

DEMOGRAPHY OF THE YELLOWSTONE GRIZZLY BEARS

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Abstract. We undertook a demographic analysis of the Yellowstone grizzly bears (*Ursus arctos*) to identify critical environmental factors controlling grizzly bear vital rates, and thereby to help evaluate the effectiveness of past management and to identify future conservation issues. We concluded that, within the limits of uncertainty implied by the available data and our methods of data analysis, the size of the Yellowstone grizzly bear population changed little from 1975 to 1995. We found that grizzly bear mortality rates are about double in years when the whitebark pine crop fails than in mast years, and that the population probably declines when the crop fails and increases in mast years. Our model suggests that natural variation in whitebark pine crop size over the last two decades explains more of the perceived fluctuations in Yellowstone grizzly population size than do other variables.

Our analysis used demographic data from 202 radio-telemetered bears followed between 1975 and 1992 and accounted for whitebark pine (*Pinus albicaulis*) crop failures during 1993–1995. We used a maximum likelihood method to estimate demographic parameters and used the Akaike Information Criteria to judge the significance of various independent variables. We identified no independent variables correlated with grizzly bear fecundity. In order of importance, we found that grizzly bear mortality rates are correlated with season, whitebark pine crop size (mast vs. nonmast year), sex, management-trapping status (never management-trapped vs. management-trapped once or more), and age. The mortality rate of bears that were management-trapped at least once was almost double that of bears that were never management-trapped, implying a source/sink (i.e., never management-trapped/management-trapped) structure. The rate at which bears move between the source and sink, estimated as the management-trapping rate (h), is critical to estimating the finite rate of increase, λ . We quantified h by estimating the rate at which bears that have never been management-trapped are management-trapped for the first time. It differed across seasons, was higher in nonmast than mast years, and varied with age. We calculate that $\lambda = 1.00$ from 1975 to 1983 (four mast and five nonmast years) and 1.02 from 1984 to 1995 (seven mast and five nonmast years). Overall, we find that $\lambda = 1.01 \pm 0.04$ (mean ± 1 SE) from 1975 to 1995.

Our models suggest that future management should concentrate on the threats to whitebark pine, such as those posed by white pine blister rust, global warming, and fire suppression. As is currently widely recognized by Yellowstone land managers, our model also suggests that future management must compensate for the increased grizzly bear mortality that is likely to be caused by an increasing number of humans in Yellowstone.

Key words: Akaike information criterion; behavior; conditioning to humans; conservation; demography; generalized Leslie matrix; grizzly bear; maximum likelihood; radiotelemetry; source–sink; *Ursus arctos*; whitebark pine.

INTRODUCTION

Management of grizzly bears (*Ursus arctos*) native to the Yellowstone ecosystem of Wyoming, Montana, and Idaho revolves around several obvious yet difficult questions. Are there more or fewer grizzly bears now than there were over two decades ago when this population was first protected under the U.S. Endangered

Species Act? Are different bears subject to different mortality risks? What should future grizzly bear management focus on?

Although the demography of Yellowstone's grizzly bears has been intensively studied (Cowan et al. 1974, Craighead et al. 1974, Shaffer 1978, Knight and Eberhardt 1984, 1985, Suchy et al. 1985, Dennis et al. 1991, Eberhardt et al. 1994, Foley 1994, Boyce 1995, Eberhardt 1995, Knight et al. 1995), controversies remain (Shaffer 1992, Mattson and Craighead 1994, Boyce 1995). For the most part, these disputes arise not from different scientists choosing to rely on different data sets and finding them in conflict, but rather from dif-

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ferent scientists relying on different assumptions when analyzing essentially the same data. Our present analysis uses these same data, makes its own assumptions (some novel and some not), incorporates previous analyses as special cases, and endeavors to explain how and why our results differ from those of previous studies.

Our analysis capitalizes both on earlier Yellowstone grizzly bear demographic research and on previous studies of grizzly bear behavior. Because humans have directly caused 70–90% of known grizzly bear deaths in the Yellowstone ecosystem since the 1970s (Mattson et al. 1996b, Mattson 1998), factors that influence the rates at which humans encounter and kill bears are preeminently important, not only in informing management but also in explaining heterogeneity in grizzly bear mortality rates. Previous work identified season, size of whitebark pine seed crop, and the habituation of bears to humans as important factors mediating human–bear interactions and affecting grizzly bear death rates (Mattson et al. 1991b, 1992, Blanchard and Knight 1995, Mattson 1998). However, most previous work did not involve direct estimates of the effect of these factors on the grizzly bear mortality rate itself. It instead computed relative, rather than absolute, mortality risks, or measured the effects of these variables on indirect surrogates of mortality, such as propensity to forage near roads.

The present analysis was motivated by these insights and several other issues. First, several large sampling biases contaminate the available demographic data from radiotelemetered bears (Eberhardt et al. 1994, Eberhardt 1995). Many of these biases have been previously identified and some have been accounted for. However, no existing analysis accounts for all known potentially significant sampling biases. Second, previous analyses rely on subsets of the available data and on conventional independent variables such as sex and age, rather than undertaking a systematic analysis of all available data and considering a wider class of potentially useful and conceptually relevant independent variables such as whitebark pine seed crop size and season. Last, although some previous analyses distinguish between bears that have never been management-trapped and those that have (Mattson et al. 1992, Boyce 1995, Eberhardt 1995), no analysis has considered an explicit source–sink demographic model of a population containing two coexisting behavioral types (never management-trapped/management-trapped at least once), or has estimated the rate at which bears move from the source to the sink (which we quantify using the management-trapping rate).

METHODS

Data

From 1975 to 1992, 202 grizzly bears were radiotelemetered in the Yellowstone ecosystem. Knight et al.

(1976), Blanchard (1985), and Knight and Eberhardt (1985) describe the procedures used to trap and handle bears and relocate radio-collared individuals during aerial overflights. Appendix A describes the four raw data sets containing demographic information gathered from these radiotelemetered bears. Some of these data were placed in the public domain in response to requests filed under the U.S. Freedom of Information Act.

We derived from the raw data, and included in our summary files, every date that an uncollared bear was trapped and fitted with a radio collar, the date of every relocation of each radio-collared bear (from *Flight reports*; see Appendix A), and the event that ended each such monitoring sequence. A monitoring sequence ended either when a bear died while wearing an active radio collar or when a live bear dropped its radio collar. We define collar drop broadly to include not only collars physically dropped but also those that became inactive for any reason. The summary files also list each bear's sex and year of birth and, for each relocation, whether it was visual or by radio signal only. The files also list the first date each bear was management-trapped, if any. On each date that a mature female was visually relocated, the summary files list the number of cubs (whether collared or not) seen accompanying her. Throughout, we use the term "cubs" narrowly, to mean cubs-of-the-year.

While constructing the input computer files, we identified various ambiguities and inconsistencies in the raw data. As detailed in Appendix A, we either resolved these problems or, in fewer cases, explicitly decided that they could not be resolved.

Parameter estimation

Sampling problems and bias.—Several major problems affect the Yellowstone grizzly bear demographic data obtained from radiotelemetered individuals.

1) Grizzly bear mortality rates are elevated in some seasons and years as compared to others (e.g., in the fall as compared to the winter, and in whitebark pine nonmast years as compared to mast years), and for some bear classes as compared to others (e.g., subadult males as compared to adult females, and for management-trapped bears as compared to those never management-trapped; Mattson et al. 1992). The potential for bias arises because relatively more data were obtained for certain seasons, years, and bear classes than others, implying that some were oversampled and others undersampled. This bias, if uncorrected, will cause mortality estimates to be biased high if high-mortality seasons, years, and bear classes were oversampled, and biased low in the opposite situation. Oversampling can occur because relatively more bears had an active radio collar during some seasons and years (because of variation in trapping intensity across seasons and years), or because certain bear classes were relatively more or less likely to be trapped and fitted with a radio collar.

2) Some cubs died between emergence from the den

TABLE 1. Model dependent variables. All females ≥ 4 yr old are assumed to be sexually mature.

Variable	Definition
Demographic parameters	
d	Instantaneous mortality rate (per day)
a_0	Probability of no reproduction (dimensionless) ($a_0 = 1 - a_1 - a_2 - a_3$)
a_1	Probability of a one-cub litter (dimensionless)
a_2	Probability of a two-cub litter (dimensionless)
a_3	Probability of a three-cub litter (dimensionless)
h	Instantaneous management-trapping rate (per day)
Sampling bias and sampling process parameters	
c	Instantaneous collar drop rate (per day)
r	Instantaneous relocation rate (per day)
s	Sighting probability (dimensionless)
g	Cub sighting probability (dimensionless)

and when their mother was first seen, and not all cubs were seen each time that their radio-collared mother was. If uncorrected, these biases cause fecundity estimates to be biased low.

3) The available data often did not provide the exact date of death or collar drop. Instead, the date of death or collar drop was known only to be between the dates of the penultimate and last relocations.

4) To compute a mortality rate, all analyses essentially divide the total number of deaths of bears with an active radio-collar by the total number of days these bears were monitored. In considering bears that lost their radio collar and were subsequently recollared and again monitored, some previous analyses incorrectly include the time between collar drop and recollaring in the denominator of the mortality estimator (Knight and Eberhardt 1985, Eberhardt et al. 1994; but see Eberhardt 1995 and Hovey and McLellan 1996). If uncorrected, this will cause the mortality rate to be biased low (Hovey and McLellan 1996).

Of these biases and problems, previous analyses accounted for the first three incompletely or not at all. We use the model discussed next to quantify both grizzly bear demography and these sampling processes that affect the data that we analyze. In this way, we address these four sampling problems and biases.

Dependent variables.—Our model contains five dependent variables describing grizzly bear demography (Table 1). These are the mortality (d) and management-trapping (h) rates and the annual probabilities of an adult (≥ 4 yr old) female giving birth to a one-, two-, or three-cub litter (a_1 , a_2 , and a_3 , respectively).

The model also contains four dependent variables describing sampling biases and sampling processes. These dependent variables are the collar drop rate (c) and relocation (r) rates, the probability of seeing a radio-collared bear when it is relocated (s ; henceforth "sighting probability"), and the probability of seeing a cub that is accompanying its collared mother, given that its mother was relocated and seen (g ; henceforth "cub sighting probability"). These are not of biological

interest themselves. The variables r and c are needed to estimate how sampling intensity changes across time and bear classes, allowing us to account for the sampling bias in the demographic variables (problem 1 in the preceding section). They are also needed to overcome the difficulty of uncertainty in the dates of death and collar drop (problem 3). The variable g allows us to account for the fecundity bias (problem 2). None of the demographic parameters depends on s . We estimate it to quantify heterogeneity across seasons and bear classes in sightability, a question of some current debate (Mattson 1997a).

Independent variables.—Each of the nine dependent variables is, potentially, a function of any or all independent variables. Indeed, the goal of the parameter estimation procedure described next is to determine, for each dependent variable, which independent variables have a statistically significant effect on it.

The independent variables that we consider (see Table 2) include sex, age (Age-1, Age-2, and Age-3), whether a bear has ever been management-trapped (Mgt), whitebark pine mast year status (Wbp-1, Wbp-2, Wbp-3), time period (before or after 1983), and season (Season-2, Season-3, and Season-4). Throughout, our notation suppresses the functional dependence of the dependent variables on the independent variables.

We scored age as three categorical variables that allowed us to isolate differences attributable to cubs (0 yr old), subadults (1–3 yr old) and senescent adults (≥ 13 yr old; Table 2). We classified each year as a whitebark pine mast or nonmast year, based on the frequency of pine seed in feces and evidence of use of pine seed at feeding sites associated with locations of

TABLE 2. Model independent variables.

Variable	States
Sex	state 0: male; state 1: female.
Age-1	state 0: 0 yr old; state 1: ≥ 1 yr old
Age-2	state 0: 0–3 yr old; state 1: ≥ 4 yr old
Age-3	state 0: 0–12 yr old; state 1: ≥ 13 yr old
Mgt	state 0: no management-trappings; state 1: one or more management-trappings
Season-2	state 0: January–May; state 1: June–December
Season-3	state 0: November–April; state 1: May–July; state 2: August–October
Season-4	state 0: December–February; state 1: March–May; state 2: June–August; state 3: September–November
Time period	state 0: 1975–1982; state 1: 1983–1992
Wbp-1	state 0: nonmast year; state 1: mast year†
Wbp-2	state 0: previous year was a mast year; state 1: previous year was a nonmast year
Wbp-3	state 0: 2 or more of 3 preceding years were nonmast years; state 1: 2 or more of 3 previous years were mast years

† Mast years: 1976, 1978–1980, 1985–1987, 1989–1992. Nonmast years: 1975, 1977, 1981–1984, 1988.

radio-marked bears. Our definition of a mast year corresponds roughly, but not precisely, to a year when >20 cones per tree, on average, were counted in permanent transects across the Yellowstone ecosystem. There was potential for error in this classification, in that there is considerable spatial heterogeneity in whitebark pine production not accounted for by average ecosystem production data. We included time period in our analysis to investigate Eberhardt's (1995) hypothesis that grizzly bear management activities differed enough before and after 1983 to warrant separate analyses of data over these two time periods.

Previous analyses of Yellowstone grizzly demography have not accounted for variation across the seasons in grizzly mortality or in other dependent variables. We accomplished this using independent variables that divide the months of the year into two, three, or four states (Season-2, Season-3, and Season-4, respectively). Each season variable corresponds to known differences among months in food availability, grizzly bear physiology, grizzly bear behavior, and/or human sampling effort. Specifically, the states of the Season-2 independent variables correspond to the period of hibernation (ending when the last age/reproductive classes emerge) vs. the remainder of the year; the states of Season-3 correspond to the main hibernation exclusive of late denning classes, active-season hypophagia (the period of little feeding activity) and hyperphagia (the period of heightened feeding activity); and the states of Season-4 correspond to the core period of hibernation, the period of foraging on ungulate carcasses (including hibernation of females with cubs of the year), the hiatus between carcass and pine seed availability, and the period of foraging on pine seeds (Table 2; see Judd et al. 1986).

Different seasonal variables were used to model the various dependent variables. The decisions were based primarily, but not entirely, on the amount of data available; the more data, the more seasons we considered. We used Season-2 to model g , primarily because of the paucity of data available. We used Season-3 for d , h , and c because relatively more data were available, and because Season-3 emphasizes known seasonal variation in levels of grizzly bear activity. Season-4 was used for r and s because even more data were available. Moreover, Season-4 should capture variation across the months in human effort expended in relocating radio-collared bears. This said, the season variables are somewhat arbitrary. We will discuss this in a more general context when we consider the inherently arbitrary nature of deciding what independent variables to include, or exclude, from an analysis.

The Individual Grizzly Bear Histories and Annual Reports of the Interagency Grizzly Bear Study Team databases (see Appendix A) explicitly distinguish between trappings done for management and research purposes. In our analysis, the management-trapping status independent variable (Mgt) has only two states.

On any given date, each bear has either never been management-trapped, or has been management-trapped at least once.

Nearly all of the management-trapping events that we identified were based on information in the Individual Grizzly Bear Histories or Annual Reports databases (see Appendix A). We scored any trapping listed in either of these two data sets as being for management purposes as a management trapping. These two databases were compiled well before our analysis commenced, and were the primary sources that we relied on in scoring management-trapping status. In addition, we also scored any trapping that satisfied one or more of the following criteria as being for management purposes: (1) the bear was transported after being trapped; (2) the Annual Reports indicate that the bear was euthanized after being trapped; (3) the trapping occurred in the following areas that have high human densities or are otherwise known to attract human-habituated bears: Big Springs, Idaho, Blanding Ranger Station, Brook Creek Lodge, Canyon development, Cooke City, Mikloich residence, Gardiner, Lake development, Madison Fork Ranch, Madison Junction, Pahaska, Rainbow Point, Sawtell Estates, Shoshone Lodge, Terpin Meadow, Tressell Ranch, or West Yellowstone.

Later in the paper, we show how the management-trapping status independent variable leads one to conclude that this population has a source-sink population structure. In the model to be presented, the source will consist of those bears never management-trapped, and the sink will consist of those management-trapped at least once. To fully specify this source-sink model, we made some assumptions about the inheritance of management-trapping status. In this regard, any cub born to a sow after she was management-trapped was scored as having one management-trapping at birth (Herrero 1985, Meagher and Fowler 1989). This is tantamount to assuming that the management-trapping status variable has perfect maternal inheritance.

We assume no density dependence. The independent variables that we include are easily and unambiguously scored. By contrast, allowing density-dependent mortality and fecundity would require including population density as an independent variable. The "unduplicated females with cubs of the year" measure used by Boyce (1995) and Knight et al. (1995) to quantify population size is subject to several large sampling biases (USFWS 1993, Craighead et al. 1995, Mattson 1997a). Moreover, although there are compelling theoretical reasons to believe that mortality and/or natality rates are necessarily density dependent, this has been difficult to actually demonstrate in bear populations (Taylor 1994, Craighead et al. 1995).

Simultaneous risk model.—The parameters that we estimated describe how the nine dependent variables (rates or probabilities) change as a function of independent variables (season, age, etc.). We estimated a

base value for each dependent variable, giving its value when all independent variables included in the model were in state 0. (In this context, "category" and "class" are synonyms for "state.") For each dependent variable, we estimated additional parameters describing the extent to which its base value is modified when a particular independent variable is in a state other than 0. As described in Appendix B, the terms modifying the base value combine multiplicatively to determine the dependent variable value. Our analysis assumes that each radio-collared bear is simultaneously subject to risks of mortality (d), management-trapping (h), collar drop (c), and relocation (r).

Maximum likelihood parameter estimation.—Following Heisey and Fuller (1985) and Pollock et al. (1989), we used a maximum likelihood approach to estimating demographic parameters from this radiotelemetry data set (Appendix B). Each model that we considered has a number of parameters whose numerical values are initially unknown. The maximum likelihood procedure starts with guesses at the value of these unknown parameters; our computer program then determines the probability of each datum (or more precisely, transition; Appendix B) contained in the actual data set, given the assumed numerical value of the model parameters. The numerical value of one or more model parameters is then changed slightly, and the process is repeated until the program converges on a set of numerical parameter values that maximize the overall probability of observing the series of transitions contained in the actual data. We used the downhill simplex method of Nelder and Mead (1965; see Press et al. 1992) to do this maximization.

Using AIC to choose among alternative models.—The most general model that could be described using the dependent and independent variables in Tables 1 and 2 has a huge number of parameters, well beyond the capability of computers available to us. Consequently, we started by investigating reduced models. These models differed from one another in the assumptions that they made concerning exactly which independent variables affected each dependent variable. We used the Akaike information criterion (AIC; Akaike 1973, Burnham and Anderson 1992, Lebreton et al. 1992, Burnham et al. 1995) to compare the fit to the data provided by alternative models. AIC is simply twice the sum of the negative of the log of the likelihood value plus the number of parameters that the model contains. We continued to iteratively add and delete independent variables (and hence, parameters) until this procedure arrived at a model that was locally stable. In other words, when we added or deleted each independent variable affecting each dependent variable, one at a time, we obtained an AIC value higher than that of the best model.

The difference between the AIC value of the best model and of an alternative model obtained by adding or deleting a particular independent variable is a rea-

sonable measure of the relative importance of that independent variable. Using an obvious notation, we define $\Delta = \text{AIC}_{\text{Alt}} - \text{AIC}_{\text{Best}}$. We further distinguish between values of Δ obtained by deleting an independent variable from our best model (Δ_-) and those obtained by adding an independent variable to it (Δ_+). By definition, all independent variables included in the best model have positive values of Δ_- , and all those omitted have positive values of Δ_+ . Large values of Δ_- indicate independent variables that have a major effect. Values of Δ_- and Δ_+ near 0 indicate independent variables whose effects are moderate. Large values of Δ_+ indicate independent variables whose effect is trivial.

Our parameter estimation procedure involved two levels of optimization. First, we specified a model by stating which independent variables did and did not influence each dependent variable, and determined the numerical values of this model's parameters by maximizing the likelihood function. Second, we compared models by minimizing the AIC.

Finite rate of increase

The finite rate of increase, $\hat{\lambda}$, gives the annual percentage change in population size. In organizing its calculation, we account for some subtle but critical differences in the effects of sex, age, management-trapping status, season, and whitebark pine seed crop size on grizzly mortality and fecundity. For each independent variable, we specify if and how bears move between its states.

Obviously, because bears do not change sex, they never move between states 0 and 1 of the independent variable Sex. By contrast, individuals move from one age class to the next at a fixed constant rate; in a year's time, each bear ages by exactly 1 yr. Bears also move from never management-trapped to management-trapped status, although not at a fixed rate. The seasons follow one another in the same fixed sequence, whereas mast and nonmast years appear in an unpredictable sequence.

In simple age-structured demographic models, there is no need to empirically estimate the rate at which individuals move between age classes, as this is known a priori. By contrast, because our analysis classified individuals by management-trapping status, to estimate the elements of our transition matrix, we first estimated the rate at which bears move from the non-management-trapped to the management-trapped subpopulations. This is simply the rate at which bears with no management-trapping events acquired their first management-trapping, a quantity that we estimated from the available data. This rate and an emigration probability estimated from mark-recapture data are analogous, in that both describe movement of individuals between subpopulations (Arnson 1972, Hestbeck et al. 1991, Spendlow et al. 1995).

Generalized Leslie matrix.—We accounted for the diverse effects of these independent variables on griz-

zly bear mortality and fecundity using a generalized Leslie matrix (Goodman 1969, Land and Rogers 1982). In contrast to a standard Leslie matrix, which classifies individuals according to age alone, this generalized Leslie matrix simultaneously classified individuals according to both age and management-trapping status. There are five age states (0, 1, 2, 3, and ≥ 4 yr) and two management-trapping states (management-trapped or not), so the population vector associated with this matrix has $5 \times 2 = 10$ elements. The generalized Leslie matrix has $10 \times 10 = 100$ elements. It contains four submatrices (Appendix C). The two diagonal submatrices correspond to the Leslie matrices for the non-management-trapped and management-trapped subpopulations, whereas the two off-diagonal submatrices quantify movement between the two subpopulations.

Each element in this matrix is the annual transition probability from one (age, management-trapping) pair to another. Many of these annual transition probabilities are 0, because certain transitions are prohibited. In particular, the entire upper right submatrix is entirely zeros, because the nature of the Mgt independent variable that we employ implies that no management-trapped bears ever become non-management-trapped, and because we assume that management-trapped sows produce only management-trapped offspring.

The elements of these generalized Leslie matrices are calculated from the demographic parameters estimated from the likelihood model (Table 3), using the procedures in Appendix C. Most matrix elements are computed using both the management-trapping (h) and mortality (d) rates (Appendix C). Some also involve fecundity (a_1 , a_2 , and a_3). These calculations account for sex in the usual manner, by using only female vital rates (Caswell 1989). They account for seasonal variation in the vital rates by breaking each annual transition probability into several pieces, corresponding to various seasons, and then reconstructing it from its seasonal parts. To account for the large differences in grizzly bear vital rates between whitebark pine mast and nonmast years, we derived a separate generalized Leslie matrix for each. Our overall estimate of $\hat{\lambda}$ is the appropriate geometric average of the lead eigenvalues of these two generalized Leslie matrices.

Uncertainty in $\hat{\lambda}$

We used three methods to quantify uncertainty in $\hat{\lambda}$. First, using methods described in Appendix C, we estimated the standard error of $\hat{\lambda}$. Second, some errors in the $\hat{\lambda}$ that we report arise not from sampling error per se, but from somewhat arbitrary decisions that we made. For example, we were unable to distinguish between collar loss and death in a few cases (Appendix A). Our best model assumes that these were all collar drops; however, we also estimated $\hat{\lambda}$ under the assumption that they were all deaths. The *Results* report on the $\hat{\lambda}$ estimated under this and several other alternative models.

Third, no analysis can consider all possible independent variables. Future analyses of this population's demography will undoubtedly focus on a somewhat different set of independent variables than we have, just as several independent variables that appeared to us to be important, but that had not been included previously, were important in motivating the present study. We do not consider spatial variables or interaction terms, for example, nor have we considered all ways in which the months of the year could be grouped (season variables). Thus, the independent variables that we investigated are a sample from a larger universe of independent variables that might conceivably be included in a Yellowstone grizzly bear demographic analysis.

We used a generalized jackknife procedure to investigate uncertainty introduced by using a limited subset of independent variables. In particular, we deleted each independent variable from our best model, one independent variable at a time, and recomputed $\hat{\lambda}$. This is analogous to a standard jackknife that sequentially deletes each datum from the actual data set and then recomputes parameter estimates.

We carried out this procedure separately on the demographic and the sampling independent variables. In particular, we computed $\hat{\lambda}$ for each model obtained by deleting a single significant independent variable from one of the demographic dependent variables (d , h , a_1 , a_2 , a_3). We then computed the sample standard deviation among the values of $\hat{\lambda}$ estimated from these reduced models and denoted it by $SE_{\Omega(\Delta)}$. We repeated this procedure for the sampling dependent variables (c , r , and g , but not s , because the demographic parameters that we estimated are completely independent of it). We denoted the sample standard deviation among the $\hat{\lambda}$ obtained from these reduced models by $SE_{\Omega(\Sigma)}$.

$SE_{\Omega(\Delta)}$ and $SE_{\Omega(\Sigma)}$ quantify a null case of randomly sampling the space of all conceivable independent variables. In practice, decisions about what variables to include and exclude from an analysis are very much art, and, one hopes, not random. It is useful to calculate $SE_{\Omega(\Delta)}$ and $SE_{\Omega(\Sigma)}$ because this forces one to explicitly acknowledge that any analysis of Yellowstone grizzly bear demography necessarily must sample from the space of all conceivable independent variables. We do not claim that past or future researchers have sampled, or will sample, this space randomly. But sample it they must. Null models are often useful, not because they are fully accurate, but because they force one to be more precise in quantifying and explicating sampling issues.

RESULTS

Our best model contains 43 parameters (Table 3). This includes seven parameters describing the mortality rate (d), three for fecundity (a_1 , a_2 , a_3), seven for the management-trapping rate (h), five for the collar drop rate (c), nine for the relocation rate (r), eight for

TABLE 3. Grizzly bear demography parameter estimates, with additional parameter estimates describing sampling biases and processes.

Dependent variable interpretation	Exponent [†] ± 1 SE	Multiplier [‡] ± 1 SE
Mortality rate (<i>d</i>)		
Base rate (all in state 0)	-9.1 $\pm$ 0.1	0.00012 d ⁻¹ $\pm$ 0.00001
Females§ (Sex state 1)	-0.56 $\pm$ 0.2	0.57 $\pm$ 0.09
Yearlings and older (Age-1 state 1)	-0.14 $\pm$ 0.1	0.87 $\pm$ 0.09
Management-trapped (Mgt state 1)	0.63 $\pm$ 0.1	1.9 $\pm$ 0.3
Summer (Season-3 state 1)	2.1 $\pm$ 0.2	8.5 $\pm$ 2
Autumn (Season-3 state 2)	2.9 $\pm$ 0.1	18 $\pm$ 2
Most years (Wbp-1 state 1)	-0.48 $\pm$ 0.1	0.62 $\pm$ 0.09
Probability of a 1-cub litter (<i>a</i> ₁)	-3.3 $\pm$ 0.6	0.04 $\pm$ 0.02
Probability of a 2-cub litter (<i>a</i> ₂)	-1.9 $\pm$ 0.2	0.16 $\pm$ 0.04
Probability of a 3-cub litter (<i>a</i> ₃)	-1.7 $\pm$ 0.2	0.19 $\pm$ 0.04
Management-trapping rate (<i>h</i>)		
Base rate (all in state 0)	-10.0 $\pm$ 0.1	0.000045 d ⁻¹ $\pm$ 0.000004
Yearlings and older (Age-1 state 1)	-1.0 $\pm$ 0.1	0.37 $\pm$ 0.04
Adults (Age-2 state 1)	-0.50 $\pm$ 0.1	0.61 $\pm$ 0.08
Management-trapped (Mgt state 1)	2.1 $\pm$ 0.1	8.5 $\pm$ 0.9
Summer (Season-3 state 1)	3.0 $\pm$ 0.2	20 $\pm$ 4
Autumn (Season-3 state 2)	4.0 $\pm$ 0.1	52 $\pm$ 6
Most years (Wbp-1 state 1)	-0.86 $\pm$ 0.2	0.42 $\pm$ 0.07
Collar drop rate (<i>c</i>)		
Base rate (all in state 0)	-7.2 $\pm$ 0.06	0.00077 d ⁻¹ $\pm$ 0.00005
Females (Sex state 1)	-0.43 $\pm$ 0.09	0.65 $\pm$ 0.06
Summer (Season-3 state 1)	1.4 $\pm$ 0.1	4.0 $\pm$ 0.4
Autumn (Season-3 state 2)	1.3 $\pm$ 0.1	3.8 $\pm$ 0.4
After 1983 (Time Period state 1)	0.26 $\pm$ 0.07	1.3 $\pm$ 0.1
Relocation rate (<i>r</i>)		
Base rate (all in state 0)	-4.412 $\pm$ 0.009	0.0121 d ⁻¹ $\pm$ 0.0001
Females (Sex state 1)	0.26 $\pm$ 0.01	0.77 $\pm$ 0.02
Adults (Age-2 state 1)	0.05 $\pm$ 0.01	1.05 $\pm$ 0.01
Management-trapped (Mgt state 1)	0.16 $\pm$ 0.01	1.17 $\pm$ 0.02
Spring (Season-4 state 1)	1.69 $\pm$ 0.02	5.4 $\pm$ 0.1
Summer (Season-4 state 2)	2.39 $\pm$ 0.01	10.9 $\pm$ 0.2
Autumn (Season-4 state 3)	2.09 $\pm$ 0.02	8.1 $\pm$ 0.1
After 1983 (Time Period state 1)	-0.58 $\pm$ 0.01	0.561 $\pm$ 0.007
Most years (Wbp-1 state 1)	0.11 $\pm$ 0.01	1.12 $\pm$ 0.01
Sighting probability (<i>s</i>)		
Base probability (all in state 0)	-3.88 $\pm$ 0.03	0.0206 $\pm$ 0.0006
Females (Sex state 1)	0.16 $\pm$ 0.04	1.17 $\pm$ 0.05
Oldtimers (Age-3 state 1)	0.28 $\pm$ 0.07	1.33 $\pm$ 0.09
Management-trapped (Mgt state 1)	0.18 $\pm$ 0.04	1.20 $\pm$ 0.05
Spring (Season-4 state 1)	1.61 $\pm$ 0.06	5.0 $\pm$ 0.3
Summer (Season-4 state 2)	1.44 $\pm$ 0.05	4.2 $\pm$ 0.2
Autumn (Season-4 state 3)	1.02 $\pm$ 0.06	2.8 $\pm$ 0.2
After 1983 (Time Period state 1)	0.14 $\pm$ 0.04	1.15 $\pm$ 0.05
Cub sighting probability (<i>g</i>)		
Base probability (all in state 0)	-0.29 $\pm$ 0.02	0.75 $\pm$ 0.01
Management-trapped (Mgt state 1)	-0.30 $\pm$ 0.09	0.74 $\pm$ 0.07
Summer and later (Season-2 state 1)	0.11 $\pm$ 0.02	1.12 $\pm$ 0.02
After 1983 (Time Period state 1)	0.12 $\pm$ 0.02	1.13 $\pm$ 0.02

[†] This is k_{ij} or v_{ij} ; see Appendix B.

[‡] This is $e^{k_{ij}}$ or $e^{v_{ij}}$ of Appendix B. As discussed in Appendix B and the text, these values combine multiplicatively to determine the rate or probability value.

§ Applies only to yearlings and older; see Appendix B.

the sighting probability (*s*), and four for the cub sighting probability (*g*).

Using the data in Table 3, one can reconstruct the value of any dependent variable. For example, the sighting probability of a management-trapped female in the autumn of 1980 is 0.08, computed as the base probability (0.0206), multiplied by the modifier terms for females (1.17), management-trapping (1.20), and autumn (2.8). The base probability is not multiplied by the time period modifier, because this independent vari-

able is in its ground state in 1980 (Table 2). As a second example, the management-trapping rate of a sexually mature, wary female during the autumn of a whitebark pine mast year is (0.000045)(0.37)(0.61)(52)(0.42) = 0.00022 female/d. On average, it would take 1/0.00022 = 4545 d, or ~12 yr, before this bear was management-trapped for the first time, assuming that it did not die beforehand and that the mortality rate of a mast-year autumn applied to this entire 12-yr period.

Because the 202 bears in our analysis are a sample

of the entire population, there is uncertainty in the estimated parameter values presented in Table 3. We quantify this uncertainty by presenting the SE (standard error) of each parameter. Importantly, SE is not a measure of the temporal variation in any parameter due, for example, to environmental stochasticity. It is a measure of the uncertainty in the parameter that arises from the parameter being estimated from a finite sample (Pease and Fowler 1997). By contrast, the different mortality rates estimated for mast and nonmast years are an estimate of environmental stochasticity.

Demographic parameter estimates.—Grizzly bear mortality rate (d) varies significantly as a function of Season-3 ($\Delta_- = 57$), management-trapping status (Mgt, $\Delta_- = 4.6$), Sex ($\Delta_- = 4.3$), and whitebark pine crop size (WBP-1, $\Delta_- = 1.8$). We find no effect of Age-2 ($\Delta_+ = 0.7$), Time period ($\Delta_+ = 1.8$), or Age-3 ($\Delta_+ = 2.0$). The effect of season on mortality, as quantified by its Δ_- value, is an order of magnitude larger than the effect of any of the other independent variables. This is also true for the effect of season on other dependent variables.

The management-trapping rate (h) varies with Season-3 ($\Delta_- = 103$), management-trapping status (Mgt, $\Delta_- = 52$), whitebark pine crop size (WBP-1, $\Delta_- = 11$), Age-1 ($\Delta_- = 3.1$), and Age-2 ($\Delta_- = 2.5$). It is not a function of Time Period ($\Delta_+ = 1.0$), Sex ($\Delta_+ = 1.2$), or Age-3 ($\Delta_+ = 2.0$). Previous analyses have not estimated the management-trapping rate.

Fecundity (a_1 , a_2 , and a_3) is not affected by current-year whitebark pine crop size (WBP-1, $\Delta_+ = 1.2$), Time period ($\Delta_+ = 3.0$), prior year whitebark pine crop sizes (WBP-2, $\Delta_+ = 5.7$; WBP-3, $\Delta_+ = 5.1$), the mother's management-trapping status (Mgt, $\Delta_+ = 4.1$), or her age (Age-3 $\Delta_+ = 5.7$).

Our model parameterizes fecundity using the annual probabilities of producing a litter of various sizes, whereas most analyses of large-mammal demography parameterize it using age at first reproduction, mean litter size, and interbirth interval. Although we need not explicitly compute these latter three quantities to compute $\hat{\lambda}$, doing so facilitates comparison with other studies and expresses our results in an intuitively understandable way. We estimate that a fraction ($0.04 + 0.16 + 0.19 = 0.39$) of the females give birth each year. Because our model implicitly assumes a geometric distribution of interbirth intervals, the mean interbirth interval is $\sum_{i=1}^{\infty} 0.39i(1 - 0.39)^{i-1} = 2.6$ yr. Our estimate of mean litter size at den emergence on 15 April is $(0.04 + 2 \times 0.16 + 3 \times 0.19)/0.39$, or 2.4 cubs. Our analysis assumes that age at sexual maturity is 4 yr, and we estimate that mean age of first reproduction is $0.39 \sum_{i=0}^{\infty} (i + 4)(1 - 0.39)^i$, or 5.6 yr. We assume a 1:1 primary sex ratio.

Sampling parameter estimates.—The collar drop rate is influenced by Season-3 ($\Delta_- = 57$), Sex ($\Delta_- = 6.5$), and Time period ($\Delta_- = 1.2$), but not by whitebark pine crop size (WBP-1, $\Delta_+ = 0.3$), management-trapping

status (Mgt, $\Delta_+ = 1.8$), or age (Age-1, $\Delta_+ = 2.0$; Age-2, $\Delta_+ = 0.6$; Age-3, $\Delta_+ = 1.2$). The relocation rate is influenced by Season-4 ($\Delta_- = 3191$), Time period ($\Delta_- = 618$), Sex ($\Delta_- = 129$), management-trapping status (Mgt, $\Delta_- = 46$), white bark pine crop size (WBP-1, $\Delta_- = 22$), and Age-2 ($\Delta_- = 0.9$). It is not influenced by Age-1 ($\Delta_+ = 0.8$) or Age-3 ($\Delta_+ = 1.9$). The sighting probability is influenced by Season-2 ($\Delta_- = 71$), Age-3 ($\Delta_- = 10$), management-trapping status (Mgt, $\Delta_- = 6.0$), Sex ($\Delta_- = 3.2$), and Time period ($\Delta_- = 2.7$), but not by whitebark pine crop size (WBP-1, $\Delta_+ = 1.9$), Age-1 ($\Delta_+ = 1.8$), or Age-2 ($\Delta_+ = 1.0$). The cub sighting probability is influenced by management-trapping status (Mgt, $\Delta_- = 9.2$), Time period ($\Delta_- = 1.0$), and Season-2 ($\Delta_- = 0.1$), but not by whitebark pine crop size (WBP-1, $\Delta_+ = 1.6$).

Estimate of $\hat{\lambda}$.—The generalized Leslie matrices for mast and nonmast years are given in Table 4. We denote the lead eigenvalues of these two matrices by $\hat{\lambda}_M$ and $\hat{\lambda}_N$, respectively. The population declines 5% in whitebark pine nonmast years ($\hat{\lambda}_N = 0.95 \pm 0.04$ [mean ± 1 SE]) and increases 7% in mast years ($\hat{\lambda}_M = 1.07 \pm 0.04$). Accounting for the 11 mast and 10 nonmast years between 1975 and 1995, $\hat{\lambda} = \hat{\lambda}_M^{(11/21)} \hat{\lambda}_N^{10/21} = 1.01 \pm 0.04$. For the 1975–1983 and 1984–1995 intervals (four mast and five nonmast; seven mast and five nonmast, respectively), we find $\hat{\lambda} = 1.00$ and 1.02, respectively.

Sources of uncertainty and error in $\hat{\lambda}$.—The standard error of λ (see Appendix C) quantifies uncertainty arising from sampling error. Because a Gaussian distribution with mean 1.01 and standard deviation of 0.04 has ~40% of its probability mass below 1.00, there is an approximate 40% probability that the number of Yellowstone grizzlies has declined from 1975 to 1995, and, conversely, a 60% chance that the population increased over this time.

In a few cases, we were unable to distinguish between collar loss and death (Appendix A). The model in Table 3 assumes that they were all collar drops; when we instead assume they were all deaths, we obtain $\hat{\lambda} = 1.00$. When we assume that management-trapped sows produce all non-management-trapped cubs, we obtain $\hat{\lambda} = 1.04$. Finally, we estimated λ under the assumption that collar drops and deaths whose exact time of occurrence was unknown occurred at either the first conceivable date of collar drop or death ($\hat{\lambda} = 1.01$), or the last ($\hat{\lambda} = 1.04$; Appendix A). By contrast, the model in Table 3 effectively, although implicitly, estimates the exact time of collar drop or death when it is not known exactly. Although, in our view, these models are all less defensible than our best model, there is scope for different interpretations of the available data.

We computed $\hat{\lambda}$ for each of the nine models obtained by deleting a single significant independent variable from one of the demographic dependent variables (d , h , a_1 , a_2 , a_3 ; see Table 3). (One cannot remove Age-1 from d ; see Appendix B.) The average $\hat{\lambda}$ for these nine models was 1.01. The sample standard deviation among

TABLE 4. Generalized Leslie matrices for females in mast and nonmast years.†

$L_{\text{nonmast}} =$	0	0	0	0.35	0.37	0	0	0	0	0
	0.60	0	0	0	0	0	0	0	0	0
	0	0.77	0	0	0	0	0	0	0	0
	0	0	0.77	0	0	0	0	0	0	0
	0	0	0	0.77	0.80	0	0	0	0	0
	0	0	0	0.04	0.04	0	0	0	0.35	0.35
	0.19	0	0	0	0	0.68	0	0	0	0
	0	0.09	0	0	0	0	0.76	0	0	0
	0	0	0.09	0	0	0	0	0.76	0	0
	0	0	0	0.02	0.02	0	0	0	0.76	0.76
$L_{\text{mast}} =$	0	0	0	0.40	0.41	0	0	0	0	0
	0.78	0	0	0	0	0	0	0	0	0
	0	0.87	0	0	0	0	0	0	0	0
	0	0	0.87	0	0	0	0	0	0	0
	0	0	0	0.87	0.89	0	0	0	0	0
	0	0	0	0.02	0.01	0	0	0	0.39	0.39
	0.10	0	0	0	0	0.79	0	0	0	0
	0	0.04	0	0	0	0	0.84	0	0	0
	0	0	0.04	0	0	0	0	0.84	0	0
	0	0	0	0.04	0.03	0	0	0	0.84	0.84

† The population vector has 10 elements. The first five correspond to non-management-trapped individuals aged 0, 1, 2, 3, and ≥ 4 , respectively. The second five describe the management-trapped subpopulation.

these nine models was $SE_{\Omega(\Delta)} = 0.02$. Repeating this procedure on the sampling dependent variables (c , r , and g , but not s , because the demographic parameters we estimate are completely independent of it), we find that the average $\hat{\lambda}$ of these 12 models is 1.01, with a sample standard deviation of $SE_{\Omega(\Sigma)} = 0.004$.

DISCUSSION

We conclude that, within the limits of uncertainty implied by the available data, the size of the Yellowstone grizzly bear population changed little from 1975 to 1995. The population probably increased in whitebark pine crop mast years and declined in years when this crop failed.

Uncertainty.—We used three methods to measure uncertainty. Here, SE measures the expected error, because our results are based on a finite sample of bears. Our estimated SE of 0.04 corresponds to a confidence interval for $\hat{\lambda}$ extending from 0.93 (7% per annum decline) to 1.09 (9% per annum increase). The alternative models obtained by changing various assumptions produced $\hat{\lambda}$ values ranging from 1.00 to 1.04, suggesting that these assumptions were relatively less important than sampling error. Finally, the null model of random sampling from the space of all conceivable independent variables suggests that future analyses that modify the independent variables assumed to affect the demographic variables may significantly change $\hat{\lambda}$ ($SE_{\Omega(\Delta)} = 0.02$), whereas modifying independent variables affecting the sampling variables may be less important to $\hat{\lambda}$ ($SE_{\Omega(\Sigma)} = 0.004$). Overall, there is large uncertainty. Thus, although our best estimate is of a slightly expanding population from 1975 to 1995, there is a substantial probability that the population actually declined over this time interval. In the face of this un-

certainty, there is every reason to implement a cautious management strategy.

What does $\hat{\lambda}$ represent?—The $\hat{\lambda}$ that we estimate is best viewed as a retrospective summary of changes in the Yellowstone grizzly bear population size from 1975 to 1995. The demographic data from radiotelemetered bears that we use to estimate the demographic parameters in Table 3 encompass the period 1975–1992. However, in estimating $\hat{\lambda}$, we use the frequency of mast and nonmast years in the entire 1975–1995 period. We have not analyzed any radiotelemetry data from 1993 to 1995; they are not currently in the public domain. Based on the whitebark pine crop failures in these three years (Knight and Blanchard 1995), we predict that future analyses will show an overall 14% reduction in grizzly population size over this 3-yr period. We do know that there were many grizzly bear deaths from 1993 to 1995 (H. Pac, Montana Department of Fish, Wildlife, and Parks, Bozeman, Montana, *personal communication*).

Our analysis is useful for making predictions about how this population will behave in the future. However, it would be naive simply to extrapolate our $\hat{\lambda}$ into the future. This would involve assuming that current environmental conditions will not change, an assumption that is contrary to the widely predicted future increases of the number of humans in Yellowstone, and to the predicted future impact of global warming. Somewhat less simplistically, one could base future management on both the estimate of $\hat{\lambda}$ itself and its confidence interval, thereby providing future management with an appropriate margin of error. The approach we advocate is even more subtle. In planning future management, we advocate using our model to identify independent variables having a crucial effect on grizzly bear vital

TABLE 5. Comparison of our results to those of Eberhardt et al. (1994), Eberhardt (1995), and Boyce (1995).

Change in our analysis	Amount that our $\hat{\lambda}$ changes from:	
	Eberhardt et al. (1994)	Eberhardt (1995) and Boyce (1995)
Mortality rate bias	+0.07	=†
Pool mortality rates of non-management-trapped and management-trapped bears	-0.05	=
Assume non-management-trapped bears never become management-trapped	+0.08	+0.08
Assume no effect of season on mortality	-0.02	-0.02
Assume no effect of whitebark pine crop size on mortality	+0.01	+0.01
Fecundity bias	-0.02	-0.02
Cub mortality rate bias	+0.00	+0.00
Use 1983–1994 data	=	+0.01
First reproduction at age 5 yr	-0.02	=
Total differences	+0.05	+0.06
Our $\hat{\lambda}$ + differences accounted for	1.06	1.07
Their $\hat{\lambda}$	1.05	1.05

† The equality sign indicates that our analysis and theirs were equivalent in this respect.

rates, and then to develop an understanding of future trends in the value of these independent variables.

Comparing Yellowstone grizzly bear studies

Comparison of $\hat{\lambda}$ to direct estimates of population size.—One can estimate the finite rate of increase either as fecundity minus mortality (as we have done, albeit with some elaborations), or by directly counting or estimating the number of individuals alive at two or more points in time. Although there is much uncertainty associated with all direct estimates of the size of Yellowstone's grizzly bear population, the available studies are broadly consistent with a population that has varied little in size over the period of our study. Studies published in the early 1980s (Blanchard and Knight 1980, Roop 1980, McCullough 1981) and in the mid-1990s (Mattson et al. 1995, Eberhardt and Knight 1996) are remarkably consistent in estimating that, at the time each estimate was made, there were, most likely, 300–350 bears. An estimate of ~200 bears made by Craighead et al. (1974) has been criticized (Cowan et al. 1974, McCullough 1981) because it assumes that the population contains few backcountry bears (non-management-trapped or wary bears, in our terminology).

The dramatic increases in Yellowstone grizzly bear numbers over the last two decades implied by the values of $\hat{\lambda}$ estimated by Eberhardt et al. (1994), Eberhardt (1995), and Boyce (1995) appear to us to be broadly inconsistent with direct estimates of population size made over this period. Starting with $\hat{\lambda} = 1.05$ estimated by Eberhardt et al. (1994) for 1975–1992, if we assume a population size of 300 bears in 1975, we predict a population of $300 \times 1.05^{18} = 720$ bears in 1992. Similarly, starting with $\hat{\lambda} = 1.05$ estimated by Eberhardt (1995) and Boyce (1995) for 1983–1994, if we assume a population of 300 grizzlies in 1983, we predict a population of 540 in 1994. Even assuming a 1975 population of 200, the $\hat{\lambda}$ of 1.05 estimated by Eberhardt et al. (1994) implies a 1992 population of 460. Starting with our $\hat{\lambda} = 1.01$ for 1975–1995, and assuming a

population of 300 bears in 1975, we predict a 1995 population of 370 bears. Ideally, one would undertake a more precise comparison of these studies, for example by comparing confidence intervals. However, this is difficult because of the nonstandard and biased methods used to directly estimate numbers of Yellowstone bears (Craighead et al. 1995, Mattson 1997a, 1998), and because the different direct estimates that we have cited were often obtained using divergent methods.

Why is our $\hat{\lambda}$ different from theirs?—To compare predictions obtained by different researchers who analyzed essentially the same data, it is wholly inadequate to rely on the confidence interval. Using data from 1975 to 1992, Eberhardt et al. (1994) estimate $\hat{\lambda} = 1.05$. Using data primarily, but not solely, from 1983 to 1994, Eberhardt (1995) and Boyce (1995) also estimate $\hat{\lambda} = 1.05$. The differences between their results and ours are real, even though their estimate falls within our 95% CI (0.93, 1.09). There is no issue of statistical significance. Our confidence interval quantifies the amount that we would expect our $\hat{\lambda}$ to change if we were to gather data from an entirely different sample of 202 Yellowstone grizzly bears and were to analyze these new data using exactly the methods that we employ here. Importantly, Eberhardt et al. (1994), Eberhardt (1995), and Boyce (1995) had essentially (although not always exactly) the same data available as we had. They got a different answer because they used a different method of analysis.

Previous analyses of these data account fully for sex and age, partially for management-trapping status, and not at all for season or whitebark pine seed crop size (Cowan et al. 1974, Craighead et al. 1974, Shaffer 1978, Knight and Eberhardt 1985, Eberhardt et al. 1994, Boyce 1995, Eberhardt 1995). In every significant respect, the analyses of Eberhardt et al. (1994), Eberhardt (1995), and Boyce (1995) are subsumed as special cases of ours (Table 5). Surprisingly, the expanded set of independent variables that we investigated, while explaining some differences between our

TABLE 6. Predicted fraction of population in various age, sex, and management-trapping classes.

Age class	Females	Males	Both sexes
Non-management-trapped			
Cubs	0.03	0.03	0.07
Subadults	0.05	0.04	0.10
Adults	0.08	0.03	0.11
All age classes	0.16	0.11	0.27
Management-trapped			
Cubs	0.09	0.09	0.18
Subadults	0.18	0.11	0.29
Adults	0.20	0.05	0.25
All age classes	0.47	0.26	0.73

analysis and others, is not the primary source of differences.

We identified several specific ways in which their method of analysis differs from ours (see Table 5). We then changed our analysis so that it corresponded to the methods they used, and recomputed our $\hat{\lambda}$ under their assumption. In this way, we dissected out, one at a time, the reasons their results differ from ours, and the impact of each difference on our $\hat{\lambda}$. The $\hat{\lambda}$ of Eberhardt et al. (1994) is higher than ours primarily because of the mortality bias discussed previously (inflating the denominator of the mortality estimator with uncollared bears; Hovey and McLellan 1996). Eberhardt (1995) and Boyce (1995) corrected this mortality bias, and recognized the existence of non-management-trapped and management-trapped subpopulations. Although their analysis recognizes that non-management-trapped bears have lower mortality rates than management-trapped bears, their $\hat{\lambda}$ is based primarily on the fecundity and mortality of the non-management-trapped subpopulation. This is tantamount to assuming that no non-management-trapped bear ever becomes management-trapped (or that there is no flow from the source to the sink), and it causes their $\hat{\lambda}$ to be biased high. However, it should be noted that they define the non-management-trapped subpopulation somewhat differently than we do, as those bears whose first trapping was not for management purposes. Their estimates of non-management-trapped mortality include mortality that occurs after a member of this subpopulation becomes management-trapped.

What fraction of this population is management-trapped?—Our analysis predicted that 73% of the population is management-trapped (Table 6); however, we believe that it overpredicted this percentage. By our definition and assumptions, the management-trapped subpopulation includes both management-trapped bears and the offspring of female management-trapped bears. Non-management-trapped bears are found primarily in the backcountry (Mattson et al. 1992) and many use army cutworm moth (*Euxoa auxiliaris*) aggregation sites on the Shoshone National Forest as an important backcountry food source (Mattson et al.

1991a, French et al. 1994). The amount of backcountry habitat available in the Yellowstone ecosystem and the number of bears seen at moth sites on the Shoshone National Forest suggest to us that <73% of this population is non-management-trapped. Potential explanations for this discrepancy include the following points. (1) Our assumption that management-trapped bears never become non-management-trapped is incorrect. (2) Our assumption that management-trapped bears always produce management-trapped offspring is incorrect. (3) We have overestimated the mortality rate of the non-management trapped subpopulation. (4) We have overestimated the rate at which non-management-trapped bears become management-trapped.

Although both (1) and (2) seem unlikely to us, given the available data and ease with which grizzly bears learn about new food resources (Meagher and Fowler 1989, Mattson et al. 1991a, b), they may be true to some small extent. Possibilities (3) and (4) are more plausible; they would arise if some of the non-management-trapped bears in our analysis already had some of the behavioral characteristics and associated mortality risks of management-trapped bears.

Behavioral demography

Our analysis builds on previous research showing that grizzly bears rapidly alter their behavior in response to humans, and that humans are the primary source of grizzly bear mortality (Joep 1985, Craighead et al. 1988, Knight et al. 1988a, McLellan and Shackleton 1988, 1989, Gilbert 1989, Dalle-Molle and Van Horn 1989, Meagher and Fowler 1989, Mattson 1990, Mattson et al. 1992, 1996a, b, Gunther 1994, Mattson 1998). For a demographic analysis to adequately account for heterogeneity in mortality risk among bears, it must categorize the behavior of each grizzly bear toward humans, and determine how mortality risk varies across behavioral categories.

Ideally, we would have directly and objectively measured the behavior of all bears in our data set. However, the only available records of directly observed grizzly bear behavior are highly anecdotal, and many of the bears in question are now dead. Moreover, bear behavior is notoriously idiosyncratic, depending on the prompts and environmental circumstances to which behavior is manifested (Herrero 1985, Gilbert 1989). Finally, we define grizzly behavior toward humans broadly, to encompass not only grizzly behavior in direct human-grizzly encounters, but also grizzly behavioral responses to roads, developments, garbage dumps, and other human features of the landscape. For these reasons, the independent variables that we employ to quantify grizzly bear behavior are all proxies for actual bear behavior.

Interpreting management-trapping status.—In interpreting our results, we consider the bears that have never been management-trapped to be wary and the management-trapped bears to be conditioned to hu-

mans. However, this proposition, although amply supported, is above and beyond what one needs to accept our estimate of λ . The λ that we present is based on the differences in mortality rates of bears according to management-trapping status, on our estimate of the rate at which bears never before management-trapped are management-trapped for the first time, and on our estimate of the effects of other independent variables on grizzly bear vital rates.

We know of no evidence supporting the idea that trapping grizzly bears causes them to become conditioned to humans. Rather, the available evidence suggests that soon after a bear becomes human-conditioned, it does something to precipitate a management response. Examples include raiding a campground, killing livestock, or foraging too close to a development. In this way, management-trapping is potentially one of the first unambiguous manifestations of conditioning to humans (Herrero 1985, Meagher and Fowler 1989), and thereby provides an objective record of a bear losing its fear of humans. This justifies our view of management-trapping status as a proxy for underlying behavioral variables, although this is best construed as a hypothesis warranting testing, rather than a firm conclusion.

There are data from Yellowstone that are useful for testing the proposition that management-trapped bears are conditioned to humans. Prior to and independent of our decision to use management-trapping as a proxy for conditioning to humans, D. J. Mattson twice classified the radio-collared bears in our data set as either wary or conditioned to humans, based on a number of subjective and objective criteria. The first classification was done with input from two members of the Inter-agency Grizzly Bear Study Team, and the second was done by D. J. Mattson alone, two years later, without reference to the first. We eventually discarded these classifications, because they implicitly assume that no bear's status changes during its lifetime, making it impossible to compute the rate at which wary bears become conditioned. The final classification of each bear's behavior using management-trapping status is correlated with D. J. Mattson's first ($r = 0.60$, $SE = 0.05$) and second ($r = 0.72$, $SE = 0.05$) prior classifications.

How sex, age, etc., measure behavior.—Similarly, we consider sex, age, season, and whitebark pine crop size to be proxies for grizzly bear behavioral patterns associated with different mortality risks. Whitebark pine is a critical fall grizzly bear food in the Yellowstone ecosystem (Mattson et al. 1991b). Grizzly bears do not starve to death when the whitebark pine crop fails. Instead, they change their behavior. Rather than foraging in the high-elevation whitebark pine stands where humans are sparse, they forage at lower elevations, where humans are more common. This behavioral shift directly increases grizzly bear mortality (Mattson et al. 1992), as well as increasing mortality

via a second, more delayed and insidious, pathway. The increased contact of humans and bears increases the number of human-conditioned bears in the ecosystem. These newly human-conditioned grizzly bears are then subject to a higher mortality rate in all future years, including mast years (Meagher and Fowler 1989).

Among Yellowstone's grizzly bears, ungulate carcass scavenging is heaviest in the spring, fish and root use are heaviest in the summer, and whitebark pine seed use is heaviest in the late summer and autumn (Mattson et al. 1991b). These food resources are found at specific locations, with associated, predictable opportunities for interactions with humans. The impetus to feed, along with potential willingness to tolerate nearness of humans, also varies with season, peaking in August to October (Mattson 1990, 1997b, Mattson et al. 1991b). In this way, the large effect of season on the mortality and management-trapping rates is likely to be a proxy for the different behaviors inherent in exploiting food resources available at different times of the year and for the underlying physiological changes.

The behavior of Yellowstone's grizzly bears also varies with sex and age, in ways likely to affect risk of mortality. For example, adult males are more mobile (Blanchard and Knight 1991), eat more ungulate meat (Mattson 1997c), and account for more predation on livestock (Mattson 1990) compared to other sex and age classes. They are also less likely to be conditioned to humans and more likely to use backcountry areas (Mattson et al. 1992). Unlike females, males <4 yr old tend to disperse to areas outside their natal ranges (Blanchard and Knight 1991). Thus, young males are predisposed to conflict with humans because they are mobile, use unfamiliar areas, and are often conditioned to humans, especially in contrast to adult males. Conversely, adult males precipitate disproportional conflict with humans where they prey on livestock.

Demography and behavior in general.—Those researchers wishing to combine behavior and demography have perhaps been stymied by the difficulty of objectively measuring behavioral determinants of fecundity and mortality. Common independent variables employed by demographic analyses, such as sex and age, may often be proxies for underlying behavioral variables. Inasmuch as animals are distinguished from the nonliving world by their ability to reproduce and learn, it is sensible that demography and behavior should play a central role in ecological theory.

Yellowstone grizzly bear management

Past management.—If our main conclusion that the Yellowstone grizzly bear population has changed little in size over the last two decades is correct, how can one account for the major grizzly bear management initiatives, such as dump closures and other sanitation of human facilities, that were implemented over this period and that are widely regarded as successful (cf. Gunther 1994)? Almost all grizzlies that die in the Yel-

lowstone ecosystem are killed by humans (Mattson et al. 1996a, Mattson 1998), and the last two decades have seen increasing numbers of people living and recreating in good grizzly bear habitat, aided by increases in road and trail access (Clark and Minta 1994). We conjecture that there have, in fact, been real improvements in grizzly bear management over the last two decades. However, although these have successfully negated grizzly losses from an increasing number of humans in the ecosystem, they have not produced any substantial net improvement in the grizzly bear population's status (Mattson 1998).

We agree with Eberhardt (1995) that the 1983–1992 period was favorable for grizzly bears in Yellowstone. He compares population growth rates for the pre- vs. post-1983 time periods, and suggests that grizzly bear management was improved during 1983–1992 as compared to 1975–1982. Our analysis suggests the alternative explanation that the favorable period was due to large whitebark pine seed crops. Whitebark pine mast years were more common from 1983 to 1992 (70% mast years; $\hat{\lambda} = 1.07^{7/10} 0.95^{3/10} = 1.03$) than they were from 1975 to 1982 (50% mast years; $\hat{\lambda} = 1.07^{4/8} 0.95^{4/8} = 1.01$). We find no effect of time period (before or after 1983) on the rates of mortality or management-trapping, but do find a strong effect of whitebark pine seed crop size (Table 3). This suggests that grizzly mortality is determined by whitebark pine seed crop size.

Future management problems: whitebark pine and people.—Whitebark pine is at considerable risk of major declines within the next 100 yr. White pine blister rust (*Cronartium ribicola*), an introduced pathogen, has already devastated many whitebark pine stands in the northwestern United States, and is present in the Yellowstone area (Kendall 1995). In addition, if as expected, whitebark pine responds to global warming by shifting its range to higher elevations, geometrically diminishing habitat area will be available to it, given the acutely convex mountains in the Yellowstone ecosystem (Romme and Turner 1991). Although long-term abundance of this shade-intolerant species may also be threatened by widespread fire suppression on public and private lands (Keane et al. 1990), paradoxically, stand-replacement fires may have a near-term detrimental effect on bears. Even though whitebark pine may re-establish on sites burned by fires, such as those in Yellowstone during 1988, production of a substantial number of cones is not expected for a century (Mattson and Reinhart 1994).

The level of human activity, especially in habitat attractive to bears, is of great consequence to grizzly bear conservation (Mattson et al. 1996b). Numbers and activity of humans in the Yellowstone ecosystem continue to increase (Clark and Minta 1994), creating more opportunities for grizzly bears to become conditioned to humans. In the 1970s and early 1980s, grizzly bear management emphasized closing garbage dumps and

otherwise preventing bears from foraging on human foods (Meagher and Phillips 1983, Gunther 1994). Importantly, it appears to us that the easy management gains have already been taken. Dump closures appear to have produced greater gain per unit cost and encountered less political resistance than management options contemplated and employed more recently.

The critical distinction involves contrasting the localized, well-defined nature of dumps with more spatially diffuse human activities and features of National Forests, such as hunting, roads, and livestock grazing (Orme and Williams 1986). Because dumps occur at a relatively few discrete locations, they are comparatively easy to attack with management. By contrast, hunters, roads, and livestock are spread thin. As such, management of these activities will predictably be much more costly to implement and enforce. Moreover, when a dump is closed, there is relatively minor impact on recreational and commodity uses of public lands. By contrast, some diffuse management options, such as closing roads or restricting hunting, although favorably affecting grizzly bear survival, are also likely to have major impacts on traditionally important human uses of public lands. These difficulties compound the challenges presented by an increasing number of humans in the ecosystem (Mattson et al. 1996a, b), and suggest that it would be simplistic to assume that past management gains or holding actions can be extrapolated into the future.

The threats posed by diminishing whitebark pine and increasing numbers of people are inconsistent with an optimistic long-term prognosis for the Yellowstone grizzly bear population. Even a partial presentation of the positive management changes that might be taken in response is beyond the scope of the present paper (Mattson et al. 1996b). Simply identifying whitebark pine seed crop size and conditioning to humans as central demographic variables is itself a step forward, as this conclusion could be impetus for the reallocation of scarce management dollars toward more productive ends, and for the adoption of a more precautionary management approach.

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APPENDIX A

THE RAW DATA

The *Individual Grizzly Bear Histories* data set lists all dates on which each bear was trapped and fitted with a radio collar and all dates on which each bear's collar was dropped or became inactive. In a number of instances clearly identified in the raw data, a bear was trapped and re-collared after having dropped a previous radio collar. It also lists each bear's sex and age when first trapped and the date of any mortality of a radio-collared bear.

Each *Flight Report* records a single aerial overflight taken to relocate radio-collared grizzly bears. It lists the date of the aerial overflight, those radio-collared bears that were relocated only via their radio signal, and those that were seen by a human observer. The Flight Reports also give the age and number of cubs, yearlings, and 2-yr-olds seen by the human observer whenever a radio-collared sexually mature female was seen. Except for rare occasions, the cubs accompanying radio-collared females were not themselves radio-collared, so our only knowledge of them comes from visual observations. Our analysis relies on 1181 Flight Reports, consisting of >8791 aerial relocations of radio-collared grizzly bears.

The *Annual Reports of the Interagency Grizzly Bear Study Team* (Knight et al. 1976, 1977, 1978, 1980, 1981, 1982, 1985, 1986, 1987, 1988b, 1989, 1990, 1991, 1992, 1993, Knight and Blanchard 1983) list all bears trapped and radio-collared each year, the date and location of each trapping, and the date and location of all grizzly bear deaths recorded in the Yellowstone ecosystem each year. They also record whether each trapping was for management or research purposes.

The *Grizzly Bear Mortalities* data set (Craighead et al. 1988) lists all grizzly bear deaths in the Yellowstone ecosystem between 1959 and 1988; a date for each mortality is given.

The *Individual Grizzly Bear Histories* and *Flight Reports*

have been placed in the public domain in response to requests made under the U.S. Freedom of Information Act.

When we compared the electronic and hard copies of the Flight Reports, both obtained from the Interagency Grizzly Bear Study Team, we found numerous discrepancies. We took the hard copy Flight Reports as being correct.

The major problems that we encountered while summarizing the raw data, and our procedures for resolving them, are as follows. (1) Although the dates of all management-trapping events and relocations were known exactly, we could delimit the dates of most collar drops and of many deaths only to a time interval that started on the last date on which the bear was definitely alive with an active radio collar and ended on the last conceivable date of death or collar drop. We used several methods to fix the end date: for most of the study period, the radio collars that were used emitted two discrete frequencies, depending on whether the collar was moving ("active mode") or not ("mortality mode"); when possible, we took the end date as the date when the collar was first relocated in mortality mode. When the evidence that a collar drop or death had occurred consisted of a series of relocations from nearly the same spatial location, we took the first date of such a sequence as the end date. In some cases, the data showed that a collar drop or death had definitely occurred, but were insufficient for determining the end date; in this circumstance, we took the end date as 31 December 1992, because the raw data that we analyzed extended only until then. When a collar drop or death could only be determined to within a time interval, our summary files simply give the two dates bounding it, and the likelihood function accounts for this ambiguity. (2) In 15 cases (3% of all deaths and collar drops), the raw data were insufficient to distinguish between collar drop and bear death. We believe that most such cases were actually collar drops, but estimate model parameters under the assumption that they were all collar drops and that they were all deaths.

(3) There were some inconsistencies among the raw data sets regarding the date of death of some bears, evidently because these data did not always carefully distinguish among the actual date of death, the date when a death first became known to humans, the last date a bear was known with certainty to be alive with an active radio collar, and the last date that the bear could conceivably have been alive with an active radio collar. We either determined the correct date of actual death or a time interval containing the date of death. (4) Some Flight Reports state that "young" or

"cubs" were seen, terms that are ambiguous as to the number and/or age of the offspring present. We omitted such ambiguous records from the fecundity calculations. (5) The Flight Reports misreported the age of offspring accompanying sows 6% of the time. This problem usually arose because some "cubs" identified on the Flight Report were actually yearlings or 2-yr-olds, presumably because "cub" was sometimes used as a generic term to denote offspring. We identified and corrected such problems by looking at the entire multiyear sequence of relocations of each mother and her offspring.

APPENDIX B

MAXIMUM LIKELIHOOD PARAMETER ESTIMATION

Model probabilities and instantaneous rates.—The independent variables modify each dependent variable according to

$$w = \exp \left[k_w + \sum_{i=1}^I \beta_{wi} \sum_{j=1}^{M_i} v_{wij} \delta_{ij} \right]$$

where w represents one of the dependent variables (d , h , a_1 , a_2 , a_3 , c , r , s , or g), I is the number of independent variables (12 in our case; see Table 2), and $M_i + 1$ is the number of states of the i th independent variable. The Kronecker deltas, δ_{ij} , describe the actual data; δ_{ij} is 1 if the i th independent variable is in state j ; otherwise, it is 0. If, under the model being estimated, the i th independent variable contributes to dependent variable w , β_{wi} is 1; if not, it is 0. (In essence, we use the AIC procedure to determine which β_{wi} are 0, and which are 1.) Thus, one specifies a particular model by stating, for each dependent variable, whether each β_{wi} is 0 or 1. All independent variables that we consider are categorical and are numbered starting with state 0, using consecutive integers.

Once we specify a model, we desire to estimate the k_w and the v_{wij} . When all independent variables are in ground state (i.e., state 0), $w = \exp(k_w)$. The parameters v_{wij} quantify the extent to which this baseline value is modified when the i th independent variable is in state j , where $j > 1$. Note that there are no v_{wi0} terms; if an independent variable is in state 0, there is no modification term. Terms of the form $\exp(k_w)$ and $\exp(v_{wij})$ combine multiplicatively to determine the overall probability or rate (Table 2). We thus assume that hazards act proportionally (Cox and Oakes 1984).

Given a model specified by the β_{wi} , given assumed or estimated values of k_w and the v_{wij} , and given the actual data as specified by the values of δ_{ij} , one can determine the numerical value of any dependent variable.

Data interpreted as transitions.—On each date, each bear in the data set can be assigned a four-tuple, $\sigma = (\sigma_1, \sigma_2, \sigma_3, \sigma_4)$; σ_1 is 0 if the bear is alive and 1 if it is dead; σ_2 is 0 if the bear has an active radio collar and 1 otherwise; σ_3 is 0 if the bear has never been management-trapped and 1 if it has been; σ_4 counts the number of times the bear has been relocated, and can be any non-negative integer. Similarly, on each date that each sexually mature female with an active radio collar is sighted, we assign her a scalar, ω , which records the number of cubs seen accompanying her on this date. Moreover, on each date, we also know the state of all independent variables affecting a particular bear; for the sake of a compact notation, we do not express this symbolically.

All of the available data can be summarized as either "mortality transitions" or "fecundity transitions." A mortality transition describes the change in σ observed for a particular radio-collared bear between two dates. For example, a bear that had never been management-trapped or collared, that was first collared on 15 July 1976, was relocated on 22 July 1976, and that died on 1 August 1976, would contribute two mortality transitions to the data. The values of σ on 15 July, 22 July, and

1 August 1976 are (0, 0, 0, 0), (0, 0, 0, 1), and (1, 0, 0, 1), respectively. The first transition extends from 15 to 22 July 1976 and consists of the first two four-tuples. The second transition extends from 22 July to 1 August 1976 and consists of the second and third four-tuples. A fecundity transition describes the change in ω for a particular radio-collared sexually mature female between two dates. Consider, for example, a radio-collared female that overwintered with an active collar, was relocated and seen on 1 June with two cubs, and was relocated and seen on 15 June with three cubs. This female would contribute two fecundity transitions to the data. The first extends from 15 April 1976 (the assumed date of den emergence) to 1 June 1976, and would be associated with $\omega = 2$. The second fecundity transition starts at 1 June and goes to 15 June, and is associated with $\omega = 3$. Mortality transitions of bears with an active radio collar but no change of state contribute to the data for the same reason that, in computing a mortality rate, we must consider the numbers of bears monitored that did not die, as well as those monitored that did die. Similarly, if a female was seen on a particular date and no cubs were observed, this fecundity transition contributes to the data.

For a given model specified by β_{wi} and assumed parameter values specified by the k_w and v_{wij} , the formulas given next can be used to obtain the numerical probability of each and every mortality and fecundity transition in the actual data. We then take the log of each of these probabilities and sum the numbers so obtained to produce the log likelihood of a particular model (recall that each particular model is specified by setting the β_{wi} values). This log likelihood is maximized using the downhill simplex method (Nelder and Mead 1965, Press et al. 1992).

Mortality transition probabilities.—We seek to derive formulas that give the value of each mortality transition, in terms of the underlying rates and probabilities. The data provide the exact dates of all relocations and management-trapping events, and the exact dates of some deaths and collar drops. However, we do not know the exact date of some deaths and collar drops; in these circumstances, we know only that the death or collar drop occurred within a certain interval of time. The likelihoods associated with these two circumstances must be computed using different formulas.

Define $P(\sigma_E, t_E | \sigma_B, t_B)$ as the likelihood that a radio-collared bear with status σ_B on date t_B survives to date t_E with no status transitions of any sort, and then undergoes a transition to status σ_E at exactly t_E . Because each radio-collared bear is subject to competing risks of death, collar drop, relocation, and management-trapping,

$$P(\sigma_E, t_E | \sigma_B, t_B) = \exp(-[d + c + r + h][t_E - t_B])$$

$$P(\sigma_E, t_E | \sigma_B, t_B) = K_P(\sigma_B \rightarrow \sigma_E)$$

$$\times \exp(-[d + c + r + h][t_E - t_B])$$

where $K_P(\sigma_B \rightarrow \sigma_E)$ is d , c , h , r , or $h + c$, depending on whether the transition involves a death, collar drop, manage-

ment-trapping, relocation, or simultaneous management-trapping and collar drop. It is understood that independent variables change state only on the cusp between transitions; this can always be arranged by splitting a single transition into two on any and all dates on which an independent variable changes state.

When the exact date of death or collar drop is known only to within a time interval, matters are more complicated. The likelihood of a death occurring sometime between time t_B and t_E , and before any death, management-trapping, relocation or collar drop is

$$\int_{t_B}^{t_E-t_B} d \exp(-[d+h+r+c]y) dy \\ = \frac{d}{d+h+r+c} (1 - \exp(-[d+h+r+c](t_E-t_B))).$$

To obtain the analogous formula that holds when the exact date of a collar drop is known only to within a time interval, substitute $c \leftrightarrow d$. One final problem, dealt with in the next paragraph, is that the dependent variables d , h , r , and c are not constant over the time interval t_B to t_E ; for example, these dependent variables will, in general, change on the cusp between two states of a season-independent variable. To account for this, we break the transition into several pieces and apply the above integral separately to each part.

Define $Q(\sigma_E, t_E | \sigma_B, t_B)$ as the likelihood that a bear with status σ_B at date t_B undergoes transition to status σ_E sometime before date t_E , and before suffering any other transition. To account for independent variables (Age, Season, Year, and Wbp) that may change state within the interval (t_B, t_E) , we divide it into $N+1$ subintervals, such that the independent variables change state only on the cusp between subintervals, and are constant within each. Defining t_{B+j} as the date of the cusp between the j and $j+1$ subintervals,

$$Q(\sigma_E, t_E | \sigma_B, t_B) \\ = \sum_{j=1}^{N+1} S(t_{B+j-1}) \frac{K_Q(\sigma_B \rightarrow \sigma_E)}{d_j + c_j + h_j + r_j} \\ \times (1 - \exp(-[d_j + c_j + h_j + r_j][t_{B+j} - t_{B+j-1}]))$$

where d_j , c_j , h_j , and r_j denote the instantaneous mortality, collar drop, management-trapping, and relocation rates, respectively, on the subinterval (t_{B+j-1}, t_{B+j}) . We define $K_Q(\sigma_B \rightarrow \sigma_E)$ as d_j when the transition involves a death, and as c_j when the transition involves a collar drop. $S(t_{B+j-1})$ is the probability of no transition of any sort before date t_{B+j-1} computed iteratively as

$$S(t_B) = 1 \\ S(t_{B+j}) = S(t_{B+j-1}) \exp(-[d_j + c_j + h_j + r_j][t_{B+j} - t_{B+j-1}]) \\ j \geq 1.$$

Our analysis extends that of Bart and Robson (1982), who assume that death occurred after a fixed portion of this time interval had elapsed, and of White (1983), who assumes that all collars fail at a fixed time after being put into use.

Fecundity transition probabilities.—Let the fecundity transition for which we wish to compute the likelihood start at time t_B and end at time t_E . By the definition of a fecundity transition, the adult female in question is not seen at all between t_B and t_E (although she may be relocated, but not seen). She is seen on date t_E , accompanied by ω cubs.

Define the vector $\mathbf{a}(t_B)$ so that element $a_f(t_B)$ ($0 \leq f \leq 3$) of it is the probability that f cubs are actually alive and accompanying a particular adult female at time t_B . By assumption, $a_0 = 1 - a_1 - a_2 - a_3$. Define the vector $\mathbf{a}(t_E)$ so that element $a_f(t_E)$ of it is the probability that there are actually f cubs alive and accompanying an adult female at

time t_E , conditioned on $\mathbf{a}(t_B)$ cubs being alive and accompanying her at time $t_B < t_E$. Under this formulation, the number of cubs actually alive and accompanying a female at any particular time is generally not known exactly, but is instead given by a probability distribution. If cub deaths occur independently of one another,

$$a_f(t_E | \mathbf{a}(t_B)) = \sum_{k=f}^3 a_k(t_B) \binom{k}{f} R(t_B, t_E)^f [1 - R(t_B, t_E)]^{k-f} \\ 0 \leq f \leq 3 \quad (\text{A.1})$$

where

$$R(t_B, t_E) = \exp\left(-\sum_{j=1}^{N+1} d_j[t_{B+j} - t_{B+j-1}]\right) \quad (\text{A.2})$$

is the probability of a cub surviving from t_B to t_E . It is understood that Eq. (A.2) divides the interval (t_E, t_B) into $N+1$ subintervals so that the independent variables are constant over each subinterval and change states only at the cusps between subintervals. This is necessary because certain independent variables, such as Season, may change state between t_B and t_E , also causing the cub mortality rate to change its numerical value. With this definition, the cub mortality rate within each subinterval is constant.

The data that we have to compute grizzly bear fecundity do not consist of the actual number of cubs accompanying a female on various dates, as can be computed from Equations (A.1) and (A.2). Instead, we know only the number of cubs observed with a female when she was herself seen. The actual and observed numbers of cubs are not equivalent, because not all cubs are seen when their mother is. To account for this, let V_ω be the probability of observing ω cubs at time t_E , conditioned on both the number of cubs actually alive and accompanying her at time t_E , as given by $\mathbf{a}(t_E | \mathbf{a}(t_B))$, and on their mother being seen at time t_E . For convenience, the notation suppresses this conditioning:

$$V_\omega = \sum_{k=\omega}^3 a_k(t_E | \mathbf{a}(t_B)) \binom{k}{\omega} g^\omega (1-g)^{k-\omega}. \quad (\text{A.3})$$

To apply Eq. A.3, start with the first fecundity transition for a particular female in a particular year. For females that overwinter with an active radio collar, this fecundity transition commences on 15 April. The calculation of the first fecundity transition probability involves assuming, in Eq. A.3, that $a_0(t_B) = 1 - a_1 - a_2 - a_3$, $a_1(t_B) = a_1$, $a_2(t_B) = a_2$, and $a_3(t_B) = a_3$, for t_B equal to 15 April, and where a_1 , a_2 , and a_3 are model-dependent variables, to be estimated. Then use Eq. A.3 to compute the probability of seeing the number of cubs observed. This probability determines the contribution of the first fecundity transition to the likelihood function.

Computing the probability associated with the second (and subsequent) fecundity transitions, for a given sexually mature female in a given year, involves applying the above equations iteratively. To accomplish this, we need an estimate of the number of cubs actually alive at time t_E at the end of the first fecundity transition. Note that Eqs. A.1 and A.2 are inadequate, because they do not account for the fact that we observed ω cubs accompanying this female at t_E . We denote the estimate of the number of cubs actually alive and accompanying a female at time t_E by $\mathbf{a}(t_E)$, and estimate it as

$$a_f(t_E) = 0 \quad f < \omega \quad (\text{A.4})$$

$$a_f(t_E) = \frac{a_f(t_E | \mathbf{a}(t_B)) \binom{f}{\omega} g^\omega (1-g)^{f-\omega}}{V_\omega} \quad f \geq \omega. \quad (\text{A.5})$$

It is understood that $\mathbf{a}(t_E)$, as specified by Eqs. A.4 and A.5, is conditioned on $\mathbf{a}(t_B)$ cubs being present at time t_B , on no visual

sightings of the female between t_B and t_E , and on ω cubs being observed with the female at time t_E . To iterate these equations, use the estimated value of $a(t_E)$ computed from Eqs. A.4 and A.5 as the new value of $a(t_B)$ in Eqs. A.1 and A.2.

Because the sex of uncollared cubs accompanying their

collared mother is generally unknown, and because the uncollared cub data contribute heavily to our estimate of cub mortality, our analysis assumes that male and female cubs have the same mortality rate. Consequently, we are forced to always include Age-1 when estimating d .

APPENDIX C

GENERALIZED LESLIE MATRIX

Because there are five age classes within both the non-management-trapped and management-trapped subpopulations, the population vector has 10 elements. The generalized Leslie matrix has the structure

$$\begin{pmatrix} 0 & 0 & 0 & f_{3m} & f_{4m} & 0 & 0 & 0 & 0 & 0 \\ s_{0m} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{1m} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{2m} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{3m} & s_{4m} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & f_{3f} & f_{4f} & 0 & 0 & 0 & f_{3m} & f_{4m} \\ s_{0f} & 0 & 0 & 0 & 0 & s_{0m} & 0 & 0 & 0 & 0 \\ 0 & s_{1f} & 0 & 0 & 0 & 0 & s_{1m} & 0 & 0 & 0 \\ 0 & 0 & s_{2f} & 0 & 0 & 0 & 0 & s_{2m} & 0 & 0 \\ 0 & 0 & 0 & s_{3f} & s_{4f} & 0 & 0 & 0 & s_{3m} & s_{4m} \end{pmatrix}.$$

To reduce notation, we have suppressed the dependence of the matrix elements on the whitebark pine independent variable; there is one transition matrix for most years and one for nonmast years.

Let d_{xyz} and h_{xyz} denote the instantaneous mortality and management-trapping rates of an individual with age x , management-trapping status y , and season z . It is understood that $x = 0, \dots, 4$ (where $x = 4$ represents all ages ≥ 4), $y = 0$ or 1 (these states are consistent with those of Mgt), and $z = 0, 1$, or 2 (these states are consistent with those of Season-3). Our transition matrix assumes that the population is censused on 15 April, upon emergence from the den. The following formulas are valid for $x = 0, \dots, 4$:

$$\begin{aligned} s_{xm} &= \exp(-t_0[d_{x00} + h_{x00}] - t_1[d_{x01} + h_{x01}] \\ &\quad - t_2[d_{x02} + h_{x02}] - t_3[d_{x00} + h_{x00}] \\ &\quad - t_4[d_{x+1,00} + h_{x+1,00}]) \\ s_{xm} &= \exp(-t_0d_{x10} - t_1d_{x11} - t_2d_{x12} - t_3d_{x10} - t_4d_{x+1,10}) \\ s_{xf} &= \sum_{j=0}^4 \exp\left(-\sum_{k=0}^{j-1} t_k[d_{x0k} + h_{x0k}]\right) \exp\left(-\sum_{k=j+1}^4 t_kd_{x1k}\right) \\ &\quad \times \frac{h_{x0j}}{d_{x1j} - d_{x0j} - h_{x0j}} \\ &\quad \times (\exp(-t_j[d_{x0j} + h_{x0j}]) - \exp(-t_jd_{x1j})) \end{aligned}$$

where $t_0 = 15$, $t_1 = 92$, $t_2 = 92$, $t_3 = 61$, and $t_4 = 105.25$ d. By special definition, $d_{5yz} = d_{4yz}$ and $h_{5yz} = d_{4yz}$ in the first and second equations. In the last equation, by special definition, $d_{x+3} = d_{x0}$, $h_{x+3} = h_{x0}$, $d_{x+4} = d_{x+1,0}$ for $x < 4$, $d_{x+4} =$

d_{x0} , $h_{x+4} = h_{x+1,0}$ for $x < 4$, $h_{x+4} = h_{x0}$, $\exp(-\sum_{k=0}^4 t_k[d_{x0k} + h_{x0k}]) = 1$, and $\exp(-\sum_{k=5}^4 t_kd_{x1k}) = 1$.

The cub mortality rates that we estimated from the fecundity transition data are conditioned on the survival of the cub's mother. Because few cubs in the dataset are themselves radio-collared, the fecundity transition data weigh heavily in determining how to interpret the cub mortality rate that we estimate. Because it is thought that cub death is probable whenever the mother dies before 1 July (Craighead et al. 1988), we set the overall instantaneous cub mortality rate between 15 April and 1 July as being equal to the sum of the cub and adult female instantaneous mortality rates.

Only adults that survive an entire year from the census date are able to reproduce, and some individuals reproduce on their fourth birthday; thus,

$$f_{xm} = 0.5(a_1 + 2a_2 + 3a_3)s_{xm} \quad x = 3, 4$$

and an analogous formula holds for f_{xm} .

The upper right submatrix of this matrix is all zeros. Consequently, the finite rate of increase, λ , is determined by the largest of the lead eigenvalues associated with the upper left (non-management-trapped) and lower right (management-trapped) 5×5 submatrices. For our best model, λ is determined by the non-management-trapped subpopulation lead eigenvalue, because, in our case, it is always larger than the management-trapped subpopulation lead eigenvalue. There is no guarantee that this will always be true, however; the s_{xm} terms must account for both mortality and management-trapping losses, whereas the s_{xm} terms need only account for mortality losses.

We compute the standard errors of the parameter estimates reported in Table 3 from the curvature of the likelihood function at its maximum (Stuart and Ord 1991: Eq. 18.64):

$$\text{var}\{\Theta_i\} = -1 \left/ \frac{\partial^2 \ln L(\Theta)}{\partial \Theta_i^2} \right|_{\Theta=\hat{\Theta}}$$

where L is the likelihood function, the vector Θ contains all of the parameter values of the best model in Table 3, and $\hat{\Theta}_i$ is the i th element of this vector. In applying this formula, we computed the second partial derivative numerically. Note also that our approach assumes that the covariance terms in the obvious generalization of this equation are 0.

We estimated the standard error of λ using the standard errors of the underlying demographic parameters (Stuart and Ord 1987: Eq. 10.12):

$$\text{var}\{b(\Theta)\} = \sum_{i=1}^N \left\{ \frac{\partial b}{\partial \Theta_i} \right\}^2 \text{var}\{\Theta_i\}$$

where b can be taken as λ when computing its SE, or as exp as in Table 3 when computing the SE of terms of the form $\exp(k_{xy})$ and $\exp(v_{xy})$. Once again, we computed the partial derivatives numerically.