

**International Association of
Bear Research and Management**

Monograph Series Number 4

**Population Viability
for
Grizzly Bears:
A Critical Review**

**Mark S. Boyce
Bonnie M. Blanchard
Richard R. Knight
Christopher Servheen**

2001

**International Association for Bear Research and Management
Monograph Series Number 4**

**Population Viability for Grizzly Bears:
A Critical Review**

by

Mark S. Boyce
Bonnie M. Blanchard
Richard R. Knight
Christopher Servheen

A paper presented at the
11th International Conference
on
Bear Research and Management
Gatlinburg, TN
April 1998

Editors

Michael R. Vaughan
Todd K. Fuller

Suggested citation:

Boyce, M.S., B.M. Blanchard, R.R. Knight, and C. Servheen. 2001. Population viability for grizzly bears: a critical review. International Association for Bear Research and Management Monograph Series Number 4. 45pp.

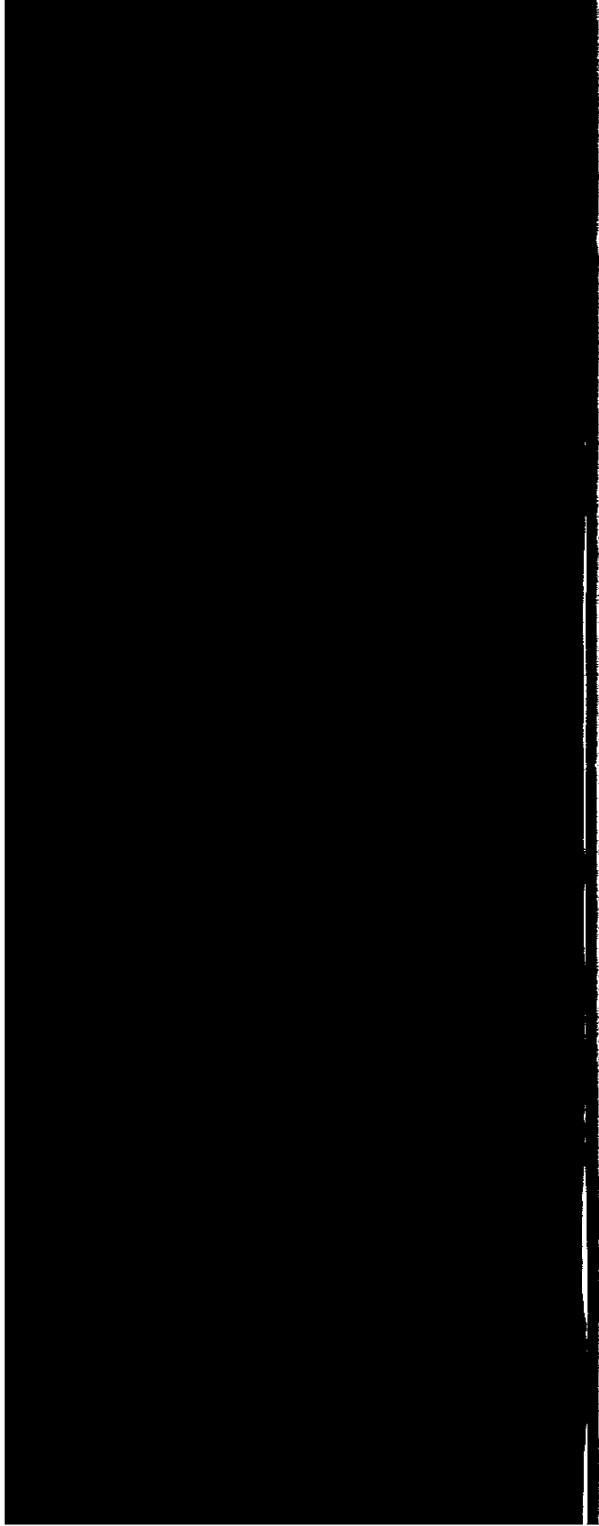
2001

International Association for Bear Research and Management

Prepared for publication by Charissa Reid, Yellowstone National Park, Wyoming.
Printed by Thomson-Shore Inc., Dexter, Michigan.

ISBN 0-944740-10-3

Available from Terry White, Department of Forestry, Wildlife and Fisheries, University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, USA. Phone (865) 974-0739; Fax 865 974 4714; e-mail tdwhite@utk.edu.



Survival of the grizzly bear in the Yellowstone ecosystem will be dependent on preservation of habitat, enlightened adaptive management, agency understanding, political support, and objective research. The price for survival will be constant citizen concern and support and scientific
y Milo Burcham.

TABLE OF CONTENTS

PREFACE	vii
INTRODUCTION	2
Purpose of PVA	2
Expectations	3
COUNT TRAJECTORIES: TIME-SERIES APPROACHES	3
Counts of Females with Cubs of the Year	3
Bias Correction for the COY Counts	4
Counts of Grizzly Bears in the Tetons	7
Stochastic Time-series Models	7
Discussion	11
STRUCTURED-POPULATION MODELS	12
Review	12
<i>Minimum Viable Population</i>	12
<i>Updated MVP (Suchy, et al.)</i>	13
<i>Stable-Age Distribution Methods</i>	14
<i>Projection Matrix Methods</i>	15
<i>Canned PVAs: Mills et al.(1996)</i>	17
Discussion and Further Analysis	18
Survival Analysis	18
Using RAMAS/GIS for the GYE	23
Using RAMAS/GIS for the Metapopulation of US Grizzly Bears	25
Using ALEX	29
DISCUSSION	29
Demographics	29
Habitat-Based PVA	31
Implications for Management	32
CONCLUSIONS	33
ACKNOWLEDGMENTS	34
LITERATURE CITED	35

PREFACE

Grizzly bears in the conterminous United States have been reduced to <2% of their former geographic range. The remaining 4 populations have been protected under the Endangered Species Act since 1975. To meet its conservation mandate, the U.S. Fish and Wildlife Service has developed a Recovery Plan, which includes recommendations and guidelines for ensuring the persistence of grizzly bear populations (USFWS 1993).

This document is the result of a cooperative effort to address task #38 in the Grizzly Bear Recovery Plan (USFWS 1993) – the application of population viability analysis (PVA) to grizzly bear recovery. As such, it represents yet another step to further understand the needs of the grizzly bear for recovery. This effort has resulted in a comprehensive review of PVA techniques and application of these state-of-the-art approaches to try and understand factors influencing the probability of persistence of grizzly bear populations. This document relies upon the many years of comprehensive data collected on grizzly bears in the Yellowstone ecosystem and on other grizzly populations in the United States, and we recognize the enormous efforts of many people to develop the data used in this report. One of the products of this effort is highlighting further issues that need additional work to better understand the relationship of the grizzly to its habitats. This work to link demographics and habitat values for grizzly bears is now ongoing.

The long-term future of the grizzly depends on adaptive management that takes new information such as that presented in this volume and reacts to it with both necessary management and additional research and analysis as warranted. Grizzly recovery will require this type of responsiveness to changing conditions because we live in a world where changing conditions are a continual challenge to wildlife conservation. We are committed to adaptive management and to continually working to improve our knowledge of the needs of the grizzly into the next century. This document represents a commitment to that approach.

Christopher Servheen
Grizzly Bear Recovery Coordinator
U.S. Department of Interior
Fish and Wildlife Service
Missoula, Montana
U.S.A.

Mark S. Boyce
Alberta Conservation Association Chair in Fisheries and Wildlife
University of Alberta
Edmonton, Alberta
CANADA

POPULATION VIABILITY FOR GRIZZLY BEARS: A CRITICAL REVIEW

MARK S. BOYCE, Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada, email: mark.boyce@ualberta.ca

BONNIE M. BLANCHARD, U.S.G.S., Biological Resources Division, Montana State University, Bozeman, MT 59717, USA

RICHARD R. KNIGHT, U.S.G.S., Biological Resources Division, Montana State University, Bozeman, MT 59717, USA

CHRISTOPHER SERVHEEN, U.S. Fish and Wildlife Service, University of Montana, Missoula, MT 59812, USA, email: grizz@selway.umt.edu

Abstract: We review and update population viability analyses (PVA) conducted for grizzly bears (*Ursus arctos horribilis*) in the Rocky Mountains of the United States. Our analysis focused on grizzly bears of the Greater Yellowstone Ecosystem (GYE) because this population has been most studied.

Counts of unduplicated adult female bears accompanied by cubs of the year (COY index) have been used to document grizzly bear population trends in the GYE but the method is biased by annual variation in the intensity of survey effort and in the sightability of bears. With new methods for estimating population size based on cumulative counts, we are able to correct these biases and come up with unbiased estimates of the total number of adult females with COY. The trend in the adjusted number of adult females with COY corroborates other data indicating that the GYE bear population increased during 1983-1997.

Using the COY data we computed expected time to extinction and extinction probabilities at 100 years using stochastic models. Recent data provide optimistic projections of the likelihood of persistence for grizzly bears in the GYE; a 99.2% probability that the GYE grizzly bear population will persist for 100 years. Extending to a 500-year period, we find that probability of persistence decreases to 96.1%.

Survival analysis of radiocollared bears in the GYE based on the Andersen and Gill (1982) method demonstrates significant differences in survival among bear sex and age classes: young (0-4 yr) and old (>20 yr) bears have lower survival than bears aged 5-20; males (especially prereproductives) have lower survival rates than females; and females with young have significantly lower survival rates than other bears. Other factors also influence survival rates. For example, bears with home ranges completely outside Yellowstone National Park (YNP) have significantly higher risk of mortality than bears with home ranges partially or completely within YNP, and grizzly bears relocated after management conflicts suffer a higher mortality rate than bears that have not been relocated.

Hunters are the second greatest source of grizzly bear mortality in the GYE. Hunters shoot grizzly bears deliberately, in self-defense, or because they mistake grizzlies for black bears. Reducing hunter-related mortalities could increase the probability of long-term persistence of grizzlies in the GYE.

Count data, demographic analysis, and grizzly bear distribution all indicate that the GYE bear population increased during the past decade, probably as a result of cooperative efforts by state and federal agencies and the public to reduce conflicts between humans and bears. Prior to the closure of garbage dumps in Yellowstone National Park in 1970-71 recruitment was density dependent. However, recent increases in grizzly bear population density have resulted in reduced survival. We hypothesize that the change from density-dependent recruitment to density-dependent survival may be attributed to more frequent contact between cubs and infanticidal males (Swenson et al. 1997) when bears foraged at dumps, and more frequent contact between bears and humans now.

We studied spatially structured population models using RAMAS/GIS and ALEX software and drew some parameter estimates from our survival analysis results. We found 100-year persistence probabilities for grizzly bears in the conterminous states are high, bolstered by a large population in the Northern Continental Divide Ecosystem (NCDE). Using RAMAS/GIS and ALEX, we found that high variance in our estimates of carrying capacity for bears in the GYE lowered the probability of persistence, but this may be inappropriate because this variance is redundant with the variance in demographic parameters in the model. Dispersal among subpopulations of grizzly bears in the U.S. Rocky Mountains has not been observed, although data from Canada and Alaska show that bears, especially subadult males, sometimes disperse considerable distances. Using RAMAS/GIS to model conservative levels of dispersal among subpopulations illustrates that managing to ensure capability of dispersal for bears among subpopulations through linkage-zone management (Servheen and Sandstrom 1993) and/or by transplants (Servheen et al. 1995) can improve prospects for long-term viability of grizzly bear populations.

We believe that the population models reviewed here would be greatly improved if they interfaced with data on habitat relationships, which is now possible with resource selection probability function estimation (Manly et al. 1993). Habitat data in the GYE already compiled for a cumulative-effects evaluation can be used to parameterize a resource selection function for grizzly bears, and then interfaced with a population model to produce a habitat-based PVA. Our ability to evaluate the effects of natural resource management on grizzly bear populations in the Rocky Mountains would be greatly improved with such a habitat-based PVA.

Key words: bear, demography, density dependence, extinction, grizzly bear, population viability analysis, PVA, survival analysis, *Ursus arctos*, Yellowstone National Park.

"They are the untamed soul of the Rockies."
- D. Chadwick, 1995

INTRODUCTION

The grizzly bear is a symbol of wilderness in western North America (Peek 1986). Habitat loss and human-caused mortality have resulted in the elimination of grizzly bears from 98% of their former range in the conterminous USA. Currently grizzlies remain in blocks of land essentially uninhabited by humans. Increases in the human population and encroachment into grizzly habitats continue to erode the species' range and threatens their long-term persistence in the conterminous United States (Peek et al. 1987, Servheen 1993, Harting et al. 1994). As a result, the grizzly bear was listed as threatened under the U.S. Endangered Species Act on 28 July 1975. Recovery plans for the species prepared by the U.S. Fish and Wildlife Service were approved in 1982 and 1993 (Servheen 1993).

A task recommended in the 1993 Recovery Plan was the completion of a PVA. Population viability analysis evaluates the likelihood of long-term persistence of a population, and ideally enables the development of a model to predict a population's dynamics and future abundance.

Scope of this Monograph

We provide a critical review of PVA and related modeling efforts for grizzly bears, primarily in the GYE. We updated many of these models using data collected since the initial studies were completed. Included are both analytical models and simulation approaches. Several PVA software packages recently were compared using grizzly bear data by Mills et al. (1996). We expand on their evaluation by providing an overview of modeling results obtained from 2 new PVA software packages: RAMAS/GIS and ALEX.

We believe that all PVA approaches have limitations and we will attempt to explain the most serious of these. The existence of limitations and assumptions does not invalidate the models. After all, by definition, models are a simplification of nature to help us to better understand "how it all works" (Grant 1986).

This monograph is not intended to suffice as a PVA for GYE grizzly bears—a principal conclusion is that including habitats in a PVA model would greatly improve our ability to assess population viability. New methods for linking habitats with population models using geographical information systems (GIS) offer important opportunity that will help managers evaluate the

consequences of their natural resource management decisions (Manly et al. 1993, Boyce et al. 1994).

Purpose of PVA

Even though we often have insufficient data to perform PVA with statistical rigor, a PVA model can be useful for framing our understanding of the principal processes that shape the species' dynamics. As such, the model can provide the basis for an adaptive management protocol whereby we perpetually improve the model by performing population management and monitoring and then iterating the model to incorporate new information (Walters 1986, Boyce 1997).

Often PVA is focused on the estimation of minimum viable population (MVP) size under the premise that population size is a major consideration in the likelihood of extinction for a population (Caughley 1994). Others have suggested the approach of determining whether a population is increasing or decreasing and evaluating which factors are responsible for population trends (Caughley 1994, Eberhardt and Knight 1996). Included among such evaluations of population viability are calculations of population growth rates based on estimates of vital rates (Eberhardt et al. 1994).

We find each of these approaches unsatisfactory. For example, population size alone is inadequate for evaluating long-term viability, and it would be dangerous to hang viability on numbers of bears. We know, for example, securing reliable estimates of grizzly bear populations in forested areas can be difficult (Eberhardt and Knight 1996; Servheen et al. 1994, 1996). Furthermore, the disturbance to bears necessary to secure good estimates may jeopardize bears, and such an effort might exceed the entire budget of the recovery program (Servheen et al. 1996). We also know that wildlife populations undergo fluctuations due to changes in the environment, but that these need not portend a poor future for the bears. Even though a population may have increased or decreased for the past 10-20 years, this offers no indication that the population will continue on the same trajectory in the future. Indeed, because of density dependence, no populations can continue to grow indefinitely (Sinclair 1989). We are seldom able to anticipate population trends very far into the future (except possibly by anticipating habitat trends), so demographic trajectories will be of use only in the near term.

Fundamentally, PVA implies that we are interested in the long-term prospects for the grizzly bear populations under study. Also, we could benefit from an improved understanding of factors that influence population fluctuations, and how we might manipulate these factors.

The exercise of modeling, in itself, may improve our understanding of a population. But ecological modeling is unreliable because of the inherent complexity and unpredictability of ecosystems (Ludwig 1999). For PVA to be a useful management tool, methods should be standardized as much as possible (Akçakaya 1994), but our understanding of PVA has not progressed sufficiently to permit such standardization. Because of inherent uncertainties, modeling scenarios should project the worst case, using conservatively small estimates of population size and conservatively high estimates of variance for parameter estimates.

This is not to imply that PVA is a hopeless cause. Quite the contrary—PVA is the best method available for integrating conservation science and management. PVA is the very basis for adaptive management in which the model poses a formal statement of our understanding of the system and hypothesizes the consequences of management actions (Boyce 1997). Monitoring the results of management actions then provides data that are used to evaluate the model's predictions with consequent revisions to the model and a new set of predictions (Walters 1986). Given our current level of understanding of ecological science and natural resource management, active adaptive management offers the best, safest, and most rigorous approach toward successful conservation (Walters and Holling 1990).

Expectations

Uncertainty is fundamental to PVA (Soulé 1987). We are attempting to evaluate risks to populations due to randomness in population processes and risks associated with management actions. But, because our models use data that may be insufficient, biased, or even made up, we must not garner unrealistic expectations of PVAs. And because we are still learning how to perform such analyses, we might not get it right.

Regrettably, our naiveté with PVA has negative ramifications for those not familiar with the vagaries of ecological modeling, and this threatens acceptance of any such efforts by management. Schullery (1992) noted that PVAs have provided wildly different estimates of the number of grizzly bears required to ensure long-term persistence in the GYE. Shaffer's (1978) first estimates suggested that only 35 bears were necessary to ensure a 95% probability of persistence for 100 years. Recently,

the same results in a PVA. Unfortunately, instead of attempting to understand the reasons for the various assumptions that lead to differing results, resource managers commonly distrust models and modelers. In the context of cumulative effects modeling for grizzly bears, Robert Barbee, former Superintendent of YNP remarked:

"...There's this whole notion of cumulative effects modeling in grizzly bear management, for example. Scientists tell us about the quantification of all the complex sets of variables out there, that leads to overlays in a formula that ultimately could be factored down to a certain kind of actionable result in the loss of one tenth of a bear or half a bear in the system over five years. I am highly skeptical of that, and I think most people of the management mentality are also. And yet I see us heading into it more and more, and I can assure you that science and management are on divergent paths here. There's great skepticism in offices like mine, and a great infatuation with the science of modeling among the scientific people. ...I'm skeptical about where it's taking us. It's a big money sump. I think it's gimmicky and it may deserve more respect, but I'm telling you that it doesn't have that respect in the management community. A lot of managers might keep their mouths shut because they don't want to admit how absolutely ignorant they are about all of this new technology" (Schullery 1995).

For any of this modeling to be of use, it must ultimately be accepted by managers. Some technical details in this monograph may be inaccessible for readers unfamiliar with population biology. But we attempt to explain the assumptions and major conclusions of the models so that the results can be understood and considered by the managers who must make the tough decisions.

COUNT TRAJECTORIES: TIME-SERIES APPROACHES

Counts of Females with Cubs of the Year

Because grizzly bears often occupy forested habitats where they can be difficult to detect, reliable estimates of population size or densities have proven elusive (Harris 1986, Miller et al. 1997). Servheen (1993) used the COY index to evaluate grizzly bear population status and re-

sightings from April through October. The COY index has the advantage of being less intrusive and expensive than an extensive mark-recapture program.

Trend in the COY index (Fig. 1) has been cited as evidence that the GYE grizzly bear population is increasing (Knight et al. 1995, Eberhardt and Knight 1996), despite disclaimers in the Recovery Plan (Servheen 1993) that the index "is not adequate to characterize population trend or precise population size." Eberhardt et al. (1986) estimated that on average approximately 33% of adult female bears breed in any year, thus a 3-year moving sum of the unduplicated number of adult females with COY offers an estimate of the minimum number of adult females (N_p) in the population (Fig. 2). Based on capture data and age and sex composition of the GYE population, Eberhardt and Knight (1996) estimated that adult females constitute ~27% of the population. Therefore, an approximate minimum population size can be obtained by $\hat{N}_{\min} = (3\text{-yr moving sum COY index})/0.27$.

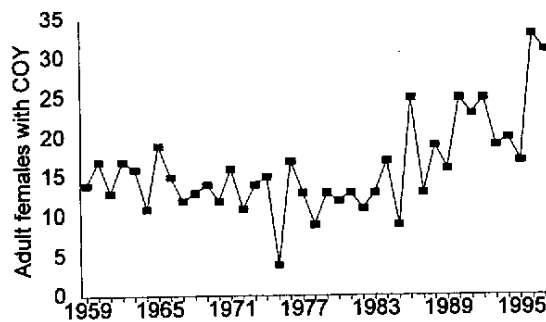


Figure 1. Unduplicated counts of the number of adult females with cubs of the year in the Greater Yellowstone Ecosystem, 1959-1996.

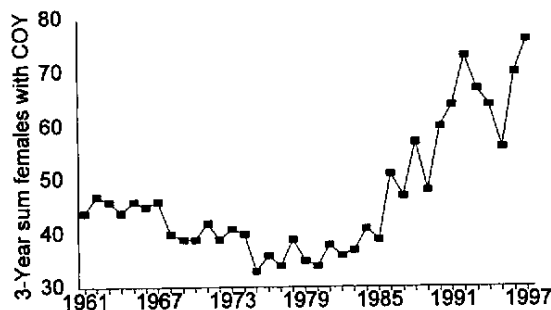


Figure 2. Moving 3-year sum of the COY index as an estimate of the number of adult females in the Greater Yellowstone Ecosystem, 1959-1996.

Bias Correction for COY Counts

Although family groups are probably the most visible population segment (Knight et al. 1995), COY index has been criticized because bear-sightability appears to vary from year-to-year (Mattson 1997). In dry years when food is scarce, bears ranged widely while foraging and were more likely to be observed (Eberhardt et al. 1994). Furthermore, survey effort varied due to weather conditions and flight budgets (Mattson 1997).

Mattson and Pease (1994) and Mattson (1997) argued that the COY index has little value as a population estimator because of sightability variation. To correct for this, Mattson and Pease (1994) developed 2 sightability indices: (1) percentage of sightings of females with COY observed during flights to relocate radiocollared bears, and (2) percentage of telemetry flights in which a radiocollared female with COY was actually seen. The rationale behind the first measure of sightability is that if females with COY are more easily observed than other bears, this index will increase. This assumes that the proportion of females with COY remains a constant fraction of the population, and this certainly need not be true because reproductive success clearly varies from year-to-year (cf. Fig. 14 and 15 below). Thus, their first index is an invalid measure of sightability.

The second sightability index may be a more reliable measure of the sightability of females with COY. Using 1979-1990 data, Mattson and Pease (1994) found a correlation between the 3-year sums of females with COY and the arcsin transformed proportion of successful relocation efforts where the female with COY was seen ($r^2 = 0.63$, $n = 12$, $P = 0.002$). Multiple regression of the number of hours flown did not yield significant results ($P = 0.162$).

Knight et al. (1995) attempted a similar adjustment for COY index bias using the log of the number of distinct family groups related to the mean frequency of sightings of family groups in a given year. This log-linear model was then used to adjust the number of bears sighted (Fig. 3).

Time-series trends present problems for statistical analysis because observations are not independent, and it is easy to find spurious correlations in time series. We find all of the attempts to adjust the COY index to be inadequate, partly because they are based upon adjustments in 2 time series, each containing a temporal trend. Although a relationship between the logarithm of the COY index and frequency of sightings is possible these time series are not necessarily causally linked and adjustments might be spurious. For example, the actual number of females with COY may have increased between 1979 and 1990, and is simply a reflection of the

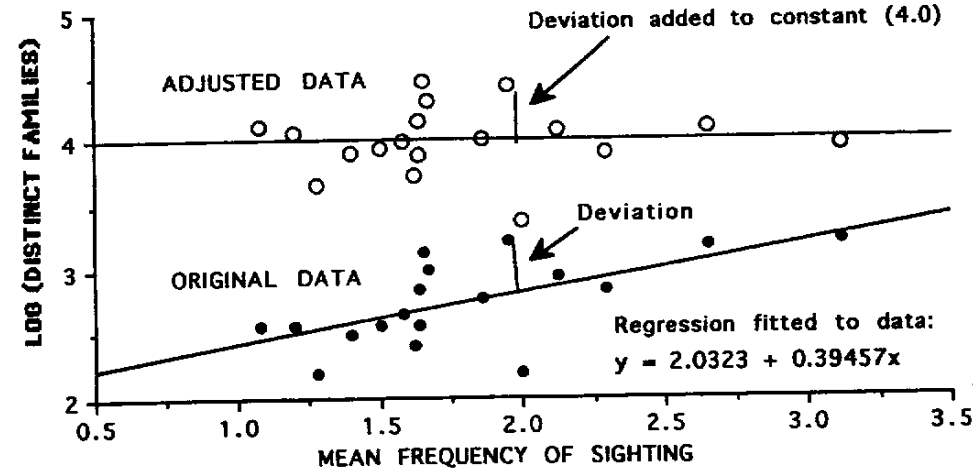


Figure 3. Log of the number of unduplicated adult females with COY as a function of the mean frequency of sightings. This relationship indicates that the more observations of bears were accumulated the higher the COY index. The open circles represent an adjusted COY index removing the linear pattern (from Knight et al. 1995).

increased GYE grizzly bear population size. Because more bears are being sighted in alpine areas foraging on army cutworm moths (*Euxoa auxiliaris*, Mattson et al. 1991, French et al. 1994), sightability has increased during the same time interval. Therefore, the mean frequency of sightings increased. Making adjustments for the change in sightability that occurred during a period of increasing population size is likely to overcompensate for the true relationship between sightability and the COY index.

The model proposed by Knight et al. (1995) appears to oversimplify the actual relationship, which we believe must be asymptotic. As survey effort and frequency of sightings increase, we expect the COY index to increase asymptotically up to a maximum equal to the actual number of females with COY in the population. Assuming that the model is loglinear causes much too great an adjustment in the index for years during which an extensive search effort was made. This yields a smaller population size estimate than is warranted.

We developed a method for estimating the actual number of females with COY based on cumulative counts of unique individuals during each field season (Boyce et al., unpublished manuscript). As the number of females with COY sightings increases, eventually one would expect to see all of the bears. Thus, we expect the cumulative

effort, such as the DeLury method commonly used in fisheries (DeLury 1947, Moran 1951).

A statistically defensible method for estimating population size is based on maximum likelihood estimation (Lewontin and Prout 1956). This method assumes that the probability of a bear not being seen after i observations is

$$\theta_i = [(N-1)/N]^i \quad (1)$$

and then the probability of a bear being seen is

$$1 - [(N-1)/N]^i. \quad (2)$$

Thus, the expected number of unique sightings after a total of observations, S_p , is

$$E(S_p) = N\{1 - [(N-1)/N]^{S_p}\}. \quad (3)$$

where E denotes expectation. With this model we assume that all females with COY are equally likely to be observed. We used the principle of maximum likelihood to estimate N ; 10,000 simulations were used to obtain standard errors (SE) for the estimates (Table 1, Fig. 4).

The MLE fits the grizzly bear data fairly well (Fig. 5), but in a few occasions a bit more flexibility in the underlying model would ensure a closer fit to the data (Fig. 6). The fundamental problem is that the MLE assumes that

Table 1. Confidence intervals (95%) for the maximum likelihood estimates (MLE) of the number of adult female grizzly bears with cubs of the year computed from 10,000 randomized trials for each year.

Year	Lower Limit	MLE	Upper Limit
1986	25*	27	34
1987	14	22	56
1988	19*	23	33
1989	16*	21	35
1990	26	32	46
1991	23*	27	36
1992	31	47	91
1993	21	29	53
1994	21	28	46
1995	20	34	89
1996	41	56	91

* The probability of an estimate as high as that observed is more than 0.025 if the population size equals the number of bears actually seen.

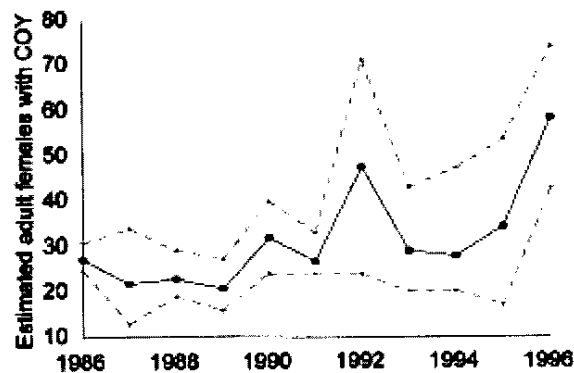


Figure 4. MLE estimates of the number of females with COY (solid oval dots) in the GYE, surrounded by SE (dashed lines) for 1986-1996.

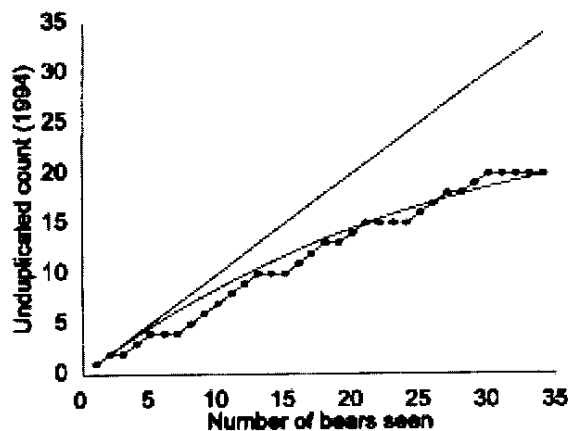


Figure 5. Cumulative unduplicated counts (COY index) versus number of bears seen for year 1994. The MLE (eq. 2) is fitted to the observed data. The straight line has a slope of 1. In most years the MLE fits well as illustrated by this example.

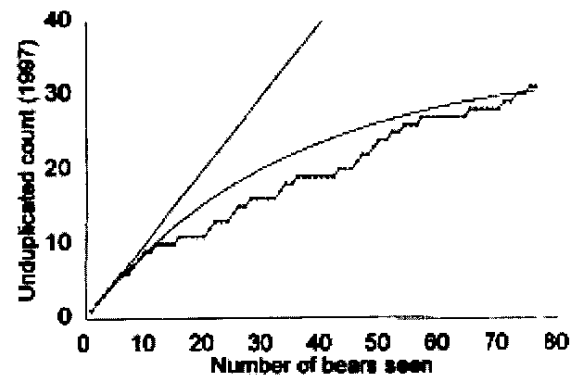


Figure 6. Cumulative unduplicated counts (COY index) versus bears observed in 1997. The MLE has been fitted to the data. The straight line has a slope of 1. In 1986 and 1997 the MLE offers a poor fit to the data apparently due to heterogeneity in sighting probabilities among bears.

they are easily seen resulting in heterogeneity in sighting probability.

This occasional heterogeneity in sighting probability motivated us to develop a model to estimate population size using the negative binomial distribution (Boyce et al. unpublished manuscript). The negative binomial frequently offers a good characterization of heterogeneous or aggregated ecological data (Krebs 1999), and there is theoretical justification for its application to the bear data. The fit of data to this model is reasonable, and the estimator appears to have good properties given the relatively small sample sizes available for analysis in most years. Alternative estimators exist, e.g., the Chao non-parametric estimator (Chao and Lee 1992). But by identifying the underlying distribution, our negative binomial estimator has greater power yielding estimates with tighter confidence intervals than more general methods. This is particularly important given the few counts available in some years. A comparison of the Chao, MLE and negative binomial estimates (Fig. 7) indicates that the MLE is relatively conservative and all estimators provide estimates substantially higher than the COY index. Based on the results of simulation studies, we caution that reliable estimates using the MLE require that unduplicated sightings should be >75% of the estimated female grizzly bears with COY in any year (Boyce et al. unpublished manuscript). Our bias-corrected estimates based on the negative binomial distribution are better able to accommodate the small sample sizes that have been observed in some years.

These estimation methods overcome the criticism that using cumulative counts to estimate the minimum number of bears ignores the influence of annual variation in search effort and sightability (Mattson 1997). Estimates

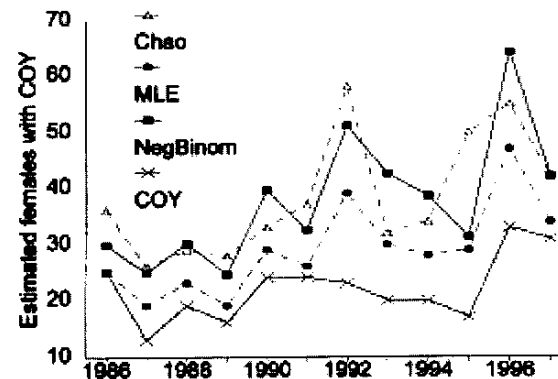


Figure 7. Estimated number of unduplicated females with cubs of the year based upon the Chao estimator (open triangles, dashed lines), the MLE (round dots, dashed line), and the negative binomial model (square symbols, solid line). Also plotted for comparison is the COY index (X).

of asymptotic population size are not affected by variation in search effort and sightability. This point is illustrated by the plot in Figure 5. Even if a smaller or larger proportion of the population were counted, the true asymptote will not be affected. Furthermore, in recent years the Interagency Grizzly Bear Study Team (IGBST) has developed protocols for aerial searches in an attempt to standardize search patterns from year-to-year so that counts are comparable among years.

An alternative way to conceptualize the cumulative count data is as a mark-release-recapture (MRR) problem with previously seen bears classified as "marked" (Eberhardt and Knight 1996). Indeed, we note that our MLE method is identical to a multiple MRR method with individuals sampled 1 at a time (Darroch 1958, Samuel 1969).

Counts of Grizzly Bears in the Tetons

An interagency effort was launched in 1983 to reduce grizzly bear mortality in the GYE. These efforts are credited with the increasing 3-year sum of the COY index from 1983-1997 (Fig. 2; Servheen 1993). In addition, agency personnel reported bear sightings increased in areas of the GYE surrounding YNP, but no systematic procedure has been in place to document range expansion of the bears. S. L. Cain (National Park Service, unpublished data) has reports of grizzly bear sightings in Grand Teton National Park and the John D. Rockefeller

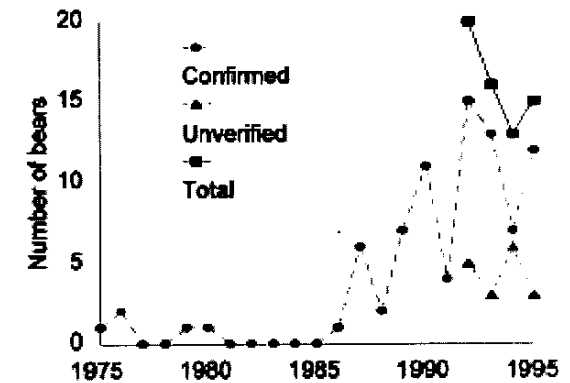


Figure 8. Number of bears counted in Grand Teton National Park and the John D. Rockefeller Memorial Parkway, 1975-1995 (S. Cain, unpublished data). Included are verified, unverified, and total counts.

the COY index ($r = 0.84$, 18 df, $P < 0.001$) are consistent with demographic data that indicate grizzly bear population increases throughout the GYE (Eberhardt 1995).

Stochastic Time-series Models

Time series of population estimates can be used to characterize a stochastic process that then may be projected into the future, permitting the estimation of persistence times, risk of extinction, and other long-term population parameters. Dennis et al. (1991) summarized a number of statistical methods derived from a stochastic model of exponential population growth that have been used for PVA. A more realistic model structure that includes density dependence and autocorrelation is reviewed by Foley (1994). Both works used 1959-87 GYE COY index data to demonstrate their methods.

Dennis et al. (1991) used annual estimates of the 1959-73 female bear population made by Craighead et al. (1974) and the 3-year moving sum of the number of adult females with COY for 1975-1987 (Eberhardt et al. 1986). We are uncertain of the origin of the 1974 count.

An MLE of population growth can be calculated from the ratio of beginning, n_0 , and ending, n_q , population sizes:

$$\hat{\mu} = [\ln(n_q/n_0)]/t_q \quad (4)$$

where t_q is the number of counts in the series. The vari-

chastic population trajectories are paralleled for each component of the population (e.g., each age class), we expected the same characteristics for the female with COY segment of the population as for the population as a whole (Tuljapurkar and Orzack 1980).

Next we must define an extinction threshold, n_e , which is largely arbitrary. The probability of extinction depends upon the threshold that one sets for n_e , and to illustrate the magnitude of effect for grizzly bears we have plotted this relationship (Fig. 9). The value of n_e will be the number of adult females accompanied by COY at the time which we presume extinction to occur. Following Shaffer (1983) we set $n_e = 1$ for one threshold, and 10 for another (Dennis et al. 1991). The distance between the current population size and the arbitrary n_e value (in natural logarithms) we will term

$$x_d = x_0 - x_e = \ln(n_0/n_e) \quad (6)$$

where x_0 is the natural log of n_0 and x_e is the natural log of n_e . These parameters provide sufficient information to estimate the probability of extinction, π , based upon the population trajectory over the interval t_0 to t_q :

$$\pi(x_d, \hat{\mu}, \hat{\sigma}^2) = \begin{cases} 1, & \hat{\mu} \leq 0; \\ \exp(-2\hat{\mu}x_d/\hat{\sigma}^2), & \hat{\mu} > 0 \end{cases} \quad (7)$$

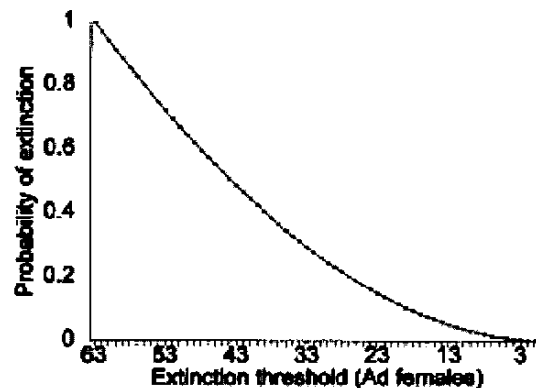


Figure 9. Probability of reaching an extinction threshold for the Yellowstone grizzly bear population as a function of the number of adult females selected for the extinction threshold. The decision for extinction threshold size is largely arbitrary.

The mean time to reach the extinction threshold population size is

also calculate the most likely (modal) extinction time:

$$t^* = t^*(x_d, \hat{\mu}, \hat{\sigma}^2) = x_d / |\hat{\mu}| [(1 + 9/4\nu^2)^{0.5} - 3/2\nu] \quad (9)$$

where $\nu = x_d / |\hat{\mu}| \hat{\sigma}^2$.

Using estimates of the number of adult females with COY for 1959 through 1987, Dennis et al. (1991) estimated these measures of growth trajectory and extinction parameters to conclude that the GYE grizzly bear population is "doomed to extinction, though not in our lifetimes." We updated this analysis with data to 1994 using the same models, and found the long-term outlook progressively more optimistic (Table 2). Instead of a probability of extinction of 1, we calculated only 0.0004. If the population should decline to extinction, it will do so quickly, but according to our calculations it has a very low probability of doing so.

We attempted to reconstruct the exact estimates for the period calculated by Dennis et al. (1991), but were unsuccessful although we obtained values quite close to

Table 2. Estimated growth and extinction parameters based upon the estimated number of adult females in the Greater Yellowstone Ecosystem.

	1959-1987 COY data	1959-1994 COY data
μ^a	-0.0075	0.0106
$\sigma^{2(b)}$	0.0089	0.0112
\bar{r}^c	-0.003	0.016
λ^d	0.0097	1.0109
\bar{a}^e	0.993	1.0106
q^f	27	34
t_q^g	27	33

	Extinction Parameters			
	$n_e = 1$	$n_e = 10$	$n_e = 1$	$n_e = 10$
x_d^b	3.85	1.55	4.14	1.84
π^i	1	1	0.0004	0.032
θ^j	514	207	392	174
t^{*k}	333	79	269	80

^a estimated population growth rate, eq. 5

^b Variance in growth rate, eq. 6

^c Mean per capita growth rate, $\ln[N(t+1)/N(t)]$

^d Finite population growth factor

Autocorrelation in growth rates, r , has the potential to cause populations to run for a series of bad years, greatly increasing the risk of extinction. This has been accommodated by adjusting v_r in the previous 2 equations

$$v_r = v_r(1 + \rho)/(1 - \rho). \quad (13)$$

Plotting the autocorrelation function (Fig. 12), we find that the first lag gives a strong negative autocorrelation, which has a stabilizing effect on a population, essentially preventing it from taking a run toward extinction. This is probably due in part to density dependence, so there is probably some redundancy in the effect of ρ and r_d .

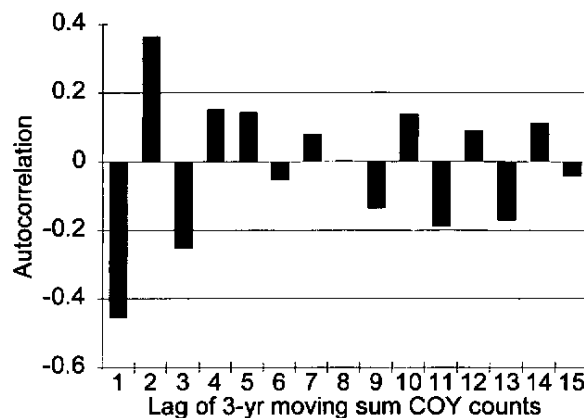


Figure 12. Autocorrelation function for the per capita growth rate based on the estimated number of adult females (3-yr moving sum of the COY Index), 1959-1994. The significant negative autocorrelation in the first lag implies density dependence. The first lag autocorrelation is used to adjust random process trajectories as developed by Foley (1994).

These parameters, based on the density-dependent model, were computed for the GYE grizzly bear data by Foley (1994) to compare with the exponential growth model of Dennis et al. (1991) (Table 3). In the updated estimates we employed an independent estimate of carrying capacity based upon the survival analysis described below, and a plausible $r_d = 0.1$ based upon the review by Miller (1990b). As carrying capacity increases, the probability of extinction declines exponentially (Foley 1994). To ensure a conservative estimate of extinction risk, we used a low value for carrying capacity; recent estimates of population size (Eberhardt and Knight 1996) suggest population sizes 50-75% higher than the K we used. Also, there is probably an interaction between the per capita growth rate, r , and the carrying capacity, K . For example, by managing to reduce bear mortalities and targeting mortality sinks since 1983 (Gunther 1994) the bear population has been able to expand into areas where

Table 3. Extinction parameters for the GYE grizzly bears based upon density-dependent diffusion models (Foley 1994). Foley's values were for adult female bears only. We divided by 0.27 to estimate the total grizzly bear population (Eberhardt and Knight 1996). Notation follows Foley (1994) where the triple subscripted variables are for use of r , r_d , or k in the models (e.g. a 0 for r means that no autocorrelation term was considered in estimating the expected time to extinction, T_e , or the probability of persistence to 100 years, P_{100}).

Estimates	Foley's values 1959-1987	Updated 1959-1994
T_e^a	28	33
k^b	4.06	5.44
r_{do}^c	0.0031	0.011
r_{dl}^d	0.0179	0.1 ^e
ρ^f	-0.46	-0.455
v_r^g	0.011	0.011
v_{re}^h	0.004	0.004
$T_e(0,0,k)$	1,488 yr	2,690 yr
$T_e(0,\rho,k)$	3,995 yr	7,398 yr
$T_e(r_{do},0,k)$		12,446 yr
$T_e(r_{dl},0,k)$	9×10^6 yr	91,370 yr
$T_e(r_{dl},\rho,k)$	1.4×10^{16} yr	6.78×10^5 yr
$P_{100}(0,0,k)$		0.964
$P_{100}(0,\rho,k)$		0.987
$P_{100}(r_{do},0,k)$		0.992
$P_{100}(r_{dl},0,k)$		0.999
$P_{100}(r_{dl},\rho,k)$		1.00

^a Time periods

^b $\ln(\text{carrying capacity}) = \ln K$

^c Drift coefficient, assuming r is small

^d Expected value of the per capita growth rate

^e Potential growth rate for a grizzly bear population (see Miller 1990b).

^f Autocorrelation in growth rates

^g Variance in per capita growth rate

^h Effective environmental variance taking ρ into account

death rates were previously too high to sustain a population. To illustrate this we plot density-dependent birth and death rates as a function of population size (Fig. 13). A decrease in death rate, say due to management, has the consequence of increasing the equilibrium population size where b equals d . Thus, we can see how increasing r might also increase K . Such interactions are not included in the present analysis.

Under all assumptions, the GYE grizzly bear population appears reasonably secure with expected times to extinction >2,690 years. But expected time to extinction is a poor measure of the distribution of extinction times

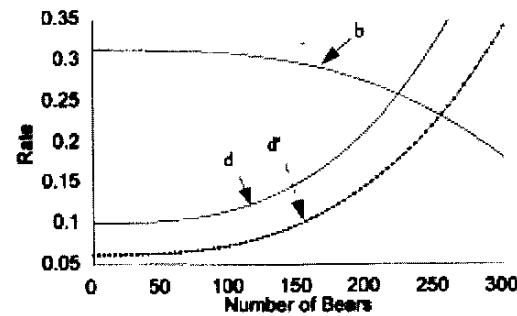


Figure 13. Density-dependent rates of birth (b) and death (d) illustrating how increased bear survival attributable to IGBC management initiated in 1983 can increase carrying capacity, K , i.e., the population size at which $b = d$ (adapted from Murray 1979).

because it is highly skewed (Ludwig 1996). We think it better to estimate the probability of persistence to some time in the future—the time horizon is typically 100 years (Shaffer 1978, Akçakaya 1994). If one assumes a Poisson extinction process, which seems reasonable given that the population process is Poisson with $v_r = r_{do}$, persistence probability to 100 years can be estimated by

$$P_{100} = \exp(-100/T_e). \quad (14)$$

In the most conservative case, allowing the population to fluctuate randomly (i.e., pursue a random walk), we find that the probability of persistence well exceeds 95%. Precise estimates of extinction or persistence risk are not possible (Ludwig 1999), but given the assumptions of the Foley (1994) model we consistently calculate values suggesting an optimistic future for the population.

We believe that the analytical approaches reviewed by Foley (1994) are the most appropriate of those available for study of the grizzly bear data. Foley (1994) conducted simulations comparing the analytical results to those from a logistic growth model, finding reassuring concordance. We can compare the predictions of MVP from this approach to that calculated by Shaffer (1983) given the following rationale. To ensure a 95% probability of surviving 100 years, we must have

$$T_e = 100\text{yr}/(-\ln 0.95) = 1,950 \text{ yr}. \quad (15)$$

In the simplest case with $r_d = 0$, $T_e = k^2/v_r$. We can solve

of persistence for 100 years equals only 16 bears (but as we noted above, this may incorporate density dependence twice and thus is too small). Ignoring the effect of the negative autocorrelation (as did Shaffer), we find a value of 103 bears. Shaffer (1978, 1983) incorporated density dependence into his simulations, and his estimates were between our 2 values.

On a final note, we found the customary time horizon of 100 years too brief. For a long-lived species such as the grizzly bear, 100 years is only 3 to 4 times their maximum life span. Even though these models do not possess age structure, this effect is reflected only by the low potential growth rates and dampened variance in growth rates for the species. We believe that a longer target time for persistence (e.g., 200–500 yrs) should be used.

Recomputing the probability of persistence calculations (Table 3) for longer time horizons, we find $P_{200}(r_{do}, 0, k) = 0.984$, $P_{300}(r_{do}, 0, k) = 0.976$, $P_{400}(r_{do}, 0, k) = 0.968$, and $P_{500}(r_{do}, 0, k) = 0.961$. Thus our calculations indicate that the probability of persistence for the GYE grizzly bear population exceeds 95% even for a 500-year time horizon.

Discussion

Information derived from counts of females with COY can be improved by using methods that accommodate annual variation in the intensity of survey effort and sightability. Calculations presented above and this discussion were based upon analyses of biased counts, which should be revisited after appropriate adjustments are made. Using the unadjusted counts is conservative because adjusted counts indicate a greater increase in recent years (Fig. 7).

The prognosis by Dennis et al. that the Yellowstone grizzly bears are doomed to extinction appears largely based upon their estimate of the probability of extinction, $p = 1$. We believe that the threshold behavior of this parameter is unreasonable, i.e., if the time series shows any decline, $p = 1$. Adding 7 years of data to the time series decreased the probability of extinction from 1 to 0.0004, a dramatic improvement. Our new estimates of the expected and modal times to extinction are actually shorter than in Dennis et al.'s (1991) analysis, but these are contingent upon the population taking a first passage to extinction, which is extremely unlikely. The reason for the rapid declines is that we maintained all annual transitions in the analysis, whereas the previ-

effect on the low mortality case, but decreased MVP to 100 for Case 2. Estimates of population growth rate for average vital rates indicated that the population was increasing by 1.4% to 3.7% per year. Consistent with Shaffer's observations, MVP estimates were more sensitive to survival than to reproduction (see also Caswell 1978). To be conservative, Suchy et al. (1985) recommended that a population size ≥ 125 be maintained to ensure a high probability of a viable bear population in the GYE for at least 100 years.

The original PVA conducted by Shaffer (1983) was reasonable, given the available data. With additional data we see stronger evidence for density dependence in survival than in reproduction (see below). But including density-dependent survival would have minor effects on the performance of the model (depending on the degree of density dependence). Shaffer's (1983) footnote regarding unrealistic sojourns above carrying capacity for some population trajectory suggests that the strength of density dependence he used was insufficient to stabilize the population. This does not bear on the appropriateness of the structure of his model, however.

Stable-age Distribution Methods.—The IGBST used demographic estimates from their long-term radiotelemetry study to calculate the growth rate for the GYE grizzly bear population (Eberhardt et al. 1994). This calculation is an improvement over a similar exercise a decade earlier (Knight and Eberhardt 1985) because it is based upon a larger sample size, uses only females in the estimates for survival of subadults, and employs bootstrapping methods to estimate the variance in the estimate of growth rate.

Combining estimates of survival and reproduction by iterating the familiar Lotka-Euler model,

$$1 = \sum \lambda^{-x} l_x m_x \quad (18)$$

Eberhardt et al. (1994) estimated a growth rate, $\lambda = 1.046$. Bootstrapped estimates of λ (see Meyer et al. 1986) provided a 95% confidence interval from 1.00 to 1.09, indicating that the population was almost certainly increasing or at least not decreasing. This interpretation was bolstered by trend counts using the COY index (see above). Sensitivities of growth rate to demographic components (i.e., $\partial\lambda/\partial x$) were presented (Table 6) that illustrated the well-known result that for a long-lived species like the grizzly bear, the sensitivity of growth rate is highest for adult survival (see Emlen and Pikitch 1989, Lebreton and Clobert 1991, Meyer and Boyce 1994). Eberhardt et al. (1994) also presented a decomposition of the variance in growth rate into the effect attributable to respective vital rates indicating that survival to age 5 contributed

Table 6. Sensitivity of growth rate, λ , to vital rates and the proportion of the variance in λ attributable to these vital rates as estimated by Eberhardt et al. (1994) and Eberhardt (1995).

	Sensitivity ($\partial\lambda/\partial x$)	Eberhardt et al. (1994) Proportion of variance	Eberhardt (1995) Proportion of variance
Adult survival	0.567	0.443	0.19
Survival to age 5	0.2	0.46	0.77
Reproduction	0.32	0.097	0.04
Σ		1.000	1.00

at least as much to variation from year-to-year as did variation in adult survival. This is important because although adult survival is a highly sensitive parameter, it does not vary much. So an understanding of prereproductive survival is much more important to understanding factors causing the population to fluctuate than is implied by sensitivities.

Eberhardt et al. (1994) estimated survival, s , based upon known deaths of bears that were at one time radiocollared, i.e., $s = 1 - \text{deaths}/(\text{bear-years})$. They recognized later that this produced a biased estimate because (1) the estimate of bear-years did not include only the days that the radiotransmitter was functioning, and (2) all radiocollared bears were included in the analysis, including "management bears" (i.e., those collared because they were involved in conflicts or potential conflicts with humans) which have much higher mortality than "research bears." Eberhardt (1995) redid these calculations, included in the 1994 annual report of the IGBST, using exposure time instead of bear years and estimating survival for "research bears."

The new population growth rate estimate was slightly higher ($\lambda = 1.053$), but because fewer animals were used in the calculations, the sampling variance was higher and consequently the 95% confidence intervals overlapped 1 (Eberhardt 1995). The results and interpretation are the same, however, and the calculated role of prereproductive survival in determining variation in λ becomes much greater (Table 6).

Servheen et al. (1994) performed a similar Lotka-Euler analysis of demographic parameter estimates for bears in 2 areas in the NCDE and the Selkirks. Sample sizes for each of these areas were smaller than for the GYE, therefore sampling errors were large and bootstrapped confidence intervals were sometimes substantial (Table 7). Two estimates from the North Fork of the Flathead River indicated the population was increasing, i.e., $\lambda >$

Table 7. Estimates of population growth, λ , for demographic data based on radiotracking studies. Estimates of λ were obtained by iterating the Lotka-Euler stable-age-distribution equation, and confidence intervals were computed using bootstrap procedures. Statistics for GYE from Eberhardt (1995) and Servheen et al. (1994) for all others.

Area	Years	λ	95% CI
NCDE: Area 1 ^{a,c}	1978-1994	1.08	1.01 - 1.12
NCDE: Area 1 ^{a,d}	1978-1994	1.06	0.98 - 1.11
NCDE: Area 2 ^b	1987-1994	0.96	0.8 - 1.05
Selkirk Mountains, MT	1983-1994	0.99	0.79 - 1.1
GYE	1983-1994	1.053	0.97 - 1.12
Cabinet-Yaak Mountains	--	Insufficient data	
Washington Cascades	--	Insufficient data	

^a North Fork Flathead River

^b South Fork Flathead River

^c excluding 1993-94 USA bears

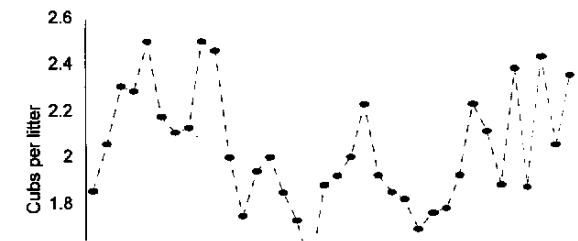
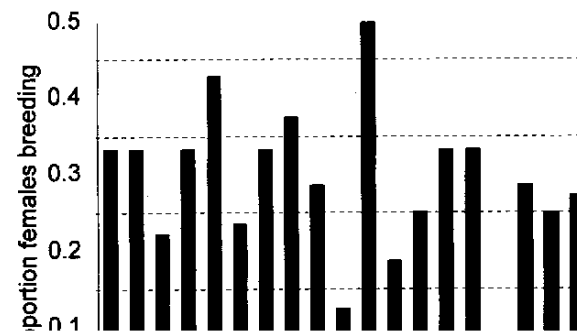
^d including 1993-94 USA bears

1, whereas data from the South Fork study area (cf. Mace et al. 1994, Mace and Waller 1998) produced $\lambda = 0.96$. The Selkirk Mountain grizzly bear data suggested a 1% rate of decline. However, the confidence intervals surrounding both the South Fork estimate and the Selkirk estimate were large so that one cannot reject the null hypothesis of no trend in population size.

Projection Matrix Methods.—Ample evidence exists that grizzly bear populations do not exist in a stable age distribution, including population fluctuations such as the decline that occurred after closure of refuse dumps in Yellowstone around 1970-1971 (Eberhardt et al. 1985) and reproduction fluctuates from year-to-year (see Figs. 14 and 15). In fact, vital rates are random variables and this temporal variance can have important ramifications for population growth (Boyce 1977). Stochastic demography can involve complex mathematics and therefore much of the theory has been overlooked by conservation biologists, but the consequences can be very substantial

(Tuljapurkar 1990).

The usual approach to studying these processes is to rewrite the Lotka-Euler equation (eq. 18) in matrix form facilitating explicit incorporation of random vital rates. Some important properties of projection matrices include the following: (1) In stochastic environments, population size assumes a skewed distribution in which very large populations occur only rarely (Lewontin and Cohen 1969). As a consequence of this skewness, mean population size tends to overestimate most populations. (2) Stochastic growth rates are lower than deterministic growth rates of projection matrices composed of average vital rates (Boyce 1977, Tuljapurkar and Orzack 1980). Ignoring temporal variation in estimates of demographic parameters may lead to serious overestimates of the actual growth rate. (3) Increased variation in vital rates produces lower growth rates (Tuljapurkar 1990). (4) Variation in vital rates with high sensitivity has greater impact on stochastic growth rate, i.e., deterministic sen-



cally falls differently on various vital rates, altering the age structure and potentially complicating population dynamics (Lande and Orzack 1988). Although we agree with Mills et al.'s (1996) caveat that one ought to understand density dependence because it can have marked consequences on extinction dynamics, we disagree with their implication that the consequences of density dependence are unpredictable. In general, density dependence reduces extinction probability because it dampens the effects of stochastic perturbations (Ferson et al. 1989). But for difference equations, this can be confounded through interactions with deterministic instability such that populations might actually have higher risk of extinction under density dependence (Ginzburg et al. 1990). Erratic behavior from simulation models emerges because of the attempt to emulate the INMAT ceiling for population size by adjusting density-dependent functions. Such abrupt density-dependent functions can destabilize the underlying difference equations, yielding bifurcations ultimately leading to chaotic behavior.

We believe that such complex dynamics do not apply to grizzly bear populations, and we doubt that we could justify such an abrupt density-dependent function in bear populations, even though there is evidence for density dependence (Shaffer 1983, Stringham 1985, McCullough 1986). INMAT's approach of setting $N_t = K$ in the next time step whenever $N_t > K$ will not yield such rich dynamical behavior. We believe that attempting to emulate the ceiling accounts for the inconsistent results among simulation packages reported by Mills et al. (1996).

A clear message emerged from the Mills et al. (1996) review that selection of a software package for performing PVA should be based on its ability to model population processes as they occur in the population of interest. Performing simulations with input data for which no empirical estimates exist is dangerous and is almost guaranteed to yield spurious results. Because data are often limited to a small fraction of the inputs possible in canned programs, simple analytical models (e.g., Tuljapurkar and Semura 1979, Foley 1994) may actually provide more defensible approaches to PVA.

Discussion and Further Analysis

Structured population models combine vital rates to determine population growth. These vital rates vary due to demographic stochasticity and as a function of environmental variables. Ultimately one may envisage all ecological influences on an organism by the way in which they influence vital rates. This offers great flexibility and permits the development of population models that incorporate considerable complexity. The cost is that many more parameters need to be estimated and the abil-

ity to find general analytical results is diminished because the models become mathematically intractable. Consequently, simulation methods are commonly used or simplifications are made (such as the assumption of a stable age distribution).

The density-dependent simulation methods reviewed in this section appear useful, especially when the structure of the variance is studied. Shaffer (1983) pooled sampling variance along with temporal variance because sample sizes were too small to do otherwise. Decomposing variance remains a problem in such detailed simulation models, and the more detailed the model the less likely one will be able to characterize the variance structure. Methods for partitioning variance are reviewed by Burnham et al. (1987) and these should be applied when sample sizes allow. Shaffer's approach of keeping the sampling variance in the simulations means that the simulations will reflect all sources of uncertainty, including the reliability of data. But confounding the sources of variance guarantees overly pessimistic estimates of the probability of extinction.

Stable-age-distribution calculations offer much less insight for PVA, even if corrected for bias associated with the stable-age-distribution assumption. Estimates of growth rate are of limited value for long-term computations because under the assumption of a stable-age distribution one cannot sort out factors influencing population fluctuations, including density dependence. Sensitivity analysis might be argued to help identify where the action is in the life table, but this is unlikely to have any bearing on whether management can manipulate the respective demographic components.

More useful, we believe, would be an analysis of the ecological factors shaping variation in the vital rates. Because this has not been done systematically, in the next section we will present the results of a survival analysis designed for the purpose. Then we will pursue some additional simulations employing several of the new software packages designed for performing PVA. Spatial structure can be accommodated in these computer programs so that we can evaluate the consequences of dispersal and fragmentation.

Survival Analysis

Reviewing the survival values used in the structured population models discussed in the previous section revealed considerable range in estimates and diversity in methods used to obtain the estimates. None of these analyses tie survival estimates to environmental variables, yet much of our understanding of the ecology of grizzly bears points to the importance of such relationships. For example, density dependence probably operates through

effects on survival (Stringham 1985, Miller 1990a), but the Shaffer model (Shaffer 1978, 1983; Shaffer and Samson 1985) only invokes density dependence in reproductive rates. High sensitivity of population growth rate to adult female survival has helped to shape management policies for grizzly bears (Knight et al. 1988), yet ecological factors influencing survival remain largely unstudied.

The extensive long-term radiotelemetry studies of the IGBST afford an opportunity to better understand factors influencing survival of grizzly bears. Statistical methods for survival analysis developed mostly by human demographers (Gross and Clark 1975), recently have begun to appear in the wildlife literature (Pollock et al. 1989). Radiotelemetry data present particular challenges for statistical analysis because animals are collared at various times and different ages, animals may die or lose their collars, or the radio may fail (White and Garrott 1990). Based upon total documented deaths in the GYE, it is apparent that mortality varies with season (e.g., grizzly bears are most likely to die during July through October (Fig. 16)), and from year-to-year (Fig. 17 and 18). Indeed, Eberhardt et al. (1994) acknowledged that their survival estimates may be biased due to loss of radiocollars or battery failure.

The proportional hazards analysis, or Cox regression, is a statistical method for detecting the relationship between mortality and covariates. The underlying structure for survival is assumed to follow an exponential function where the hazard, $h(t;x)$, (proportion of bears dying at time t as a function of a vector of covariates, x) is of the general form

$$h(t; x) = h_0(t)e^{\beta'x} \quad (24)$$

where β is a vector of regression coefficients for the corresponding x value, and h_0 is a baseline survival function. One can view this model as an exponential variation on multiple regression where β_i is a regression coefficient for the i th covariate, x_i , and β_0 is subsumed into h_0 . Cox (1972) proposed a partial-likelihood method for estimating the β 's that are usually evaluated using a likelihood ratio test. The method easily accommodates right-censored data, e.g., radio failure or cast collar where the fates of the bears are unknown. For discrete covariates, such as (0,1) variables, Cox regression provides the same estimates of survival as the Kaplan-Meier

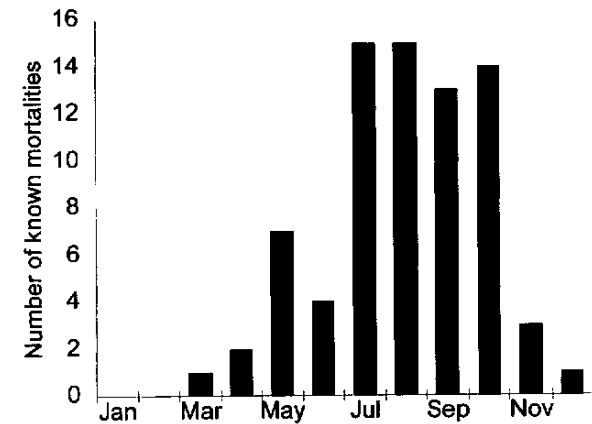


Figure 16. Temporal distribution of bear mortalities throughout the year. Bears are most likely to die July-October.

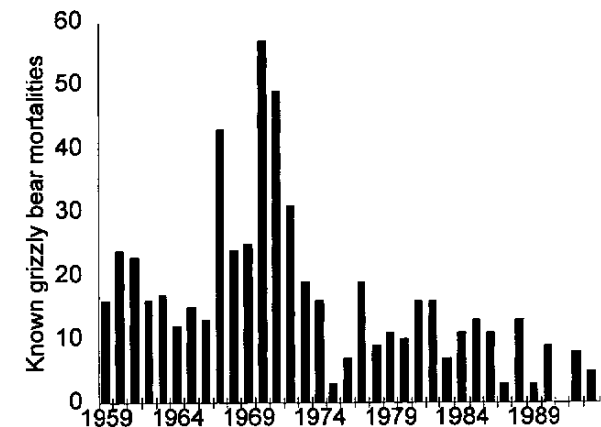
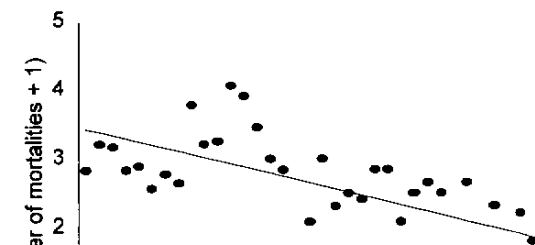


Figure 17. Year-to-year variation in total known bear mortalities in the GYE, 1959-1994.



to conflicts with humans are predisposed to conflicts resulting in their death.

We were surprised that the hazard increased over the 1975-1994 time period (Table 10) because total known mortalities appeared to have decreased (Fig. 18), and because in 1983 state and federal management agencies began an effort to reduce bear mortalities (Servheen 1993). However, increasing mortality rates are consistent with density-dependent mortality as documented in other bear populations (Miller 1990a,b). Evidence clearly indicates that density is increasing in the GYE as previously discussed (see Fig. 1, 2, 7 and 8). To confirm the relation with density dependence, we entered the COY index into another Andersen-Gill model along with sex, age, $(age)^2$ (i.e., quadratic as in Fig. 20) data. The estimated minimum number of adult females contributed significantly to the model ($P = 0.045$; Table 11) which supported the role of density dependence and provides the underpinnings for an age-structured population model for grizzly bears (Fig. 22).

Again we confront the problem of sorting out patterns involving temporal trends (see COY index above). Because the estimated number of adult females and year were correlated ($r = 0.52$, 32 df), suggesting a trend, we

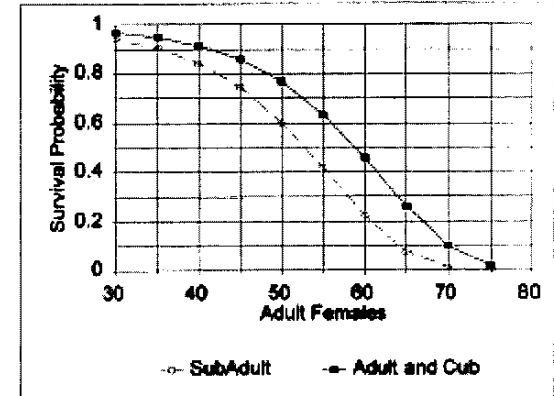


Figure 22. Density-dependent survival estimated by the Andersen-Gill method. Adult females are estimated by the 3-yr moving sum of the number of unduplicated females with cubs of the year (Knight et al. 1995).

Table 10. Andersen-Gill hazard model showing temporal trends in the hazard function after accounting for sex and age. This indicates that mortality has increased over the period 1975 to 1994. See footnote for Table 9 for variable definitions.

	Coef.	exp(coef.)	SE(coef.)	z	P
SEX	0.20295	1.225	0.27272	0.744	0.4568
AGE	-0.14455	0.865	0.07238	-1.997	0.0458
(AGE) ²	0.00808	1.008	0.00314	2.573	0.0101
YEAR	0.51349	1.671	0.21123	2.431	0.0151
	exp. (coef.)	exp(-coef.)	lower .95	upper .95	
SEX	1.225	0.816	0.718	2.091	
AGE	0.865	1.156	0.751	0.997	
(AGE) ²	1.008	0.992	1.002	1.014	
YEAR	1.671	0.598	1.105	2.528	

Likelihood ratio test = 15.8 on 4 df, $P = 0.0033$

Efficient score test = 17.1 on 4 df, $P = 0.0018$

Table 11. Andersen-Gill proportional hazards model showing relation between the hazard function and the minimum number of females based upon the unadjusted COY index (that increases over time). Variable definitions are listed as a footnote to Table 9.

	Coef.	exp(coef.)	SE(coef.)	z	P
3-YR FEM W/COY	0.10842	1.115	0.05417	2.002	0.04533
SEX	0.17346	1.189	0.2721	0.637	0.5238
AGE	-0.14597	0.864	0.07186	-2.031	0.04222
(AGE) ²	0.00859	1.009	0.00312	2.751	0.00593
	exp. (coef.)	exp(-coef.)	lower .95	upper .95	

could not rule out the possibility that natural mortalities were increasing, and independently, bear counts are increasing as well. Due to this confounded relation between the estimated number of adult females and year, neither variable has a significant effect on the hazard function in a model containing both (Table 12). Bears captured in YNP in recent years are significantly smaller in body size, again reflecting evidence for density dependence; body size prior to 1972 was likely artificially inflated due to availability of significant amounts of garbage, which ceased by 1975 (R. R. Knight unpublished). Experimental verification of density-dependent mortality is virtually impossible for grizzly bears, but basic principles of population biology suggest that density dependence must be present (Stringham 1985, Sinclair 1989, McCullough 1990, Taylor 1994). In our judgment this is the best interpretation of these results.

USING RAMAS/GIS FOR THE GYE

RAMAS/GIS is a software package (Applied Biomathematics, 100 N. Country Rd., Setauket, NY 11733) that simulates structured populations with metapopulation (Gilpin and Hanski 1991) structure on actual maps of landscapes (Akçakaya 1994). As such, it integrates spatial and demographic approaches for performing PVA. The package is menu driven and has a long list of output displays to summarize results of simulations. A host of options exist for incorporating ecological influences, offering great flexibility for applications (Boyce 1996).

Using RAMAS/GIS, we simulated the GYE population of grizzly bears, and then built a model that included all 6 metapopulations, i.e., GYE, NCDE, Cabinet/Yaak, Selkirk, North Cascades, and the proposed reintroduction area in the Bitterroot Mountains of east central Idaho (Servheen 1993). Throughout our simulations we tried to ensure that the model was reasonably parameterized, and that we could estimate error associated with variables included in the model. Once reasonable parameters were chosen, we used "What if?" exercises to explore the dynamics of populations under hypothetical scenarios.

We chose the stage-structured population matrix as described above (eq. 18) with 3 stage classes: COY, subadults, and adults. Although complete life tables have been calculated for grizzly bears (e.g., Craighead et al. 1974; Servheen 1993; Servheen et al. 1994), in practice estimates for individual ages are often based upon small sample sizes thereby burdening these estimates with large sampling variances. By pooling ages together into these 3 stages we were able to greatly reduce the standard errors associated with estimates of survival (Table 8) and fecundity.

Estimates of baseline values and standard errors for each of the survival rates were obtained using maximum likelihood estimation (Cox and Oakes 1984) of deaths of radiocollared bears for age and sex class *i*:

$$S_i = [1 - (\text{number of deaths}/R)] \quad (25)$$

where *R* is exposure time in days (Table 8). These estimates were taken to the 365.25th power to obtain annual

Table 12. Andersen-Gill proportional hazards model attempting to include both the COY index and year in the model. Contribution to the model for the COY index and year is no longer significant, apparently due to the confounded trend in these 2 correlated variables. Variable definitions are listed as a footnote to Table 9

	Coef.	exp (coef.)	SE (coef.)	z	P
3yr FEM W/COY	0.06692	1.069	0.06120	1.094	0.2742
SEX	0.18872	1.208	0.27390	0.689	0.4908
AGE	-0.14662	0.864	0.07235	-2.027	0.0427
(AGE) ²	0.00828	1.008	0.00314	2.64	0.0083
YEAR	0.41701	1.517	0.22324	1.868	0.0618
	<u>exp(coef)</u>	<u>exp(-coef.)</u>	<u>lower .95</u>	<u>upper .95</u>	
3yr FEM W/COY	1.069	0.935	0.948	1.205	
SEX	1.208	0.828	0.706	2.066	
AGE	0.864	1.158	0.740	0.005	

associated with vital rates by the same proportion as the fraction of the variance in survival attributable to density dependence (Boyce 1996). Instead, we left all variances in the model, inflating the true variance. This conservative approach will overestimate extinction risk and decrease population growth rates (Boyce 1977, Boyce and Daley 1980).

For 100 replications of 100-year trajectories each (summarized in Figs. 24-26), first note that the population size declines to approximately 67% of K . This is due in part to the high variance in K and the underlying concavity of growth rate as a function of N (Boyce and Daley 1980). Reducing the variance in K by increasing sample size or partitioning out the sampling variance from the among-years variance (see Burnham et al. 1987: ch. 4) will result in larger projected population sizes, closer to K . The programmed decline in K also contributed to population decline.

Of the options available in RAMAS/GIS, Fig. 25 probably most completely captures the population risks emerging from the simulations. Here the probability of population declines of various magnitudes or greater during the 100-year interval is plotted. Note that it is virtually guaranteed that N will decrease by 50% and there is a 5-10% probability that the population will decline to extinction.

The probability of reaching various magnitudes of decline at the end of a 100-year run indicates the odds are about 90% that the population will remain constant or decline, and there exists a 40% chance that we will see at least a 50% decline in population size at the end of 100 years (Fig. 26). The pattern of decline is at least in part attributable to the assumed -0.5% per annum change

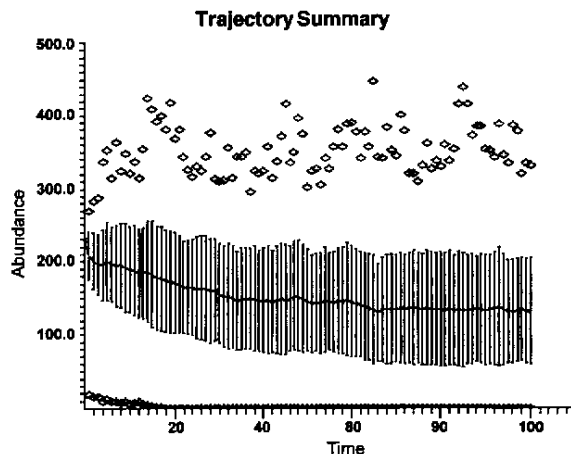


Figure 24. Population trajectory with \pm SE bars for a RAMAS/GIS simulation of the GYE grizzly bear population. High variance in K ($SE = 70$) results in a declining population. Open jagged dots are extreme values during the course of 100 replications of a 100-yr trajectory.

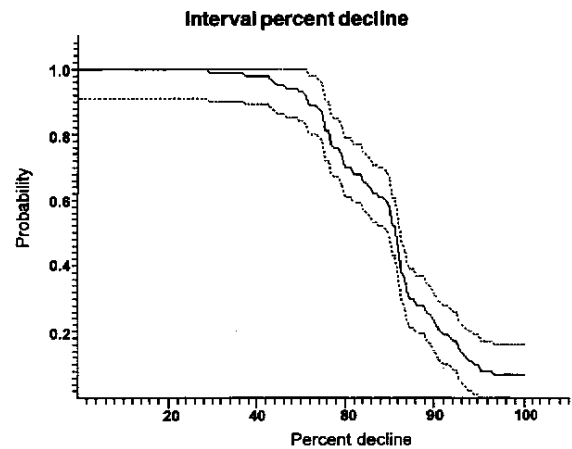


Figure 25. Cumulative probability of occurrence for declines of various magnitudes anytime during the course of 100 trials of 100-yr projections. During each of the repeated 100 yr trajectories, population declines of about 40% were observed. Very few population trajectories declined to extinction (i.e., 100% decline). Simulations were based on data from the GYE grizzly bear population.

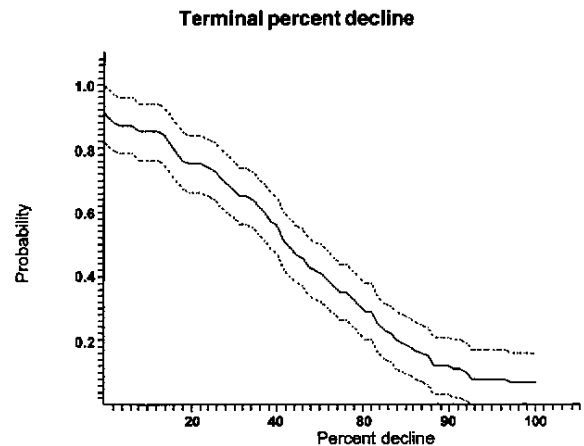


Figure 26. Probability of observing declines of 1 - 100% at the end of a 100-yr trajectory for the GYE grizzly bear population using RAMAS/GIS simulations.

in K . But there remains a low chance that declines could approach 100%.

Using RAMAS/GIS for the Metapopulation of U.S. Grizzly Bears

We built a spatially structured simulation for all 6 sub-populations of bears. This analysis used carrying capacities presented as recovery levels in the Recovery Plan (Servheen 1993). For population characteristics such as survival and fecundity, age distribution, and density dependence, we followed the same patterns as for GYE data. Indeed, underlying demographic structure cannot be

changed for each subpopulation using RAMAS/GIS. GIS data were used only to delineate habitat areas for metapopulations and no attempt was made to include an interface with habitat suitability.

Results of the metapopulation simulations mirror those for the GYE with $N \approx 2/3(K)$ (Fig. 27). Again, this could be attributed to the high variance surrounding estimates of the density-dependent function that renders high σ_K . After 100 years we expect to find the majority of bears in the NCDE and the fewest in the North Cascades (Fig. 28). Low numbers of bears in the North Cascades and the Bitterroot Mountains in Idaho are due, in large part, to uncertainty associated with their hypothetical establishment because we allowed for an initial population size (release) of only 10 bears in each of these areas. So, in many of the runs these populations go extinct (Fig.

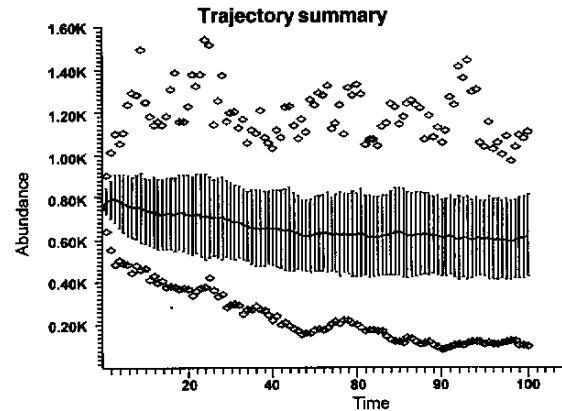
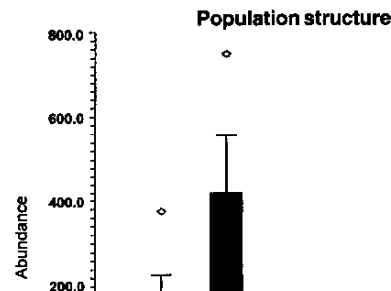


Figure 27. Trajectory of decline for the metapopulation of 6 subpopulations of grizzly bears in the conterminous United States. Mean population sizes are bracketed by S.E.s; extreme values are represented by open jagged dots. Note that none of the 100 runs of 100-yr trajectories went extinct. Dispersal among subpopulations was assumed to be rare.



29). There is a 20% chance of extinction in either the Selkirk or Cabinet/Yaak ecosystems (Fig. 30), ignoring the possibility of restoration efforts (Servheen et al. 1995).

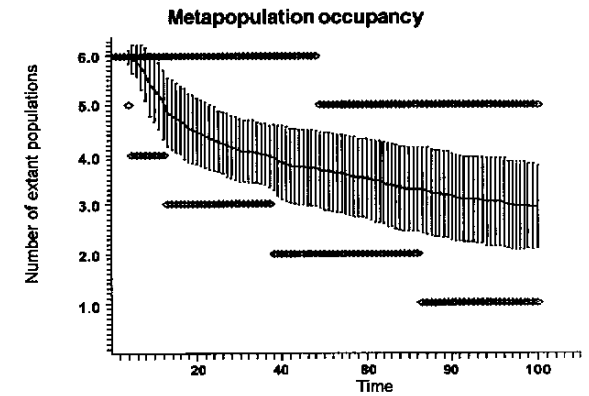


Figure 29. Occupancy of subpopulations in the simulations summarized by Figures 27 and 28. At the end of 100 yrs on average only 3 of the subpopulations are occupied.

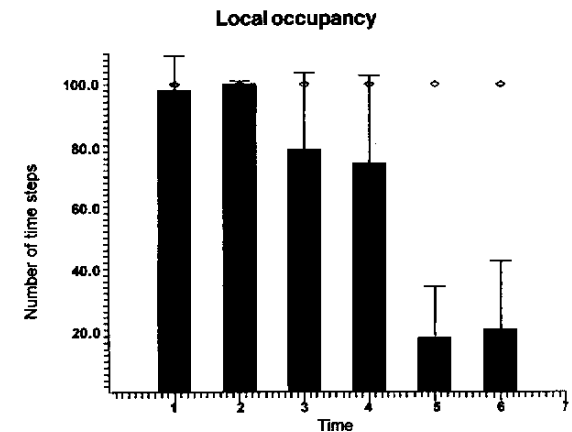


Figure 30. Time steps (yrs) that each of the 6 subpopulations listed under Figure 28 were occupied. The Cascades and Idaho populations were least likely to be occupied largely due to risks associated with population establishment. Average occupancy times of 75-80 yrs for the Cabinet-Yaak and Selkirk populations do not take into account the probable rescue of these subpopulations by dispersers from Canada or from transplant programs (Servheen et al. 1995).

The probability that declines $> 80\%$ would occur during the 100-year interval is virtually nonexistent (Fig. 31). But declines $> 50\%$ have a 40% probability. After a 100-year interval populations are unlikely to be $< 40\%$

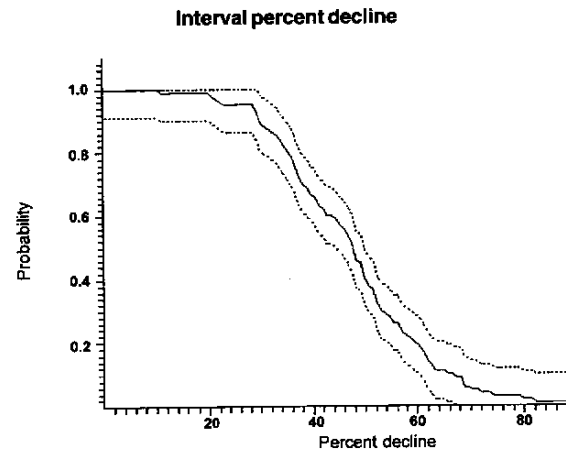


Figure 31. Probability of declines of 0-90% anytime during the 100-yr projections for the metapopulation. Declines greater than about 80% are exceedingly unlikely to occur.

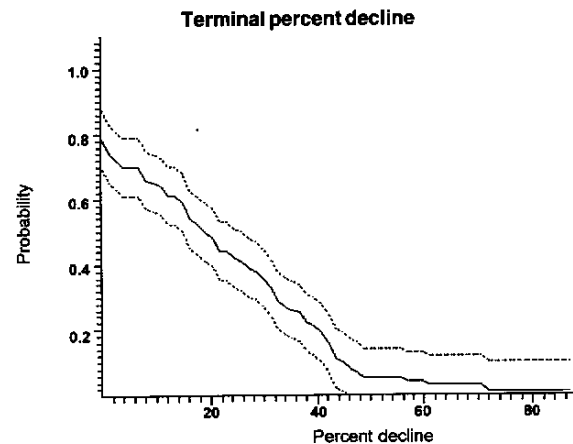


Figure 32. Probability that the population at the end of 100 yrs will have declined by 0-90% for the metapopulation of grizzly bears with limited dispersal capability.

duce extinction risks below current levels, yet, such management reactions are bound to happen (e.g., Servheen et al. 1995). Indeed, an active recovery effort is underway that is designed to be responsive to changes in numbers of bears by implementation of active management (Servheen 1993).

In our initial simulations we assumed virtually no dispersal among subpopulations. This assumption was based on the fact that only one of 500 radio-collared bears stud-

age zones linking subpopulations and to manage these lands in innovative ways that will not inhibit dispersal (Servheen and Sandstrom 1993). In view of this effort, we conducted simulations assuming modest dispersal capability with dispersal approximated by a decay function (see Fig. 33). Results were striking. Total population size increased to about 0.8K (Fig. 34) and, on average, about 5 subpopulations were occupied after 100 years (Fig. 35). Occupancy approached 100% for each subpopulation with the exception of the North Cascades and the Bitterroot Mountains in Idaho—these areas may not be occupied because of failure to establish (Fig. 36). Declines in population size are still likely, but there exists essentially no chance that the total population will decline > 70% during the next 100 yrs (Fig. 37 and 38). Models incorporating dispersal project that grizzlies will

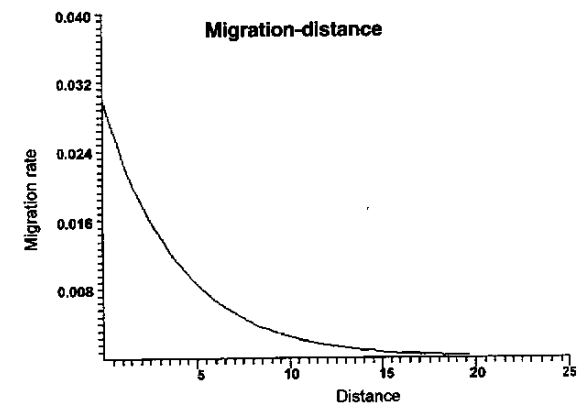
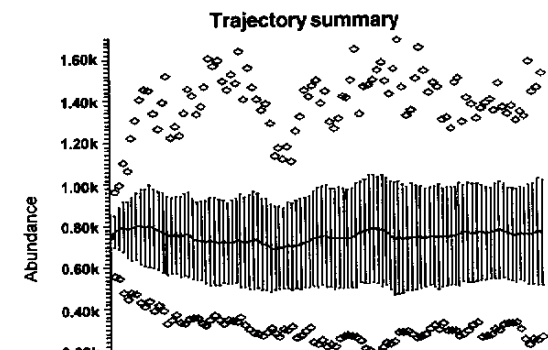


Figure 33. Decay function used to simulate the dispersal of bears among subpopulations. Rate of dispersal is plotted as a function of distance from source population in km.



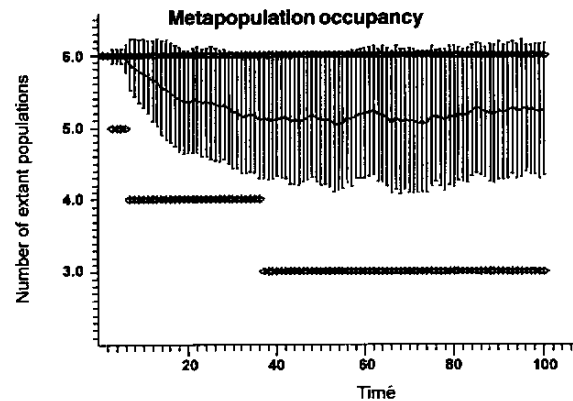


Figure 35. Occupancy of subpopulations with dispersal as illustrated at Figure 33. On average only 1 subpopulation will be extinct after 100 yrs, but as many as 3 may go extinct.

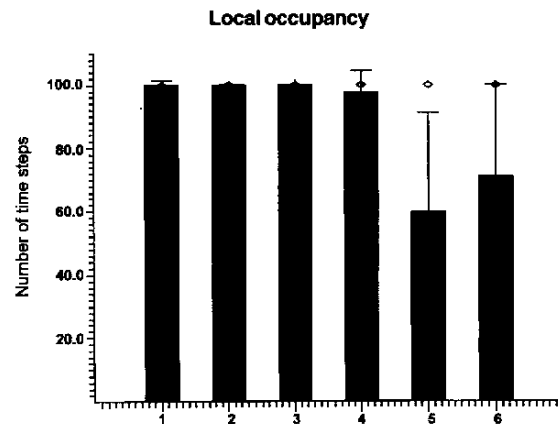


Figure 36. Occupancy of each of the 6 subpopulations as listed in the caption to Figure 28. On average the Cascades population is expected to persist only 60 yrs, but persistence is highly dependent on initial establishment. Persistence is slightly higher for the Idaho subpopulation, and again, the main mechanism resulting in short occupancy times is failure to establish initially. Currently no grizzly bears are known to occur in the Selway-Bitterroot wilderness of Idaho but a release plan is being developed (MacCracken et al. 1994).

be better distributed among subpopulations than under the low-dispersal assumption (Fig. 39).

Modeling the grizzly bear populations as metapopulations is somewhat misleading because only the GYE subpopulation is thought to be truly isolated from Canadian grizzly bears (Servheen 1993). There-

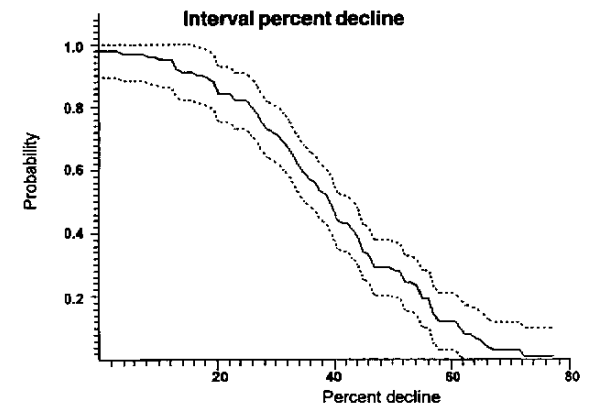


Figure 37. Probability of declines of specified magnitude or larger during the 100-yr trajectories over all 6 subpopulations of grizzly bears listed in the Recovery Plan (Servheen 1993). Dispersal is assumed to follow the function plotted in Figure 33.

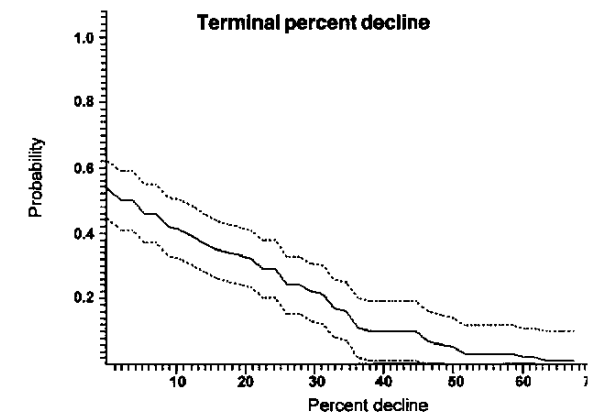
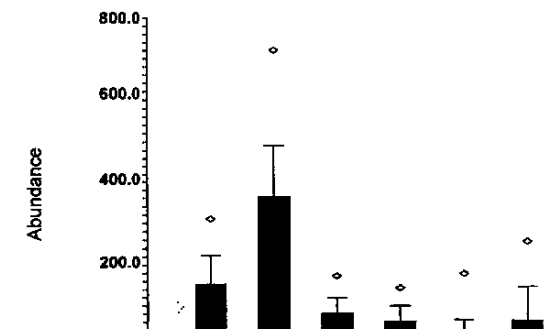


Figure 38. Terminal % decline over all 6 subpopulations of grizzly bears at the end of 100-yr projected populations.



Using ALEX

Like RAMAS/GIS, ALEX (Analysis of the Likelihood of Extinction) is a second generation software package that estimates the probability that a population will become extinct. The focus in ALEX is on characterizing individual subpopulations by dynamic characteristics of the habitats in each area. Stochastic characteristics of habitat quality of individual areas can be incorporated, allowing extinction risks in various metapopulations to be modeled in some detail. Metapopulation structure includes dispersal attributes similar to RAMAS/GIS.

The ALEX software includes interesting ideas about habitat characterization that are unique among PVA models. In RAMAS/GIS, for example, carrying capacity can vary among sites and stochastic perturbations can be made to fluctuate with a specified correlation structure, but the underlying demographic structure of each subpopulation remains the same. In ALEX, the mechanisms of population regulation potentially can be different in each subpopulation. The package includes nice graphical displays of results and allows one to monitor subpopulations through time to witness all details of population fluctuations including extinction and recolonization processes. The program is menu driven, easy to use, and a new ALEX-for-Windows version is available.

On the other hand, parameterizing the model is difficult. Incorporating environmental stochasticity requires massaging data into "habitat quality" measures to achieve the desired effect. For example, to model declining habitats, one must build in a regular catastrophe to cause an exponential decline in habitat quality. If the catastrophe causes a fixed percentage loss in habitat quality and catastrophes are set to occur with sufficient frequency, one can indirectly make the habitat quality decline.

Although we made the program do most anything we wanted, deciding on an objective way to estimate parameters seemed elusive. Using our best guesses for parameters we generated simulations for a 6-subpopulation model of grizzly bears. Our results were quite similar to results of RAMAS/GIS, but ALEX could be run for longer periods, e.g., 500 years. In general, our simulations did not differ substantially from those of RAMAS/GIS, except that we had no statistical basis for justifying the inputs for habitat variables that are necessary to the functioning of the model.

DISCUSSION

Demographics

Conservation modeling offers such an enormous di-

versity of alternatives that managers often are unable to sift through the complex variations. A prerequisite to sound modeling is a clear statement of objectives (Grant 1986). But PVA modelers do not have a consensus on objectives. Shaffer (1983) focused on the minimum viable population size, presuming that there exists some critical population level below which extinction occurs. Soulé (1987) expressed concern about this approach because a focus on the minimum may imply that this population size is somehow adequate for long-term viability. Others have argued that we must seek a sufficiently large population size so that evolution can continue to take place (Franklin 1980, Foose et al. 1995). In practice we are often more urgently concerned about the prevention of extinction. Eberhardt and Knight (1996) suggested that managers should be more concerned with population trend or growth rates than population size. For long-term management considerations, "persistence" implies that growth rate will be zero so short-term fluctuations are of little consequence. Nevertheless, understanding the reasons for increases or decreases in population size can provide valuable information to managers (Caughley 1994).

In the management discussions of the Grizzly Bear Recovery Plan (Servheen 1993), the focus is on evaluating whether current management is sufficient or whether current management is a "blueprint for extinction" (Shaffer 1992). Therefore, we have reviewed models and data for evaluating the long-term prognosis for bears, given what we know about their population characteristics. Granted such a long-term prognosis becomes ever more difficult to make as the future time horizon expands, and arbitrarily we have adopted mostly the convention of modeling population trajectories for 100 years into the future. We cannot know the future—a few years ago most people worried of a world shattered by nuclear holocaust. For our view of the future we must make some realistic assumptions about the environment over the next 100 years.

The simplest assumption is no change—that population, environmental, and stochastic processes will continue to operate as they have over the past 100 years. This projection of trajectories is the approach used in the exponential growth models of Dennis et al. (1991). Given the rapid development of the western United States and the rapid decline in grizzly bear numbers, if we follow such a trajectory, clearly this species will become extinct before 100 years. And one must accept Dennis et al.'s (1991) conclusion that the bear is "doomed to extinction."

Such an assumption appears inconsistent with current management efforts. We believe that there is basis for

assuming that existing national parks and wilderness areas will remain in place, the laws requiring recovery of listed species will persist, and these lands and laws will continue to afford habitat for grizzly bears. Furthermore, there is evidence that people are learning to cope with the management needed to conserve bears and threats to bears may be less on some private lands and multiple-use forests in the future (Chadwick 1999). So we believe it is unreasonable to anticipate that the rate of decline observed during the past will continue into the future. There exists strong motivation and effort to increase available and occupied bear habitat, and future habitat deterioration is less likely than it was in the past. Yet it remains clear that maintaining sufficient habitat is a fundamental requirement and further losses of habitat can only result in decreased probability of the grizzly bear population persisting.

Perhaps this discussion seems like simple common sense and it goes without saying. Yet, it is fundamental to the structure of models used by some to forecast the future of grizzly bears. Specifically, models by Dennis et al. (1991) and some by Mills et al. (1996) assumed exponential growth models where the population trajectory dominates in the calculations of extinction risk. To our way of thinking, any modeling effort for grizzly bears without density dependence in survival and/or reproduction could be defensible only if factors leading to declines were changing exponentially.

The rub, however, is that estimating density-dependent functions can be exceedingly difficult (Ginzburg et al. 1990, McCullough 1990) and seldom do we have sufficient data. Density dependence can influence the behavior of bears, but securing sufficient data to document these responses may be impractical or impossible. For the GYE grizzly bears, our analysis of survival demonstrates density dependence so that this issue need not plague further analysis. But even when such evidence does not exist (e.g., for the other 5 subpopulations), it is still essential to assume a simple density-dependent model as the underlying structure. From an hypothesis-testing context, the principle of parsimony requires that we view a density dependent model as the null model (Boyce 1994).

Ecologists will agree that stochasticity is fundamental to extinction, and therefore, a structural element in any PVA must be randomness. Indeed, we believe that an effective PVA attempts to understand the variance structure and how it is propagated in the system. Shaffer (1981) has categorized stochasticity into (1) demographic stochasticity relating to chance events associated with birth and death processes, (2) environmental stochasticity caused by vagaries of the environment changing through

time, (3) catastrophes such as floods, extensive wildfire, epidemics, and (4) genetic stochasticity including drift and inbreeding depression.

Taking a pragmatic perspective, demographic stochasticity should be in any PVA model, but its influence will be felt only within subpopulations that become quite small, say fewer than 30-50 individuals. Environmental stochasticity is the most important type of randomness in determining extinction risk (Lande 1988), however, and its influence can have overwhelming consequences. Attempting to tease apart the factors contributing to environmental stochasticity is perhaps one of the most important outcomes of a PVA. How to model the influence of catastrophes is highly controversial, but we follow Caughley (1994) in viewing catastrophes as events on the tail of the distribution of environmental stochasticity. Young's (1994) analysis of catastrophes in large mammal populations did nothing to persuade us that catastrophes are other than an arbitrary collection of population declines singled out solely on the basis of the magnitude of decline (Erb and Boyce 1999).

Finally, genetic stochasticity is ultimately important, but as Boyce (1992) reviewed in detail elsewhere, we have insufficient basis of understanding about the population genetics of grizzly bears to defend the results of conservation-genetics models. Clearly there exist basic principles of population genetics that carry important messages for population management. But explicitly characterizing the population genetics of grizzly bears is beyond our current abilities. Still, one feature of great significance is inbreeding depression. We know that species vary widely in their response to inbreeding (Ralls et al. 1988), probably due to historical events permitting the accumulation of deleterious recessive alleles in the genome. Captive brown bears in Europe show inbreeding depression expressed by reduced reproductive success (Laikre et al. 1996). An estimate of 47 for the effective population size (N_e) for the Yellowstone grizzly bears has been calculated (Bolger et al. 1987), but we have no sound basis for determining whether $N_e = 47$ constitutes a sufficient population size to avoid extinction due to genetic causes (Ewens 1990). Theoretical work on the accumulation of genetic load through mutations in small populations has led Lande (1995) to suggest that populations of 2,000 to 5,000 may be necessary to ensure long-term viability. Recently, however, an empirical evaluation of the importance of mutation in genetic load appears to contradict the theoretical predictions (Gilligan et al. 1997). To conclude, we have insufficient data or understanding of grizzly bear genetics on which to base a PVA, and we agree with Lande (1988) that environmental stochasticity is of greater magnitude conse-

quence in evaluating population viability for conservation.

Most software packages available for PVA do a respectable job of simulating demographic patterns through time, and each package provides useful insights into how bear populations might function. The more complex the model, the more detailed one's data must be to do a reasonable job of parameterizing the model. The ALEX software, in particular, appears to require a level of understanding about temporal and spatial variation in bear habitats that far outstrips our empirical basis. This does not imply that the model has flawed structure, but rather that we need to sort out these habitat attributes.

Grizzly bears are notorious for their adaptability in foraging. Some bears become specialists on elk (*Cervus elaphus*) calves in spring, others learn to forage on army cutworm moths in the alpine, and still others become really good at catching cutthroat trout (*Oncorhynchus clarki*; Reinhart and Mattson 1990). Given that each food resource upon which bears depend fluctuates through time, the ability of bears to adapt to new resources cushions them from negative effects of environmental stochasticity. We have evidence that some bears are predisposed to die in conflicts with humans while other bears appear to learn to avoid roads and other places where they might encounter humans. And we saw evidence from our survival analysis that some individuals make high reproductive investments and assume mortality risks as a consequence, whereas other bears that are not breeding enjoy higher survival to some future opportunity to breed (Williams 1966).

Individual heterogeneity also exists in bears' behavior around humans, with subsequent consequences for survival. For example, translocation of bears is a management action designed to remove bears from areas where they have been in conflict with humans (Blanchard and Knight 1996). The distribution of translocations of female bears by age in the GYE is significantly different from expected based upon age frequency in the sampled population ($\chi^2 = 11.3$, 4 df, $P < 0.025$). This difference is because young bears (age classes 0-2) are less likely to be translocated, whereas the age distribution of female bears older than age 3 being translocated does not differ significantly from random expectation ($\chi^2 = 0.76$, 3 df, $P > 0.75$).

These facts point to the importance of individually based modeling for grizzly bears (Łomnicki 1990). Individual heterogeneity in the context of PVA is likely to enhance persistence and reduce the risk of extinction (White 2000). The difficulty, however, is securing sufficient information about individual bears to parameterize complex individually based models. Radiotelemetry data

on individual bears may permit the development of such models, and we believe that this might prove to be a fruitful research area.

Habitat-based PVA

Most "canned" software for PVA focuses on demographic projections. But PVA models need not include details of age and sex structure and in many cases we would learn more about the long-term persistence of populations by better understanding their ecology and resource base. For example, Foin and Brenchley-Jackson (1991) developed a model for the light-footed clapper rail (*Rallus longirostris*) based on hydrology, salinity, soil moisture, and transpiration in salt marshes that had important ramifications for conservation management of the species. The importance of long-term habitat changes for evaluating long-term population viability appears almost certainly true for grizzly bears as well (Mattson and Craighead 1994). Although it is clear from demographic studies that mortality rates need to be kept low to ensure viable bear populations, long-term persistence of a grizzly bear population certainly will depend also on ensuring large expanses of good habitat.

Land use is perhaps the most fundamental issue in management of grizzly bears. Bears require large expanses of undeveloped landscapes. Most grizzly bears die near roads, and in many areas habitat use is significantly reduced near roads (McLellan and Mace 1985, McLellan and Shackleton 1988, Mace et al. 1996). This appears to be true even in Yellowstone National Park where adult females and subadult males are displaced by dominant bears into areas near roads and developments where they are more likely to die (Mattson et al. 1987). In *Blueprint for the Future*, the Greater Yellowstone Coalition identifies road construction for timber management as one of the most serious concerns regarding bear management in national forests of Montana, Idaho, and Wyoming (Harting et al. 1994).

Using a simple source-sink model, Doak (1995) argued that habitat degradation can result in precipitous declines in bear populations that are not likely to be detected by monitoring the population. The time lag in the response of the population suggests that even though demographic parameters for the bear population would suggest a viable population, declines would not be detected until habitats deteriorated so seriously that recovery was impossible. Given the extent of wilderness and national park lands in the GYE, we find this scenario unlikely for grizzly bears, but the message is important: population monitoring independent of habitats may yield misleading indicators of population viability.

To characterize the cumulative effects of various types

of development on grizzly bear habitat, Weaver et al. (1985, 1986) developed a cumulative effects model (CEM). The model integrates a number of possible factors that may influence habitat effectiveness of an area. The cumulative effects assessment (Weaver et al. 1985) identified several important habitat variables. In addition, using a Delphi survey, Weaver et al. (1985) established a list of disturbance and displacement coefficients for a CEM. None of the coefficients in the CEM have been validated. A GIS map of key habitat variables was completed for the GYE, however, and we believe that these GIS databases could be useful in parameterizing a resource selection function (Mace et al. 1996), with statistically defensible underpinnings (Manly et al. 1993).

Despite the obvious importance of these landscape-level resource management issues, none of the existing viability models provides opportunity to evaluate the consequences of roads, climate change, timber sales, oil and gas exploration and development, campground placement, or housing developments on grizzly bear population viability (Mattson and Reid 1991, Craighead et al. 1995).

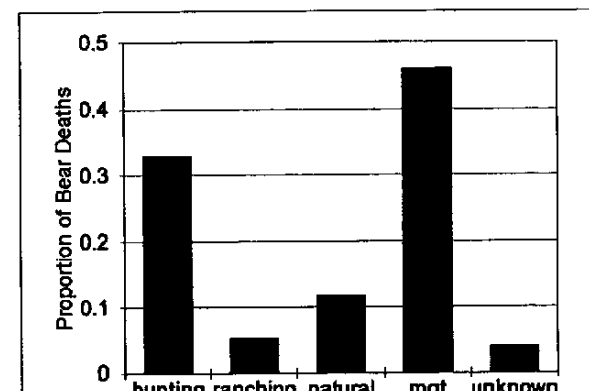
The RAMAS/GIS software attempts to move PVA modeling in this direction by allowing an interface between landscape variables and subpopulations. To do this well, however, we must be able to evaluate the probability that a particular tract of land constitutes grizzly bear habitat. Manly et al. (1993) developed statistical procedures (logistic regression and discriminant analysis) for doing this using resource selection probability functions. Models are constructed that evaluate the probability of occurrence at a site based upon a multiple-variable assessment of the habitat. For example, Mace et al. (1996) successfully applied a model for grizzly bear habitat on the South Fork of the Flathead River, Montana using logistic regression. Such models can be interfaced with population models to evaluate the consequences of land management decisions on the future viability of grizzly bear populations (see Boyce et al. 1994; Boyce and McDonald 1999; Mladenoff et al. 1995, 1997).

Boyce (1997) offers a PVA for grizzly bears as an example of adaptive resource management. Several analyses of data and population models provided input into the present management programs for grizzly bears. Models have been revised as new data have been compiled (e.g., Suchy et al. 1985). But adaptive manage-

Management Implications

We cannot be completely satisfied with any projection of the future of grizzly bears in the Rocky Mountains without a habitat-based PVA. This carries the assumption that ultimately habitat is limiting population size for grizzly bears. Belovsky et al. (1994) warn, however, that although habitats prevail in many endangered species management issues, other forms of intervention management may be necessary. [Extinction times are not just a function of K and its variance, $\text{var}(K)$, but also r and its variance, $\text{var}(r)$ (Tuljapurkar and Semura 1979, Akçakaya 1994, Foley 1994).] For grizzly bears such intervention management might include developing schemes to reduce hunter-caused mortalities.

As revealed by the survival analysis, bear mortality risk is significantly higher for bears living outside YNP. Although wilderness areas in the GYE are posted with signs warning hunters that they are in "Grizzly Country," and required to use bear-proof panniers and hang game carcasses out of bears' reach, hunters remain a leading cause of grizzly bear mortality (Fig. 40). These deaths have been especially common in recent years (Fig. 41). In YNP, where culling of elk was terminated in 1968, an increased number of elk has provided opportunities for bears to feed on winter-killed elk; and some bears have learned to prey on elk calves (Singer et al. 1997). Hunting in areas near YNP may reduce opportunities for grizzlies to scavenge winter-killed elk. Artificial feeding of elk, such as at the National Elk Refuge and State of Wyoming feedgrounds, reduces overwintering mortality for elk (Boyce 1989). Yet, overall elk numbers are enhanced due to such feeding.



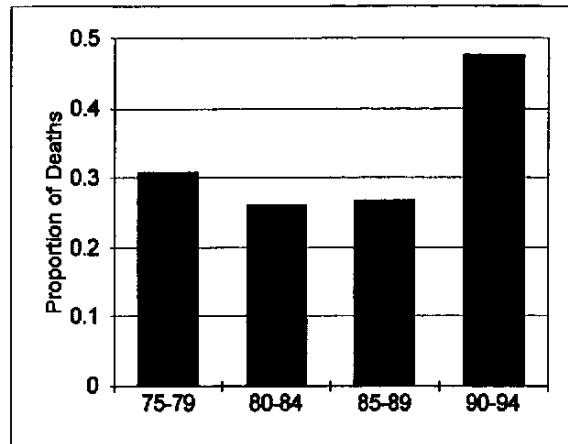


Figure 41. The proportion of total known death³ attributable to hunting-related causes during 5-yr intervals from 1975-1994.

Aggressive education and possible restrictions on hunters appear to be necessary to reduce the number of bears being killed. During spring, bear hunters sometimes mistake grizzly bears for black bears. Hunters inexperienced with grizzly bears appear prone to shoot when confronted by a grizzly. None of the 3 state wildlife management agencies in the GYE require that hunters undergo bear identification and conflict avoidance training prior to hunting in bear country. Research of the details associated with hunter-related grizzly bear deaths could give insight into the types of restrictions and education programs that would be most effective at reducing hunting conflicts with grizzly bears.

Properly managed, hunting can be an important tool for bear management. Eberhardt and Knight (1996) suggest that the increasing grizzly bear populations in the GYE might require management efforts to curb further expansion. Proposed release of grizzly bears into the Bitterroot Mountains of Idaho may provide a way to remove "excess" bears from the GYE, or limited hunting may be reinstated outside of the national parks. Hunting can negatively condition bears to humans and select against those bears unwary of humans thereby potentially reducing conflicts (M. Shaffer *personal communication*). Harvesting strategies require careful consideration, however. Removal of large males by trophy hunting, for example, may negatively affect reproduction if older males are replaced by infanticidal immigrant males (Wielgus 1993, Swenson et al. 1997).

tion that the bear population was precariously small prompted transplants of bears from Canada (Servheen et al. 1995). Similarly, high mortality of bears in and adjacent to YNP led to the closing of the tent campground at Fishing Bridge, and termination of sheep grazing allotments in Targhee National Forest (Schullery 1992). Surely, future management will help to ensure persistence of grizzly bears throughout their current range.

CONCLUSIONS

At this point we would like to make a final assessment as to the viability of grizzly bear populations, but do not have sufficient understanding of the genetics and ecology of grizzly bears to make a defensible statement. According to the early work of Shaffer (1978, 1983) and Shaffer and Samson (1985) the Yellowstone and Northern Continental Divide ecosystems have populations far greater than the projected minimum viable population. But Shaffer (1992) argued that targeting MVP population levels is not sound conservation strategy and that larger populations are necessary if we are to ensure the long-term persistence of the species.

The Grizzly Bear Recovery Plan (Servheen 1993:54) calls for a PVA for GYE grizzly bears. Shaffer (1992) recognized the need for a PVA, and identified 5 specific objectives for such an effort that focus on demographic approaches:

1. Provide an up-to-date, integrated summary of sex and age-specific mortality and fecundity rates and the variances of these rates.
2. Partition the estimated variability in these demographic parameters and overall population growth rate to that attributable to sampling error, changes in density, and chance events (demographic, environmental, catastrophic, and genetic).
3. Refine the model of Shaffer and Samson (1985) or other appropriate model to incorporate the full range of chance events that can affect population lifetimes.
4. Use the results of the data re-analysis and the refined model to estimate the population lifetimes of an array of population sizes (say 50 to 5,000).
5. Use the model to generate specific hypotheses about population status and trend that can be tested by ongoing management activities.

As an evaluation of this review, we will comment on

We find Shaffer's second suggestion to partition variability more problematic. Our survival analyses partitioned survival variance into various components attributable to selected covariates including density. However, we do not have sufficient information to permit partitioning of variance into demographic, environmental, catastrophic and genetic components. Even though there were years of low reproduction (cf. Figs. 14 and 15), and years when the bears suffered extensive mortality subsequent to dump closures (Craighead et al. 1995), we find no evidence of catastrophes affecting grizzly bear vital rates. Anticipating some future epidemic or severe climate change is beyond our vision without some historical basis. One might imagine that burning more than 33% of YNP might constitute a catastrophe, but apparently few bears died in the fires, and no evidence exists of increased mortality or reduced reproduction related to the fires (Blanchard and Knight 1990). If anything, bear populations have been increasing since the fires of 1988 due possibly in part to increased availability of herbaceous forage in burned areas and ungulate carcasses immediately after the fires. We have no basis whatsoever for characterizing genetic stochasticity for grizzly bears or any other species of which we are aware.

The third charge to update a PVA model, is probably accomplished with this monograph, although we make no pretenses of having evaluated the "full range of chance events that can affect population lifetimes." We would argue, however, that chance events are not as serious a concern for the future of grizzly bears in the Rocky Mountains as the deterministic erosion of habitats for the species associated with human development and resource extraction. Furthermore, management will find it easier to cope with the deterministic trends.

Estimated population lifetimes for an array of population sizes from 50 to 350 were calculated (Fig. 11). Expected times to extinction became so large for larger populations that plotting them obscures values in the more plausible range.

Finally, Shaffer's suggestion that models should generate hypotheses that then should be tested by experimental management programs is precisely the message of adaptive management (Walters 1986). Previous efforts postulated that reducing mortality would allow bear populations to increase (Knight et al. 1988). This ap-

and refine the model until we have a model with true predictive capability.

Adaptive management approaches will be crucial to grizzly bear management in the future, because the future is uncertain. A number of questions surround the future of grizzly bear food resources and habitats in the GYE, for example: The introduction of lake trout (*Salvelinus namaycush*) into Yellowstone Lake may decrease the availability of cutthroat trout (Knight 1998). Pesticide use may reduce army cutworm moths or have toxic consequences for bears. Agricultural interests have called for reduced populations of both elk and bison to reduce risks of transmission of brucellosis to cattle (Cheville et al. 1998). White-pine blister rust may gradually eliminate whitebark pine (*Pinus albicaulis*) in the GYE as it has in the NCDE (Knight 1998). And increasing human demand for recreational areas and development will pose ever-increasing conflicts with grizzly bears.

We do not believe that this monograph or any of the studies that we have reviewed constitute a sufficient PVA for grizzly bears. We believe that the next step in PVA is linking grizzly bear population viability to habitats. Such an effort will increase confidence in assessments of the viability of grizzly bear populations in the GYE and throughout the Rocky Mountains. The necessary theory (Manly et al. 1993), model structures (Boyce et al. 1994, Mladenoff et al. 1995), technology (GIS), and baseline data (CEM) exist to perform such an analysis. Our ability to manage for the long-term viability of grizzly bears depends upon such an integration of population biology and GIS at a broad landscape scale.

ACKNOWLEDGMENTS

The National Fish and Wildlife Foundation coordinated funding for this project with financial assistance from the U.S. Fish and Wildlife Service and from the sale of an art print donated by Robert Bateman. Additional funds came from the Boone and Crockett Club. S. L. Cain provided unpublished data for our analysis. C. Johnson helped with data entry. We thank R. Mace, D. Mattson, E. Merrill, P. Schullery, J. Varley, L. Eberhardt, L. Metzgar, S. Mills, C. Pease, and S. and M. French for discussion on grizzly bears. B. F. J. Manly, D. MacKenzie, K. Pollock, M. Riggs, S. Sheriff, G. White,

LITERATURE CITED

- Aalen, O. O. 1978. Nonparametric inference for a family of counting processes. *Annals of Statistics* 6:701-726.
- Akçakaya, H. R. 1994. RAMAS/GIS: linking landscape data with population viability analysis. Applied Biomathematics, Setauket, New York, USA.
- Andersen, P. K. 1982. Testing goodness of fit of Cox's regression and life model. *Biometrics* 38:67-77.
- _____, and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. *Annals of Statistics* 10:1100-1120.
- Belovsky, G. E., J. A. Bissonette, R. D. Dueser, T. C. Edwards, Jr., C. M. Luecke, M. E. Ritchie, J. B. Slade, and F. H. Wagner. 1994. Management of small populations: concepts affecting the recovery of endangered species. *Wildlife Society Bulletin* 22:307-316.
- Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91-96.
- Blanchard, B. M., and R. R. Knight. 1990. Reactions of grizzly bears, *Ursus arctos horribilis*, to wildfire in Yellowstone National Park, Wyoming. *Canadian Field-Naturalist* 104:592-594.
- _____, and _____. 1996. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. *Journal of Wildlife Management* 59:560-565.
- Bolger, D. T., C. C. Biehl, M. Soric, and M. Gilpin. 1987. Estimating effective population size for the Yellowstone grizzly bear population: effects of non-Poisson family size distribution and breeding sex ratio. Pages 3-16 in F. Singer, ed. *Conference on science in the national parks*, vol. 2. Wildlife management and habitats. George Wright Society & National Park Service, Washington, D.C., USA.
- Boyce, M. S. 1977. Population growth with stochastic fluctuations in the life table. *Theoretical Population Biology* 12:366-373.
- _____. 1989. *The Jackson elk herd*. Cambridge University Press, Cambridge, United Kingdom.
- _____. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.
- _____. 1994. Population viability analysis exemplified by models for the northern spotted owl. Pages 3-18 in D. J. Fletcher and B. F. J. Manly, eds. *Statistics in ecology and environmental management*. University of Otago Press, Dunedin, New Zealand.
- _____. 1996. RAMAS/GIS: linking landscape data with population viability analysis. *Quarterly Review of Biology* 71:167-168.
- _____. 1997. Population viability analysis: adaptive management for threatened and endangered species. Pages 226-236 in M. S. Boyce and A. Haney, eds. *Ecosystem management: applications for sustainable forest and wildlife resources*. Yale University Press, New Haven, Connecticut, USA.
- _____, and D. J. Daley. 1980. Population tracking of fluctuating environments and natural selection for tracking ability. *American Naturalist* 115:480-491.
- _____, and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14:268-272.
- _____, J. S. Meyer, and L. L. Irwin. 1994. Habitat-based PVA for the northern spotted owl. Pages 63-85 in D. J. Fletcher and B. F. J. Manly, eds. *Statistics in Ecology and Environmental Monitoring*, Otago Conference Series No. 2, University of Otago Press, Dunedin, New Zealand.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5:1-437.
- Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theoretical Population Biology* 14:215-230.
- Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47:906-918.
- _____. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- Chadwick, D. H. 1995. Grizzly country: northern Montana's wildlands may be the last best hope for grizzlies in the lower 48. *Nature Conservancy* 45(4):10-15.
- _____. 1999. Helping a great bear hang on. *National Wildlife* 37(1):22-31.
- Chao, A., and S. M. Lee. 1992. Estimating the number of classes via sample coverage. *Journal of the American Statistical Association* 87:210-217.
- Cheville, N. F., D. R. McCullough, and L. R. Paulson. 1998. *Brucellosis in the greater Yellowstone area*. National Research Council, Washington, D.C., USA.
- Cohen, J. E. 1979. Comparative statics and stochastic dynamics of age-structured populations. *Theoretical Population Biology* 16:159-171.
- Cox, D. R. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society B34*:187-202.
- _____, and D. Oakes. 1984. *Analysis of survival data*. Chapman and Hall, London, United Kingdom.
- Craighead, J. J., F. C. Craighead, and J. Sumner. 1974. A population analysis of the Yellowstone grizzly bears. *Montana Forestry and Conservation Experiment Station Bulletin* 40. University of Montana, Missoula, USA.
- _____, J. S. Sumner, and J. A. Mitchell. 1995. *The grizzly bears of Yellowstone: Their ecology in the Yellowstone ecosystem, 1959-1992*. Island Press, Washington, D.C., USA.
- Darroch, J. N. 1958. The multi-response census. I. Estimation of a close population. *Biometrika* 45:343-359.
- DeLury, D. B. 1947. On the estimation of biological populations. *Biometrics* 3:145-167.
- Dennis, B. P., L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 61:115-143.
- Doak, D. F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology* 9:1370-1379.
- Eberhardt, L. L. 1987. Population projections from simple models. *Journal of Applied Ecology* 24:103-118.
- _____. 1995. Population trend estimates from reproductive and survival data. Pages 13-19 in R. R. Knight and B. M.

- Blanchard. Yellowstone grizzly bear investigations, 1994. National Biological Service, Bozeman, Montana, USA.
- _____, B. M. Blanchard, and R. R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology* 72:360–363.
- _____, and R. R. Knight. 1996. How many grizzlies in Yellowstone? *Journal of Wildlife Management* 60:416–421.
- _____, and B. M. Blanchard. 1986. Monitoring grizzly bear population trends. *Journal of Wildlife Management* 50:613–618.
- Emlen, J. M., and E. K. Pickett. 1989. Animal population dynamics: identification of critical components. *Ecological Modelling* 44:253–273.
- Erb, J. D., and M. S. Boyce. 1999. Distribution of population declines in large mammals. *Conservation Biology* 13:199–201.
- Ewens, W. J. 1990. The minimum viable population size as a genetic and a demographic concept. Pages 307–316 in J. Adams, D. A. Lam, A. I. Hermalin, and P. E. Smouse, editors, *Convergent issues in genetics and demography*. Oxford University Press, Oxford, United Kingdom.
- Ferson, S., L. Ginzburg, and A. Silvers. 1989. Extreme event risk analysis for age-structured populations. *Ecological Modelling* 47:175–187.
- Foin, T. C., and J. L. Brenchley-Jackson. 1991. Simulation model evaluation of potential recovery of endangered light-footed clapper rail populations. *Biological Conservation* 58:123–148.
- Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8:124–137.
- _____. 1997. Extinction models for local populations. Pages 215–246 in I. Hanski and M. E. Gilpin, editors, *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, New York, New York, USA.
- Foose, T. J., L. de Boer, U. S. Seal, and R. Lande. 1995. Conservation management strategies based on viable populations. Pages 273–294 in J. D. Ballou, M. Gilpin, and T. J. Foose, eds. *Population management for survival and recovery: analytical methods and strategies in small population conservation*. Columbia University Press, New York, New York, USA.
- Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–149 in M. E. Soulé and B. A. Wilcox, editors, *Conservation biology*. Sinauer, Sunderland, Massachusetts, USA.
- French, S. P., M. G. French, and R. R. Knight. 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *International Conference on Bear Research and Management* 9:389–400.
- Furstenberg, H., and H. Kesten. 1960. Products of random matrices. *Annals of Mathematical Statistics* 31:457–469.
- Gilligan, D. M., L. M. Woodworth, M. E. Montgomery, D. A. Briscoe, and R. Frankham. 1997. Is mutation accumulation a threat to the survival of endangered populations? *Conservation Biology* 11:1235–1241.
- Gilpin, M. E., and I. Hanski. 1991. *Metapopulation dynamics*. Acad. Press, London, United Kingdom.
- Ginzburg, L. R., S. Ferson, and H. R. Akçakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63–70.
- Grant, W. E. 1986. *Systems analysis and simulation in wildlife and fisheries science*. John Wiley, New York, New York, USA.
- Gross, A. J., and V. A. Clark. 1975. *Survival distributions: reliability applications in the biomedical sciences*. John Wiley & Sons, New York, New York, USA.
- Gunther, K. A. 1994. Bear management in Yellowstone National Park, 1960–93. *International Conference of Bear Research and Management* 9:549–560.
- Harris, R. B. 1986. Grizzly bear population monitoring: current options and considerations. Montana Forestry and Conservation Experiment Station, University of Montana, Miscellaneous Publication No. 45.
- _____, and F. W. Allendorf. 1989. Genetically effective population size of large mammals: An assessment of estimators. *Conservation Biology* 3:181–191.
- Harting, A., D. Glick, C. Rawlins, and B. Ekey. 1994. Sustaining Greater Yellowstone, a blueprint for the future. Greater Yellowstone Coalition, Bozeman, Montana, USA.
- Heyde, C. C., and J. E. Cohen. 1985. Confidence intervals for demographic projections based on products of random matrices. *Theoretical Population Biology* 27:120–153.
- Kalish, S., and M. A. McPeck. 1993. Extinction dynamics, population growth and seed banks. *Oecologia* 95:314–320.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457–481.
- Knight, R. R. 1998. Holding on to Yellowstone's grizzlies. *Yellowstone Science* 6:2–9.
- _____, B. M. Blanchard, and L. L. Eberhardt. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1974–1985. *Wildlife Society Bulletin* 16:121–125.
- _____, _____, and _____. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. *Wildlife Society Bulletin* 23:245–248.
- _____, and L. L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology* 66:323–334.
- Krebs, C. J. 1999. *Ecological methodology*. Second edition. Benjamin-Cummings, Menlo Park, California, USA.
- Lacava, J., and J. Hughes. 1984. Determining minimum viable population levels. *Wildlife Society Bulletin* 12:370–376.
- Laikre, L., R. Andren, H. O. Larsson, and N. Ryman. 1996. Inbreeding depression in brown bear, *Ursus arctos*. *Biological Conservation* 76:69–72.
- Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology* 6:505–512.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–1460.
- _____. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes.

- American Naturalist 142:911-927.
- _____. 1995. Mutation and conservation. *Conservation Biology* 9:782-791.
- _____, and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87-123 in M.E. Soulé, editor, *Viable populations for conservation*. Cambridge University Press, Cambridge, United Kingdom.
- _____, and S. H. Orzack. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proceedings of the National Academy of Sciences, USA* 85:7418-7421.
- Lebreton, J.D., and J. Clobert. 1991. Bird population dynamics, management and conservation: the role of mathematical modelling. Pages 105-124 in C. M. Perrins, J.D. Lebreton, and G. J. M. Hiron, eds. *Bird population studies: their relevance to conservation and management*. Oxford University Press, Oxford, United Kingdom.
- Lewontin, R. C., and D. Cohen. 1969. On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences, USA* 62:1056-1060.
- _____, and T. Prout. 1956. Estimation of the number of different classes in a population. *Biometrics* 12:211-223.
- Lomnicki, A. 1990. *Populations of individuals*. Princeton University Press, Princeton, New Jersey, USA.
- Ludwig, D. 1996. The distribution of population survival times. *American Naturalist* 147:506-526.
- _____. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298-310.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- MacCracken, J. G., D. Goble, and J. O'Laughlin. 1994. Grizzly bear recover in Idaho. Idaho Forestry, Wildlife and Range Experiment Station, Report No. 12.
- Mace, G. M., and R. Lande. 1991. Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5:148-157.
- Mace, R. D., S. Minta, T. Manley, and K. Aune. 1994. Estimating grizzly bear population size using camera sightings. *Wildlife Society Bulletin* 22:74-83.
- _____, and J. S. Waller. 1998. Demography and population trend of grizzly bears in the Swan Mountains, Montana. *Conservation Biology* 12:1005-1016.
- _____, J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology* 33:754-772.
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. *Resource selection by animals*. Chapman & Hall, London, United Kingdom.
- the lessons, improving the process. Island Press, Washington, D.C., USA.
- _____, and C. M. Pease. 1994. Performance of demographic indices used in the 1993 grizzly bear recovery plan. *Administrative Record on Public Comments on the Grizzly Bear Recovery Plan*, 1994. US Fish and Wildlife Service, Missoula, Montana, USA.
- _____, and M. M. Reid. 1991. Conservation of the Yellowstone grizzly bear. *Conservation Biology* 5:364-372.
- _____, R. R. Knight, and B. M. Blanchard. 1987. The effects of development and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *International Conference on Bear Research and Management* 7:259-273.
- _____, C. M. Gillin, S. A. Benson, and R. R. Knight. 1991. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology* 69:2430-2435.
- McCullough, D. A. 1986. The Craigheads' data on Yellowstone grizzly bear populations: relevance to current research and management. *International Conference on Bear Research and Management* 6:21-32.
- _____. 1990. Detecting density dependence: Filtering the baby from the bathwater. *Transactions of the North American Wildlife and Natural Resources Conference* 55:534-543.
- McKelvey, K., B. R. Noon, and R. Lamberson. 1992. Conservation planning for species occupying fragmented landscapes: The case of the northern spotted owl. Pages 424-450 in P.M. Kareiva, J.G. Kingsolver, and R.B. Huey, editors, *Biotic interactions and global change*. Sinauer, Sunderland, Massachusetts, USA.
- McLellan, B. N., and R. D. Mace. 1985. Behaviour of grizzly bears in response to roads, seismic activity, and people. British Columbia Ministry of Environment, Cranbrook, British Columbia, Canada.
- _____, and D. M. Shackleton. 1988. Grizzly bears and resource extraction industries: effects of roads on behaviour, habitat use, and demography. *Journal of Applied Ecology* 25:451-460.
- Merrill, E. H., and M. S. Boyce. 1991. Summer range and elk population dynamics in Yellowstone National Park. Pages 263-273 in R. B. Keiter, and M. S. Boyce, eds. *The Greater Yellowstone Ecosystem: redefining America's wilderness heritage*. Yale University Press, New Haven, Connecticut, USA.
- Metzgar, L. H., and M. Bader. 1992. Large mammal predators in the northern Rockies: grizzly bears and their habitat. *North West Environmental Journal* 8:231-233.
- Meyer, J. S., and M. S. Boyce. 1994. Life historical consequences of pesticides and other insults to vital rates. Pages 363-377 in R. J. Kendall and T. E. Lacher, eds. *Wildlife toxicology and population modeling*. Lewis

- _____. 1990b. Population management of bears in North America. International Conference on Bear Research and Management 8:357-373.
- _____, G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. 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-resight techniques. Wildlife Monographs 133:1-55.
- Mills, L. S., S. Hayes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conservation Biology 10:863-873.
- Mladenoff, D. J., R. G. Haight, T. A. Sickley, and A. P. Wydeven. 1997. Causes and implications of species restoration in altered ecosystems. BioScience 47:21-31.
- _____, T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes Region. Conservation Biology 9:279-294.
- Moran, P. A. P. 1951. A mathematical theory of animal trapping. Biometrika 38:307-311.
- Murray, B. G., Jr. 1979. Population dynamics: alternative models. Academic Press, New York, New York, USA.
- Nations, C., and M. S. Boyce. 1997. Stochastic demography for conservation biology. Pages 451-469 in S. D. Tuljapurkar and H. Caswell, eds. Structured-population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York, New York, USA.
- Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 in D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: populations. Elsevier Applied Science, London, United Kingdom.
- Peek, J. 1986. A review of wildlife management. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- _____, M. B. Pelton, H. D. Picton, J. W. Schoen, and P. Zager. 1987. Grizzly bear conservation and management: a review. Wildlife Society Bulletin 15:160-169.
- Pielou, E. C. 1977. Mathematical ecology. John Wiley & Sons, New York, New York, USA.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132:757-785.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.
- Ralls, K., J. D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conservation Biology 2:185-193.
- Reinhart, D. P., and D. J. Mattson. 1990. Bear use of cutthroat trout spawning streams in Yellowstone National Park. Schullery, P. 1992. The bears of Yellowstone. High Plains, Worland, Wyoming, USA.
- _____. 1995. A bee in every bouquet. Yellowstone Science 3(1):8-14.
- Servheen, C. 1993. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- _____, F. Hovey, B. McLellan, R. Mace, W. Wakkinen, W. Kasworm, D. Carney, T. Manley, K. Kendall, and R. Wielgus. 1994. Report of the northern ecosystems researchers on grizzly bear population trends in the North and South Forks of the Flathead, and the Blackfeet Indian Reservation of the NCDE; the Cabinet-Yaak ecosystem; and the Selkirk ecosystem; and future data needs to improve trend estimates. Report to the Interagency Grizzly Bear Committee, Missoula, Montana, USA.
- _____, W. F. Kasworm, and T. J. Thier. 1995. Transplanting grizzly bears *Ursus arctos horribilis* as a management tool—results from the Cabinet Mountains, Montana, USA. Biological Conservation 71:261-268.
- _____, R. Mace, R. Harris, W. Kasworm, W. Wakkinen, B. McLellan, D. Carney, A. Sokkalla, T. Wittinger, J. Waller, F. Hovey, S. Gnidak, K. Kendall, and T. Manley. 1996. Report of methods to determine population size and rate of change for grizzly bears at the ecosystem scale. Report to the Interagency Grizzly Bear Committee, Missoula, Montana, USA.
- _____, and P. Sandstrom. 1993. Ecosystem management and linkage zones for grizzly bears and other large carnivores in the Northern Rocky Mountains in Montana and Idaho. Endangered Species Technical Bulletin 18:10-14.
- Shaffer, M. L. 1978. Determining minimum viable population size: a case study of the grizzly bear (*Ursus arctos* L.). Ph. D. Dissertation, Duke University, Durham, N.C.
- _____. 1981. Minimum population sizes for species conservation. BioScience 31:131-134.
- _____. 1983. Determining minimum viable population sizes for the grizzly bear. International Conference on Bear Research and Management 5:133-139.
- _____. 1992. Keeping the grizzly bear in the American West: a strategy for real recovery. The Wilderness Society, Washington, D.C., USA.
- _____, and F. B. Samson. 1985. Population size and extinction: a note on determining critical population sizes. American Naturalist 125:144-152.
- Sinclair, A. R. E. 1989. The regulation of animal populations. Pages 197-241 in J. M. Cherrett, ed., Ecological concepts. Blackwell, Oxford, United Kingdom.
- Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12-25.

- University of Tennessee, Knoxville, USA.
- Suchy, W., L. L. McDonald, M. D. Strickland, and S. H. Anderson. 1985. New estimates of minimum viable population size for grizzly bears of the Yellowstone ecosystem. *Wildlife Society Bulletin* 13:223-228.
- Swenson, J. E., F. Sandegren, A. Söderberg, A. Björvall, R. Franzen, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450-451.
- Taylor, M. 1994. Density-dependent population regulation of black, brown, and polar bears. *International Conference on Bear Research and Management* 9, Monograph Series Number 3.
- Thomas, C. D. 1990. What do real population dynamics tell us about minimum viable population sizes? *Conservation Biology* 4:324-327.
- Tuljapourkar, S. D. 1982a. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theoretical Population Biology* 21:114-140.
- _____. 1982b. Population dynamics in variable environments. III. Evolutionary dynamics of r-selection. *Theoretical Population Biology* 21:141-165.
- _____. 1990. Population dynamics in variable environments. *Lecture Notes in Biomathematics* No. 85. Springer-Verlag, New York, New York, USA.
- _____, and S. H. Orzack. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theoretical Population Biology* 18:314-342.
- _____, and J. S. Semura. 1979. Stochastic instability and Liapunov stability. *Journal of Mathematical Biology* 8:133-145.
- U.S. Department of Interior. 1982. Grizzly bear recovery plan. U.S. Department of Interior, Fish and Wildlife Service, Denver, Colorado, USA.
- Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan Co., New York, New York, USA.
- _____, and C. S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060-2068.
- Weaver, J., R. Escano, D. Mattson, T. Puchlers, and D. Despaigne. 1985. A cumulative effects model for grizzly bear management in the Yellowstone ecosystem. Pages 234-246 in G. P. Contreras and K. E. Evans, eds. *Proceedings—Grizzly bear habitat symposium*. U.S. Forest Service General Technical Report INT-207.
- _____, R. Escano, and D. S. Winn. 1986. A framework for assessing cumulative effects on grizzly bears. *Transactions of the North American Wildlife and Natural Resources Conference* 52:364-376.
- White, G. C. 2000. Population viability analysis. Pages 288-231 in L. Boitani and T. Fuller, eds. *Research techniques in animal ecology*. Columbia University Press, New York, New York, USA.
- _____, and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.
- Wielgus, R. B. 1993. Causes and consequences of sexual habitat segregation in grizzly bears. Ph.D. Thesis, University of British Columbia, Vancouver, British Columbia, Canada.
- Williams, G. C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. *American Naturalist* 100:687-690.
- Young, T. P. 1994. Natural die-offs of large mammals: implications for conservation. *Conservation Biology* 8:410-418.