MANAGING RISKS OF DECLINE FOR HUNTED POPULATIONS OF GRIZZLY BEARS GIVEN UNCERTAINTY IN POPULATION PARAMETERS

Official Release

Final Report

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Preamble

This report was commissioned by the Independent Scientific Panel on Grizzly Bears for the Government of British Columbia in April, 2002. The mandate was to provide an independent assessment of the management risks associated with harvesting grizzly bear populations given uncertainty in population characteristics such population size, vital rates (survival, reproduction), and how close harvest approximates the natural finite rate of increase. I also examine risks of population decline for grizzly bear populations in British Columbia based upon documented population size and standard error, offtake, and vital rates assumed for populations inhabiting good, moderate, and poor areas of habitat quality. I wrote this progress report without solicitation of comments from the Government of British Columbia; this report rests on my own judgement. The conclusions contained in this report reflect the professional opinions of the author without any form of editing or censuring by the Government of British Columbia or any other concerned parties.

March 5, 2003

Dr. Philip D. McLoughlin

Executive Summary

A better understanding of how sampling error influences results of population viability analysis (PVA) will serve to focus research aimed at improving the applicability of PVA for management purposes. In Section 1.0 of this report, I evaluate the relative contributions of sampling error in initial population size and sampling errors in vital rates to the outcome of PVA for grizzly bears (*Ursus arctos*) in western North America. I used a 2-way, random-effects analysis of variance to estimate the components of variance in PVA outcomes explained by errors (standard errors applied between 0–30% of parameter estimates) in vital rates and initial population size. Error in population size accounted for the largest source of variation in the model ($F_{35,5} = 10.8$, $P = 0.00001$), explaining 60.5% of the variance. In contrast, error in vital rates contributed very little to simulation outcomes ($F_{35,5} = 0.61$, $P = 0.70$), accounting for only 2.4% of model variation. The results demonstrate that error in initial population size can be an important determinant of simulation outcomes, and that removing sampling error from process variation in models of PVA in order to make them more realistic is perhaps not as critical as is currently thought. Errors in estimates of initial population size, if ignored in models of PVA, have the potential to leave managers with estimates of population persistence that are of little value for making management decisions.

In Section 2.0, I quantify management risks associated with how close harvest approximates a population's finite rate of increase. I describe the existence of a threshold of human-caused mortality for grizzly bears (*Ursus arctos*) in North America, which, if exceeded, accelerates declines in the persistence probabilities of populations. Using population viability analysis (PVA), I identified thresholds of annual kill for 3 simulated grizzly bear populations

with a common population size from breakpoints in slopes of regression curves relating annual

kill to persistence probabilities of populations. The position of the threshold is shown to shift

with changes in vital rates (natural survival, reproduction) and life history that varied according

to net primary productivity (PP) of habitat. For populations inhabiting relatively good habitat

(PP > 1000 $g/m^2/y$), the breakpoint model suggesting a threshold at 4.9% annual kill was the

most parsimonious compared to all other breakpoint models. As habitat productivity and natural

growth rates decreased, the threshold level shifted to the left in regressions of persistence *versus*

annual kill. The threshold of kill for the simulated population inhabiting moderate habitat (PP =

700–1000 $g/m^2/y$) was best described at 2.8% of initial population size. A linear decline in

population persistence as annual kill increased was the most parsimonious solution for the

population inhabiting poor habitat (PP < 700 $g/m^2/y$), suggesting that any threshold of human-

caused mortality was already surpassed even at extremely low levels of annual kill. Prior to any

management strategy to set levels of harvest for actual populations, population size, productivity

and state of habitat, life history, and estimates of population growth in the absence of human-

caused mortality should be considered to predict the response of a population to non-natural

mortality.

Section 3.0 of this study examines risks of population decline for 10 grizzly bear

populations in British Columbia based upon documented population size and standard error,

offtake, and vital rates assumed for populations inhabiting good, moderate, and poor areas of

habitat quality. Although regulated harvest rates (2.8–3.8% of *N* per year) appear reasonable

considering population viability thresholds presented in Section 2.0, they are likely unsustainable

in conjunction with uncertainty in population size plus the additional 2.2%/year estimated

unknown, non-hunter mortality observed for most study areas. The general pattern was for a

50% chance that grizzly bear populations will decline at rates exceeding 20% over 30 years. If the province plans to maintain a 2.8–3.8% annual harvest without first decreasing the amount of uncertainty in population estimates, it is imperative that non-hunting mortality be reduced substantially to develop more acceptable outcomes of PVA. If enforcement of hunting regulations cannot be improved and non-hunter mortalities reduced (e.g., road and rail deaths, kills in defense of life or property), then it is only through a reduction in quota that grizzly bear populations can be modeled sustainably using PVA. The size of reduction in quota necessary to maintain persistence of populations has yet to be modeled.

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1.0 Relative Contributions of Error in Vital Rates and Error in Initial Population Size to Outcomes of Population Viability Analysis

There are several sources of variation that affect probabilities of population persistence. Random chance in survival and reproduction, or demographic stochasticity, may be an important factor contributing to extinction events because as populations become smaller, binomial outcomes to survival and reproduction (success or failure, production of male or female offspring) can result in severe shifts in population trends (Caughley 1977; Caughley and Gunn 1996). Environmental variation describes stochasticity in survival and reproduction resulting from random fluctuations in the environment over space or time. Conditions that reduce carrying capacity or increase variance in vital rates of populations may reduce persistence probabilities (Ruggerio et al. 1994), and if spatial variation is high within a population and subpopulations are regularly depleted due to local conditions, high immigration and emigration rates among subpopulations may increase overall population persistence (White 2000). Individual variation as a result of differences in genome or sex and age status will affect population persistence because not all animals have the same chances of survival and reproduction. Increased individual variation means that some animals in a population will have both high reproduction and survival, and as populations get smaller it is likely these individuals (lowest chance of mortality) will proportionately make up the population, increasing population persistence. Taken together, demographic, environmental, and individual variation have been termed 'process' variation (White 2000), all of which act on population processes to affect persistence probabilities of populations.

Process variation contrasts with sampling error, the additional source of variation we introduce to models in our attempts to measure population persistence (i.e., population viability analysis, PVA; Boyce 1992). Sampling error exists for variance estimates of vital rates (survival, reproduction) and, unless we are dealing with a very small and visible population, the initial population size upon which we base PVA (Ludwig 1999). Of special concern to population biologists is how to handle sampling error in analyses of population viability.

Including sampling error in PVA models will result in conservative outcomes, and this has been perceived to be a problem by some researchers. Generally, sampling error in initial population size has been largely ignored in models of PVA, but methods to separate sampling error from environmental variation for estimates of vital rates have been promoted as improvements to PVA (White 2000). The utility of PVA for making 'real-world' management decisions, however, rests not only in the accuracy of parameters and our estimation of breadth of environmental variation in vital rates, but also in the precision of parameters (Ludwig 1999). Managers are forced to make decisions with data they have on hand, and to exclude sampling error for PVA may, at worst, provide a false sense of security regarding the likelihood of population persistence. If models of PVA are to be more than academic exercises and instead tools to be applied in a real-world setting, we should not ignore sampling error and its contribution to outcomes of PVA.

A better understanding of how sampling error in PVA influences results will serve to focus research aimed at improving the utility of PVA for management purposes. It would be of interest, for example, to compare the relative importance of sampling error in vital rates and uncertainty in initial population size to determining outcomes of PVA. Results may direct research efforts towards increasing precision of those parameters deemed most influential to

simulation results. The relative importance of types of sampling error in PVA will likely be specific to the life history of species and our ability to measure population parameters, but generalizations for populations of a single species or several that are closely-related and for which life history strategies are similar should be possible.

Here I evaluate the relative contributions of sampling error in initial population size and sampling errors in vital rates to the outcome of PVA for grizzly bears (*Ursus arctos*). I used mean estimates of survival and reproductive parameters from 5 populations of grizzly bears in western North America to develop models of PVA (Fig.1). To these rates and parameters I applied combinations of randomly chosen levels of sampling error, holding environmental variation constant at zero. I modeled PVA using an initial population size that was the average population size for 9 watersheds in the region estimated from DNA mark-recapture experiments, with randomly chosen levels of sampling error equal in proportion to those applied to vital rates. I used a random-effects analysis of variance (ANOVA) to estimate the components of variance in PVA outcomes explained by sampling error in vital rates and sampling error in initial population size.

1.1 METHODS

1.1.1 Population Viability Analysis

The usual approach for estimating persistence is to develop a probability distribution for the number of years before population models for a species 'go extinct', or fall below a specified threshold (White 2000). The percentage of area under this distribution where the population persists beyond a specified time period is accepted as an estimate of persistence. Here I use a

WINDOWS© compatible program named RISKMAN (RISK MANagement) to model risks of population declines for grizzly bear populations (Taylor et al. 2001). RISKMAN differs from other simulation models by providing an option to accurately model the population dynamics of species with multi-year reproduction schedules, such as bears, cetaceans, elephants, phocids, and primates (Taylor et al. 1987). The program provides a stochastic option that uses the variance of input parameters and the structure identified by the simulation options that are selected. The model obtains a random normal deviate for each survival and recruitment rate based upon the mean and standard error for a particular age/sex strata. Individuals of age/sex strata in the model are then exposed in a series of Bernoulli trials to the probability described by the annual random deviate. This process incorporates annual variability and sampling error (normal distribution), and also uncertainty associated with applying the random mean to individual trials where the result is either a success or a failure (e.g. survival or death, produce a litter or fail to produce a litter). The model uses Monte Carlo techniques to generate a distribution of results (Manly 1997), and then uses this distribution to estimate the variance of summary parameters (e.g., population size at a future time, population growth rate, and proportion of runs that result in a population decline set at a pre-determined level by the user). The model relies on a life table approach (Caughley 1977), rather than a Leslie matrix (Leslie 1945) to model population dynamics. Individuals simultaneously survive and reproduce with the Leslie matrix approach, whereas the life table approach has the females survive first, then they reproduce (Taylor and Carley 1988). Having females survive first enables heterogeneity in female survival to influence reproduction for any given year, which increases realism in models of population viability (White 2000).

1.1.2 Experimental Design

I used a 2-way, random-effects analysis of variance (Model II ANOVA; Sokal and Rohlf 1995) to estimate the relative components of variance in PVA outcomes explained by errors in vital rates (Factor 1) and errors in initial population size (Factor 2). I developed 6 randomly chosen levels of sampling error (standard error, SE) between 0–30% of estimates (Table 1.1) to apply to vital rates and initial population size. Vital rates were mean estimates of annual survival and reproductive parameters from 5 populations of grizzly bears in western North America (Fig. 1.1, Table 1.1). Initial population size ($N = 101.2$) was the average size of 9 populations for the central Rocky Mountains estimated from DNA mark-recapture experiments (Boulanger and Hamilton 2002). I assumed no environmental variation in vital rates, which, in actuality, would be additive to sampling error (i.e., model outcomes are attributed only to sampling error and effects of demographic stochasticity, and individual variation described by sex/age distribution for simulations). I used the stable age distribution to start each analysis of population viability. Cells in the ANOVA design were populated without replication as outcomes of analyses of population viability (1000 stochastic population simulations; see below). Components of variance (absolute values) were estimated using the Type III expected mean squares method (Sokal and Rohlf 1995; Statsoft, Inc. 1997). All statistics were carried out using Statistica Release 5.1 (Statsoft, Inc., Tulsa, Oklahoma, USA).

1.1.3 Required Inputs

Input required to run population projection models to estimate risks of population decline were obtained from data presented in McLellan (1989*a,b,c*), MacHutchon et al. (1993), Wielgus and Bunnell (1994), Wielgus et al. (1994), Hovey and McLellan (1996), and Mace and Waller

Fig. 1.1. Locations of grizzly bear populations in western North America for which mean vital rates were calculated to develop simulations. **A**. West Coast, British Columbia (MacHutchon et al. 1993); **B**. Selkirk Mountains, British Columbia (Wielgus et al. 1994); **C**. Flathead River Drainage, British Columbia (McLellan 1989*a*,*b*,*c*; Hovey and McLellan 1996); **D**. Kananaskis, Alberta (Wielgus and Bunnell 1994); and **E**. Swan Mountains, Montana (Mace and Waller 1998).

Table 1.1. Demographic parameters and 6 levels of SE used for RISKMAN simulations. Parameters include survival of cubs (S_c), yearlings (S_y), subadult females (S_{sf}), subadult males (S_{sm}), adult females (S_{af}), adult males (S_{am}), litter size (Lsize), the proportion of females available to mate in the previous year that are successful in producing cubs in the next year ([P] w cub), and initial population size (N). Errors were applied to all estimates according to proportions (0–30% of mean) as depicted in the first row.

		Levels of SE applied to means					
	Mean	0.035	0.045	0.071	0.201	0.274	0.292
S_c	0.797	0.028	0.036	0.056	0.160	0.219	0.233
S_y	0.844	0.030	0.038	0.060	0.170	0.231	0.246
S_{sf}	0.866	0.030	0.039	0.061	0.174	0.238	0.253
S_{sm}	0.864	0.030	0.039	0.061	0.174	0.237	0.252
S_{af}	0.943	0.033	0.043	0.067	0.190	0.259	0.275
S_{am}	0.855	0.030	0.039	0.061	0.172	0.234	0.250
Lsize	1.979	0.069	0.090	0.140	0.398	0.543	0.578
Prop. cub	0.625	0.022	0.028	0.044	0.126	0.171	0.182
N	101.2	3.6	4.6	7.2	20.4	27.8	29.6

(1998). Because RISKMAN requires an estimate of SE for all vital rates, for the West Coast population (MacHutchon et al. 1993) I used mean annual survival rates calculated using methods of Trent and Rongstad (1974) and, for bears, Eberhardt et al. (1994). Survival rates presented in Hovey and McLellan (1996) contained estimates of SE for all but adult male and subadult male grizzly bears. I used the methods of Trent and Rongstad (1974) to determine survival rates and SE for these segments of the population from data on male mortalities presented in McLellan (1989*b*). SE in vital rates for the Selkirks population were derived from 95% confidence limits presented in Wielgus et al. (1994). For all simulations maximum age of survival was set at 25 years (Mace and Waller 1998).

The proportion of females with new litters of each age class having 1, 2, or 3 cubs-of-the-year in their litters was input for reproduction in the model, along with the mean proportion of females of each age class that were available for mating in a previous year (i.e., possessed no cubs, or cubs that were at least 2-years-old), and then gave birth to a litter in the following year. In all simulations I used a minimum age of reproduction of 5 years, and a maximum of 25 years (McLellan 1994; Case and Buckland 1998).

The finite rate of population increase (λ) is not a required input by RISKMAN as the program calculates the parameter itself. Although there are provisions to model density-dependent effects in RISKMAN, I had no data to model such effects here (McLellan 1994; Boyce 1995; Mills et al. 1996; Wielgus 2002). Effects of catastrophes were not incorporated into models (Ewans et al. 1987), nor were potentially detrimental effects of inbreeding (Lacy 1993; Lindenmayer et al. 1995).

1.1.4 Simulations

Persistence was modelled over 30 years, the time in which we can reasonably expect inventory reassessments for most grizzly bear populations in North America. For each observation, 1000 stochastic population models were run to provide the proportion of outcomes falling below a set level of persistence. Here, persistence was defined as a population decline of less than 20%; thus, each observation represented the probability of the population declining by less than 20% over 30 years. A 20% decline over 3 generations (roughly 30 years for grizzly bears) is the criteria used by the IUCN to classify species or populations as 'threatened' (IUCN 1994). Stochastic population models were discontinued if populations declined by more than 20% (i.e., recovery of populations after declining by 20% before 30 years had elapsed was not permitted).

1.2 RESULTS

Error in initial population size was the largest source of variation in the model ($F_{35,5}$ = 10.8, P = 0.00001), accounting for 60.5% of the variance (Table 1.2). Error in vital rates contributed little to simulation outcomes ($F_{35,5}$ = 0.61, P = 0.70) when compared to error in population size (2.4% of model variation; Table 1.2). Effects on probability of persistence brought about by adding sampling error in initial population size to the PVA, holding errors in vital rates constant, maximally reduced probability of persistence from 0.910 at SE = 3.5% of N to 0.813 at SE = 29.2% of N. Adding error to vital rates but holding error in initial population size constant maximally reduced probability of persistence from 0.885 at SE = 3.5% of rates to

Table 1.2. Components of variation (absolute values) explained by error in initial population size (SE of N) and error in vital rates (SE of rates).

Source	Component of Variance
SE of rates	0.000057
SE of N	0.001417
Interaction	0.000870
Error	0.000000

0.874 at SE = 29.2% of rates. Interaction accounted for the remaining unexplained variation in the model (37.1% of variance; Table 1.2).

1.3 CONTEXT AND CONCLUSIONS

Despite the rapid acceptance of PVA for modelling conservation prospects of species, the validity of the method for guiding management decisions has recently been called into question (e.g., Taylor 1995; Ludwig 1996, 1999; Fieberg and Ellner 2000). For example, several authors have voiced their distrust of PVA because of the long time horizons often incorporated into models (e.g., 100 years) and the large amounts of data necessary to accurately capture environmental variation experienced by populations over such time periods. Fieberg and Ellner (2000) concluded that long-term extinction probabilities are likely to require unattainable amounts of data. Ludwig (1999) presented calculations of extinction probabilities using currently available data for several species and concluded that confidence limits were too large to provide anything useful to managers, especially with observation errors (including errors in abundance). The results of this study qualitatively agree with Ludwig (1999) and demonstrate that even for relatively short time horizons (30 years) and conservative measures of decline (20% of initial size), error in initial population size can be an important factor determining simulation outcomes. Probabilities of extinction were affected by as much as 1/10 over 30 years by including errors in initial population size quite typical for most studies of grizzly bears (average SE was 25% of N for the 9 populations of grizzly bears enumerated in Boulanger and Hamilton 2002). Errors in estimates of initial population size, if ignored in models of PVA, certainly have

the potential to leave managers with estimates of population persistence that are of little value for making management decisions.

The finding that sampling error in vital rates—including errors up to 30% of parameter estimates—should contribute so little to variation in simulation outcomes relative to error in initial population size was surprising. This result is likely related to simulation models repeatedly applying variation in vital rates at every year of a simulation—which may "average out" errors in vital rates over a simulation time horizon—but applying error in initial population size only once for a simulation run (i.e., at the beginning) where effects of variance become fixed for a simulation run. Removing sampling error from process variation in models of PVA in order to make models more realistic is perhaps not as critical as is currently thought (e.g., White 2000). Instead, the results urge us to turn our attention towards initial population size and ensuring N is estimated as precisely as possible for any model of PVA.

If error in initial population size is unknown or large, it may be prudent to model PVA using a minimum population number that has been measured without error (e.g., counts of known, tagged animals). The value of PVA to managers when error in initial population size is present may be improved if sampling error can be incorporated into intervals of PVA outcomes (in the sense of confidence limits). For example, runs may be conducted both with and without estimated error in initial population size, and lower bounds of population persistence delineated by those analyses incorporating sampling error. Conclusions as to the value of PVA when error in initial populations size is substantially large should be arrived at only after modelling best and worst case scenarios for species (i.e., with and without sampling error in N). Unfortunately, given the difficulty in enumerating populations it may be impossible to develop any reliable estimates of small extinction probabilities, especially over longer time intervals. Because effects

of error in initial population size on persistence probabilities increases with time (Ludwig 1999), persistence may need to be estimated only over time horizons suitably proportionate to the user's confidence in estimates of initial population size.

Only recently have models of PVA allowed for errors in initial population size to factor into persistence probabilities (e.g., Ludwig 1999), and only RISKMAN fully incorporates this option in so-called 'canned' PVA models thusfar (i.e., empty models ready for paramaterization by users; review in Boyce et al. 2001). I recommend here that options to include errors in initial population size be incorporated into mainstream models of PVA (e.g., RAMAS GIS, Akçakaya 1998; VORTEX, Lacy 1993) to permit users the chance to evaluate results both with and without this bias.

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2.0 Thresholds of Human-Caused Mortality and Population Viability: A Case Study with Grizzly Bears

Of particular importance to conservation biology are questions of thresholds of anthropogenic disturbance associated with population declines and loss of species diversity. Unfortunately, we have yet to fully develop methods by which to establish disturbance thresholds for species, and quantitative assessment of consequences for species when thresholds are exceeded is almost nonexistent. At the population level, one solution may be to identify disturbance thresholds by regressing persistence probabilities of populations, *sensu* population viability analysis (PVA; Boyce 1982), against some yardstick of human disturbance (e.g., human-caused mortality, population fragmentation, reduction in carrying capacity due to habitat loss). The idea would be to test for the existence of a non-linear relationship between persistence and anthropogenic disturbance, for which thresholds are identified from 'breakpoints' or points of inflection in curves of regression models (Fig. 2.1). Consequences to populations when thresholds are exceeded would be assessed in terms of probabilities of persistence.

There exists some evidence to support the hypothesis that a nonlinear relationship between the persistence of populations and human disturbance is real. At the community level, Bayne et al. (2002) observed that richness and diversity of forest songbirds showed strong threshold responses with changes in percent cover of forests subject to logging. For populations, it could be argued that all impacts that reduce population size should affect probability of persistence in a nonlinear manner because outcomes of PVA show a nonlinear relationship with population size, increasing towards a horizontal asymptote as N increases (White 2000). This is
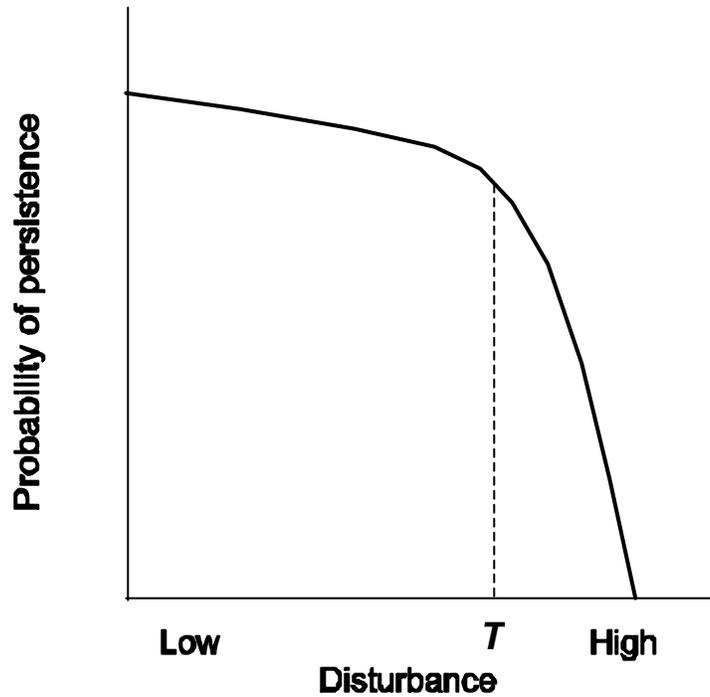
Fig. 2.1. Hypothetical example of a threshold effect in probability of population persistence with varying degrees of disturbance (solid line). The dashed line describes a potential threshold of distrubance (*T*) above which probability of persistence declines at a different rate with disturbance.

largely due to decreasing importance of random chance in survival and reproduction in determining population trends as populations increase (Caughley 1977).

Although not easy to estimate for most species, the simplest human impact to relate to population viability for the purpose of detecting a disturbance threshold would be human-caused mortality, since mortality influences population models of PVA directly. Indirect impacts on survival and reproduction (e.g., habitat fragmentation, habitat loss) would need to first be related to vital rates before PVA can be used to outline habitat disturbance thresholds. For those species in which rates of human-caused mortality are readily measured (e.g., game species, large mammals), identifying thresholds of human-caused mortality would be of considerable interest to biologists charged with regulating harvest through policy. Knowledge of how thresholds change with habitat features (e.g., productivity, amount, configuration) and life history strategy would aid biologists in assessing the vulnerability of populations living in different environments to over-harvesting.

Here I describe the existence of a threshold of human-caused mortality for grizzly bears (*Ursus arctos*) in North America, which, if exceeded, accelerates declines in the persistence probabilities of populations. Using PVA, I identified thresholds of annual kill for 3 simulated grizzly bear populations from breakpoints in slopes of regression curves relating annual kill to persistence probabilities of populations. The position of the threshold is shown to shift with changes in vital rates (natural survival, reproduction) and life history that vary according to net primary productivity of habitat.

2.1 METHODS

2.1.1 Population Viability Analysis

Population viability analysis uses measures of vital rates for populations and effects of demographic and environmental stochasticity on population growth to evaluate probabilities of population persistence for a specified period of time (Boyce 1992). The usual approach for estimating persistence is to develop a probability distribution for the number of years before population models for a species 'go extinct', or fall below a specified threshold. The percentage of area under this distribution where the population persists beyond a specified time period is equated to persistence. For a review of PVA, including its merits and shortfalls, I refer the reader to White (2000).

Effects of human-caused mortality on populations can be incorporated into PVA in a variety of ways, ranging from detailed simulations that include the age-specific vulnerability and selectivity of the kill to simple apportionment of the kill according to the abundance of sex and age types in the population. A WINDOWS© compatible program named RISKMAN (see, e.g., Eastridge and Clark 2001) was developed for the full range of options described above (Taylor et al. 2001). The model is available freely from M. K. Taylor upon written request (P.O. Box 1000, Department of Sustainable Development, Government of Nunavut, Iqaluit, NU X0A 0H0, Canada).

Here I use RISKMAN to model population viability for grizzly bears in the presence of human-caused mortality. RISKMAN differs from other simulation models by providing an option to accurately model the population dynamics of species with multi-year reproduction schedules, such as bears, cetaceans, elephants, phocids, and primates (Taylor et al. 1987). The

program provides a stochastic option that uses the variance of input parameters and the structure

identified by the simulation options that are selected. The model obtains a random normal

deviate for each survival and recruitment rate based upon the mean and standard error for

particular age/sex strata. Individuals of age/sex strata in the model are then exposed in a series

of Bernoulli trials to the probability described by the annual random deviate. This process

incorporates annual variability and sampling error (normal distribution), and also uncertainty

associated with applying the random mean to individual trials where the result is either a success

or a failure (e.g., survival or death, produce a litter or fail to produce a litter).   The model uses

Monte Carlo techniques to generate a distribution of results (Manly 1997), and then uses this

distribution to estimate the variance of summary parameters (e.g., population size at a future

time, population growth rate, and proportion of runs that result in a population decline set at a

pre-determined level by the user). The model relies on a life table approach (Caughley 1977),

rather than a Leslie matrix (Leslie 1945) to model population dynamics. Individuals

simultaneously survive and reproduce with the Leslie matrix approach, whereas the life table

approach has the females survive first, then they reproduce (Taylor and Carley 1988). Having

females survive first enables heterogeneity in female survival to influence reproduction for any

given year, which increases realism in models of population viability (White 2000).

2.1.2 Populations

I compared effects of harvest on the viability of three simulated populations of grizzly

bears in North America (Fig. 2.2; Table 2.1) exhibiting finite rates of increase (λ) that vary with

productivity of habitat (poor, moderate, good) and reflected plasticity in life history traits
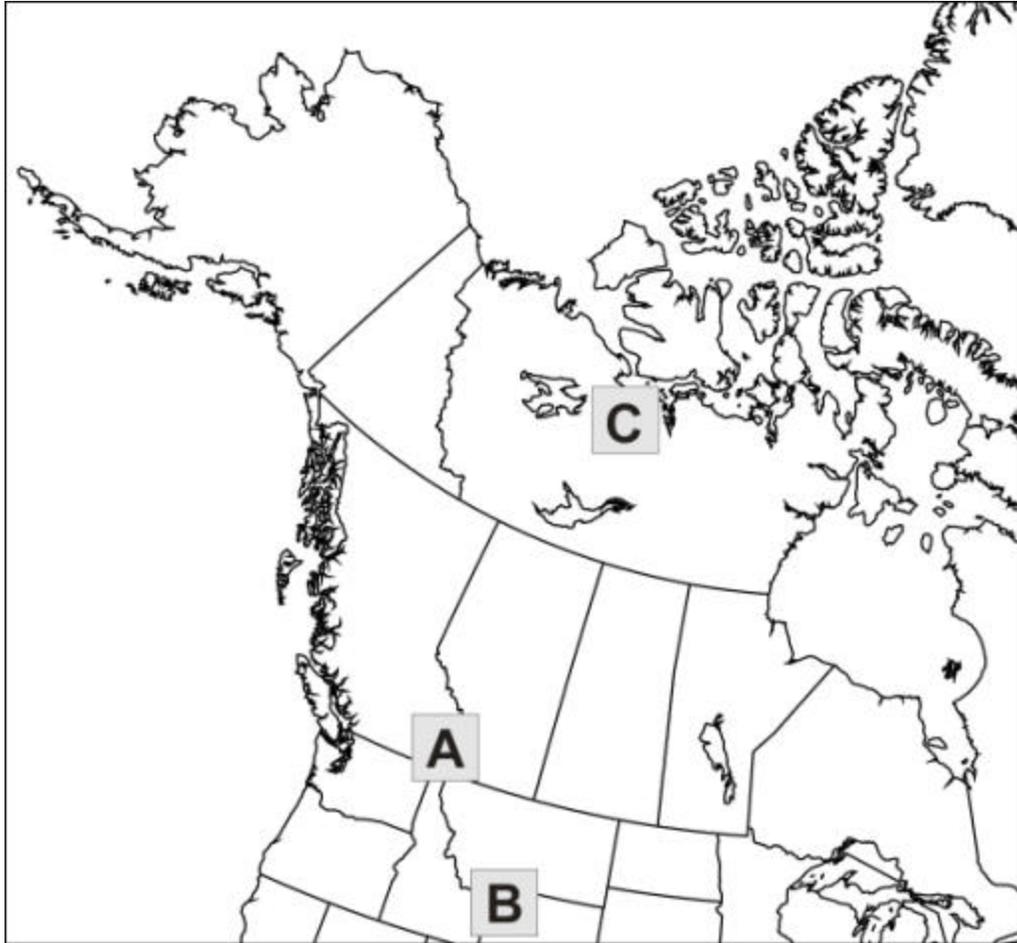
Fig. 2.2. Locations of grizzly bear populations in western North America for which mean vital rates were calculated to develop models of PVA. **A**. Central Rocky Mountains; **B**. Greater Yellowstone Ecosystem; **C**. Central Canadian Arctic.

Table 2.1. Demographic parameters used for PVA in this study. These are the base rates upon which harvests were applied (see text for derivation). Parameters include survival of cubs (S_c), yearlings (S_y), subadult (ages 2-5) females (S_{sf}), subadult (ages 2-5) males (S_{sm}), adult females (S_{af}), adult males (S_{am}), litter size (L), the proportion of females available to mate in the previous year that are successful in producing cubs in the next year ([P] cub), mean age at first reproduction (R_F), age at senescence (R_L), and maximum age of survival (w). Estimates of finite rate of increase (λ) are for determinant population growth only.

	Good ($\lambda = 1.07$)		Moderate ($\lambda = 1.05$)		Poor ($\lambda = 1.02$)	
	Mean	SE	Mean	SE	Mean	SE
S_c	0.87	0.05	0.84	0.06	0.74	0.08
S_y	0.95	0.05	0.87	0.06	0.68	0.08
S_{sf}	0.93	0.05	0.89	0.06	0.83	0.08
S_{sm}	0.91	0.05	0.89	0.06	0.83	0.08
S_{af}	0.96	0.05	0.95	0.06	0.98	0.08
S_{am}	0.93	0.05	0.95	0.06	0.98	0.08
L	2.3	0.12	2.4	0.10	2.2	0.13
[P] cub	0.60	0.07	0.60	0.07	0.60	0.07
R_F	6	.	6	.	8[a]	.
R_L	20	.	22	.	25	.
w	20	.	25	.	30	.

[a] For ages 6–7, 0.20 of females were allowed to produce cubs.

(Ferguson and McLoughlin 2000). Grizzly bears living in habitats of poor productivity show a shift in life history to later age at first reproduction, higher natural adult survival, later senescence and increased longevity. Bears adapted to low or unpredictable food availability concentrate resources into somatic growth before reproduction, ensuring higher chances of offspring survival when age at first parturition is attained. For grizzly bears living in poor habitat (H_P), I chose to model rates with standard errors (SE) according to those presented in McLoughlin and Messier (2001) for barren-ground grizzly bears in Canada's central Arctic. Net primary productivity for this study area, a correlate of habitat quality (McLoughlin et al. 2000), is 526 g/m^2/y (Ferguson and McLoughlin 2000).

Grizzly bears living in moderate habitats (H_M) should adopt life history strategies that show greater investment towards reproduction than those living in poor habitats, reducing age at first reproduction at the expense of longevity and natural adult survival. To model this type of population I chose to use modified rates originally developed from grizzly bears in the Greater Yellowstone Ecosystem (GYE), Wyoming (Table 2.1), including composite/reported rates of survival and fecundity information from Eberhardt et al. (1994), Pease and Mattson (2000), and Boyce et al. (2001). Net primary productivity for this region is 878 g/m^2/y (Ferguson and McLoughlin 2000). No studies presented natural survival for grizzly bears in the GYE. I estimated average annual offtake (approximately 3%) from annual reports of studies on Yellowstone grizzly bears and raised survival rates accordingly to develop estimates of base survival rates, which may include natural mortality but also unreported or unknown mortality. I assumed that human-caused mortality was additive, and not compensatory. Estimates of SE to apply to rates in RISKMAN for this population were the midpoint between those errors calculated for populations inhabiting good and poor habitats. Here I was not interested in

capturing sampling error, but rather the environmental variation experienced by bears, which I assumed to be somewhere between the SE for rates describing populations inhabiting good and poor habitats.

For interior grizzly bears, optimal habitat (H_G) is likely found in the central Rocky Mountains, the historical core of grizzly bear range in North America. For this type of habitat, I chose to model natural rates and SE for bears inhabiting the central interior Rocky Mountains (Table 2.1), primarily from data modified from Hovey and McLellan (1996) and McLellan (1989a,b,c), and verified through comparison with Wielgus et al. (1994), and Mace and Waller (1998). Where sexes experienced human-caused mortality, I tried to remove this mortality to set up the initial "natural rate" models for RISKMAN by increasing age/sex specific survival rates according to the breakdown of harvest outlined in records of the Government of British Columbia, including offtake specific to the Flathead watershed (again assuming human-caused mortality to be additive). I used the mean for all estimates of SE of survival for age/sex strata, applied equally to all rates. Net primary productivity in the Flathead area averages 1070 g/m^2/y (Ferguson and McLoughlin 2000). Life history is very similar to that of the moderate-habitat population, but overall survival is higher and longevity reduced to 20 years (Hovey and McLellan 1996).

Initial population size ($N = 101.2$) for all simulated populations, incorporated into models of PVA without error, was the average size of grizzly bear populations inhabiting 9 watersheds in the central Rocky Mountains (Boulanger and Hamilton 2002). For modeling purposes, the H_G, H_M, and H_P simulated populations were assumed to be below carrying capacity. Finite rates of increase calculated for each type of population, using base survival rates, are presented in Table 2.1. Note that natural finite rates of increase are not necessarily specific to any real

population, including Yellowstone National Park or the Flathead population, but rather represent hypothesized rates of increase for grizzly bear populations below carrying capacity without regulated harvest in areas of good, moderate, and poor habitat. I did not develop simulated population models to represent the extremes of growth potential for natural grizzly bear populations, but instead what I considered simulated populations with good, moderate, and poor natural growth potential. Estimated natural rates of mortality, although falling within ranges of published estimates of natural mortality (e.g., for adult females, Mace and Waller 1998; Wielgus et al. 1994), should probably be considered maximum rates for grizzly bears.

2.1.3 Simulations

Persistence was modeled for simulated populations of each habitat type over 30 years, the time in which we can reasonably expect inventory reassessments for most grizzly bear populations in North America. For each observation, 1000 stochastic population models were run to provide the proportion of outcomes falling below a set level of persistence, defined here as a population decline of less than 20%. Thus, each observation in the analysis represented the probability of the population declining by less than 20% over 30 years. A 20% decline over 3 generations (roughly 30 years for grizzly bears) is a criterion used by the IUCN to classify species or populations as 'threatened' (IUCN 1994). Stochastic population models were terminated if populations declined by more than 20% during a trial (i.e., recovery of populations after declining by 20% before 30 years had elapsed was not permitted). I added human-caused mortality to simulated populations in 0.33% increments from 0.33–8.00% of initial population size (roughly 0–8 animals per year), discontinuing further simulations when probability of persistence dropped below 0.05. Kill was applied to all populations in ratios according to hunter

selectivity of age/sex strata for grizzly bears in British Columbia based upon past records (1978–2000) of sport, subsistence, problem, and known, illegal human-caused mortality (Appendix 4.1; from Austin and Hamilton 2001), and initially with vulnerability ratios from the standing sex/age structure of the well-studied Flathead grizzly bear population (McLellan 1989*a,b,c*). Note that females with cubs were assumed protected for all simulations. For all populations I began simulations with the stable age distribution.

Effects of catastrophes were not incorporated into models (Ewans et al. 1987), nor were potentially detrimental effects of inbreeding (Lacy 1993; Lindenmayer et al. 1995). Although there are provisions to model density-dependent effects in RISKMAN, I had no data to model such effects here (McLellan 1994; Boyce 1995; Mills et al. 1996; Wielgus 2002). I assumed annual random deviates of parameter values were independent for lack of data on temporal variability, although it is possible and perhaps likely parameters were correlated (White 2000).

2.1.4 Statistics

Linear regression was used to relate human-caused mortality to persistence probabilities of populations. I used breakpoint modeling (see, e.g., Bayne et al. 2002) to determine if there was evidence of a change in slope for regressions, and if so where the breakpoint (threshold) in the regression lay. Breakpoint models allow the slope of the relationship between a dependent and independent variable to change over the range of independent values (Neter et al. 1985). The limitation of this approach is that the user is forced *a priori to* choose the location of the breakpoint. Because I did not know *a priori* whether breakpoints existed in the data, nor where they might be, I chose to compare the fit of up to 40 different breakpoint models to a model that assumed a linear response. I tested whether the dependent variable (probability of persistence)

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changed at a certain rate with percentage annual kill until the breakpoint, whereafter the relationship changed at a different rate. To model this, I included the kill term along with a breakpoint term. I created the breakpoint term by subtracting a set breakpoint value from the kill value. If the remainder was <0, I gave that breakpoint term a value of 0. If the remainder was >0 it was given the value of the remainder. For example, if a population simulation experienced human-caused mortality at 5.0% per year and I hypothesized that a breakpoint in population viability occurred at 3.0% per year, the breakpoint variable was given a value of 2.0 (Neter et al. 1985). For each type of population, I generated up to 40 models that varied the location of the breakpoint in increments of 0.1% of annual kill.

Different breakpoint models were ranked relative to the linear model based upon their explanatory power, with the best fitting model having the lowest Akaike Information Criteria (AIC) score (Burnham and Anderson 1998). I assessed whether there was a particular breakpoint model that was a better predictor of the dependent variable than all others and whether the linear model was included in the confidence set. I considered the linear model to be the most parsimonious explanation and only considered there to be strong evidence for a breakpoint if the change in AIC relative to the linear model was >2.0 units.

2.2 RESULTS

The results strongly suggest there exists a threshold of human-caused mortality for grizzly bears, which, if exceeded, accelerates declines in the persistence probabilities of populations. There was strong evidence that breakpoint functions were better predictors of persistence probability than linear functions for the simulated populations inhabiting good and

moderate habitats (Table 2.2). For good habitat, the breakpoint model suggesting a threshold at 4.9% annual kill was the most parsimonious compared to all other breakpoint models (Fig. 2.3; Table 2.2). As habitat productivity and natural growth rates decreased, the threshold level shifted to the left in regressions of persistence *versus* annual kill (Figs. 2.3–2.4). The threshold of kill for the simulated population inhabiting moderate habitat was best described at 2.8% of initial population size (Fig. 2.4; Table 2.2). For both the good and moderate habitats, probabilities of population persistence declined by –0.207 for every value of annual kill beyond mortality thresholds (Figs. 2.3–2.4).

A linear decline in population persistence as annual kill increased was the most parsimonious solution for the population inhabiting poor habitat (Fig. 2.5; Table 2.2), suggesting that any threshold of human-caused mortality was already surpassed even at extremely low levels of annual kill. Whereas simulated populations inhabiting good and moderate habitats maintained relatively high and steady probabilities of persistence at low levels of annual kill, probability of persistence for the simulated population living in poor habitat declined immediately upon the addition of human-caused mortality.

2.3 CONTEXT AND CONCLUSIONS

The results suggest that most grizzly bear populations in North America can tolerate approximately 3–5% total annual kill before declines in probability of persistence accelerate to unsatisfactory levels. I base this conclusion on the fact that most extant grizzly bear populations inhabit areas of at least moderate-good productivity in North America (Ferguson and McLoughlin 2000), and exist in demographic units near or in excess of 100 individuals. Since

Table 2.2. Comparison of the optimal breakpoint (nonlinear) model with the linear model for describing persistence/annual kill curves for simulated grizzly bear populations inhabiting good (H_G), moderate (H_M), and poor habitat (H_P). Data include Akaike Information Criteria (AIC) scores and unstandardized coefficients with persistence probability as the dependent variable, including a constant (c), slope before the breakpoint (K), slope after the optimal breakpoint (B_0), and adjusted-r^2. An asterix (*) indicates significance of presented coefficients at $P < 0.01$.

	H_G ($B_0 = 4.9\%$)		H_M ($B_0 = 2.8\%$)		H_P ($B_0 = 1.1\%$)	
	Breakpoint	Linear	Breakpoint	Linear	Breakpoint	Linear
AIC	-1079.9	-1074.7	-858.3	-855.4	-278.1	-279.3
c	1.019	0.975	1.022	0.956	0.908	0.771
K	-0.015*	.	-0.032	.	-0.145	.
B_0	-0.188*	-0.215*	-0.174*	-0.214*	-0.174	-0.332*
r^2	0.843	0.839	0.890	0.888	0.646	0.648

Fig. 2.3. Plot of persistence probability versus percentage annual kill for the simulated population inhabiting good habitat (H_G). Equations for lines are calculated separately for data subsets as divided by breakpoint analysis (all $P < 0.05$).

Fig. 2.4. Plot of persistence probability versus percentage annual kill for the simulated population inhabiting moderate habitat (H_M). Equations for lines are calculated separately for data subsets as divided by breakpoint analysis (all P <0.001).
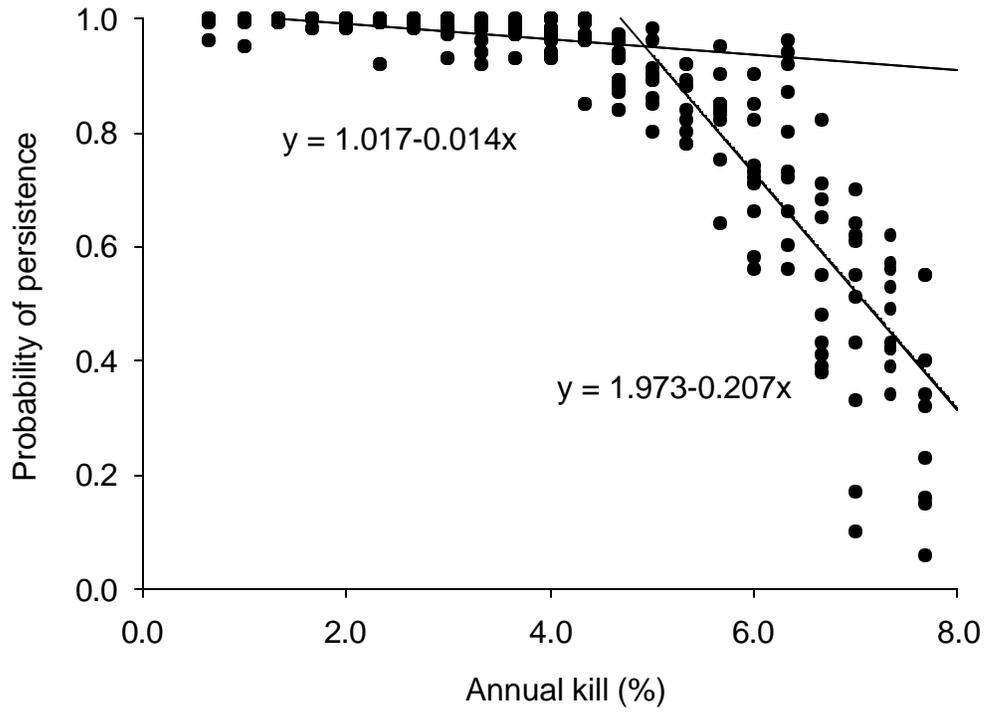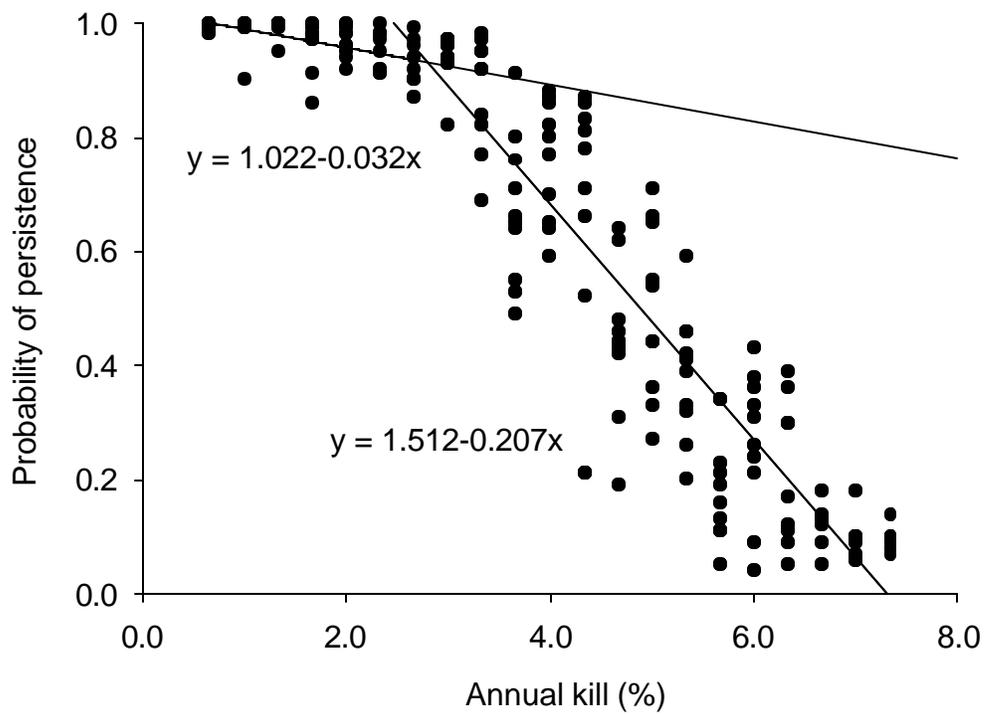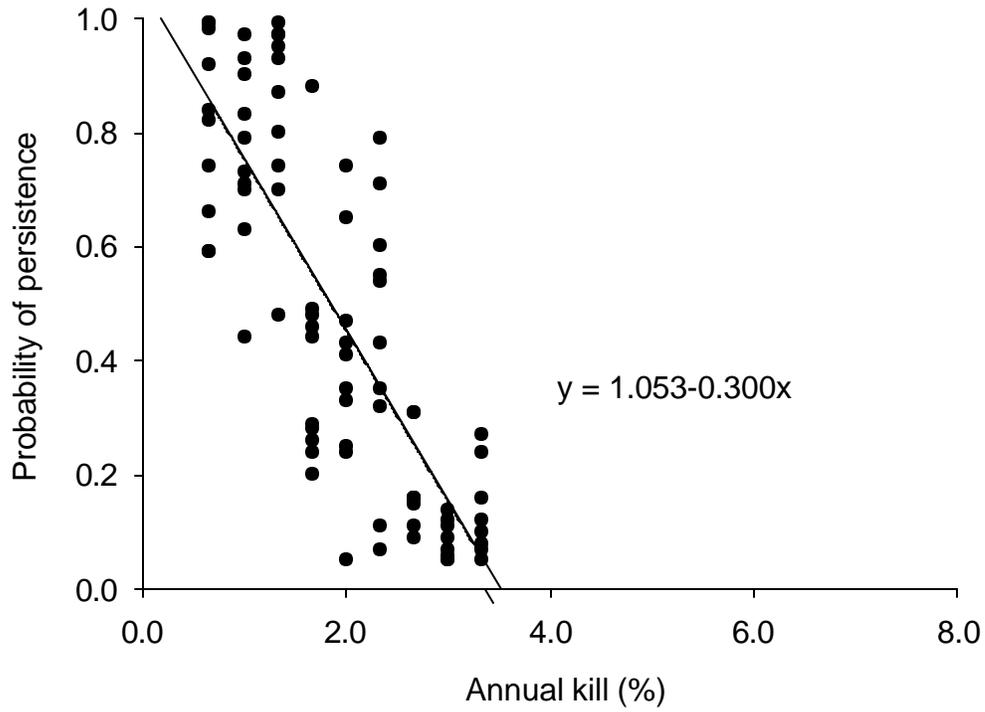
Fig. 2.5. Plot of persistence probability versus percentage annual kill for the simulated population inhabiting poor habitat (H_P). The equation for the line was calculated separately from the breakpoint analysis ($P < 0.001$).

The equation shown on the figure is:

$$y = 1.053 - 0.300x$$

population size is a primary determinant of probability of persistence (White 2000), grizzly bear populations less than 100 individuals will likely tolerate less than 3-5% annual kill, regardless of quality of habitat. For grizzly bear populations inhabiting poor quality habitats, such as those of the Arctic coastal plain or areas where human disturbance has lowered overall abundance and availability of foods, percentage allowable human-caused mortality must be minimized. Populations inhabiting these habitats will show steep declines in probability of persistence even with low levels of annual kill. Populations inhabiting good quality habitats, whose demographic parameters would suggest a natural finite rate of increase in excess of 1.07, may be able to absorb human-caused mortality up to 5% of initial population size without experiencing unsatisfactory low levels of probability of persistence.

Although I use primary productivity as a correlate of habitat quality, and suggest that habitat quality through effects on life history strategy drive susceptibility of populations to decline with the addition of human-caused mortality, I caution that estimates of primary productivity alone will not detail prospects of conservation for grizzly bear populations. For all simulated populations susceptibility of populations to decline was driven by the natural finite rate of increase of populations. I would suggest that prior to any management strategy to set levels of harvest for an actual population, life history and estimates of population growth in the absence of human-caused mortality should all be considered to predict the response of a population to non-natural mortality. These responses may or may not meet expectations from productivity estimates of habitat, depending, for example, on the current state of human or natural disturbance in the area, or current size of the population in question.

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3.0 Risks of Population Decline Given Documented Population Size, Kill, and Assumed Vital Rates for Grizzly Bear Populations in British Columbia

In this section I interpret models of grizzly bear population viability in British Columbia using simulations of population viability analysis (PVA) to quantify management risks associated with documented bear numbers from DNA mark-recapture programs, documented offtake (hunting and non-hunting, human-caused mortality), and natural vital rates for populations living in areas of good, moderate, and poor grizzly bear habitat. Specifically, I determine the potential risk of declines of 20% or more over the next 30 years for populations (Fig. 3.1) described in Appendix 7.1 of Boulanger and Hamilton (2002)—*A comparison of DNA mark-recapture and Fuhr-Demarchi/stepdown population and density estimates for grizzly bears in British Columbia*—given maximum allowable kill (including estimated non-hunting kill), and vital rates (natural survival) expected for given populations.

3.1 METHODS

3.1.1 Population Viability Analysis

Population viability analysis uses measures of vital rates for populations and effects of demographic and environmental stochasticity on population growth to evaluate probabilities of population persistence for a specified period of time (Boyce 1992). The usual approach for estimating persistence is to develop a probability distribution for the number of years before population models for a species 'go extinct', or fall below a specified threshold. The percentage
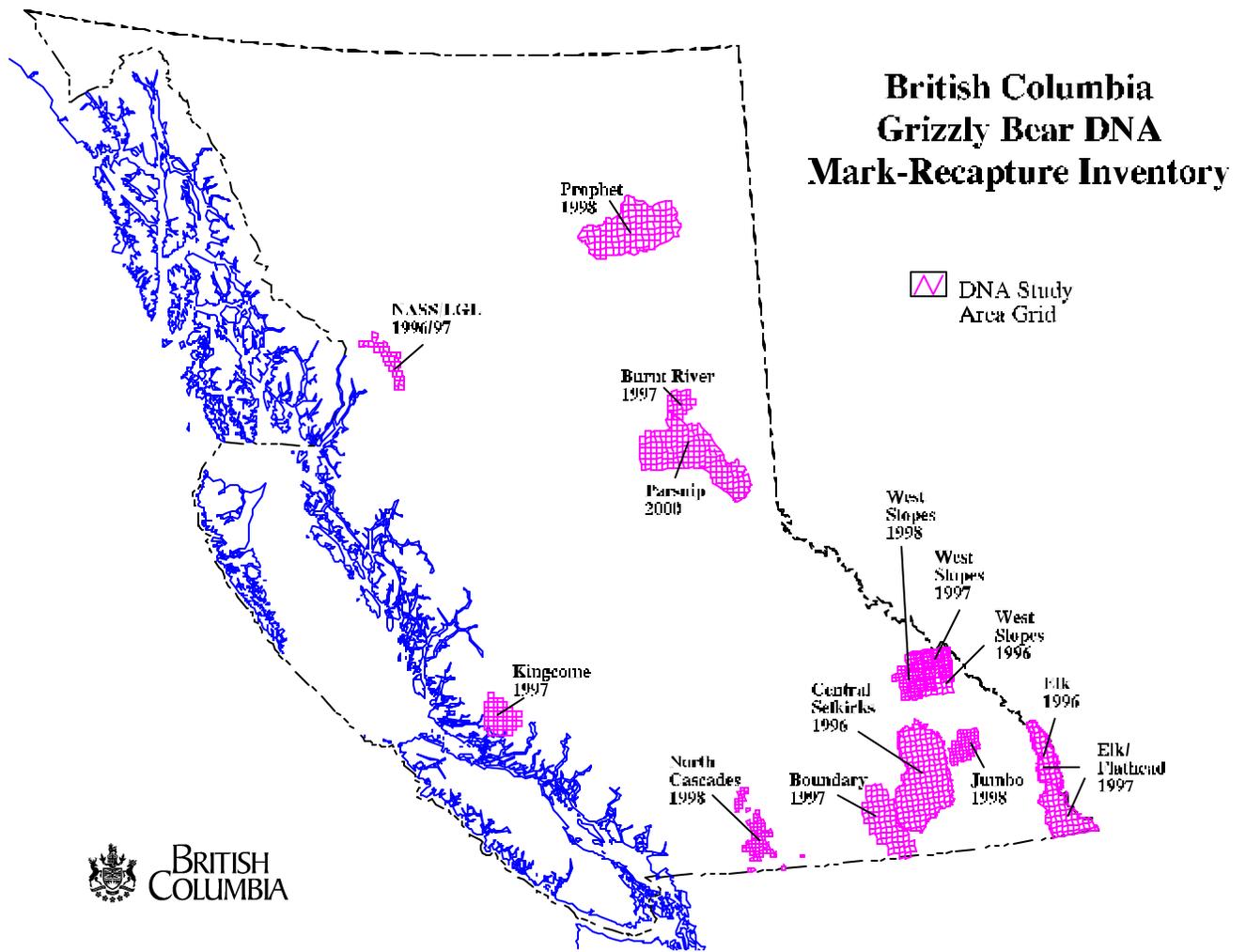
Fig. 3.1   Study area grids for most DNA mark-recapture programs included in this study (from Austin and Hamilton 2001).

of area under this distribution where the population persists beyond a specified time period is equated to persistence. For a review of PVA, including its merits and shortfalls, I refer the reader to White (2000).

Effects of human-caused mortality on populations can be incorporated into PVA in a variety of ways, ranging from detailed simulations that include the age-specific vulnerability and selectivity of the kill to simple apportionment of the kill according to the abundance of sex and age types in the population. A WINDOWS© compatible program named RISKMAN (see, e.g., Eastridge and Clark 2001) was developed for the full range of options described above (Taylor et al. 2001). The model is available freely from M. K. Taylor upon written request (P.O. Box 1000, Department of Sustainable Development, Government of Nunavut, Iqaluit, NU X0A 0H0, Canada).

Here I use RISKMAN to model population viability for grizzly bears in the presence of human-caused mortality. RISKMAN differs from other simulation models by providing an option to accurately model the population dynamics of species with multi-year reproduction schedules, such as bears, cetaceans, elephants, phocids, and primates (Taylor et al. 1987). The program provides a stochastic option that uses the variance of input parameters and the structure identified by the simulation options that are selected. The model obtains a random normal deviate for each survival and recruitment rate based upon the mean and standard error for particular age/sex strata. Individuals of age/sex strata in the model are then exposed in a series of Bernoulli trials to the probability described by the annual random deviate. This process incorporates annual variability and sampling error (normal distribution), and also uncertainty associated with applying the random mean to individual trials where the result is either a success or a failure (e.g., survival or death, produce a litter or fail to produce a litter).   The model uses

Monte Carlo techniques to generate a distribution of results (Manly 1997), and then uses this distribution to estimate the variance of summary parameters (e.g., population size at a future time, population growth rate, and proportion of runs that result in a population decline set at a pre-determined level by the user). The model relies on a life table approach (Caughley 1977), rather than a Leslie matrix (Leslie 1945) to model population dynamics. Individuals simultaneously survive and reproduce with the Leslie matrix approach, whereas the life table approach has the females survive first, then they reproduce (Taylor and Carley 1988). Having females survive first enables heterogeneity in female survival to influence reproduction for any given year, which increases realism in models of population viability (White 2000).

3.1.2 Populations

I compared effects of harvest and non-hunting, human-caused mortality on the viability of 10 simulated populations of grizzly bears in British Columbia (Table 3.1) exhibiting finite rates of increase (λ) that were assumed to vary with productivity of habitat (poor, moderate, good). Productivity of habitat was assigned to study populations according to Government of British Columbia assessments of the maximum total allowable kill for grizzly bears in areas of study, which was habitat-based in its assessment (Table 3.1). Assumed vital rates leading to finite rates of increase were obtained from models of populations inhabiting poor, moderate, and good grizzly bear habitats as presented in Section 2.1.2 of this report (Table 2.1). Population sizes and standard error (SE) of initial population estimates for modeled populations (Table 3.1) were the closure-corrected grid-based estimates from DNA mark-recapture projects (Fig. 3.1) presented in Appendix 7.1 of Boulanger and Hamilton (2002). Maximum annual allowable human-caused mortality, inclusive of maximum harvest and estimated non-hunting, human-

Table 3.1 Population parameters including maximum allowable regulated harvest, estimated annual non-harvest kill, population size (*N* and SE), and assumed vital rates for grizzly bear populations inhabiting grids of DNA mark-recapture studies presented in Boulanger and Hamilton (2002) and Mowat et al. (2002).

DNA Mark-Recapture Study Area	Vital Rates[a]	Current Allowable Regulated Harvest (bears/year)[b]	Current Estimated Non-Harvest Kill (bears/year)[c]	N[d]	SE[d]
Central Selkirks	H_M	7.8	5.8	262	23
Flathead	H_G	5.9	3.4	156	48
Granby Kettle	H_M	0.0[e]	0.8	38	13
Jumbo	H_M	1.1	0.9	39	6
Kingcome	H_M	4.1	1.0	102	21
Parsnip	H_M	11.4	7.0	367[f]	55[f]
Prophet	H_M	4.6	1.3	131	16
West Slopes 96	H_M	2.2	1.7	77	40
West Slopes 97	H_M	1.3	1.0	47	16
West Slopes 98	H_M	1.7	1.3	59	34

[a] Determined from habitat-based assessments of productivity of populations. Vital rates for population models are presented in Section 2.1.2 and Table 2.1. H_M refers to the Yellowstone model; H_G refers to the Flathead model (see Section 2.1.2).

[b] Current regulated harvest allowed on a DNA study grid, determined from habitat-based assessments of population productivity, and determined as the total allowable annual kill less estimated non-hunter kill. Converted from proportion provided by M. Austin and A.N. Hamiltion (BC Ministry of Water, Land and Air Protection) by multiplying with *N*.

[c] Estimated non-hunter kill on a DNA study grid, including kills in defense of life or property, aboriginal harvest, collisions on rail or road, and poaching. Converted from proportion provided by M. Austin and A.N. Hamilt ion (BC Ministry of Water, Land and Air Protection) by multiplying with *N*.

[d] Closure-corrected DNA mark-recapture population estimate (*N*) for populations and standard error (SE) presented in Boulanger and Hamilton (2002).

[e] Harvest is closed in Granby Kettle (M. Austin, BC Ministry of Water, Land and Air Protection, *personal communication*).

[f] From Mowat et al. (2002) and G. Mowat, *personal communication*.

caused mortality were obtained for each DNA mark-recapture study area (Table 3.1) from Government of British Columbia databases (M. Austin and A.N. Hamilton, Ministry of Water, Land, and Air Protection, Government of British Columbia, *personal communication*). Kill was applied to all populations in ratios according to hunter selectivity of age/sex strata for grizzly bears in British Columbia based upon past records (1978–2000) of sport, subsistence, problem, and known, illegal human-caused mortality (Appendix 4.1; from Austin and Hamilton 2001), and initially with vulnerability ratios from the standing sex/age structure of the well-studied Flathead grizzly bear population (McLellan 1989*a,b,c*). Note that females with cubs were assumed protected for all simulations.

3.1.3 Simulations

Persistence was modeled for simulated populations over 30 years, the time in which we can reasonably expect inventory reassessments for most grizzly bear populations in North America. For each population, 1000 stochastic population models were run to provide the proportion of outcomes falling below a set level of persistence, defined here as a population decline of less than 20%. Thus, each observation in the analysis represented the probability of the population declining by less than 20% over 30 years. A 20% decline over 3 generations (roughly 30 years for grizzly bears) is a criterion used by the IUCN to classify species or populations as 'threatened' (IUCN 1994). Stochastic population models were terminated if populations declined by more than 20% during a trial (i.e., recovery of populations after declining by 20% before 30 years had elapsed was not permitted). For all populations I began simulations with the stable age distribution.

Effects of catastrophes were not incorporated into models (Ewans et al. 1987), nor were potentially detrimental effects of inbreeding (Lacy 1993; Lindenmayer et al. 1995). Although there are provisions to model density-dependent effects in RISKMAN, I had no data to model such effects here (McLellan 1994; Boyce 1995; Mills et al. 1996; Wielgus 2002). I assumed annual random deviates of parameter values were independent for lack of data on temporal variability, although it is possible and perhaps likely parameters were correlated (White 2000).

3.2 RESULTS

Cumulative probabilities of population declines of ≥20% are presented for up to 30 years for study populations of grizzly bears in Figs. 3.2–3.11. Current maximum allowable harvest levels (2.8–3.8% of N), combined with relatively high levels of unknown, non-hunting kill (generally 2.2% of N) and uncertainty in estimates of initial population size, generated population viability models whose outcomes regularly surpassed declines of 20% over 30 years. For most populations, there appears to be a 1 in 2 chance that under current management practices grizzly bears will decline at rates exceeding this threshold target. Current management practices in only the Flathead and Granby Kettle study areas appear likely to prevent significant declines in population size over the next 30 years; however, prevention of declines for even these populations are by no means assured (e.g., 30% chance of 20% decline over 30 years).
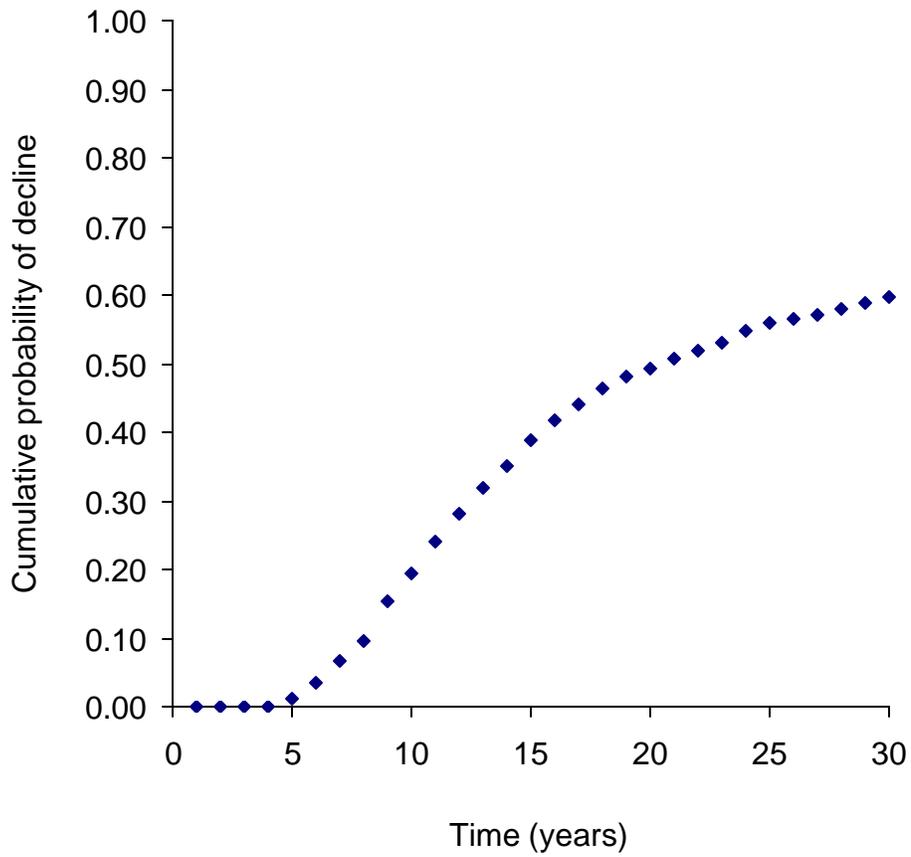
Fig. 3.2   The cumulative proportion of RISKMAN population simulation runs for the
Central Selkirks grizzly bear population having reached reductions of 20% from
initial population size as a function of time (future projection).
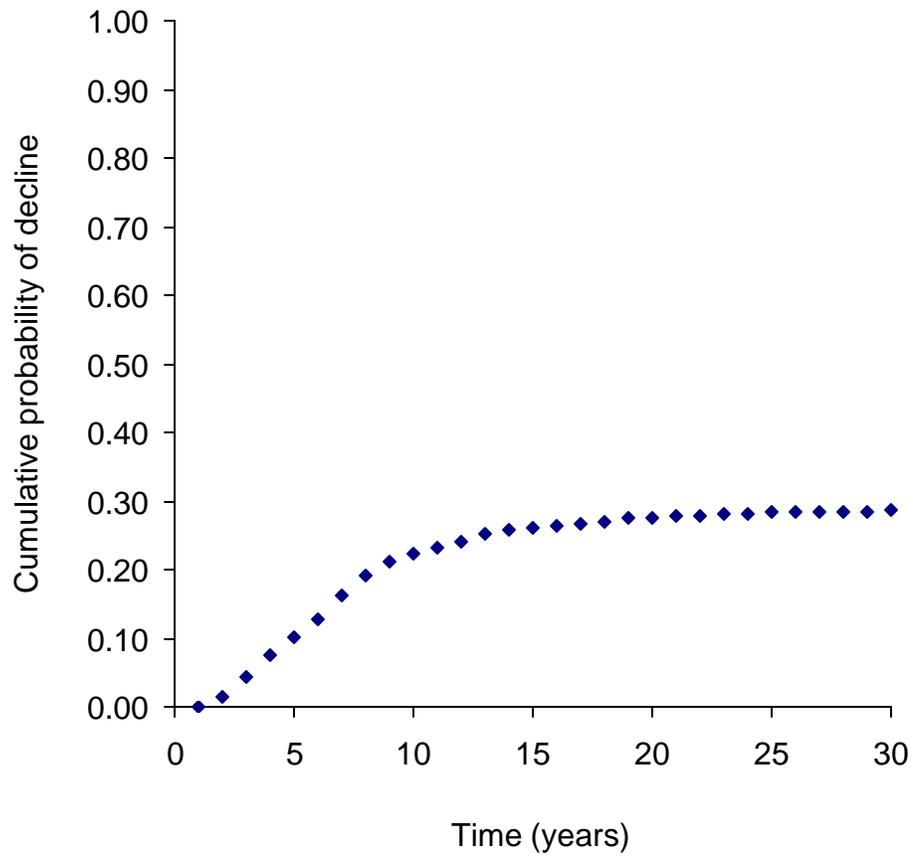
Fig. 3.3   The cumulative proportion of RISKMAN population simulation runs for the
Flathead grizzly bear population having reached reductions of 20% from initial
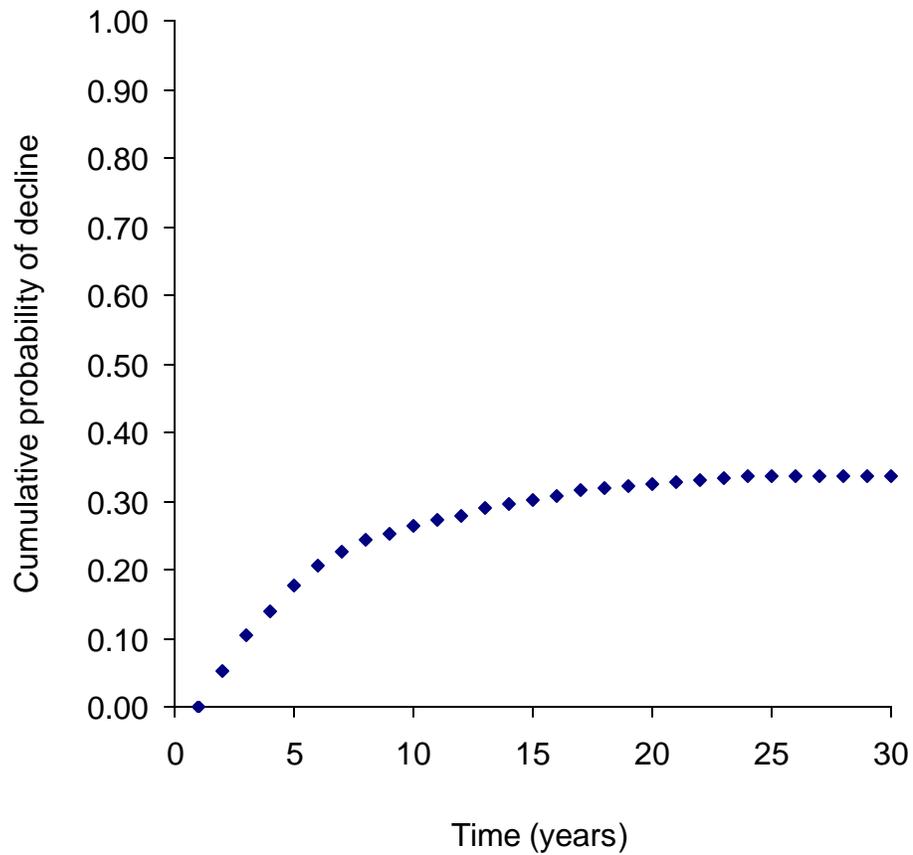population size as a function of time (future projection).

Fig. 3.4   The cumulative proportion of RISKMAN population simulation runs for the
Granby Kettle grizzly bear population having reached reductions of 20% from initial
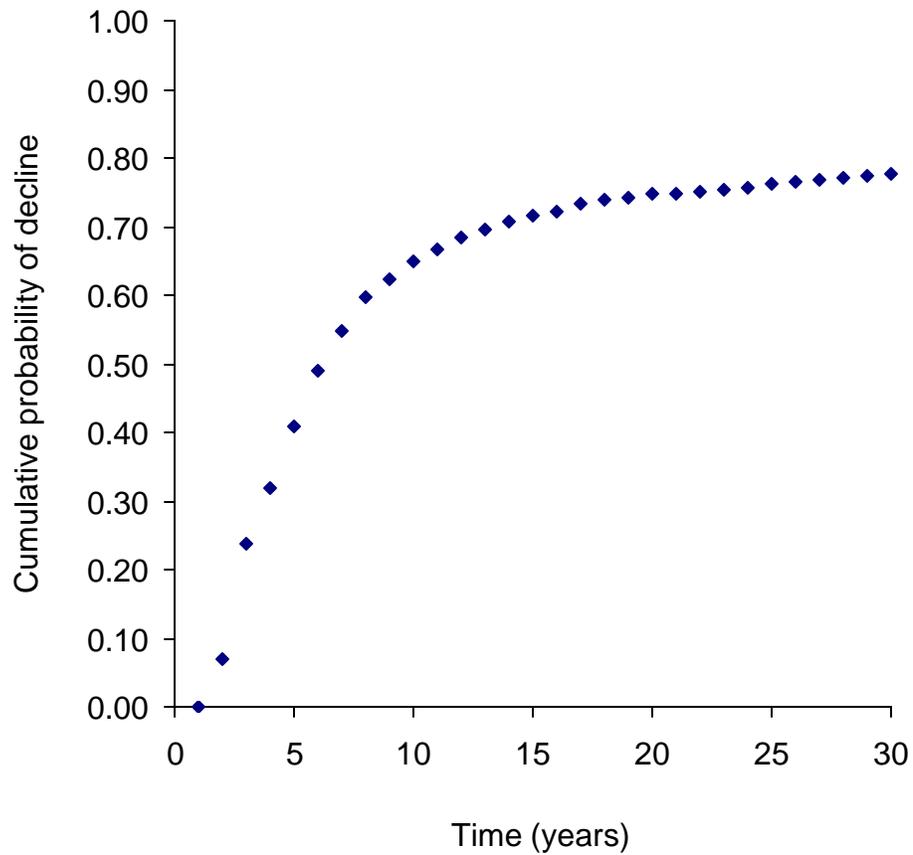population size as a function of time (future projection).

Fig. 3.5   The cumulative proportion of RISKMAN population simulation runs for the **Jumbo** grizzly bear population having reached reductions of 20% from initial population size as a function of time (future projection).
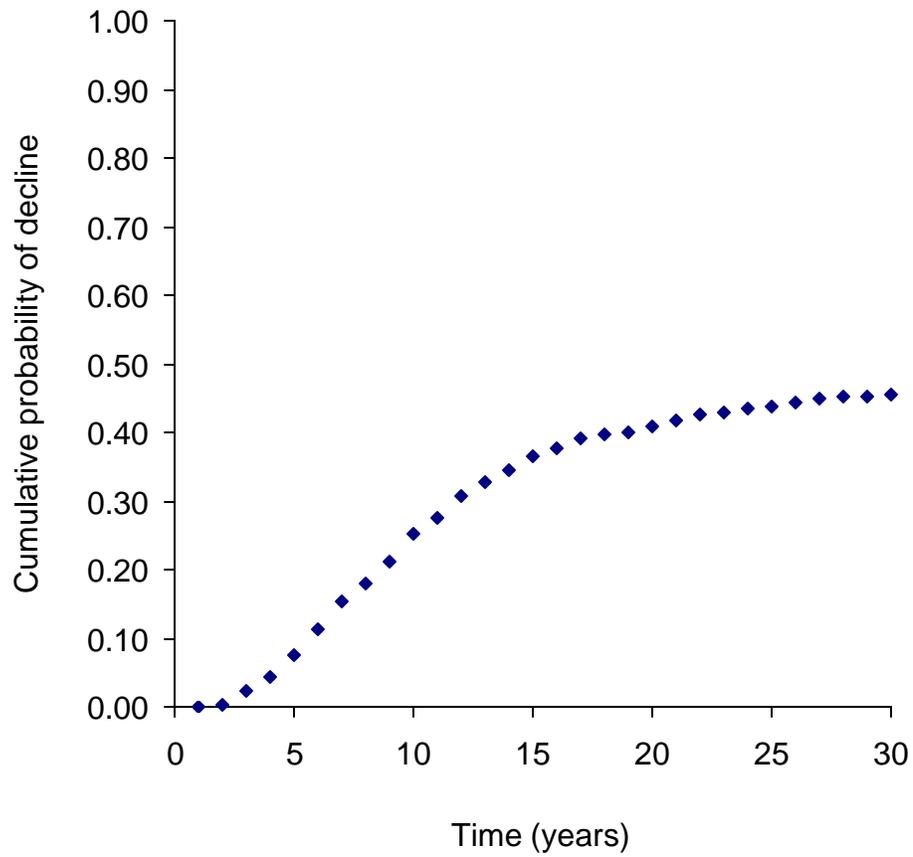
Fig. 3.6 The cumulative proportion of RISKMAN population simulation runs for the **Kingcome** grizzly bear population having reached reductions of 20% from initial population size as a function of time (future projection).
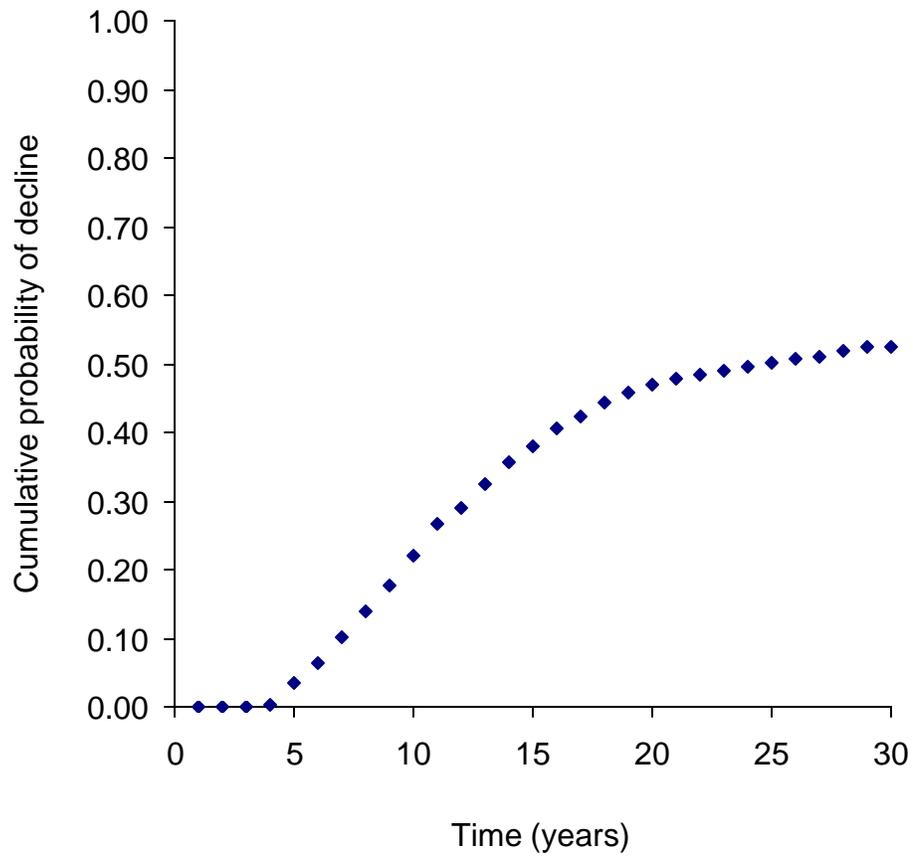
Fig. 3.7   The cumulative proportion of RISKMAN population simulation runs for the
Parsnip grizzly bear population having reached reductions of 20% from initial
population size as a function of time (future projection).

Fig. 3.8   The cumulative proportion of RISKMAN population simulation runs for the **Prophet** grizzly bear population having reached reductions of 20% from initial population size as a function of time (future projection).
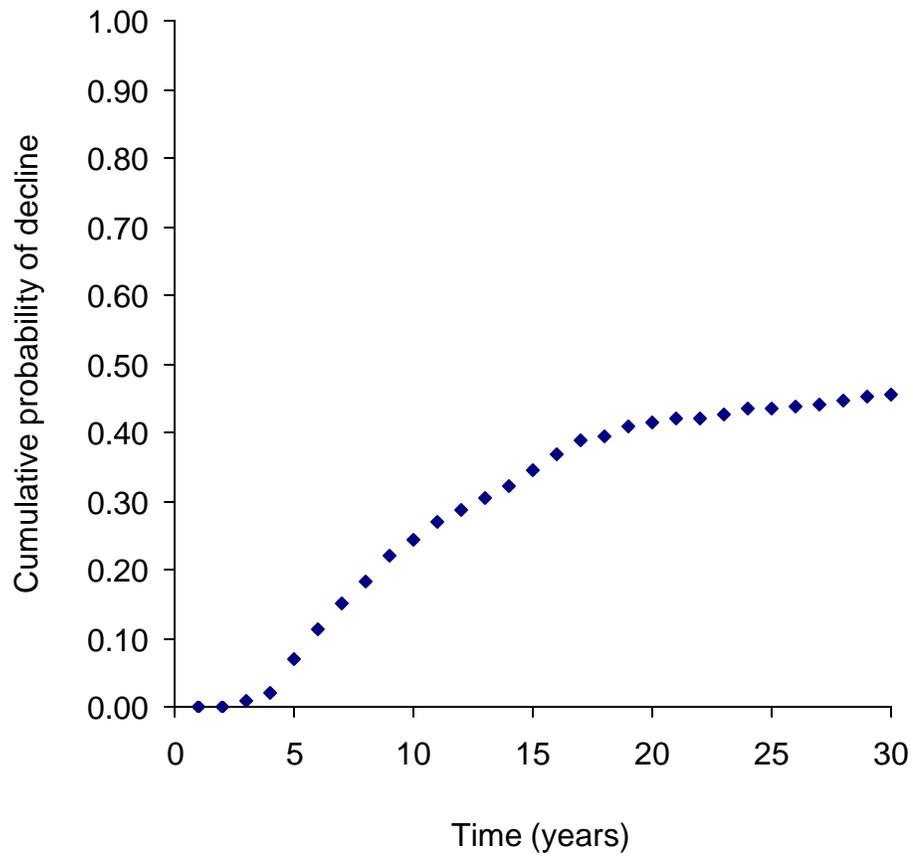
Fig. 3.9   The cumulative proportion of RISKMAN population simulation runs for the
West Slopes 96 grizzly bear population having reached reductions of 20% from initial
population size as a function of time (future projection).

Fig. 3.10 The cumulative proportion of RISKMAN population simulation runs for the
West Slopes 97 grizzly bear population having reached reductions of 20% from initial
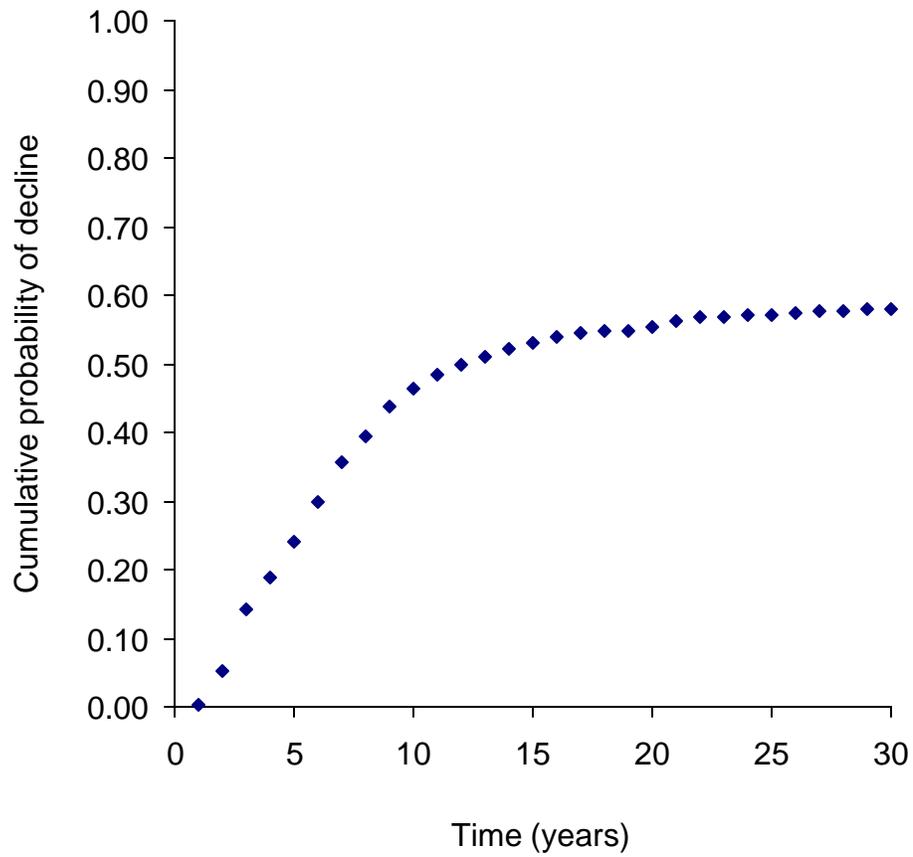population size as a function of time (future projection).

Fig. 3.11 The cumulative proportion of RISKMAN population simulation runs for the
West Slopes 98 grizzly bear population having reached reductions of 20% from initial
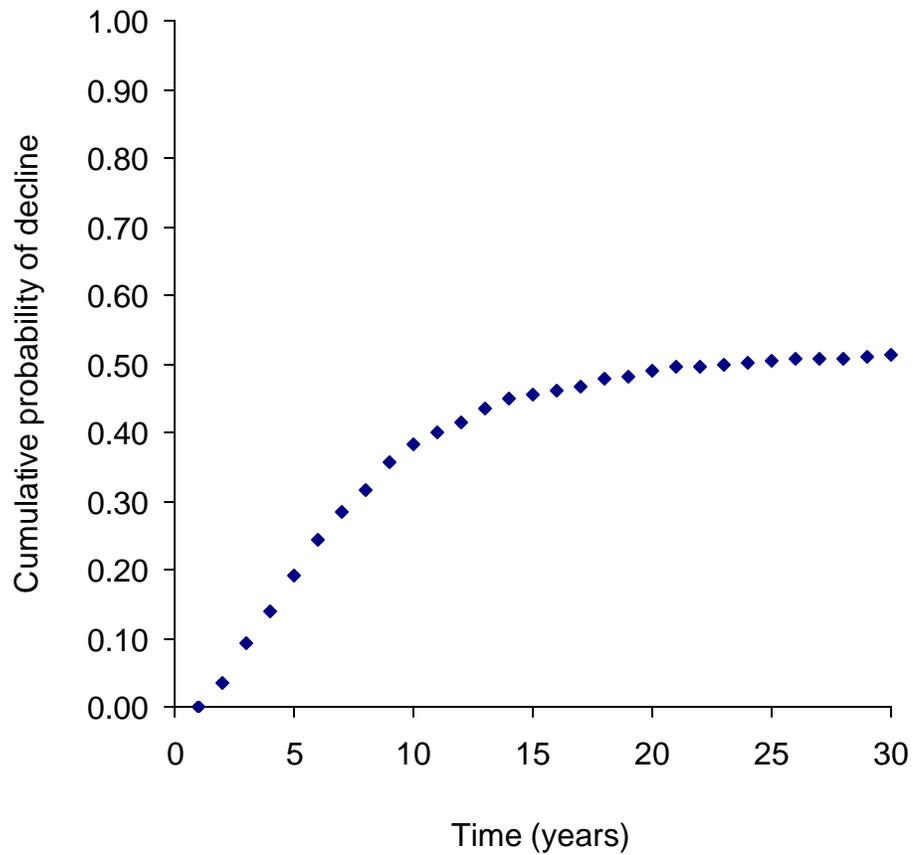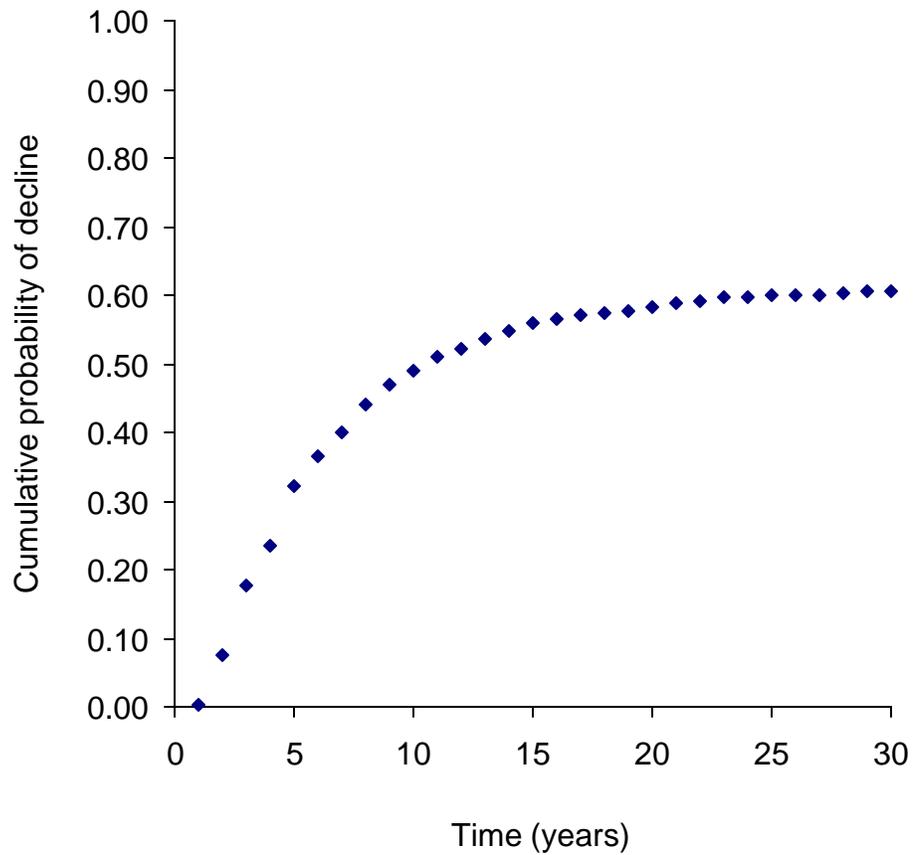population size as a function of time (future projection).

3.3 CONTEXT AND CONCLUSIONS

Probabilities of persistence were highest for the Flathead and Granby Kettle populations. Although possessing relatively high rates of harvest and estimated unknown kill, the Flathead population also assumed a higher natural finite rate of increase compared to all other populations (Table 3.1). Persistence for the Granby Kettle population was higher because the area is currently closed to regulated harvest (Table 3.1). The lowest probability of persistence was for the Jumbo population, likely because of the very low population size associated with this study area grid ($N = 39$). Large standard errors in initial population size appeared to lower probabilities of persistence (i.e., increase probabilities of decline). For example, the West Slopes 96, 97, and 98 populations were all harvested at the same rate with the same unknown mortality, but varied in probability of persistence more with the SE, rather than size, of the initial population.

Although regulated harvest rates (2.8–3.8% of N per year) appear reasonable considering population viability thresholds presented in Section 2.0, they are likely unsustainable in conjunction with uncertainty in population size plus the additional 2.2%/year estimated unknown, non-hunter mortality observed for most study areas. Having roughly a 1 in 2 chance that grizzly bear populations inhabiting grid study areas will decline at rates exceeding 20% over 30 years is probably unsatisfactory. If the province plans to maintain a 2.8–3.8% annual harvest without first decreasing the amount of uncertainty in population estimates, it is imperative that non-hunting mortality be reduced substantially to develop more acceptable outcomes of PVA for DNA-grids. If enforcement of hunting regulations cannot be improved and non-hunter mortalities reduced (e.g., road and rail deaths, kills in defense of life or property), then it is only

through a reduction in quota that grizzly bear populations can be modeled sustainably using PVA. The size of reduction in quota necessary to maintain persistence of populations has yet to be modeled.

The large standard errors associated with estimates of N provided by current DNA mark-recapture programs make it difficult to model population viability. Section 1.0 of this report summarizes the relatively large contribution of SE in initial population size to outcomes of PVA. Only when the precision of estimated population sizes are improved can estimates of population viability provide, with certainty, higher probabilities of persistence. It is possible that several populations examined in this study can be harvested at current rates, but I cannot say this with any certainty because of large estimates of SE in initial population size. Our only recourse in these situations is too err on the side of caution, and formulate management decisions based upon the models of PVA that include SE in initial population size. The utility of PVA for making 'real-world' management decisions rests not only in the accuracy of parameters and our estimation of breadth of environmental variation in vital rates, but also in the precision of parameters (Ludwig 1999). Managers are forced to make decisions with data they have on hand, and to exclude sampling error for PVA may, at worst, provide a false sense of security regarding the likelihood of population persistence. If models of PVA are to be more than academic exercises and instead tools to be applied in a real-world setting, we cannot ignore sampling error and its contribution to outcomes of PVA.

I would caution the applicability of these results for those areas for which DNA-grid population sizes, as estimated, do not represent unique, demographic units. PVA is modeled using an initial population size for which analysis is sensitive. Although grids sampled in Boulanger and Hamilton (2002) are often quite large (Fig. 3.1), it is possible that some do not

attempt to enumerate all bears in a demographic unit (e.g., watershed). Effective population size

for these populations may be greater than enumerated on DNA-grids; thus, population

persistence for grizzly bears in these regions may in actuality be higher than reported here.

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4.0   Appendix

Appendix 4.1 Relative distribution of average annual harvest for different age/sex strata in British Columbia (1978–2000) used for modeling kill (hunter and non-hunter) (from Tables 9 and 12 in Austin and Hamilton 2001). Note that females with cubs were assumed protected for all simulations.

Ages	Males	Females
0–2	22.74	12.35
3–4	48.65	26.44
5–9	64.52	34.30
10–14	28.13	15.87
15+	22.57	10.04