.g., 1.0 = no change, 0.9 = 10% decline yearly)

USFWS – U.S. Fish and Wildlife Service

WBP – whitebark pine (*Pinus albicaulis*), the seeds of which form an important dietary component for Yellowstone grizzly bears

WSI – a winter severity index incorporating minimum daily temperature, snowpack, and precipitation the previous summer

[◀ Back to contents](#)

Options for estimating population size considered but not recommended

[◀ Back to estimating population size](#)

Perhaps no class of methods for estimating the population size of animal populations has more history than “mark-recapture”. The basic idea is simple: first, capture and mark a sample of animals in the population. Later on, capture another sample from the same population. Some of the animals in this later sample will have marks from the earlier capture, some not. The proportion having marks provides an estimate of the probability of capture during the marking phase (e.g., if half the captured animals have marks, this suggests that roughly half the population was captured during the initial marking period and thus the probability of capture was about 0.5). Now, equipped with an estimate of the probability of capture (\hat{p}) and the number of animals captured in the subsequent sampling (r for “recapture”), one automatically has an estimate of the population (\hat{N}), that is,

$$r / \hat{p} = \hat{N}$$

That’s the basic idea, but needless to add, it gets a lot more complex than that, particularly if you’d rather avoid making restrictive assumptions. Many, many technical articles and books have been written on this subject, and even an introduction to it is well beyond the scope of this report. However, two applications of this basic technique have recently been used on grizzly bears in other situations, and were considered by the [Study team](#): mark-resight using radio-collars as marks, and mark-recapture using each individual bear’s DNA as the “mark”.

Mark-resight using aircraft

Population size can be estimated by treating radio-collars as the marks in a mark-recapture experiment, and then conducting observation flights in which marks are “recaptured” via sighting (and then by confirming the marked status of these animals by checking all the radio-frequencies to confirm that the observed animal is or isn’t marked). One complication in the case of bears is that because they move about so much (but, for logistical and analytical reasons, survey areas need to be fixed), the number of marked animals *available* for recapture can vary from session to session (standard “closed-population” mark-recapture experiments assume that the number of marked animals is known with certainty). Thus, in these types of surveys, after observations are conducted, the number of marked animals that could potentially have been found must be determined (because assuming that all marks are within the survey area could well be wrong). A number of surveys in Alaska have used this method, with reasonably precise results.

The [Study team](#) conducted experiments with this method during 1998-2000. Unfortunately, the low recapture rate of marked bears resulted in high variability in estimates. Thus, this method was deemed inappropriate for further application in the greater Yellowstone ecosystem, at least given samples sizes of marked animals similar to those existing at the time. For more information on these experiments in the Greater Yellowstone Ecosystem, a summary of results, and the reasons they’ve not been pursued further, click [here](#).

[◀ Back to estimating population size](#)

Mark-recapture using DNA as the mark

In recent years, wildlife researchers have increasingly been using genetic techniques to obtain data that are difficult to get in other ways. Although the majority of the DNA in each individual animal is identical, molecular ecologists have been increasingly successful in isolating and amplifying small bits of DNA that contain much more inter-individual variability than does most of the DNA molecule, even from such body parts as hair, sloughed skin cells, and feces. These bits of DNA, called hypervariable micro-satellites, are probably not terribly important in producing proteins for the animal, and as such, are more susceptible to random mutation than portions of DNA that contain the instructions for making proteins that actually function in the animal's daily life. Thus, if one compares enough of these DNA bits (which are often abbreviated as "genetic markers") – usually 7 to 9 will suffice – it is possible, through various numeric algorithms, to separate individuals from one another. Thus, each animal already carries its own individual "mark", and if some bit of its tissue can be physically obtained, mark-recapture procedures can be employed without the need for further physical marking.

Now, the concept of "identifying individuals from their DNA" (in human applications, referred to as "genetic fingerprinting") needs to be understood for what it can and cannot do. If one merely has DNA from, say the hair of bear, one can say, usually with high statistical confidence, that that bear was *not* the same bear as another one that also left hair for analysis. But that's not quite the same thing as saying that we know exactly *who* each bear is. Other, relatively simple genetic techniques can distinguish the sex of the bear (and of course, yet other genetic analyses are first performed to ensure that the hair indeed came from a grizzly

bear and not some other species). And yet more sophisticated analyses can classify each individual as more likely to have come from one group of bears than another, and can provide quantitative evidence of the relative closeness of relatedness among individually identified bears. But only in the case of extremely intensive field studies can one use these data on genetic relatedness to create an entire pedigree (i.e., identify each animal in its relation to the others). One important reason for this is that DNA contains no information whatsoever on an animal's age. Thus, for example, although it is quite possible to identify hair from a particular site as coming from 2 unique, closely-related females, it's impossible to tell, from DNA information alone, whether they are sisters or a mother-daughter group (and if the latter, which is the mother and which the daughter).

Given the sophistication with which genetics laboratories have progressed in this field, it is easy to assume that identifying individuals through DNA analysis has become easy. But errors in identification still occur. In the mark-recapture setting, those of concern are erroneously lumping two different individuals together and calling them a single one, and, even more insidiously, "creating" non-existent animals by observing unique genetic markers that result from subtle errors in the lab procedures rather than subtle differences in the real animals. Geneticists are well aware of these potential problems, and have been active in developing protocols to minimize them. And indeed, most good labs can reduce these errors to inconsequential levels --- but not without more work, and hence greater cost.

Similarly, given the aura and mystique involved when we analyze DNA, the very blueprints for our lives, there is a tendency to

view population estimates based on them as perfect or complete in ways that are unattainable through traditional methods of marking. But tissue must still be obtained from the animals, and to date, nobody has invented a method to guarantee that every single individual in a population will make the requisite donation. Thus, just as in every other method one can imagine, investigators must make do with a *sample* of animals. That means that even if laboratory procedures identify individuals with no error at all, one still has the problem of estimating the number of animals that were never captured. Fortunately, we have powerful statistical procedures – alluded to above – to make such estimates. Alas, the end result is just that: an *estimate*, and even the best of these estimates will contain uncertainty (called “sampling error” in statistical jargon). The oft-heard term “DNA census” is a misnomer; identification of genetic markers from techniques that have come to be called “non-invasive” presents a novel and oft-times useful way to obtain samples of marked animals. But from there, mark-recapture estimates proceed no differently than if animals were marked by people putting things on them. There will be imprecision (in the newspapers, often called “margin of error”).

Just as in traditional mark-recapture experiments, large samples and high recapture rates are critical if the resultant numbers are to be precise. Theoretically, the fact that all animals already have marks, and the fact that investigators can obtain samples through such means as plucking hairs from baited stations surrounded by barbed wire (or simply from trees or power-poles which bears rub upon) means that large sample sizes are a definite possibility. But there is still a substantial field effort involved in obtaining these samples, and there is also a considerable effort

required in the lab to accurately identify the thousands of samples that result from large-scale surveys. So while the expense of physically capturing bears is avoided, conducting a large-scale mark-recapture survey using DNA from hair is hardly cheap.

A number of DNA-based mark-recapture surveys have recently been conducted in Alberta and British Columbia, but they have generally been on a smaller scale than would be required were a Greater Yellowstone grizzly bear estimate to be attempted. The most applicable model from which to estimate the cost of a Yellowstone survey is that effort currently underway in northwestern Montana (the Northern Continental Divide Grizzly Bear Ecosystem). Field work is completed, and much raw data has been analyzed as of this writing, and statistical results are not yet available from this study. However, based on the budgets from this study, the **Study team** estimated that it would require approximately \$4.5 million and at least 3 years to conduct a **GYE**-wide survey with yielding sufficient data to produce a population estimate whose 95% confidence limits were $\pm 20\%$ of the point estimate (e.g., if the estimate was 600, that one could be confident that the population was no fewer than 480 or more than 720). Needless to add, were this survey to be conducted multiple times, the cost would raise proportionally.

The **Study team** recognized potential value in pursuing a mark-recapture population estimate using this method, and it was included on a number of “unfunded tasks” lists at various government committee meetings. However, funding was never found for such a task. For more detail on DNA-based mark-recapture populations, click [here](#).

[◀ Back to options considered](#)

(yet more...) estimating population size by mark-resight methods

[◀ Back to mark-resight](#)

In the case of estimating bear populations, this basic formula has been used most often in a slightly different guise, called “mark-resight” (as opposed to “mark-recapture”). In mark-resight, animals must be captured and marked once, but then subsequent “recaptures” are not physical recaptures of the animal, but rather some sort of observation in which marks can be identified (and of course, animals without marks can be correctly categorized as not having been marked). In mark-resight, the sample size of marked animals is fixed by the number of animals marked initially, but because it is so much cheaper and easier to observe animals than to capture them physically, the sample size of “recapture” events can be fairly high. There are a few different mathematical models that are well explored and can be used in “mark-resight” estimations of this sort (White 1996), and a radio-collar can be used as the “mark” in addition to a physical mark (so that there is very little chance of mistaking a marked animal for an unmarked one). This method has been used with some success on grizzly and black bears in Alaska (Schwartz and Franzmann 1991, Miller et al. 1997).

During summer 1998, the **Study team** began to experiment with using this technique to estimate the total number of grizzly bears in the greater Yellowstone ecosystem. A series of fixed-wing aircraft surveys were conducted from July 15 through August 6, 1998, in which pilots and observers in the plane looked for bears, and when

one was found, checked all the radio-frequencies to determine whether or not it was marked. In addition, after each day’s search, all the bears’ frequencies were checked to determine which marked bears were present within the search area, and thus capable of being observed. (Simple mark-resight assumes that all marks can be observed at any time, but the large distances grizzlies can move requires that this extra step be taken).

But there were two problems. The first was that very few marked (i.e., radioed) animals were re-sighted. In almost 141 hours of flight time, 113 groups of bears were observed, but only 5 bears wore radio-collars. (The number of radioed bears within the survey areas during the period varied from 20 to 27). This resulted in the population estimation having very poor precision (e.g., the confidence limits were very broad). Secondly, many bears were observed at moth-feeding sites in alpine areas in the southeast portion of the ecosystem, where they were relatively easily observed. This was a problem because it was known that bears in this area had been under-sampled for marking. (Generally, the method assumes that marks are distributed randomly among all population members, and that the probability of re-sighting an animal is the same as capturing it to begin with). The combination of high “sightability” of these moth-eating bears with their low likelihood of having been captured and marked, meant that population estimates from these surveys were likely to be inflated (Schwartz 1999).

Only slightly deterred, the research team tried the method again in 1999, this time conducting the aerial flights earlier during the summer, before any bears traveled to the alpine areas in the southeast part of the ecosystem to feed on moths. This allowed the **Study team** to

avoid the problem of having a segment of the population that was difficult to mark but easy to see. In fact, with the additional complexity of having to determine which marked animals were actually present in any given survey area taken care of, this survey came about as close to meeting the assumptions of mark-resight estimation as any field survey can be expected to.

But the first problem encountered during the 1998 survey remained: although pilots and aerial observers found grizzly bears, they still found very few *marked* grizzly bears. As in any mark-recapture effort, if the proportion of captured (or sighted, in this case) animals wearing marks is low, not only will the resultant population estimate be high, it will also be uncertain. Precision is improved by having many animals marked, and by having the probability of capture (i.e., marks as a proportion of all those resighted) be high. In 1999, in some 154 hours of flying time, pilots and observers found 85 bears (in 50 bear groups; some bears were in family groups). But of these, only a *single* bear wore a radio-collar (despite there being 29 and 31 available to be observed during the 2 observation periods). After correcting for the fact that not all collared bears were available for re-sighting (due to movement out of the survey area), the resultant estimate was that there were from 369 to 26,377 bear groups in the overall survey area! Considering that groups consisted of, an average, 1.7 bears, this equated to 95% confidence limits of from 627 to (gulp...) an astounding 44,841 grizzly bears! (Schwartz 2000 didn't actually report this latter figure, probably because it is so outlandish, but it follows directly from the math).

During the year 2000, the [Study team](#) continued to monitor the number of radio-collared bears seen during aerial flights (Schwartz and Haroldson 2001). But despite an almost

doubling of the rate at which bears were observed per flight hour over that in 1999, the percentage of marked bears seen remained abysmally low: 3 of 84 bears (3.6%).

Now, it is not terribly useful to know only that if one were one to somehow be able to replicate this survey many times under the same conditions, 95% of such surveys would return an estimate of between 627 and 44,841 bears! The difference between the lower and upper bounds is, to put it charitably, rather large.

Why were the results of this survey so imprecise? Why were so few radio-collared bears observed? The answer to that question remains a mystery, but not because members of the [Study team](#) haven't thought about it quite a bit. The most obvious concern would be that, for some reason, radio-collared bears were harder to find or to see, perhaps because of some differential habitat preference or perhaps because they hid from fixed-wing aircraft. But there is no evidence supporting either of these possibilities. Marked and unmarked bears showed no obvious difference in habitat preference (marked bears *were* found after the observation flights, during the radio-relocation portion of the effort). Marked bears did have a history of being handled (whereas unmarked bears did not), but they were not captured from aircraft. If anything, bears with radio-collars would probably have had more experience with low-flying aircraft that posed no threat to them, and thus would have been more likely to ignore airplanes than those naïve about such machines.

Regardless of the reason, with such a low "recapture" rate, there appeared to be no way to provide an estimate with a usefully narrow confidence bound short of capturing many more animals to begin with (which was beyond the budget capability of the study). Thus, although

fundamental assumptions of the method were tolerably met, low “recapture” rates doomed these estimates to such a low level of precision that they were simply useless. The full reports can be seen by clicking on Schwartz [1999](#), [2000](#), [2001](#).

[◀ Back](#)

(yet more..) estimating population size mark-recapture using DNA

[◀ Back to DNA estimates](#)

For more technical literature on estimating population size of grizzly bears using DNA from hair, the reader is referred to the following:

- Boulanger, J., M. Proctor, S. Himmer, G. Stenhouse, D. Paetkau, and J. Cranston. 2006. An empirical test of DNA mark-recapture sampling strategies for grizzly bears *Ursus* 17: 149-158.
- Boulanger, J., B. N. McLellan, J. G. Woods, M. F. Proctor, and C. Strobeck. 2004a. Sampling design and bias in DNA-based capture-mark-recapture population and density estimates of grizzly bears. *Journal of Wildlife Management* 68:457-469.
- Boulanger, J., G. Stenhouse, and R. Munro. 2004b. Sources of heterogeneity bias when DNA mark-recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. *Journal of Mammalogy* 85:618-624.
- Boulanger, J., G. C. White, B. N. McLellan, J. G. Woods, M. F. Proctor, and S. Himmer. 2002. A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia. *Ursus* 13:137-152.
- Mowat, G., D. C. Heard, D. R. Seip, K. G. Poole, G. Stenhouse, and D. Paetkau. 2005. Grizzly *Ursus Arctos* and black bear *U. americanus* densities in the interior mountains of North America. *Wildlife Biology* 11:31-48.
- Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair

capture, DNA profiling, and mark-recapture analysis. *Journal of Wildlife Management* 64(1):183-193.

- Poole, K. G., G. Mowat, and D. A. Fear. 2001. DNA-based population estimate for grizzly bears *Ursus Arctos* in northeastern British Columbia, Canada. *Wildlife Biology* 7:105-115.
- Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging free ranging black and brown bears. *Wildlife Society Bulletin* 27:616-627.

[◀ Back to DNA estimates](#)

Distinguishing duplicate observations of the same female from those of unique females

[◀ Back \(to counting females with cubs\)](#)

Knight et al. (1995) developed the following rule set used to distinguish sightings of unique females from repeated observations of the same female. Females were judged to be different based on 3 criteria: (1) distance between sightings, (2) family group descriptions, and (3) dates of sightings.

Minimum distance for 2 groups to be considered distinct was based on annual ranges, travel barriers, and typical movement patterns. A movement index was calculated using standard diameter of annual ranges (Harrison 1958) of all radiomarked F_{cub} monitored from 1 May–31 August (Blanchard and Knight 1991). The mean standard diameter for all annual ranges of F_{cub} was 15 km (SD = 6.7 km). They estimated the average maximum travel distance as twice the standard diameter, or 30 km, and used this distance to distinguish sightings of unique F_{cub} from repeat sightings of the same female.

Family groups within 30 km of each other were distinguished by other factors. The Grand Canyon of the Yellowstone River, from the lower falls to the confluence of Deep Creek, was considered a natural barrier. Females on either side of this canyon were considered unique. Knight et al. (1995) also discussed paved highways as impediments to travel and cited data presented by Mattson et al. (1987) which showed that grizzlies tended to stay >500 m from roads during spring and >2 km during summer. They provided one example where 2 families

considered unique were separated by 2 major highways and were 30 km apart (see Knight et al. 1995: Table 1). Family groups were also distinguished by size and number of cubs in the litter. Once a female with a specific number of cubs was sighted in an area, no other female with the same number of cubs in that same area was regarded as distinct unless (1) the 2 family groups were seen by the same observer on the same day, (2) the 2 family groups were seen by 2 observers at different locations but similar times on the same day, or (3) 1 or both of the females were radiomarked. Because of the possibility of cub mortality, no female with fewer cubs was considered distinct in an area unless (1) she was seen on the same day as the first female, (2) both were radiomarked, or (3) a subsequent observation of a female with a larger litter was made. Knight et al. (1995) assumed that all cubs in a litter were observed and correctly counted. This assumption was strengthened by only considering observations from qualified agency personnel. Observations from the air were only included if bears were in the open and easily observed. Ground observers watched family groups long enough to insure all cubs were seen; observers reported any doubt. Finally, Knight et al. (1995) referenced a time–distance criteria but did not provide specific rules for its application. The only example they provided was the separation of 2 sightings of 2 family groups observed 1 day apart and 25 km apart.

[◀ Back \(to counting cubs\)](#)

9% or 4%?

◀ [Back to new mortality guidelines](#)

[reprinted from Harris et al. 2006: 53]

Our estimate that the GYE grizzly bear population is likely to maintain a positive trajectory as long as survival of females (2+years old) remains above approximately 0.91 (i.e., 9% annual mortality) would seem, at first blush, to suggest a radical departure from the original 1993 guidelines. For example, Harris (1986:273) recommended that “the proportion of the female segment of the population that can be removed annually . . . without causing chronic decline should not exceed 3% of the female segment.” More recently, McLoughlin (2002:33) suggested that “most grizzly bear populations in North America can tolerate approximately 3% total annual kill before declines . . . accelerate to unsatisfactory levels.” Careful reading, however, reveals that, beyond some minor differences in assumptions and procedures, the apparent increase in tolerable mortality we report here arises not from real discrepancies in models or parameter values but rather from different ways of expressing a similar underlying dynamic.

Comparing our results with those of Harris (1986) is important because current management guidelines in the RZ (U.S. Fish and Wildlife Service 1993, 2003) adopt an annual mortality limit derived largely from that work. First, our approach here differed fundamentally in that the earlier work attempted to estimate the mortality level associated with sustainability indefinitely. That is, Harris (1986) used a model of grizzly bear population dynamics

that was self-regulating. Thus, bear populations equilibrated (rather than grew exponentially) in the absence of killing by humans. Adding human-caused deaths to this model engaged compensatory responses that were assumed to characterize grizzly bear populations (although parameters used to build the responses were not based directly on data but rather were interpolated from general principles).

Here, our aims were more modest: to project short-term growth rates applied under a range of plausible survival rates, making no assumptions about density-dependent (or other possible) regulating mechanisms that must, no doubt, intercede to change those trajectories at some point. Second, Harris (1986) assumed that natural mortalities, although decreasing as hunting increased, would never be entirely substituted by human-caused mortality. That is, even at the population level producing the highest sustainable yield indefinitely, background levels of natural mortality would continue. Harris’s (1986) objective was to estimate the maximum human-caused mortality rate that, when embedded into the assumed compensatory structure, equilibrated the population with its carrying capacity. Here, we declined to suppose any particular relationship between human- and non-human-caused mortalities (to say nothing of carrying capacity). Indeed, we had no data to do otherwise, given that not a single independent female mortality in the GYE attributable to nonhuman causes was documented during 1983–2001 (Haroldson et al. 2006). Dependent young experienced natural mortality, but because cubs and yearlings were not collared, cause of death was undetermined in many cases (Schwartz et al. 2006c).

Thus, contrasting our results directly with the 3% sustainable mortality rate of females estimated by Harris (1986) is inappropriate. Harris (1986) also assigned survival rates to 3 subadult female classes (2, 3, and 4 years old) in addition to 3 adult age classes, complicating any attempt to compare the total mortality rate sustained by adult females in his model populations with those we report here. Fortunately, we were able to rehabilitate the Harris (1986) model for application here and develop a common currency for comparison with our results. We discovered that maximum hunting rates he found consistent with sustainability (i.e., 6.85 female kills/year from a population of 193.5 females, or 3.54% of the female component killed annually; Harris 1986:276) corresponded to an annual survival rate of all females (cubs through the oldest class) of 0.851 (SD = 0.035, $n = 3,000$ iterations). For comparison, our survival rates of all females (regardless of age) consistent with low probability of decline were 0.847 (SD = 0.022, $n = 3,000$ iterations) when independent female survival was 0.91 (under low process variation) and 0.852 (SD = 0.077, $n = 6,000$) when independent female survival was 0.92 (under high process variation). Thus, although the approaches and presentation of results were quite divergent, overall female survival rates consistent with nondeclining populations in both Harris (1986) and our present effort were almost identical.

McLoughlin (2002) reported that a simulated population modeled approximately on the GYE grizzly bear data through 1995 displayed a break point (at which persistence probability declined rapidly with additional kills) at a mortality rate of about 2.8%. However, human-caused mortalities in his model were assumed additive to natural mortality, which was

set at 4.9% for females aged ≥ 6 years and 11.4% for females 2–5 years old (McLoughlin 2002:table 2.1). With approximately 30% of the female population in ages 2–5 years and 46% >6 years old (approximately the case if the population had achieved its stable age distribution prior to additional harvest), the mean natural mortality rate for females ≥ 2 years old would thus be approximately 6.4%. This, added to the 2.8% annual kill, yields 9.2% total mortality of females ≥ 2 years old (i.e., annual survival of 0.908), which is again similar to our conclusion that λ will be

1 with high probability when annual female (≥ 2 years old) survival rates are approximately 0.90–0.91.

Eberhardt (1990) also provided a simple **Deterministic** model relating grizzly bear life history rates to stable trajectories. Application of the mean survival rates from our simulations to his equation 1 (Eberhardt 1990:587) produced $r = 0$ (i.e., $\lambda = 1.0$) with independent female (≥ 2 years old) survival of 0.898 and age of first reproduction set to 5 years, as well with as with independent female survival of 0.906 and age of first reproduction set to 6 years (GYE mean during 1983–2002 was 5.81 years, but Eberhardt's [1990] equation did not allow for fractional ages). Although abstract, his model further confirmed our estimates of female survival rates consistent with non-declining trajectories.

◀ [Back to new mortality guidelines](#)

Chao2

[◀ Back to new estimate of yearly \$F_{cubs}\$](#)

One well-explored family of techniques for estimating population size uses the frequencies of captures. That is, each animal that is captured is categorized as having been captured once, twice, three times, four times, and so on. From this, one has a series of numbers (usually abbreviated f_1, f_2, f_3 , etc.) that refer not to individual animals, but to the number of animals that were captured exactly this many times. Now logically, if one could also figure out f_0 , (the number of animals *never* captured), then one would have covered all the possibilities and thus have an estimate of the total population size.

A number of models have been proposed for filling in this missing value (the number of animals captured exactly zero times), and they vary in their assumptions and in how accurately and precisely they perform under various conditions. For example, a simple method would be to simply fit a curve to the frequencies observed, and extrapolate this curve backward to include zero. This simple technique assumes, however, that all animals have an identical probability of being captured, and it performs poorly if this is not true. (Given the way that animals – in this case, females accompanied by cubs – are “captured”, it’s likely that they vary in their “capture-ability”).

Taiwanese biometrician Elaine Chao has been among the more active researchers in this field, and she has developed and published a few estimators for f_0 (and thus for the population). Among these, the one she published in 1989 (Chao 1989) relaxes the assumption that all animals must have the same probability of

capture; indeed, it allows every animal to have a unique capture probability. Although the derivation of it involved some complex math, this estimator, which we’ve nick-named Chao2 (because it was the 2nd such model she proposed), reduces to the equation

$$\hat{N} = m + \frac{f_1^2 - f_1}{2(f_2 + 1)}$$

Where \hat{N} = estimate of the total population
 m = the total number of animals captured, regardless of how often (i.e., the minimum possible number)

f_1 = number of animals captured once

f_2 = number of animals captured twice

Chao (1989) also provided ways to derive the variance for this, so that one could produce not merely a point estimate, but also a confidence interval. Following the explorations of Wilson and Collins (1992), Keating et al. (2002) and Cherry et al. (2007) conducted simulations into the behavior of this estimator under various situations. Whereas Keating et al. (2002) initially concluded that this Chao2 estimator was not quite as good as some alternatives, these authors later realized that the frequencies of bear “captures” (remember that these were not physical captures, but rather identifications of unique females accompanied by cubs using the protocol of Knight et al. 1995) was slightly different than earlier assumed. Cherry et al. (2007) conducted additional simulations under conditions that more nearly resembled the actual data from Yellowstone, and they concluded that Chao2 was equal to the other possible estimators in yielding relatively precise estimates, and that when it was biased, it was always biased low and never high. Thus even when a bit off, using Chao2 would never suggest more bears than there really were. Cherry et al. (2007) thus recommended Chao2 as

the best way to estimate the total number of females with cubs present in any year, given a series of “captures” of such animals.

[◀ Back to new estimate of yearly \$F_{cubs}\$](#)

AIC_c

[◀ Back to trend monitoring](#)

Akaike's Information Criterion (AIC) is a metric that can be used to compare and contrast alternative, competing models that have been developed to describe the same phenomenon. Rather than test a proposed model against some assumed null model and ask if the proposed model is “significantly better”, the underlying approach here is that while *no* model is capable of fully describing reality, some models are more useful than others. AIC scores are generated for each candidate model an investigator devises (and thus it cannot possibly say anything about how an existing model compares to one not yet thought up!), and the comparison of these scores gives some indication of how well the model fits the data. AIC_c is a variant of AIC that has been found to perform better when sample sizes are small.

A model that is too simple will depart from reality too much to be useful. A model that is extremely complex may track the raw data quite well, but be so specific as to have lost generality. AIC uses the principle of parsimony, i.e., making the best possible compromise between a highly-complex model (i.e., one with many “moving parts”) that tracks data but lacks generality, and one that is simple (and thus general) but imprecise.

As an example, consider the following figures, which shows some hypothetical phenomenon graphed against time:

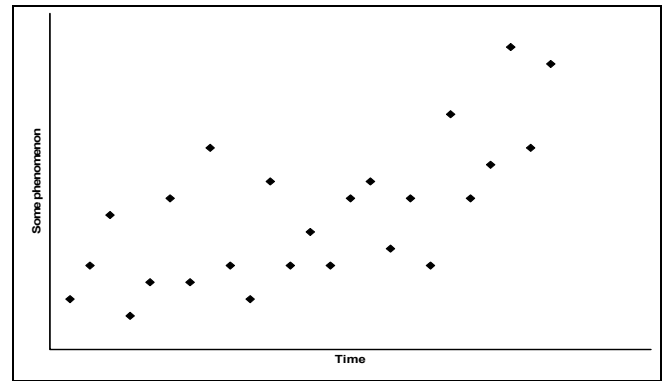


Fig. 5. Data points

It seems clear from Fig. 5. that there is *generally* an increasing trend in these data. A very simple model would be a straight line (Fig. 6):

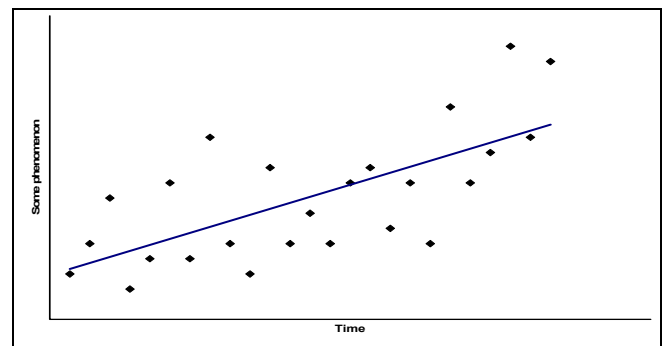


Fig 6. Data points, simple linear model

But clearly there is quite a bit of variation in these data that is unexplained by the simple straight line (note, for example, that it looks like the generally increasing trend was interrupted by a pause in the middle of the sequence). That probably means that there are other factors than simply “time” that explain all the jumping around we see in the data. Now suppose, in contrast, we threw every possible variable we could think of into a model, and ended up with a function that looked like this (Fig. 7):

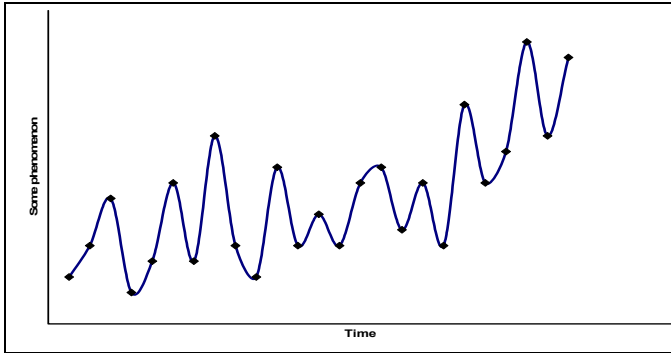


Fig. 7. Very complex model

This new model has succeeded admirably in following the data. But will this actually be a *useful* model? Can it describe the underlying process that produced these data in a slightly different context, or under slightly different conditions? (That is, after all, what we are usually after in a model; explanation and insight, not merely data tracking). A model such as this is likely to be so specifically tied to this particular set of data (i.e., include variables that pertain only to this exact manifestation of the underlying process), that it will likely fail if used to generalize to the next manifestation of the very same underlying process!

If we used **AIC** to judge these 2 models, the first (simple one) would be penalized for how much it diverges from the data, but gain from its simplicity. The second model would gain support from its tight fit to the data, but be penalized by the number of parameters (i.e., moving parts) needed to describe this very complex line.

Now if instead of these 2 extremes we could devise a compromise model (Fig. 8), one that included a few likely variables that enabled it to track the data's variation better than the simple linear model, but -- unlike the 2nd model -- did not attempt to include *every* single minor cause of the observed fluctuations, it might look something like this:

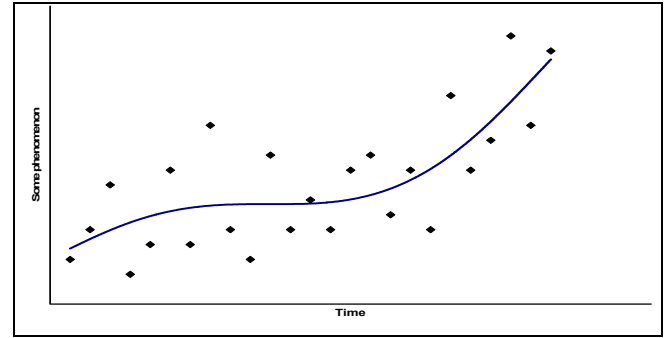


Fig. 8. Compromise model, best **AIC**

AIC would rank this as a “better” model than either of the first two.

The actual **AIC** scores are rather unimportant (they can range from very low to very high); it is the *differences* among the **AIC** scores of the models considered that are of interest. Unlike in traditional statistics, there is no “magic” threshold that distinguishes good from bad models, true from false models, or significantly better from insignificantly different models. Biometricians who’ve studied the behavior of **AIC** generally consider that any models that differ from each other by less than 2 **AIC** “units” should be viewed as having similar support.

If a suite of candidate models is considered, each model can be assigned an “**AIC** weight” as a sort of summary statistic that describes the relative strength of evidence for it, relative to the others. The weights of all the models considered sum to 1.0, so any given model gains support at the expense of all the others. Model averaging can then use these weights to produce a composite explanation that gains from the insight provided by all the candidate models, with the influence on the final model dictated by how strongly each individual model is supported.

For more information on **AIC**, see:

Burnham, K. P., and D. R. Anderson. 2002.
Model selection and multimodel inference:
a practical information-theoretic approach.
Second edition. Springer-Verlag, New
York.

[◀ Back to trend monitoring](#)

Harris 1986

[◀ Back to mortality limits](#)

The model underlying estimates of sustainable mortality is an approximation, and did not use information specifically from the GYE. It used best information that was then available on grizzly bear demographics, made some general assumptions about how grizzly bear populations operated, and added in some quantifications of opinions from experienced bear biologists (on such matters as the vulnerability of certain sex/age classes of grizzly bears to man-caused mortality relative to other sex/age classes), and combined it into what was, at the time, a state-of-the-art simulation model. In fact, the underlying model already existed at the time of the request. That the model had been parameterized well before the request — that is, that the numbers in it were developed entirely independently of its later use as means to estimate sustainable mortality — provided some assurance that it wasn't particularly biased toward finding that either particularly high or low levels of mortality were sustainable. Unfortunately, the fact that so many important elements of the model had to be generalized from a number of grizzly bear studies, and that some quantifications were made based only on general patterns of the large mammal population dynamics, meant that the model was an abstraction. It was better than anything else at the time, and it arose free from any particular bias in killing or saving bears.

In short, this model tracked the fate of individual “electronic” grizzly bears, each of which was assigned a probability of dying (and, if female, of giving birth). These probabilities were derived from various research studies that had been completed on grizzly bears at the time. The

model was designed and built for the purpose of examining what information managers could extract from the age and sex of grizzly bears killed in a recreational hunt (the state of Montana had a legal, albeit limited, hunt of grizzly bears at this time). In order to perform this function, the model had to be an “equilibrating” one, that is, it had to be equipped with “density-dependence” (otherwise, the modeled population would rapidly decline to extinction if hunting was added, or conversely, would increase exponentially if hunting was *not* added!)

The model was also *stochastic*, meaning that it incorporated variability. Rather than sustainability being defined as the mean mortality rate that would equilibrate the population, sustainability was defined as that mortality rate that produced a decline with a probability of 10% or lower. That is, most simulated population subjected to the 6% harvest equilibrated; only 1 of 10 declined. However, the proportion of declining populations increased rapidly if harvest exceeded 6%.

[◀ Back to mortality limits](#)

On non-parametric estimators of the true number of F_{cubs}

[◀ Back to estimating yearly \$F_{cubs}\$](#)

One well-researched way to estimate how many animals are never seen is to model the distribution of the number of times animals were seen, and then to use that distribution to work backward, as it were, to estimate the number seen zero times. There are various models for doing this, each making its own assumptions and behaving in various ways when the assumptions are violated. [Keating et al. \(2002\)](#) investigated a number of these. One of the results of this work was that some estimators work best when the variability in how many times each animal was observed is high, others when it is low. This variability is quantified by what is called the coefficient of variation, CV. Another result was that the estimators vary in their performance based on the overall sample size, i.e., how many total observations were made (which is not the same thing as how many individual animals there actually were).

A formalization of this work can be found in [Cherry et al. \(2007\)](#). For more information on the Chao2 estimator, the one recommended in this report, click [here](#).

[◀ Back to estimating yearly \$F_{cubs}\$](#)

0.274 or 0.284?

[◀ Back to Fcubs to total population](#)

The original proportion of adult females with cubs was listed as 0.284 in the 1993 Grizzly Bear Recovery Plan. That value was updated and changed to 0.274 by Eberhardt and Knight (1996: 417).

[◀ Back to Fcubs to total population](#)

The power of the protocol to detect a change in trend

[◀ Back to details of trend monitoring](#)

Methods

Under monitoring protocols current as of 2006, an estimate is made annually of the number of females with cubs of the year (\hat{N}_i). Unique females with cubs in each year are identified from all observations using a rule set developed by Knight et al. (1995). We consider sightings of females with cubs made with the aid of radio-telemetry biased and excluded them from the calculations (Keating et al. 2002). The Chao2 estimator (Chao 1989, Keating et al. 2002, Cherry et al. 2007) is then used to estimate the total number of females with cubs present from the estimated number observed. The trend in this segment of the population and its rate of change can be estimated from these annual estimates, providing an independent estimate of λ . However, annual estimates of \hat{N}_i can vary because of sampling error, as well as because of pulsed or synchronized reproduction. Thus, using annual estimates independently each year can result in greater variation in the estimate of total population size than is likely to characterize the true population.

Monitoring population size and λ using females with cubs. The natural logarithm of the number of females with cubs [$\log(\hat{N}_i)$] can be fit with a linear model of year ($y_i = i - 1$) to estimate λ as:

$$\log(\hat{N}_i) = \beta_0 + \beta_1 y_i + \varepsilon_i \quad (\text{Eq. 4})$$

so that the population size at time zero is estimated as $\hat{N}_0 = \exp(\hat{\beta}_0)$ and the rate of population change is estimated as $e^{(\hat{\beta}_1)}$, giving $\hat{N}_i = \hat{N}_0 \hat{\lambda}^{y_i}$. Asymmetric confidence intervals on λ can be estimated as the exponential of the

symmetric confidence bounds on β_1 . Standard errors for $\log(\hat{N}_i)$ can be computed with the usual linear model methods, and confidence intervals for (\hat{N}_i) can be estimated as the exponential of the confidence bounds on $\log(\hat{N}_i)$. When we assume a reasonably stable age and sex structure for the total population, this estimate of λ represents the rate of change of the entire population. Fitting a linear relationship makes the standard assumptions of least squares regression.

A quadratic regression can be also used to detect a change in $\hat{\lambda}$ through time. We fit the model

$$\log(\hat{N}_i) = \beta_0 + \beta_1 y_i + \beta_2 y_i^2 + \varepsilon_i \quad (\text{Eq. 5})$$

We expect that the estimate of β_2 will become negative as population growth slows (as it would, for example, if it reached carrying capacity) or reverses. Information-theoretic model selection methods (Burnham and Anderson 2002) can be used to select between the linear and quadratic models, and hence to detect changes in $\hat{\lambda}$ as additional data are collected. We used model averaging with the linear and quadratic models of the predicted population sizes of females with cubs to estimate population sizes through time (i.e., \hat{N}_i), and thus smooth the variation of the Chao2 estimates. We used AIC_c weights (Burnham and Anderson 2002) to weight the estimates from the linear and quadratic models to produce our best estimate of the current number of females with cubs and λ .

To assess the behavior of our proposed model selection procedure, we i) added 2 hypothetical years of data for 2006 and 2007, assuming $\lambda = 0.9$ for both additional years, and ii) added 4 hypothetical years of data, assuming $\lambda = 1.0$ for all additional years.

Power analysis of using \hat{N} to estimate λ . Simply adding hypothetical years with altered λ ,

as above, would not constitute a power analysis of the proposed trend monitoring method, because future years' data will also contain process and sampling variation. To estimate the power of these data to detect a true reduction in λ (i.e., correctly chose the quadratic model), we estimated variance components of the Chao2 female-cubs counts 1983–2005, and applied these in Monte Carlo projections for 10 additional years under various assumed values of λ .

To separate the sampling variance associated with each population estimate, ($\text{var}(\hat{N}_i)$) from process variance, we fitted the linear model (above), with the assumption that the variance of ε_i was the sum of the sampling variance and the process variance (earlier analyses provided no evidence for significant serial correlation, unpublished data). For the Chao2 estimator, $\text{var}(\hat{N}_i)$ was estimated with bootstrap resampling of the data, and the variance of the resampling distribution was the estimate of $\text{var}(\hat{N}_i)$. Note that the variance of $\log(\hat{N}_i)$ is estimated using the Delta method as $\text{var}(\log(\hat{N}_i)) = \text{var}(\hat{N}_i) / \hat{N}_i^2$.

To estimate the process standard deviation from the 1983–2006 Chao2 estimates, we used PROC NLMIXED in SAS (code available from GCW). This procedure maximizes the likelihood of $\log(\hat{N}_i)$ for β_0, β_1 , and the process SD, with the likelihood specified as a normal distribution with mean predicted by $\log(\hat{N}_i) = \beta_0 + \beta_1 y_i$ and variance $\text{var}(\log(\hat{N}_i)) + (\text{Process SD})^2$. This model thus explicitly includes the sampling variance of $\log(\hat{N}_i)$ plus the process variance that is estimated by the procedure. Process SD was estimated to be 0.176 with SE 0.0461 and 95% confidence interval 0.0808–0.271

To estimate the expected sampling variance of future Chao2 estimates (which assumes that future sampling effort will remain

approximately the same as used to collect the 1983–2006 data), the mean of the sampling variances of the log population estimates for the 1983–2006 data was computed. The expected sampling variance of future Chao2 estimates was then computed as a normally distributed random variable with mean zero and standard deviation equal to the square root of mean sampling variance. From this procedure, the estimated sampling standard deviation was 0.34.

To evaluate sensitivity of the linear and quadratic models to changes in \hat{N} over 1 to 10-year time intervals, we projected forward the 2006 population estimate of $N_{2006} = 52.356$ (obtained by model averaging the linear and quadratic model estimates from the fits of the 1983–2006 data), assuming alternative λ values of 0.95, 0.975, 1, 1.025, and 1.05, and using our estimates of process and sampling variation (above). Population size for each succeeding year was generated with the recursive relation $\log(N_{i+1}) = \log(N_i) + \log(\lambda) + \delta_i$, where the process variation was added as δ_i , a normally distributed random variable with mean zero and standard deviation 0.176. The estimated population size (corresponding to the Chao2 estimates) was taken as $\log(N_{i+1}) + \varepsilon_{i+1}$, where the sampling variation ε_{i+1} was added as a normally distributed random variable with mean zero and standard deviation 0.34. Each replicate was simulated independently, i.e., completely new data were added to the 1983–2006 data for each simulation.

One thousand replicates of each of the 50 scenarios (5 alternative λ X 10 alternative time-frames) were generated, from which we obtained estimates of the mean AIC_c weight of the quadratic model, the proportion of iterations in which the quadratic term was selected (weight > 0.5), and the power of the t -test to reject the null

hypothesis that the quadratic term was equal to zero. This provided a realistic simulation of the data and analyses that would be available to managers when judging whether the population had changed its trajectory.

Results

When our best estimates of process and sampling variation were added to hypothetical years 1 through 10, approximately 5 years were required of the population decreasing 5% yearly (i.e., $\lambda = 0.95$) before the preponderance of evidence (AIC_c weight > 0.5) favored the quadratic model (i.e., fundamental change in state from linear increase, Fig. 8, below). Under the scenario in which population size stabilized after year 2006 (i.e., $\lambda = 1.0$), 7 or 8 years were required for the preponderance of evidence to favor the quadratic model (depending on the criterion used, Fig. 8). Power to detect a yearly decline of 2.5% was intermediate between these 2 examples. Power was lower to detect changes in λ to 1.025 or 1.05 (unpublished data), but this was neither unexpected nor worrisome under the baseline linear estimate of λ of 1.0479.

◀ Back to trend monitoring

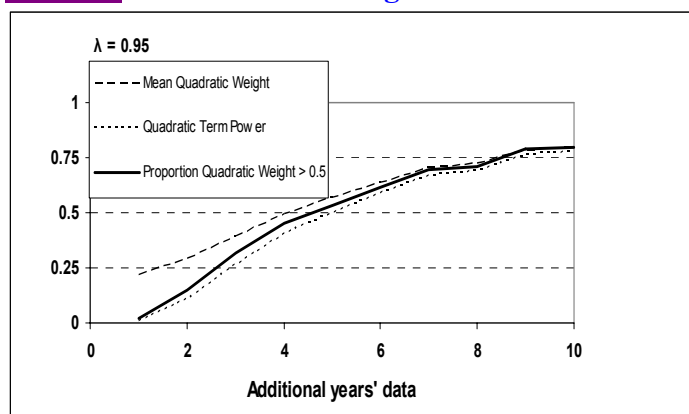


Fig. 8. Mean AIC_c weight of the (negative) quadratic term, proportion of simulations in which the quadratic model had greater AIC_c weight than

the linear model, and power of the quadratic term (i.e., probability of rejecting the linear model) when expected λ changed to 0.95 following the 1983–2006 series of estimates of females with cubs, for additional years 1 to 10 and using estimates of process and sampling variation from the data.

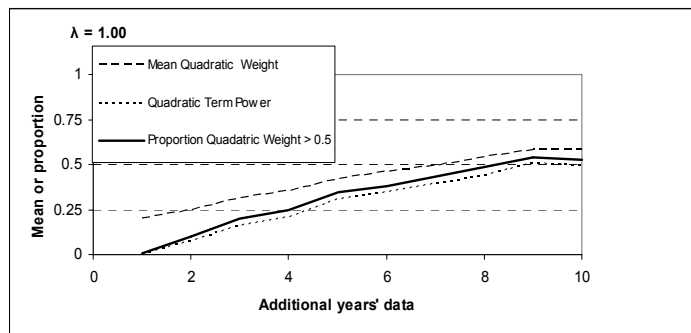


Fig. 9. Mean AIC_c weight of the (negative) quadratic term, proportion of simulations in which the quadratic model had greater AIC_c weight than the linear model, and power of the quadratic term (i.e., probability of rejecting the linear model) when expected λ changed to 1.0 following the 1983–2006 series of estimates of females with cubs, for additional years 1 to 10 and using estimates of process and sampling variation from the data.

The effect of correlation among demographic parameters on estimates of λ and the demographic vigor of the GYE grizzly bear population

[◀ Back to correlations affecting \$\lambda\$](#)

It is well known that the overall rate of population change (λ) is affected not only by mean vital rates but by their variances. Mean λ produced by a series of birth and death rates that vary annually will be lower than the λ produced by a single mean of those same rates. For this reason, **Deterministic** simplifications of growth processes are biased high, with the magnitude of the bias dependent on the magnitude of yearly variation. Clearly, if annual survival and reproductive rates covary (i.e., are positively correlated), overall variation will be greater than if they vary independently. For example, if the same underlying process causes both survival and reproduction to reach their lowest values in the same year, overall growth rate will be lower than if both reached that same lowest value in different years. Often it will be the case that vital rates are positively correlated among years.

Unfortunately, obtaining estimates of yearly co-variation is difficult. We are interested not in the appearance of yearly co-variation, but in true variation in the underlying process. If we simply calculate survival and reproductive rates annually, our estimates of covariance will largely be artifacts of sampling variation, which will tend to overwhelm the underlying process covariance. (We are interested only in the latter here, not the former). Haroldson et al. (2006) were able to estimate process variance for independent female survival (i.e., they “stripped away” sampling variance), but Schwartz et al. (2006b, c) lacked

sample size and/or procedures to do so for juvenile survival or for reproductive parameters.

However, we can approximate the amount of underlying covariance among parameters because we modeled all as functions of common covariates. As these covariates change yearly, the various rates respond in tandem. We can use these models to estimate the magnitude of correlation among rates, and to examine how this magnitude of linkage affected our estimates of overall growth rate. This procedure will tend to emphasize any existing covariance in yearly rates (and hence inflate overall variance in yearly growth rate) because much of the correlation is imposed by the model.

Methods

Correlation structure of demographic parameters and its effect on λ

We used the top models of Haroldson et al. (2006) and Schwartz et al. (2006b, c) that employed temporal covariates to predict yearly survival of cubs, yearlings, and independent females, and of reproduction (summarized by *mx*). For *mx*, we used the model with the 2nd lowest ΔAIC_c ($\Delta AIC_c = 0.58$, Schwartz et al. 2006b:21, model 2), which included **WBP** and Minpop as temporal covariates. This model predicted litter size probability. We assumed constant inter-birth intervals and ages at 1st reproduction (neither of which can be estimated annually), and adjusted results until they produced *mx* of 0.318 (used in all previous projections) when both **WBP** and MinPop were at their mean values. For cub and yearling survival, we used the 2nd highest ranking model ($\Delta AIC_c = 0.62$; model 2, Schwartz et al. 2006c:29), which included only **WSI**. In addition, we used the 3rd highest ranking model ($\Delta AIC_c =$

0.85; model 3, Schwartz et al. 2006c:29) which included only MinPop. For independent female survival, we used the 2nd highest ranking model ($\Delta AIC_c = 0.50$), which included **WBP** and **WSI** (using the C data set; Haroldson et al. 2006 did not provide AD models because they were unduly influenced by the occasional presence of unresolved-fate bears). In each case, we used the yearly covariate (Schwartz et al. 2006a:14), and calculated the model's best estimate of each demographic rate for that year (with appropriate back-transformation and conversion to an annual rate). For *mx* (via litter size), we used the **WBP** and MinPop for year $t - 1$ to estimate the rate in year t (Schwartz et al. 2006b:13).

For both of these models, we then ran 2 sets of Monte Carlo re-samplings of the 19 years of vital rates, 1) in which all rates varied in tandem, linked via their mutual association with that year's **WBP**, **WSI** and MinPop values (i.e., co-varying rates using covariate values in Schwartz et al. 2006a:14), and 2) in which all rates varied independently, i.e., sampled from the 19 possible values, but scrambled from each other (i.e., independently varying rates), in each case calculating asymptotic λ using PopTools and Eq. 3. A comparison of these 2 distributions (using identical vital rates, but one in which they were temporally correlated as suggested by our strongly supported models, and one in which rates varied independently) provided an estimate of the effect of co-varying rates on λ .

Results

Correlation structure of demographic parameters and its effect on λ

As expected, survival of adults, cubs, and yearlings were positively correlated. (The

correlation between yearly cub and yearling survival was imposed by the model; values were constrained by the fact that all had the same slopes on the logit scale). In contrast, correlations among reproduction and survival were weak and inconsistent. Although **WBP** appeared in all models (and the direction of the relationship was always the same), the reproduction model used **WBP** in the previous year, whereas survival models used **WBP** in the year of survival.

When using cub and yearling survival rates estimated from the **WSI**-only model, Monte Carlo re-sampling ($n = 5,000$) with the implied correlation structure yielded a mean λ of 1.0652 (95% CI = 1.0084–1.1276). Identical re-sampling with rates scrambled independently of one another ($n = 5,000$) yielded a mean λ of 1.0648 (95% CI = 1.0182–1.1257). When using cub and yearling survival rate estimates from the MinPop only model, Monte Carlo re-sampling ($n = 5,000$) with the implied correlation structure yielded a mean λ of 1.0720 (95% CI = 1.0063–1.1335). Identical re-sampling with rates scrambled independently of one another ($n = 5,000$) yielded a mean λ of 1.0713 (95% CI = 1.0245–1.1314).

[**◀ Back to correlations**](#)

Details on trend monitoring

◀ Back to trend monitoring

Under monitoring protocols current as of 2006, an estimate is made annually of the number of females with cubs of the year (\hat{N}_i). Unique females with cubs in each year are identified from all observations using a rule set developed by Knight et al. (1995). We consider sightings of females with cubs made with the aid of radio-telemetry biased and excluded them from the calculations (Keating et al. 2002). The Chao2 estimator (Chao 1989, Keating et al. 2002, Cherry et al. 2007) is then used to estimate the total number of females with cubs present from the estimated number observed. The trend in this segment of the population and its rate of change can be estimated from these annual estimates, providing an independent estimate of λ . However, annual estimates of \hat{N}_i can vary because of sampling error, as well as because of pulsed or synchronized reproduction. Thus, using annual estimates independently each year can result in greater variation in the estimate of total population size than is likely to characterize the true population.

The natural logarithm of the number of females with cubs [$\log(\hat{N}_i)$] can be fit with a linear model of year ($y_i = i - 1$) to estimate λ as:

$$\log(\hat{N}_i) = \beta_0 + \beta_1 y_i + \varepsilon_i \quad (\text{Eq. 4})$$

so that the population size at time zero is estimated as $\hat{N}_0 = \exp(\hat{\beta}_0)$ and the rate of population change is estimated as $e^{(\hat{\beta}_1)}$, giving $\hat{N}_i = \hat{N}_0 \hat{\lambda}^{y_i}$. Asymmetric confidence intervals on λ can be estimated as the exponential of the symmetric confidence bounds on β_1 . Standard errors for $\log(\hat{N}_i)$ can be computed with the usual linear model methods, and confidence intervals for (\hat{N}_i) can be estimated as the exponential of the confidence bounds on \log

(\hat{N}_i). When we assume a reasonably stable age and sex structure for the total population, this estimate of λ represents the rate of change of the entire population. Fitting a linear relationship makes the standard assumptions of least squares regression.

A quadratic regression can be also used to detect a change in $\hat{\lambda}$ through time. We fit the model

$$\log(\hat{N}_i) = \beta_0 + \beta_1 y_i + \beta_2 y_i^2 + \varepsilon_i \quad (\text{Eq. 5}).$$

We expect that the estimate of β_2 will become negative as population growth slows (as it would, for example, if it reached carrying capacity) or reverses. Information-theoretic model selection methods (Burnham and Anderson 2002) can be used to select between the linear and quadratic models, and hence to detect changes in $\hat{\lambda}$ as additional data are collected. We used model averaging with the linear and quadratic models of the predicted population sizes of females with cubs to estimate population sizes through time (i.e., \hat{N}_i), and thus smooth the variation of the Chao2 estimates. We used AIC_c weights (Burnham and Anderson 2002) to weight the estimates from the linear and quadratic models to produce our best estimate of the current number of females with cubs and λ .

To assess the behavior of our proposed model selection procedure, we i) added 2 hypothetical years of data for 2006 and 2007, assuming $\lambda = 0.9$ for both additional years, and ii) added 4 hypothetical years of data, assuming $\lambda = 1.0$ for all additional years.

Simply adding hypothetical years with altered λ , as above, would not constitute a power analysis of the proposed trend monitoring method, because future years' data will also contain process and sampling variation. To estimate the power of these data to detect a true reduction in λ (i.e., correctly chose the quadratic model), we

estimated variance components of the Chao2 female-cubs counts 1983–2005, and applied these in Monte Carlo projections for 10 additional years under various assumed values of λ .

To separate the sampling variance associated with each population estimate, ($\text{var}(\hat{N}_i)$) from process variance, we fitted the linear model (above), with the assumption that the variance of ε_i was the sum of the sampling variance and the process variance (earlier analyses provided no evidence for significant serial correlation, unpublished data). For the Chao2 estimator, $\text{var}(\hat{N}_i)$ was estimated with bootstrap resampling of the data, and the variance of the resampling distribution was the estimate of $\text{var}(\hat{N}_i)$. Note that the variance of $\log(\hat{N}_i)$ is estimated using the Delta method as $\text{var}(\log(\hat{N}_i)) = \text{var}(\hat{N}_i) / \hat{N}_i^2$.

To estimate the process standard deviation from the 1983–2006 Chao2 estimates, we used PROC NLMIXED in SAS (code available from GCW). This procedure maximizes the likelihood of $\log(\hat{N}_i)$ for β_0, β_1 , and the process SD, with the likelihood specified as a normal distribution with mean predicted by $\log(\hat{N}_i) = \beta_0 + \beta_1 y_i$ and variance $\text{var}(\log(\hat{N}_i)) + (\text{Process SD})^2$. This model thus explicitly includes the sampling variance of $\log(\hat{N}_i)$ plus the process variance that is estimated by the procedure. Process SD was estimated to be 0.176 with SE 0.0461 and 95% confidence interval 0.0808–0.271

To estimate the expected sampling variance of future Chao2 estimates (which assumes that future sampling effort will remain approximately the same as used to collect the 1983–2006 data), the mean of the sampling variances of the log population estimates for the 1983–2006 data was computed. The expected sampling variance of future Chao2 estimates was then computed as a normally distributed random

variable with mean zero and standard deviation equal to the square root of mean sampling variance. From this procedure, the estimated sampling standard deviation was 0.34.

To evaluate sensitivity of the linear and quadratic models to changes in \hat{N} over 1 to 10-year time intervals, we projected forward the 2006 population estimate of $N_{2006} = 52.356$ (obtained by model averaging the linear and quadratic model estimates from the fits of the 1983–2006 data), assuming alternative λ values of 0.95, 0.975, 1, 1.025, and 1.05, and using our estimates of process and sampling variation (above). Population size for each succeeding year was generated with the recursive relation $\log(N_{i+1}) = \log(N_i) + \log(\lambda) + \delta_i$, where the process variation was added as δ_i , a normally distributed random variable with mean zero and standard deviation 0.176. The estimated population size (corresponding to the Chao2 estimates) was taken as $\log(N_{i+1}) + \varepsilon_{i+1}$, where the sampling variation ε_{i+1} was added as a normally distributed random variable with mean zero and standard deviation 0.34. Each replicate was simulated independently, i.e., completely new data were added to the 1983–2006 data for each simulation.

One thousand replicates of each of the 50 scenarios (5 alternative λ X 10 alternative time-frames) were generated, from which we obtained estimates of the mean AIC_c weight of the quadratic model, the proportion of iterations in which the quadratic term was selected (weight > 0.5), and the power of the t -test to reject the null hypothesis that the quadratic term was equal to zero. This provided a realistic simulation of the data and analyses that would be available to managers when judging whether the population had changed its trajectory.

Monitoring population size and λ using females with cubs. Data for 1983–2005 were used to estimate the rate of population change. The parameter estimates and AIC_c weights for the linear and quadratic models suggested that primarily the linear model was needed to model changes in the number of females with cubs during this period. The estimate of λ using the linear model was 1.0479 with 95% confidence interval of 1.031–1.065. The estimated quadratic effect (-0.000711 , $SE = 0.0013$) was not significant ($P = 0.6$), and 79% of the AIC_c weight was associated with the linear model. Thus, the linear model was the best approximating model for 1983–2005, but we also provide the model averaged estimates.

When 2 years with $\lambda = 0.9$ were added to these data, the resulting quadratic model had an AIC_c weight of 0.67847 and an estimated quadratic effect of -0.0028 ($SE = 0.0012$) that differed from zero ($P = 0.03$). Thus, had the Chao2 counts declined by exactly 10% each year, our model selection would have detected this fundamental change in system state within 2 years. Two years would not have been sufficient to detect a change to stationary counts, but by the 3rd year, model weights would have shifted to favor the quadratic model, suggesting that population growth had stopped.

Power analysis of using \hat{N} to estimate a change in λ . When our best estimates of process and sampling variation were added to hypothetical years 1 through 10, approximately 5 years were required of the population decreasing 5% yearly (i.e., $\lambda = 0.95$) before the preponderance of evidence (AIC_c weight > 0.5) favored the quadratic model (i.e., fundamental change in state from linear increase). Under the scenario in which population size stabilized after year 2006 (i.e., $\lambda = 1.0$), 7 or 8 years were

required for the preponderance of evidence to favor the quadratic model (depending on the criterion used). Power to detect a yearly decline of 2.5% was intermediate between these 2 examples. Power was lower to detect changes in λ to 1.025 or 1.05 (unpublished data), but this was neither unexpected nor worrisome under the baseline linear estimate of λ of 1.0479.

For more on the expected power of the this trend monitoring, [click here](#).

[**◀ Back to trend monitoring**](#)

[◀ Back to contents](#)

Literature Cited

- Blanchard, B. B., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. *Biological Conservation* 58:41–67.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. *Biometrics* 45:427–438.
- Cherry, S., G. C. White, K. A. Keating, M. A. Haroldson, and C. C. Schwartz. In Press. Evaluating estimators of the numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Journal of Agricultural, Biological, and Environmental Statistics*.
- Eberhardt, L. L. 1990. Survival rates required to sustain bear populations. *Journal of Wildlife Management* 54:587–590.
- Eberhardt, L.L., and R.R. Knight. 1996. How many grizzlies in Yellowstone? *Journal of Wildlife Management* 60:416–421
- Haroldson, M. A., C. C. Schwartz, and G. C. White. 2006. Survival of independent grizzly bears in the greater Yellowstone ecosystem, 1983-2001. Pages 33–42 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildlife Monographs* 161:1–68.
- Harris, R. B. 1986. Modeling sustainable harvest rates for grizzly bears. Appendix K in A. Dood, R. Brannon, and R. Mace, editors. *The grizzly bear in northwestern Montana*. Final programmatic environmental impact statement. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA. Unit Publication, Missoula, Montana, USA.
- Harris, R. B., C. C. Schwartz, M. A. Haroldson, and G. C. White. 2006. Trajectory of the greater Yellowstone ecosystem grizzly bear population under alternative survival rates. Pages 45 --56 in C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildlife Monographs* 161:1–68.
- Interagency Grizzly Bear **Study team**. 2005. Reassessing methods to estimate population size and sustainable mortality limits for the Yellowstone grizzly bear. Interagency Grizzly Bear **Study team**, U.S.

- Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana, USA.
- Keating, K. A., C. S. Schwartz, M. A. Haroldson, and D. Moody. 2002. Estimating numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Ursus* 13:161–174.
- Knight, R. R., B. M. Blanchard, and L. L. Eberhardt. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. *Wildlife Society Bulletin* 23:245–248.
- Mattson, D.M., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *International Conference on Bear Research and Management* 7:259–273.
- McLoughlin, P.D. 2002. Managing risks of decline for hunted populations of grizzly bears given uncertainty in population parameters. Final Report, British Columbia Independent Scientific Panel on Grizzly Bears. Victoria, British Columbia, Canada.
- Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. Barnes, Jr., R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark–resighting techniques. *Wildlife Monographs* 133.
- Schwartz, C. C. 1999. Evaluation of a capture–mark–recapture estimator to determine grizzly bear numbers and density in the Greater Yellowstone Area. Pages 13–20 in C. C. Schwartz and M. A. Haroldson, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study team*, 1998. U.S. Geological Survey, Bozeman, Montana, USA.
- Schwartz, C. C. 2000. Evaluation of a capture–mark–recapture estimator to determine grizzly bear numbers and density in the Greater Yellowstone Area. Pages 15–18 in C. C. Schwartz and M. A. Haroldson, editors. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study team*, 1999. U.S. Geological Survey, Bozeman, Montana, USA.
- Schwartz, C. C. and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildlife Monographs* 113.
- Schwartz, C.C. and M. A. Haroldson, editors. 2001. *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study team*, 2000. U.S. Geological Survey, Bozeman, Montana, USA.
- Schwartz, C. C., M. A. Haroldson, K. A. Gunther, and D. Moody. 2002. Distribution of grizzly bears in the Greater Yellowstone

- Ecosystem, 1990–2000. *Ursus* 13:203–212.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2006a. Study area and methods for collecting and analyzing demographic data on grizzly bears in the greater Yellowstone ecosystem. Pages 9–16 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildlife Monographs* 161:1–68.
- Schwartz, C. C., M. A. Haroldson, and S. Cherry. 2006b. Reproductive performance of grizzly bears in the greater Yellowstone ecosystem, 1983–2002. Pages 17–24 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildlife Monographs* 161:1–68.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2006c. Survival of cub and yearling grizzly bears in the greater Yellowstone ecosystem, 1983–2001. Pages 25–31 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildlife Monographs* 161:1–68.
- Schwartz, C. C., R. B. Harris, and M. A. Haroldson. 2006d. Impacts of spatial and environmental heterogeneity on grizzly bear demographics in the greater Yellowstone ecosystem: a source-sink dynamic with management consequences. Pages 57–67 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildlife Monographs* 161:1–68.
- Schwartz, C. C., M. A. Haroldson, K.A. Gunther, and D. Moody. 2006e. Distribution of grizzly bears in the greater Yellowstone ecosystem, 1990–2004. *Ursus* 17:63–66.
- U.S. Fish and Wildlife Service. 1982. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado, USA.
- U.S. Fish and Wildlife Service. 1993. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- U.S. Fish and Wildlife Service. 2007. Final conservation strategy for the grizzly bear in the Greater Yellowstone Ecosystem. U.S. Fish and Wildlife Service, Missoula, Montana, USA.

White, G.C. 1996. NOREMARK: population estimation from mark-resight surveys. Wildlife Society Bulletin: 24: 50-52.

Wilson, R.M. and M. F. Collins. 1992. Capture-recapture experiments with samples of size one using frequency data. Biometrika 79: 542-553.

[**◀ Back to contents**](#)