

**Assessing landscape conservation efforts for the
Muskwa-Kechika region of northeastern British Columbia:
Effects of habitat connection and human-caused mortality on
source-sink dynamics in grizzly bear populations**

**Final Report to the Yellowstone to Yukon Conservation Initiative
February 7, 2005**



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Cover photo taken in the Muskwa-Kechika Management Area by Kim Heinemeyer, 2003

Abstract

Landscape analyses are increasingly being used to guide ecosystem management. Unfortunately, interest in large-scale spatial structure has largely remained isolated from population dynamics of key species within these landscapes (with some notable exceptions), even though a major assertion of conservation science has been that populations are fundamentally influenced by landscapes. The use of spatially-structured population viability analysis (PVA) is one tool that can provide insights into the influence of landscapes on population. We link grizzly bear populations to landscapes of the Muskwa-Kechika region of British Columbia's Rocky Mountains through spatially-structured PVAs to assess population responses to current and potential future landscapes.

The 19.1 million ha study area surrounds Muskwa-Kechika Management Area (MKMA), an area with special legislation aimed at maintaining the region's globally significant wildlife while allowing industrial development. To capture potentially important differences in bear productivity and density, we modeled bear population dynamics as a "metapopulation" consisting of three adjacent populations: west-side Rocky Mountain population (WRM), east-side Rocky Mountain (ERM) population and boreal forest plateau (BFP) population. We used stochastic matrix modeling to project grizzly bear populations over planning horizons of 50 years, with stochastic annual survival probabilities and both correlated environmental variations and reciprocal dispersal between populations. Demographic parameters for each population were based on data believed to capture important regional differences (i.e., higher productivity WRM, lower productivity ERM, low productivity BFP). Specifically, we used demographic parameters from the Flathead region of BC for the WRM population, from the Yellowstone region for the ERM population and from the Northwest Territories for the BFP population. Initial population sizes are based upon current estimates of grizzly bear densities; we estimated environmental correlation and dispersal rates between populations, and assumed a ceiling function for density dependence at double the initial population size. We applied hunting mortality to populations based on historic harvest of sex-stage classes.

We first explored assumed current conditions in largely undeveloped landscapes. Deterministic lambdas for the three populations are 1.09, 1.03 and 0.99 for the WRM, ERM and BFP populations, respectively. These values do not include stochastic effects, immigration/emigration, hunter mortality or density dependence. Assessment of the sensitivity and elasticity of the lambda values shows the large influence that both subadult and adult female survival has on the population growth rate (e.g., sensitivity = 0.7, elasticity = 0.64 for ERM adult females). Stochastic simulations that incorporate connectivity and hunter mortality show that the metapopulation exhibits potentially important source-sink dynamics, with the WRM population serving as an important source to the ERM and BFP populations. This is particularly true with the increased mortality experienced with hunter harvest.

The Muskwa-Kechika region is presently largely undeveloped, but facing increasing pressure for expanded natural resource extraction and development. As these activities are allowed, it would be expected that landscape changes could have substantial effects on bear populations. We performed population simulations to evaluate the potential effects of anthropogenic landscape change, as well as test the adequacy of 1) existing parks and protected areas (PPAs) and 2) MK CAD recommendations. Under these scenarios, we assume differing survival rates within each population; base survival rates are associated with the undeveloped landscape (e.g., existing parks and protected areas) and reduced survival rates are associated remaining "developed" landscapes. Assuming relatively rapid movements within each region, we calculated new population average survival rates as the area-weighted average of the two survival estimates.

Under the PPAs scenario, reduction in average population survival rates results in lambda values of 0.99, 0.92 and 0.88 in the WRM, ERM and BFP populations, respectively. Stochastic simulations assuming no hunting mortality and the maintenance of connectivity across the regions confirm that existing parks and protected areas would not likely maintain viable bear populations, and all populations are predicted to decline. In a similar fashion, our second set of scenarios assumes that recommendations of the MK CAD are implemented such that Core Areas maintain the base survival rates, connectivity areas have reduced survival and matrix lands outside these classes do not support bears. In these scenarios, deterministic lambda values are 1.03, 0.96 and 0.92 for the WRM, ERM and BFP populations, respectively. Additionally, we assume connectivity between populations is limited to shared population boundaries classified as either Core or Connectivity Areas. Stochastic simulations show WRM and BFP populations as stable or increasing, but initial declines in the ERM populations; the metapopulation appear to maintain itself or slowly increase.

To explore the importance of connectivity, particularly given these predicted source-sink dynamics, we varied the amount of dispersal between populations and recorded the metapopulation and regional population sizes at the end of the 50-year simulation, under assumptions of no hunter mortality. The loss of connectivity results in a reduced metapopulation, with only the WRM population doing well. With small to moderate amounts of connectivity, overall metapopulation numbers increase as the ERM and BFP populations benefit from emigration from the WRM. But, high levels of connectivity result in high emigration from the WRM that cause the decline of this population and eventual declines in all populations.

Our results highlight the importance of understanding how regional dynamics can be linked both to population demography (particularly female survival), movement rates and behaviors, and landscape conditions; differences in population productivity and movement can lead to spatially-explicit dynamics such as source-sink relationships.

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1 Introduction

Managers and scientists are increasingly using landscape ecology, and particularly, landscape-scale analyses (e.g., conservation area design or CAD) to guide conservation management of ecosystem processes and populations across large regions (Hawkins & Selman 2002; Howard et al. 2000; Jepson et al. 2002; Pfab 2002; Soulé & Terborgh 1999; Wisdom et al. 2002). Unfortunately, interest in large-scale spatial structure and large-scale conservation has largely remained isolated from studies of population dynamics (but see Akcakaya et al. 1995; Bergman & Kindvall 2004; Brito & Fernandez 2002; Carroll et al. 2003, 2004; Lindenmayer & Lacy 1995). In spite of this isolation from population biology, a major assertion of conservation area design (CAD) has been that population and community processes will be fundamentally influenced by the spatial configuration of habitats across landscapes, and especially by the size and location of core reserve areas and connectivity areas.

The use of population viability analysis can provide insights into the influence of landscape configuration on population numbers and dynamics. Unlike CADs, these models explicitly focus on the changing numbers and fates of individuals, and how habitat patterning and other factors impact populations by changing these fates. Thus, population assessment of wide-ranging species, linked spatially to the CAD models, can provide insights into the adequacy of conservation area and connectivity recommendations. Large carnivores are particularly appropriate for such analyses, as they may be uniquely susceptible to extinction in the face of landscape change (Newmark 1986, 1987, Peterson 1988, Schonewald-Cox et al. 1991, Bixby 1991). This sensitivity is thought to result from the low population densities and wide home ranges of most predators (Ewer 1973, Eisenberg 1981, Pimm 1982, McNab 1986, Gittleman 1989). Thus, habitat fragmentation at spatial scales that might have little effect on most plant or herbivore species could profoundly affect carnivore populations (Schoener 1983, Lindstedt et al. 1986, Fowler 1987, Bernstein et al. 1991, Huntly 1991).

Here, we present on analyses linking grizzly bear populations to landscape conservation plans, and specifically to conservation already existing in, and recommended for Muskwa-Kechika region of the northern Rocky Mountains in northeastern British Columbia. In particular, we explore the importance of potentially altered survival rates across modified habitats and the importance of connectivity in determining the region's grizzly bear population trajectories, with special attention to the conservation strategies suggested by the recently completed Muskwa-Kechika CAD (Heinemeyer et al. 2004) (004).

2 Study Area and Populations

We used the study area defined for the Muskwa-Kechika CAD to identify our study grizzly bear population extent (Figure 1). This study area encompasses 19.1 million hectares surrounding the Muskwa-Kechika Management Area (MKMA) and is centered on the northern Rocky Mountains of BC. Study area boundaries are defined by the 11 ecosections which overlap the Muskwa-Kechika Management Area, to provide an ecologically distinct study area definition and provide a regional perspective of the importance of the MKMA.

2.1 *Muskwa-Kechika Management Area*

The 6.3 million hectares Muskwa-Kechika Management Area is nationally and internationally recognized as one of North America's last remaining large wilderness areas south of the 60th parallel where extensive predator-prey systems remain largely undisturbed by human industrial development pressures. The MKMA was established in 1997 and added to in 2001 through three BC Land and Resource Management Plans (LRMPs). Based on the consensus forged at the LRMP planning tables, the MKMA was established as a unique mix of protected areas and special management areas. The overarching goal of future management is to maintain wilderness and wildlife values while allowing resource development to occur in areas where such development could be undertaken without compromising the overall values that make the MKMA so important. The MKMA region and the MK CAD study area are described in detail in Heinemeyer (2004).

In 2001, the MK Advisory Board and the BC government contracted Nature Conservancy Canada and Round River Conservation Studies to develop a Conservation Area Design (CAD) for the MKMA to delineate and prioritize environmentally important areas based on current scientific knowledge, the tenets of conservation biology, and the precautionary principle. The MK CAD project was launched in January 2003 and was completed in July 2004.

2.2 *MK Bear Populations*

There is increasing awareness that regional differences in habitat productivity may result in notable differences in grizzly bear densities, vital rates and population dynamics. In British Columbia, differences in grizzly bear

populations have been noted for the west slopes of the Rocky Mountains, the east slopes of the Rocky Mountains and the boreal forest regions (Herrero et al. 2000; McLoughlin 2002; Mowat et al. 2004a; Mowat et al. 2004b). To capture important differences in bear productivity and density, we modeled bear populations in the MK CAD study area as three connected populations: a west-side Rocky Mountain population (WRM), an east-side Rocky Mountain (ERM) population and a boreal forest plateau (BFP) population (on the east and northern fringes of the study area).

We used the BC game management units, (Mowat et al. 2004a) and recently revised BC grizzly bear population unit (BC GBPU; D. Heard, WLAP, pers. comm.) to assist us in defining the spatial extent of each bear population within the MK CAD study area (Figure 2). Generally, these definitions follow major land forms (e.g., boreal forest plateau) and conform to trends in bear population density, as estimated (Mowat et al. 2004a).

3 Methods

3.1 Model Overview

We used spatially-explicit stochastic population matrix models to project grizzly bear populations over planning horizons of 50 years. Age cohorts deterministically moved through annual classes, with survival probabilities drawn from log-normal distributions of these parameters to estimate annual or environmental variability. We assumed a spring-time, post-breeding census with a birth-pulse reproductive cycle, thus the reproductive matrix elements includes maternity (i.e., cubs/female/year) multiplied by adult female survival, as females had to survive the year prior to being able to reproduce (Caswell 2001). The effects of environmental stochasticity on survival of each age class were assumed to be perfectly correlated within populations (e.g., a good year for one age class was a good year for all ages), and, to a lesser degree, between the populations (see Environmental Correlation, below). Populations were connected through correlation in environmental stochasticity and through dispersal. Emigration rates were proportional to source population size and habitat configuration, with immigrants into each population determined by the adjacency to the other populations. Baseline survival estimates for each population excluded hunting mortality, which was then added as additional deterministic mortality based on harvest data for each population. Modeling is based on annual 1-year age-sex classes, but for ease of communication, we refer to 6 stage-sex classes of bears: cubs, yearlings, subadult female, adult female, subadult male, adult male, as vital rates are provided by stages in the existing literature. Transition from subadults into reproducing adults occurred at the age of reported first successful reproduction for each population.

3.2 Vital Rates

We estimated vital rates for each population from existing literature on bear populations in similar habitats (e.g., high productivity western habitats; Table 1) and calculated estimated annual variability for each rate by appropriately rescaling the process variation provided by Schwartz et al. (2005). We assumed that West Rocky Mountain population was similar to studied populations found on the west side of the Continental divide in regions to the south, and used vital rates estimates from the nearest of these, the Flathead region (McLellan 1989a, 1989b, 1989c; McLellan et al. 1999), after removing harvest mortality, as presented in (McLoughlin 2002).

Population data from the Greater Yellowstone region (Schwartz et al. 2005) were used to estimate the vital rates for our East Rocky Mountain population. Again, while these research efforts were conducted substantially south of our study area, they provide some the most comprehensive data available for a bear population living in east-side habitats. Additionally, the lack of hunting within the Yellowstone region enabled us to use these baseline vital rate estimates with greater confidence than those in many regions.

We were unable to find vital rate statistics for grizzly bears occupying boreal forest habitats, and used vital rates provided for barren-ground grizzly bears in the Northwest Territories (McLoughlin et al. 2003a; McLoughlin et al. 2003b). While these data may underestimate the productivity of the boreal forest plateau population, they are the best information available to characterize a low-productivity population, as we assumed the BFP population to be. This assumption is based upon the low predicted densities of the region (Mowat et al. 2004a; Mowat et al. 2004b; Poole et al. 1999; Poole et al. 2001), and conversations with regional biologists. Additionally, if population persistence or abundance is partially determined by adjacency to other populations, as indicated by Mowat et al. (2004b), then our BFP population may be affected by the absence or very low density of bears along its eastern and southern boundaries.

3.3 Hunting and other human-caused mortality

Survival estimates, as described above, exclude hunter-killed mortalities, but may include other documented forms of human-caused mortality. To account for hunter mortality, we used hunter kill information for game management units within our study area (provided by BC Ministry of Water, Land and Air Protection, WLAP). We calculated the average number of adult females, subadult females, adult males and subadult males harvested between

1976 and 1997 within each grizzly bear management unit that is completely or partially contained within each of our three defined grizzly bear population areas. For those management units that were not completely encompassed within a population, we estimated the hunting mortality as the proportion of the total mortality equivalent to the game management unit area within the population. To avoid underestimating the hunter take, in some cases we had to estimate the age (and in some cases the sex) of hunter-killed bears in which age or sex was not recorded, based on known proportions of kills across sex-stage classes.

We used the hunter-kill information in two different ways. For models of bear dynamics under current conditions, we assume that the average number of bears harvested within each sex-stage class provides the best representation of current and future harvest because harvest quotas are based on static density estimates. Under scenarios that include assumptions about landscape changes, we allow the harvest to track the population size by setting the hunter mortality in each sex-stage class equivalent to the average sex-stage population portion harvested from 1976 - 1997 (Table 2; calculated assuming static population sizes and based upon current density estimates and a stable age/sex distribution). This latter approach assumes that hunting quotas or efforts follow predicted population changes, providing more conservative mortality estimates in most cases. To check this assumption, we plotted trends in the hunter-killed data over 21 years and found no obvious changes in mortality patterns that would indicate an increase or decrease in current hunter-caused mortality. To account for undocumented, illegal and unknown human-caused mortality, we applied a 2% annual mortality randomly across all sex-stage classes (McLoughlin 2002; U.S. Fish and Wildlife Service 1993).

3.4 Initial abundances, population structure and density dependence

Bear density estimates for many areas of BC have recently been updated, using models based on habitat productivity (Mowat et al. 2004a, D. Heard, pers. comm.). We used these newest GBPU density estimates to calculate predicted initial bear abundance within each of our regional populations (Table 3). Initial age and sex class abundances were based upon the stable age/sex distribution predicted by each population's vital rates. We assumed that current bear numbers are below carrying capacity, which we set at double the initial population size. Limited data exists on density-dependence functional responses for bears, though Schwartz et al. (2005) documented potential changes in reproductive rates. Given this paucity of data, we incorporated density dependence as a simple population cap or ceiling at the carrying capacity size, with no density dependent effects below the ceilings.

3.5 Determining dispersal probability

We assumed that only subadult bears would move between the three regional populations. We estimated the probability of dispersing to an adjacent population based upon dispersal distances reported for subadult male and female grizzly bears in the Flathead region of BC (McLellan & Hovey 2001) and the amount of shared boundary between two populations and source population size (see Appendix A for additional details). A Geographic Information System (GIS) was used to calculate the length of shared borders and to establish distance strata that allowed us to estimate the proportion of each population near enough to a shared border to allow dispersal. For example, the proportion of subadults that would move from Population B to an adjacent Population A is based upon the proportion that would move sufficient distance in one year, the proportion of these animals that would then also move in the direction of Population B (we assumed that movement was equally distributed in four directions); and the relative adjacency of Population B and Population A. Final movement probabilities were determined for movement between each population (Table 4) and used to estimate immigration and emigration rates between populations. Given limitation of the modeling software, dispersal rates used in the population simulations used the subadult male rates, and assumed that subadult females moved at 0.5 this rate, which approximates the calculated rate.

3.6 Environmental and demographic stochasticity

Because of the importance of environmental stochasticity in driving population dynamics, we built stochastic models which simulate year to year variation in average survival rates. However, virtually all published estimates of temporal variation in vital rates for grizzly bears do not attempt to separate true across-year variation from demographic stochasticity or sampling error. The only good estimates of true between year variation we could find are based upon the Yellowstone data for female and male survival rates (Schwartz et al. 2005); Schwartz and collaborators also estimated process variation for cubs and yearlings. We used the Yellowstone grizzly bear process variation statistics to estimate annual variation in the survival rates of the other populations by scaling the variance values to each survival estimate, following the approach of Morris and Doak (2004). We did not attempt to estimate environmental stochasticity in fecundities or include this variation in the models.

Unlike environmental stochasticity, demographic stochasticity has little influence on overall population productivity unless the population is at low numbers. Since the bear populations were not expected to fall to low

numbers within our simulation time frame, we did not include this complication in our models. The absence of demographic stochasticity results in somewhat overly-optimistic predictions about population performance, particularly if populations fall to low numbers.

3.7 *Environmental correlation*

We assumed that the annual variability in different survival rates *within* each population are perfectly correlated and we used long-term snow monitoring data to estimate the environmental correlation that may be experienced in the survival rates *across* the three bear populations. Two snow sampling stations within or near each population were selected, approximating the northern and southern conditions for each population (Figure 3). Data on snow depth have been routinely collected at these stations monthly during winter months from 1965 - 2002. To assess year-to-year correlation across populations, we extracted the yearly maximum snow depth measurement from each of the 6 stations and estimated correlations between all pairs of stations. While there was substantial variation between the northern and southern environmental conditions within some regions, we used the average correlation between each population to estimate the level of correlation expected between all pairs of survival rates in different regions (Table 5). We did not include temporal autocorrelation in our models.

3.8 *Landscape Conditions*

The Muskwa-Kechika region is largely undeveloped at present, but faces increasing pressure for expanded natural resource extraction including natural gas development, forestry and hard-rock mining. As these activities are allowed, it would be expected that landscape changes could have substantial effects on bear populations. We performed several population simulations to evaluate the potential effects of anthropogenic landscape change, as well as test the adequacy of potential protection provided by existing protected areas and by recommendation in the MK Conservation Area Design (Heinemeyer et al. 2004).

3.8.1 **Vital rates in modified landscapes**

Within all simulations, we assume that undeveloped landscapes support bear productivity as identified in Table 1, but that modified landscapes result in reduced survival rates (Table 6). We estimate the reduced survival rates using information on population lambda estimates outside of grizzly bear recovery zones in the Yellowstone region (Schwartz et al. 2005). Estimation details are provided in Appendix A.

3.8.2 **Landscape and Population Scenarios**

We simulated several different landscape and management conditions based upon estimated current conditions, as well as upon potential future conditions. Our basic models (Base assessments, below) explore potential population trajectories under estimated current conditions. These assume that the full study area landscape supports a metapopulation of grizzly bears and that each of the 3 regional populations has average population parameters as described in Tables 1, 3 and 4. We then explore the sensitivity of the metapopulation and regional populations to changes in assumptions about population connectivity (through dispersal) and mortality imposed by hunting.

We also explore potential population consequences to changes in regional habitat suitability due to major anthropogenic modifications. One set of scenarios is based upon the existing PPAs (see Parks and Protected Areas, below) and another is based upon landscape recommendations provided by the MK CAD (see MK CAD, below). Changes in populations under each scenario assume that the identified proportion of the landscape (e.g., existing PPAs) maintain present habitat potential, but that surrounding landscapes are developed for natural resource extraction or otherwise modified to reduce survival rates in these areas, specified in Table 6. Thus, within each population (i.e., WRM, ERM, BRM), the proportion of bears within the undeveloped landscapes maintain the original survival rates (i.e., Table 1), bears outside these landscapes experiences reduced survival and the population average survival rates become the area-weighted arithmetic average of the two (Tables 7 and 8). Using the arithmetic average assumes that there is complete mixing of individuals on an annual time scale. We scaled expected annual process variation for the new survival rates (as described in Environmental Stochasticity, above); these estimates are also provided in Tables 7 and 8. Below, we describe each scenario and its assumptions regarding the maintenance of dispersal/connectivity and hunting mortality rates:

Base assessments: In this series of simulations, we assume estimated current vital rates and population parameters (Tables 1, 3, 4). We explore the metapopulation and regional population consequences of changing assumptions about connectivity between the populations and about the levels of hunting mortality:

- 1) Static hunting: This represents our best estimate of current conditions. Harvest quotas are based upon a static estimate of bear density (numbers), and so the hunting schedule removes a set number of individuals from each

sex-stage class, as indicated by the average of past harvests. These numbers do not change with changing population size.

- 2) **Proportional hunting:** This represents a more lenient assumption about hunting mortality: that it does follow population numbers and removes an average *proportion* of each sex-stage class annually, as indicated by past harvests (Table 2).
- 3) **No hunting:** To explore how hunting may be affecting population trajectories, we run a scenario that does not include hunting mortality (but does include the 2% unknown human-caused mortality, as all simulations do).
- 4) **No connectivity with proportional hunting:** This explores the importance of connectivity and dispersal between populations, allowing us to compare the metapopulation and the regional population trajectories in the absence of movement between populations, and with hunting mortality (applied to each sex-stage class proportional to population size).
- 5) **No connectivity, no hunting:** This simulation includes no connectivity between populations and no hunting mortality. It represents projections that reflect the basic stochastic population matrix dynamics within each region.

Modified Landscapes Scenarios: For each of the two landscape scenarios below, we assume that there has been major anthropogenic landscape change outside of conservation areas. Under the Parks and protected areas scenario, these conservation areas are limited to the existing PPAs; under the MK CAD scenarios, the conservation areas are limited to the Core Areas recommended by the CAD. Within the conservation areas, grizzly bear populations maintain the base survival rates (Table 1), but outside of these areas, bears experience reduced survival rates (Table 5). Assuming high mixing of individuals, we calculate the area-weighted average (product) of the survival rates for each population under the two landscape scenarios. We then modify assumptions about hunting mortality and dispersal rates, as described below:

- 6) **Parks and Protected Areas (PPAs):** These scenarios assume that current PPAs (Figure 1) maintain present habitat potential and base survival rates, but that surrounding landscapes are anthropogenically modified such that survival rates are reduced. Area-weighted population average survival rates in PPA simulations, along with calculated annual standard deviations are presented in Table 7. We assumed that the initial population size is as calculated under current population densities (Table 3), and that bears still moved between populations proportional to their adjacency (i.e., connectivity is not affected). We varied hunting under 2 scenarios: in the first, we assumed hunting continued proportional to population size and in the other scenario we assumed that there was no hunting mortality.
- 7) **MK CAD:** This scenario tests the MK CAD designation recommendations (Figure 2) and assumes that CAD core areas maintain current habitat potential, the connectivity areas support reduced survival, and the remaining landscape does not support bears. Movement between populations is restricted to boundary areas encompassed with a CAD core or connectivity area, resulting in reduced dispersal rates (Table 9). We ran scenarios assuming either that hunting is proportional to population size or that there is no hunting mortality.

Source-Sink and Connectivity Scenarios: We also ran population models to explore the importance of connectivity in the context of the potential source-sink dynamics across the three populations. For these scenarios, we assume the MK CAD landscape survival and initial dispersal conditions, and then vary dispersal rates across all populations from 0.5 to 2X of the best-estimated dispersal rates. We then projected populations to compare the metapopulation and the regional population sizes at the end of the 50-year simulation window under each dispersal condition and under 2 different hunting options: hunting proportional to population size and no hunting.

3.9 Population Projections, Lambda Sensitivities, Elasticities and Measures of Risk

We projected populations using stochastic matrix analyses in RAMAS GIS Metapopulation module (Akçakaya 2002). For each landscape and population scenario, we ran 500 replicate simulations for a 50 year time horizon. We present the average population trajectory with SD and minimum and maximum predicted population sizes for each year. These results provide information about the expected trend in population size under the scenario, and the variability around that prediction. Additionally, we calculate population lambda as the geometric average of the population size and we provide the probabilities of metapopulation decline at any point in the simulation period, by different percentages and relative to the starting metapopulation size.

For each unique matrix configuration, we also report the deterministic lambda and the sensitivity and elasticity of lambda to the estimated vital rates. These estimates do not include stochasticity, hunting mortality or density-dependence, but nonetheless provide useful summaries about expected population behavior. While the matrices are based on age classes, vital rate estimates were based on stage classes, and we report the sensitivity and elasticity of

lambda to each sex-stage class survival and fecundity parameter, rather than the less meaningful sensitivities to individual matrix elements.

4 Results

4.1 Base Assessments

4.1.1 Deterministic Lambda, Sensitivities and Elasticities

The vital rates presented in Table 1 result in sharply divergent annual population rates of increase (lambda values) in the three populations (Table 10). The WRM population has the highest deterministic lambda at 1.089, similar to the rate of increase calculated by Hovey & McLellan (1996) from similar data. The ERM population lambda was calculated at 1.03; again this rate of increase is similar to that calculated for the Yellowstone (Schwartz et al. 2005), upon which our ERM data are based. The BFP population lambda is 0.992, which is lower than the lambda (1.03) estimated using an approximation of Lotka's equation by McLoughlin et al. (2003a).

All population lambdas show a high sensitivity and elasticity in response to the survival rates of both subadult females and adult females (Table 10). This general pattern is expected for any relatively long-lived species with a substantial pre-reproductive period (Caswell 2001), and has been identified for grizzly bears in other studies (Boyce et al. 2001; Eberhardt et al. 1994; Hovey & McLellan 1996). Most important for management is the near-equality of elasticity values for subadult and adult females in each population, indicating that mortality of either age group will have strong effects on population performance.

4.1.2 Stochastic simulations varying dispersal and hunting

Varying hunting mortality: Under base assessments of current conditions with static hunting mortality, the regional metapopulation and the three regional populations are all expected to increase or remain stable over the next 50 years (Figure 4). The probability of a decline $\geq 5\%$ of the initial abundance in any time step is $\leq .35$, but there is no probability of a terminal decline (Figure 5). The calculated metapopulation lambda is 1.007. Under base assessments of current conditions with proportional hunting mortality, the regional metapopulation and the three regional populations are all expected to increase or remain stable over the next 50 years (Figure 6). The probability of a decline $\geq 5\%$ of the initial abundance in any time step is $\leq .06$, and there is no probability of a terminal decline. The calculated metapopulation lambda is 1.009. As expected from the above results, in the absence of any hunting, all populations increase and the metapopulation lambda is 1.010.

Varying dispersal assumptions: Simulations assuming no dispersal between populations and no dispersal between the WRM population and the other 2 populations show that the WRM population likely functions as a source to maintain the ERM and BFM, and thus the whole metapopulation. In the absence of connectivity, the WRM population increases rapidly to its carrying capacity, while the ERM population maintains itself (or slowly increases) and the BFP population fairly rapidly declines (Figure 7). These patterns are consistent whether or not proportional hunting is applied. Also, if connectivity is established only between the ERM and BFM populations, the ERM population declines as it loses dispersers to the BFM population (Figure 8), and eventually the BFM declines as well. While the ERM population appears to be stable in isolation, only the WRM population appears to be a robust source population able to maintain or increase in numbers as well as provide emigrants to the adjacent populations (but see Source-Sink and Connectivity section below).

4.2 Parks and Protected Areas Scenarios

Under scenarios in which the survival of bears is reduced in all areas outside of the PPAs, all population survival averages are decreased, and associated lambdas are <1 in all cases (Table 7). Stochastic simulations show consistent declines in the whole metapopulation and in each of the three populations under scenarios with and without hunting (Figure 9). Even under no hunting scenario, the metapopulation lambda is calculated at 0.890.

4.3 MK CAD Scenarios

Deterministic lambda values under the CAD landscape scenario remained > 1 (1.03) for the WRM population, but were <1 for the EMR and BFP populations (Table 8). In the absence of hunting, the metapopulation is predicted to remain stable or slowly increase (Figure 10), with lambda = 1.003; there is little probability of notable declines in the metapopulation (Figure 11). While the WRM and BFP populations are predicted to increase, the ERM population is

predicted to initially decline and then stabilizes at about half its initial size and slowly begins to increase. The initial decline may be related to the changed connectivity under the MK CAD: connectivity between the WRM and ERM populations declines by 36% over the base assumptions, while other connectivities decline by notably less (i.e., WRM-BFP declines by 13% and ERM-BFP declines by 29%). With this lower rate of movement, the WRM population still subsidized the ERM numbers, but only at a lower density, especially since the ERM is still serving as a source for the BFP population.

The addition of proportional hunting mortality results in slightly less optimistic projections with the metapopulation predicted to remain stable or decline ($\lambda = 0.999$). In this case, the WRM and BFP population numbers are maintained or increased slightly, while the ERM population declines to approximately half of its original size and stabilizes (Figure 12). There are also notable increases in the probabilities of metapopulation decline (Figure 13).

4.4 Source-Sink and Connectivity Scenarios

The level of movement, or connectivity, between regional populations within the MK area is critically important because the outcome of source-sink dynamics can depend critically on the degree of movement that exists between different populations. Given this importance, and the uncertainty concerning current or future movement rates, we plotted final metapopulation and individual population sizes at the end of 50 year trajectories under a diversity of dispersal rate scenarios that mimic levels of connectivity (Figures 14). All of these simulations assume the landscapes and responses to landscapes as described in the MK CAD scenario (above); simulations are run with and without proportional hunting mortality. Under the no hunting assumption, extremely high or extremely low levels of connectivity result in reduced regional productivity, but with contrasting effects on the source and sink populations. In the absence of significant connectivity, the WRM population reaches high numbers, but the ERM and BFP dramatically decline, resulting in a reduced regional population. Alternatively, high levels of connectivity and dispersal result in declines in the WRM as it loses high numbers of dispersers to the other, sink, populations. Under high connectivity, the ERM and BFP populations initially respond favorably to the high levels of immigrants, but subsequently also decline as the WRM source declines (and immigrants decline with it).

We also ran scenarios with proportional hunting. With this added mortality, the metapopulation maintains higher numbers in the absence of connectivity than even with low levels of connectivity (Figure 15). With the imposition of hunting, the WRM population is unable to maintain both itself and lose emigrants to the adjacent populations. While the ERM and BFP populations do better with low to moderate levels of connectivity, they decline under high connectivity conditions as the WRM population declines to low numbers (reducing the number of emigrants).

5 Discussion

The sensitivity analyses showed that the rates of increase (λ s) are highly sensitive to the both the subadult and adult female survival rates, as is expected for a long-lived species with delayed and low reproduction rates (Caswell 2001). While we searched for the most appropriate demographic rates to parameterize each population based on similarities in general habitat characteristics and productivities, we have no specific information about the demography of grizzly bears in the Muskwa-Kechika region. It is likely that the demographic rates that we chose for the WRM and ERM may be optimistic given the northern latitude of the MK compared to the Flathead and Yellowstone source studies, though the coast populations may supplement WRM to effectively increase its productivity. Alternatively, source data for the BFP population came from barren-ground grizzly bears; which might be expected to have lower productivity than BFP bears. However, this difference is rather uncertain, given the low densities of bears in the BFP area. In addition, the barren-ground grizzly study (McLoughlin et al. 2003a; McLoughlin et al. 2003b) was in a region of low human use, while much of the BFP has relatively high road densities due to extensive oil and gas development and is likely to experience increased mortality associated with these roads. While it is impossible to know how appropriate our parameterizations of the matrix models are for each population, but we feel that the rates used likely over-estimate the general grizzly bear productivity in the region.

In addition to the need to estimate the demographic parameters for the analyses, we made assumptions about a diversity of conditions that affect the stochastic population projections, based upon limited data, including dispersal rates, environmental stochasticity, environmental correlation, and change in survival rates within human-modified landscapes. Unfortunately, the uncertainty of our information on such potentially important variables is not unusual; most past studies of grizzly bears, and many other species, is similarly hampered by missing or limited information. Nonetheless, the excellent work on several other grizzly populations in western North America provide us with

enough data to be sure that the general features of our model are a good reflection of the biology of bears in the MK area.

We included hunter-kill mortality rates based on approximately 20 years harvest data from each population, and consistently saw the sensitivity of the bear population projections to these hunting levels. This is particularly true in the case of static numbers of bears removed each year, causing concern about the necessarily static nature of hunting quotas (based on static bear density estimates). But, it may be expected that hunting success (regardless of static hunting quotas) may vary with population size, as we simulated in most scenarios. Yet, even this more optimistic mortality regime caused substantial reductions in population numbers. Finally, our harvest schedule did not incorporate annual variability; in keeping with general demographic theory, we expect that including such variability would increase the impacts of hunting.

Based upon the assumptions we made about demography and other population and environmental conditions, we found that grizzly bear populations in the region are likely to exhibit source-sink dynamics, with the WRM population in the most productive western landscapes providing critical emigrants to the less productive east-side landscapes and populations, particularly the boreal forest plateau population. While these dynamics are accentuated by the hunting mortality, even without hunting mortality, the overall metapopulation and the individual population dynamics were found to be quite sensitive to the level of connectivity and movement (dispersal) between populations. Too much connectivity can cause so much emigration from source habitats into sink habitats that the source population can decline, followed by declines in the sink habitats and the overall metapopulation. Alternatively, loss of connectivity to the productive western habitats and population has severe consequences on the eastern habitats; if the BFP habitats continue to drain the ERM populations, the ERM population declines and if connectivity between these eastern populations is lost, the BFM population cannot sustain itself.

While in our simulations we could increase connectivity to the point of causing region-wide declines, the more likely threat to populations is the reduction in natural levels of connectivity and movement, particularly as potential anthropogenic changes in eastern landscapes may cause these eastern populations to become more vulnerable as “sinks”). Thus, as resource development pressure increases, the threat to the connectivity is the isolation and vulnerability of the eastern populations. These potential consequences of isolation for the ERM and BFP populations should be recognized and carefully managed, and the critical importance of connectivity between all populations should be a landscape management priority.

Schwartz et al.(2005) felt that the Yellowstone region, though supporting very different survival and lambda predictions within the region (i.e., in the park, outside the park but in recovery zones and outside recovery zones) did not have true “source-sink” dynamics, as bears are wide ranging and can move from source to sink areas with relative ease (but see Doak 1995). Similarly, we did not consider source-sink dynamics *within* each population, though under our landscape scenarios, bears within a population could be found in landscapes that supported high or low survival. We also assumed that bears *within* each population moved frequently and widely enough for population mixing and, therefore, we chose to average of the two different survival regimes present within a population (under a landscape scenario). Other assumptions (e.g., that bears in small parks and protected areas would not move freely in and out of these limited areas into unprotected landscapes) would result in very different dynamics. In our landscape scenarios, the average survival rate declined as modified habitats come to dominate the region, causing population decline. Alternatively, it would likely be demographic stochasticity (and/or genetic effects), and not actual reduced survival rates, that would endanger small and isolated populations that would result from much more limited movements. However, the movement patterns documented for bears makes this scenario appear unlikely for MK populations. Given that most landscapes within the remaining occupied and potential habitats would be a mix of secure and modified habitats, our work highlights the importance of reducing female mortality within modified habitats. While it is recognized that large carnivores are particularly sensitive to landscape change because of their wide-ranging habits, few studies have emphasized the population-level averaging of survival rates across landscapes in assessing population dynamics (as opposed to source-sink dynamics; but see Schwartz et al. 2005).

The landscape scenarios indicate that the existing PPAs would be inadequate to maintain viable bear populations, even if bears were able to maintain movement across the modified landscapes. It will be important to focus grizzly bear conservation efforts on reducing mortality in landscapes outside the PPAs, particularly if human access to and alteration of these landscapes increases (particularly for the eastern populations). The recommendations for Core Areas and Connectivity Areas presented within the MK CAD do not appear adequate to maintain independently viable ERM or BFP populations, unless hunting mortality is eliminated. The loss of some connectivity to the WRM population under the CAD recommendations appears particularly worrisome, as it is predicted to increase the vulnerability of the ERM in the face of hunter mortality.

These analyses have highlighted the importance of understanding population dynamics across landscapes and how these dynamics can drive the success of landscape-scale conservation. In particular, we found that the potential source-sink dynamics of the MK grizzly bear populations creates population vulnerability to changing connectivity conditions, particularly in the face of reduced survival from harvest and anthropogenic modification of landscapes. As

managers, scientists and conservationists continue to pursue landscape-scale planning, the long-term success in these endeavors should increasingly be evaluated at the population level, to understand how complex landscape changes will influence the dynamics of key vulnerable species.

6 Tables

Table 1. Demographic parameters for each population: survival of cubs (*Sc*), subadult females (*Ssf*), adult females (*Saf*), subadult males (*Ssm*) and adult males (*Sam*); maternity (*M*), fecundity (*f*), age at first reproduction, and senescence.

Vital Rate	West Rocky Mnt ^{a,d} Average \pm SD	East Rocky Mnt ^b Average \pm SD	Boreal Forest Plateau ^{c,d} Average \pm SD
<i>Sc</i>	0.870 \pm 0.064	0.640 \pm 0.091	0.737 \pm 0.083
<i>Sy</i>	0.947 \pm 0.060	0.817 \pm 0.101	0.683 \pm 0.125
<i>Ssf</i>	0.933 \pm 0.015	0.950 \pm 0.013	0.831 \pm 0.023
<i>Saf</i>	0.959 \pm 0.012	0.950 \pm 0.013	0.979 \pm 0.009
<i>Ssm</i>	0.913 \pm 0.025	0.874 \pm 0.030	0.824 \pm 0.034
<i>Sam</i>	0.924 \pm 0.024	0.874 \pm 0.03	0.966 \pm 0.016
<i>M</i>	0.850	0.636	0.810
<i>f</i>	0.815	0.604	0.793
Age of 1 st reprod	6	6	7 ^e
Senescence ^f	20	22	24

^a Based on data from (Hovey & McLellan 1996; McLellan 1989a, 1989b, 1989c; McLoughlin 2002)

^b Based on data in (Schwartz et al. 2005)

^c Based on data in (McLoughlin et al. 2003a; McLoughlin et al. 2003b)

^d Standard deviations based upon scaling SD estimates from Yellowstone (see text)

^e Based on information from (Pearson 1975)

^f Little information on senescence; estimates are based on existing literature

Table 2. Proportions of sex-stage classes in each population that are assumed harvested each year under the proportional hunting mortality scenarios.

Sex-Stage Class	WRM	ERM	BFP
Subadult Female	0.018	0.061	0.078
Adult Female	0.022	0.006	0.025
Subadult Male	0.038	0.045	0.140
Adult Male	0.046	0.041	0.011

Table 3. Estimates of population parameters under current conditions.

Population parameter	West Rocky Mnt	East Rocky Mnt	Boreal Forest Plateau
Initial abundance	904	789	466
Average density ^a	23.4	21.6	18.2
Population Area (ha)	38,663	36,537	25,547
Carrying Capacity ^b	1,808	1,578	932
Stable Age Distribution			
% cubs	15	17	14
% yearlings	12	10	10
% subadult females	17	14	13
% adult females	23	32	26
% subadult males	21	13	12
% adult males	12	14	25

^a Based on (Mowat et al. 2004a)

^b Assumed to be double the predicted initial population size based on density

Table 4. Dispersal rates calculated between populations, based upon area of adjacency and movement distances in McLellan & Hovey (2001).

	WRM	ERM	BFP
<u>Subadult Males</u>			
WRM	1	0.172	0.045
ERM	0.078	1	0.265
BFP	0.069	0.249	
<u>Subadult Female</u> ^a			
WRM	1	0.082	0.021
ERM	0.037	1	0.130
BFP	0.036	0.135	1

^a In simulations, dispersal for subadult female dispersal rates assumed to be 0.5X the rate calculated for subadult males.

Table 5. Environmental correlation calculated as the average correlation in snow depth across the three populations.

Population	WRM	ERM	BFP
WRM	1	-	-
ERM	0.62	1	-
BFP	0.49	0.60	1

Table 6. Survival rate estimates within human modified landscapes: human-modified survival of cubs (S_{c-hm}), subadult females (S_{sf-hm}), adult females (S_{af-hm}), subadult males (S_{sm-hm}) and adult males (S_{am-hm}).

Vital Rate	West Rocky Mnt	East Rocky Mnt	Boreal Forest Plateau
S_{c-hm}	0.817	0.443	0.587
S_{y-hm}	0.657	0.489	0.342
S_{sf-hm}	0.840	0.860	0.748
S_{af-hm}	0.863	0.860	0.881
S_{sm-hm}	0.822	0.723	0.750
S_{am-hm}	0.831	0.723	0.885

Table 7. New population vital rates and lambdas calculated under the Parks and Protected Areas scenario as the area-weighted product of the survival rates in the PPAs and in the unprotected landscapes.

Population Parameter	WRM Average \pm SD	ERM Average \pm SD	BFP Average \pm SD
Fecundity	.752	.559	.720
S_c	.830 \pm 0.071	.485 \pm 0.095	.599 \pm 0.093
S_y	.724 \pm 0.120	.559 \pm 0.133	.371 \pm 0.130
S_{sf}	.861 \pm 0.021	.879 \pm 0.020	.755 \pm 0.026
S_{af}	.885 \pm 0.022	.879 \pm 0.026	.889 \pm 0.026
S_{sm}	.843 \pm 0.029	.756 \pm 0.029	.757 \pm 0.028
S_{am}	.853 \pm 0.032	.756 \pm 0.039	.893 \pm 0.028
lambda	.992	.919	.884

Table 8. New population vital rates and lambdas calculated under the MK CAD scenario as the area-weighted product of the survival rates in the conservation areas and in the connectivity areas.

Population Parameter	WRM	ERM	BFP
	Average \pm SD	Average \pm SD	Average \pm SD
Fecundity	.781	.577	.455
S_c	.848 \pm 0.068	.545 \pm 0.094	.671 \pm 0.089
S_y	.825 \pm 0.102	.660 \pm 0.127	.533 \pm 0.134
S_{sf}	.894 \pm 0.019	.907 \pm 0.018	.794 \pm 0.025
S_{af}	.919 \pm 0.020	.907 \pm 0.025	.940 \pm 0.025
S_{sm}	.875 \pm 0.025	.802 \pm 0.026	.796 \pm 0.022
S_{am}	.885 \pm 0.029	.802 \pm 0.036	.940 \pm 0.022
lambda	1.037	0.963	0.924

Table 9. Dispersal rates assumed between populations under the MK CAD scenarios, modified from full dispersal rates based upon shared population borders classified as either Core or Connectivity Areas within the MK CAD

	WRM	ERM	BFP
<u>Subadult Males^a</u>			
WRM	1	.0112	0.039
ERM	0.050	1	0.187
BFP	0.060	0.176	1

^a Subadult female dispersal rates assumed to be 0.5X the rate calculated for subadult males.

Table 10. Lambdas, lambda sensitivities and elasticities to vital rates under the base assessments (i.e., vital rates in Table 1) for the three populations assuming no stochasticity, no density dependence and no hunting or illegal (unknown) human mortality.

	WRM	ERM	BFP
Lambda	1.089	1.0305	0.9915
S_c Sensitivity/Elasticity	0.106/0.085	0.122/0.076	0.084/0.0624
S_y Sensitivity/Elasticity	0.193/0.168	0.192/0.153	0.180/0.124
S_{sf} Sensitivity/Elasticity	0.576/0.493	0.697/0.643	0.812/0.764
S_{af} Sensitivity/Elasticity	0.593/0.523	0.692/0.638	0.605/0.598
S_{sm} Sensitivity/Elasticity	0/0	0/0	0/0
S_{am} Sensitivity/Elasticity	0/0	0/0	0/0
F Sensitivity/Elasticity	0.124/0.097	0.137/0.084	0.0885/0.072

7 Figures

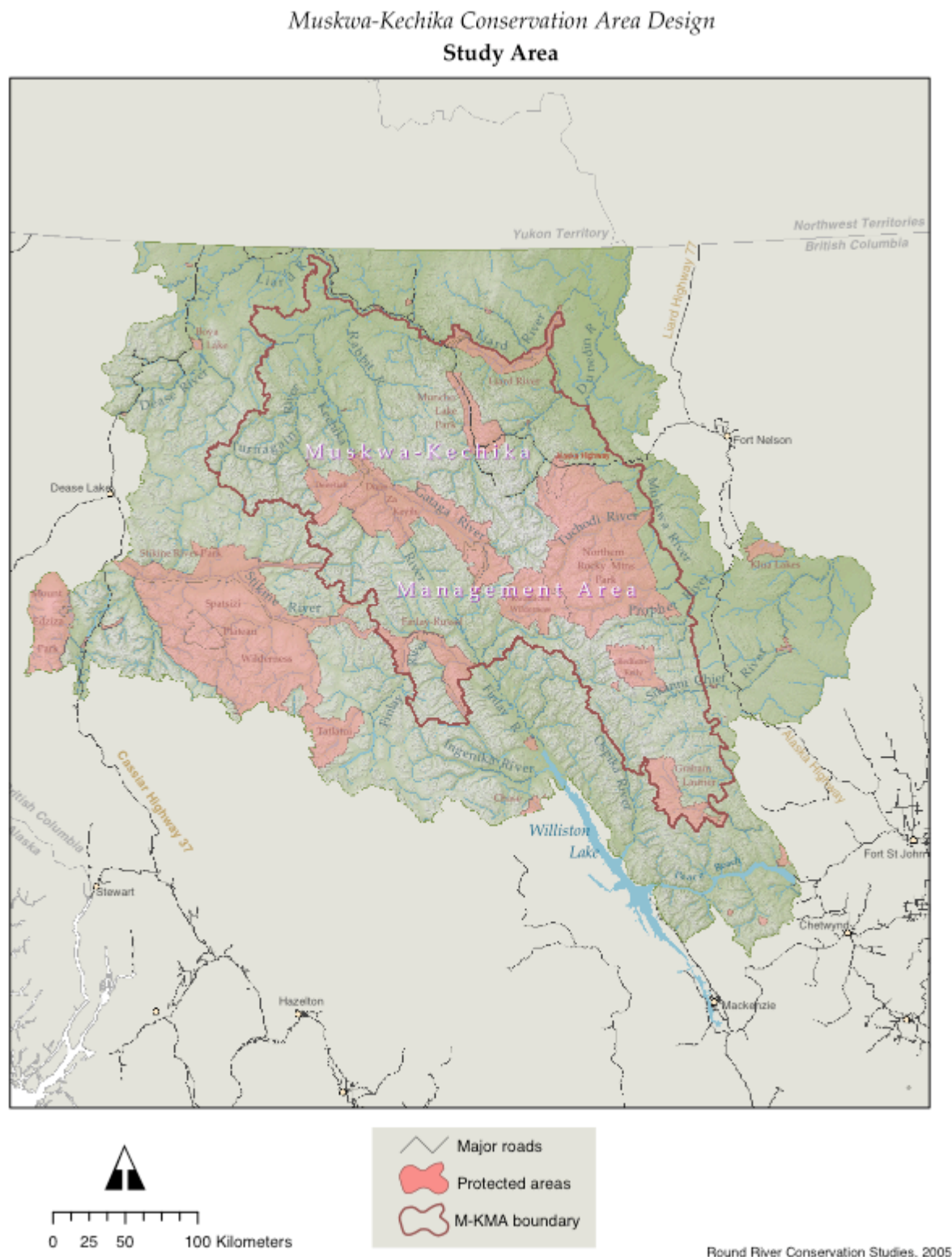
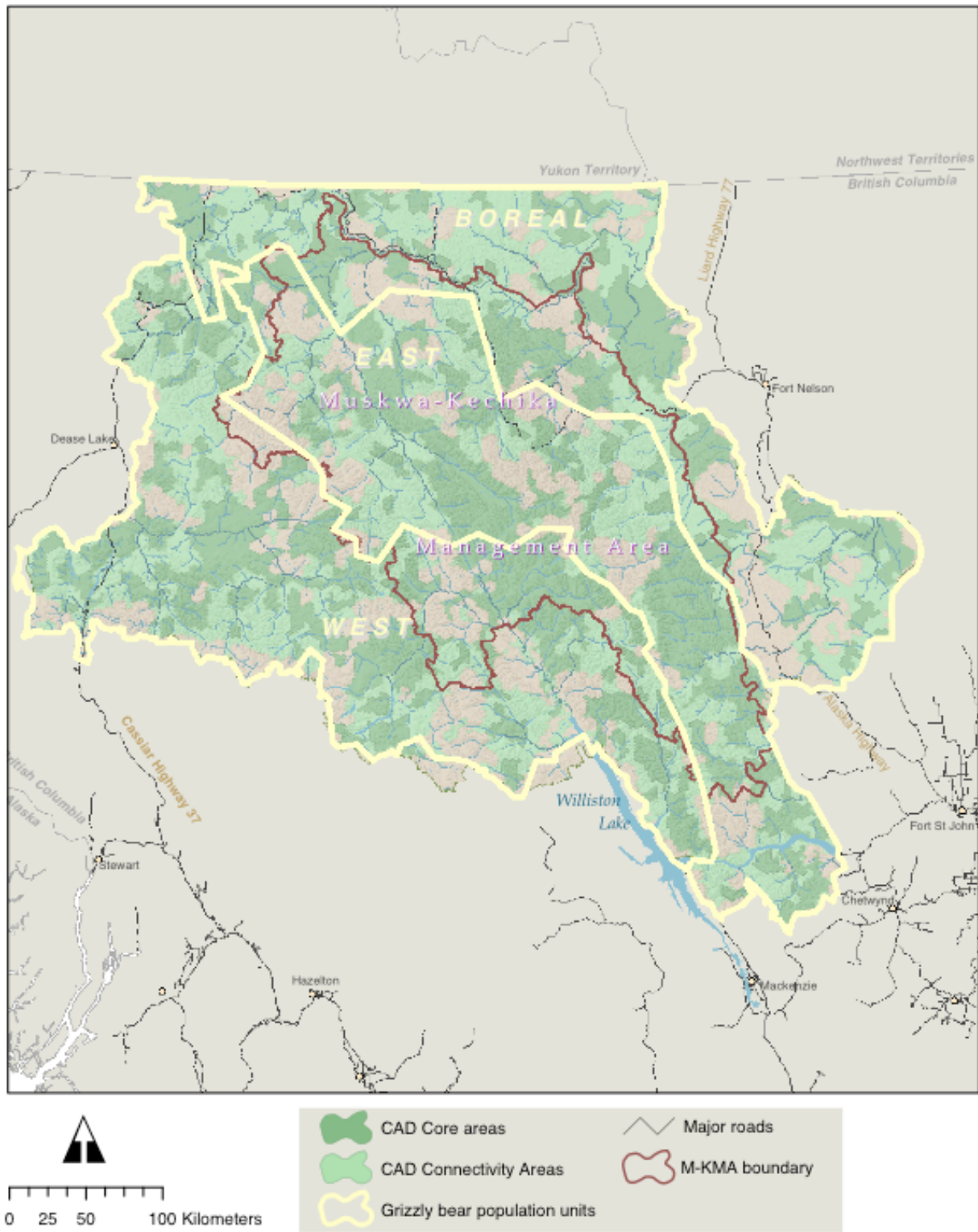


Fig 1: The MK CAD study area was used to define the extent of the PVA analyses. The map shows the distribution of existing parks and protected areas within the region, used in landscapes scenarios of bear population responses to landscape change.

Muskwa-Kechika Conservation Area Design
CAD Cores, Connectivity Areas, and Grizzly Bear Population Units



Round River Conservation Studies, 2005

Figure 2. Spatial definition of the 3 grizzly bear populations assumed to reside with the MK CAD study area and the MK CAD landscape designation recommendations.

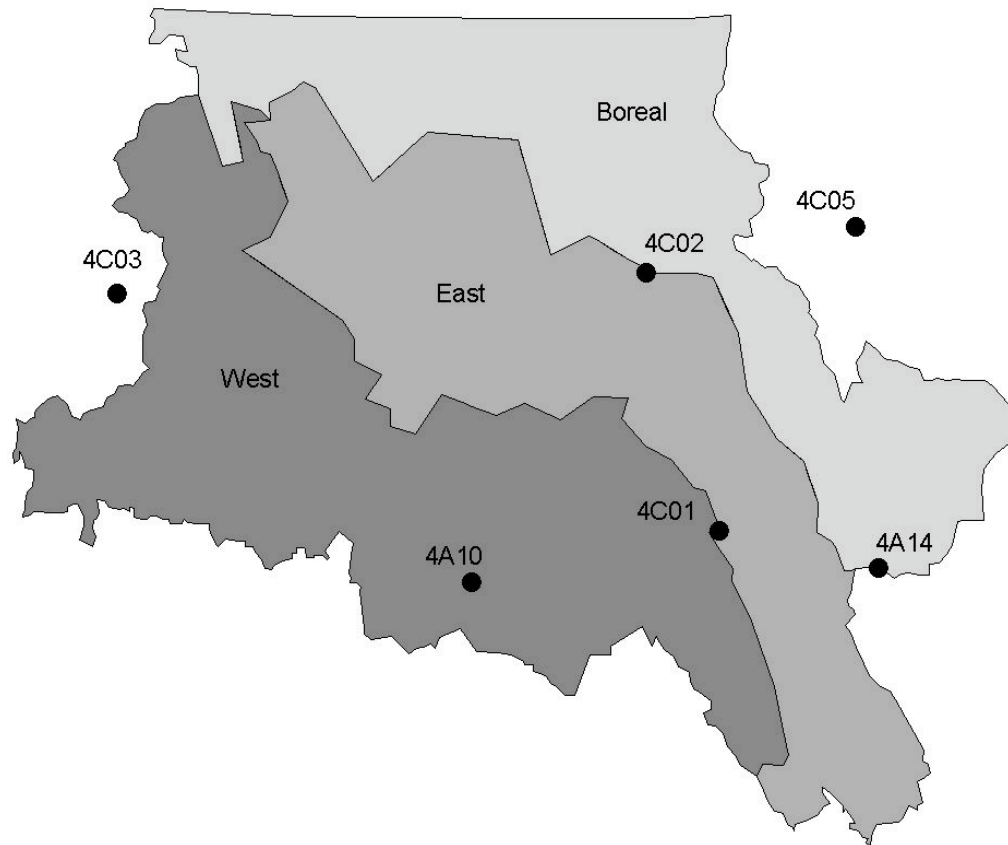


Figure 3. Two snow monitoring stations with or near each of the three populations were used to assess environmental correlation between populations, based upon yearly snow depth data.

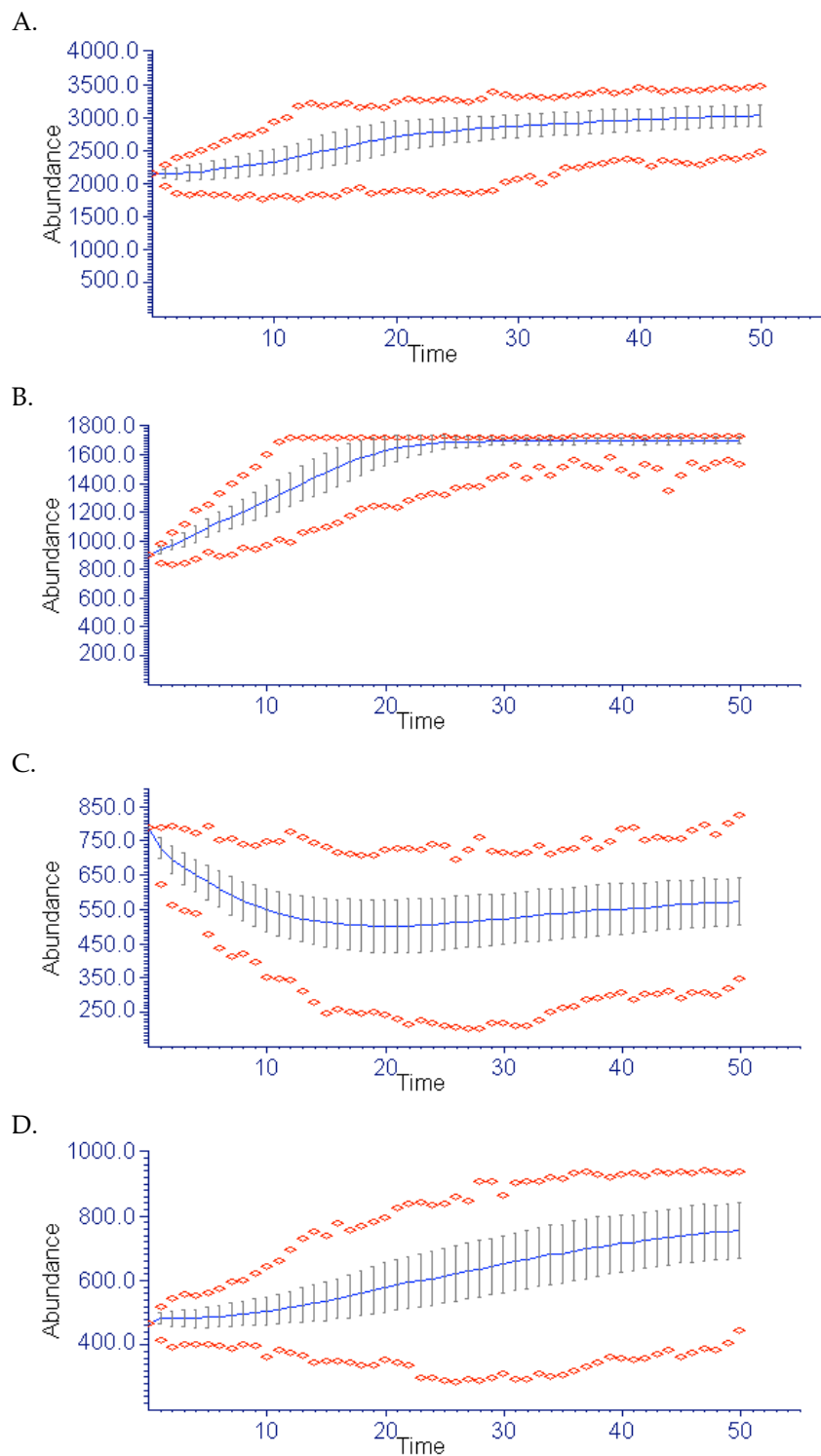


Figure 4. Population trajectories under the base assessment scenario with hunting applied as a static number of individuals removed each year from each sex-stage class. A: metapopulation (combined populations), B: West-side Rocky Mountain population, C: East-side Rocky Mountain population, D: Boreal forest plateau population.

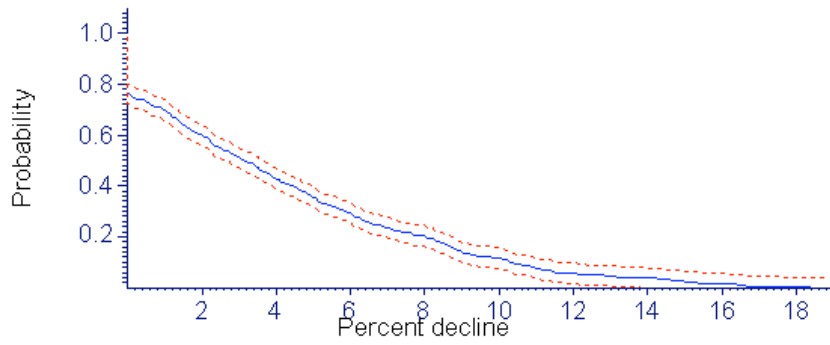


Figure 5. Risk (probability) that the metapopulation abundance will decline by the given percent below the initial population abundance at least once during the 50 year simulation window.

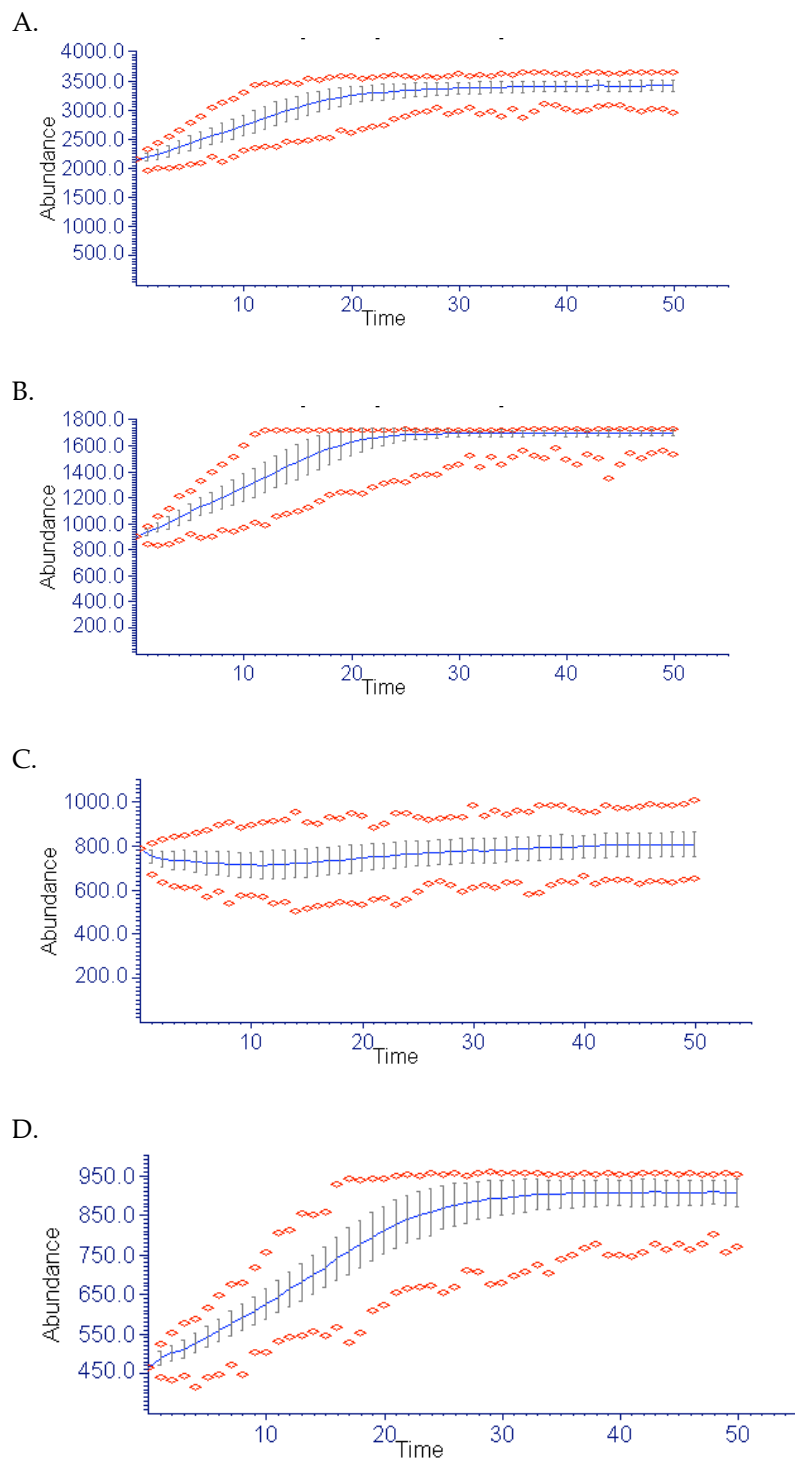


Figure 6. Population trajectories under the base assessment scenario with hunting applied as a proportion of the population removed each year from each sex-stage class. A: metapopulation (combined populations), B: West-side Rocky Mountain population, C: East-side Rocky Mountain population, D: Boreal forest plateau population.

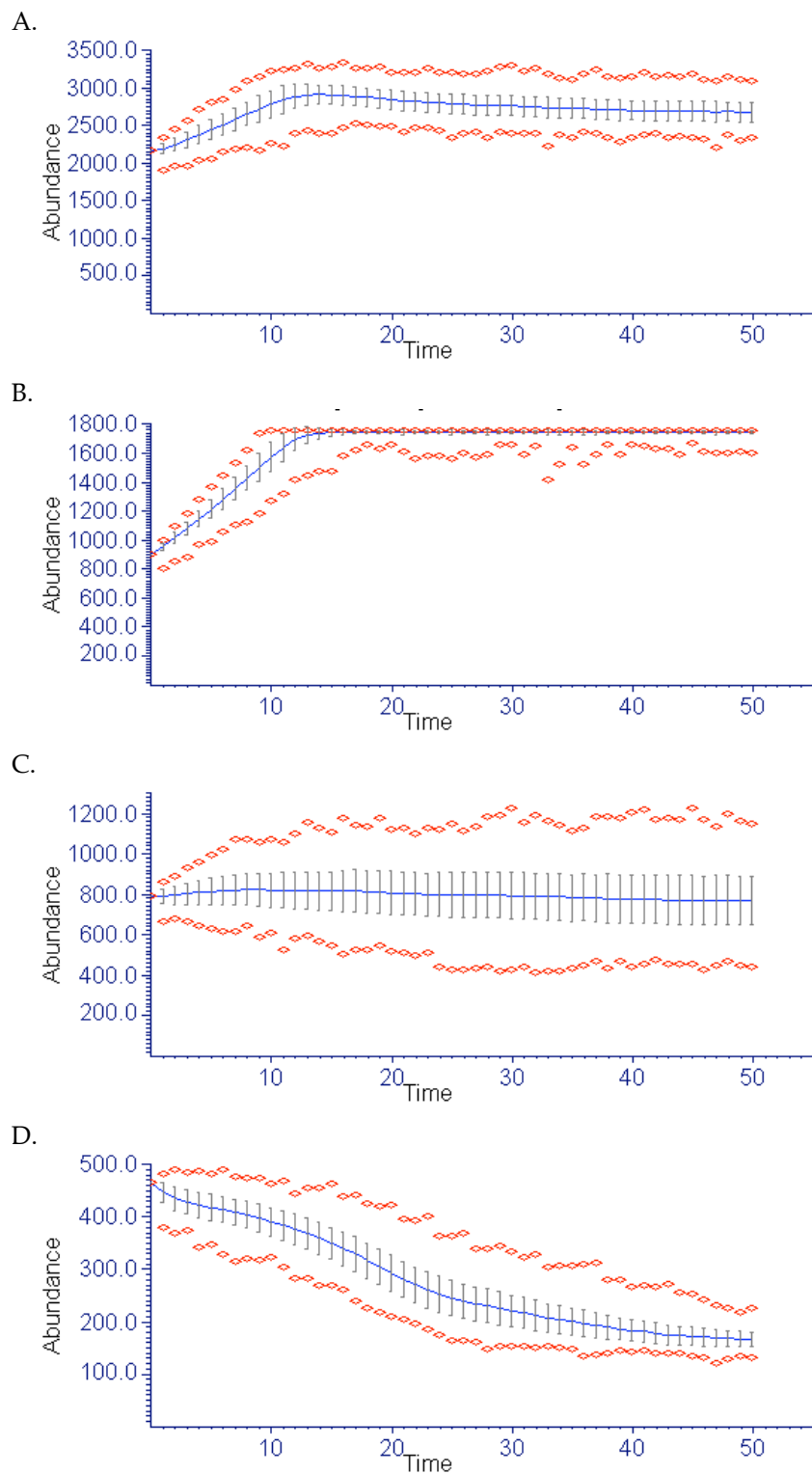


Figure 7. Population trajectories under the base assessment scenario with proportional hunting and no dispersal between populations. A: metapopulation (combined populations), B: West-side Rocky Mountain population, C: East-side Rocky Mountain population, D: Boreal forest plateau population.

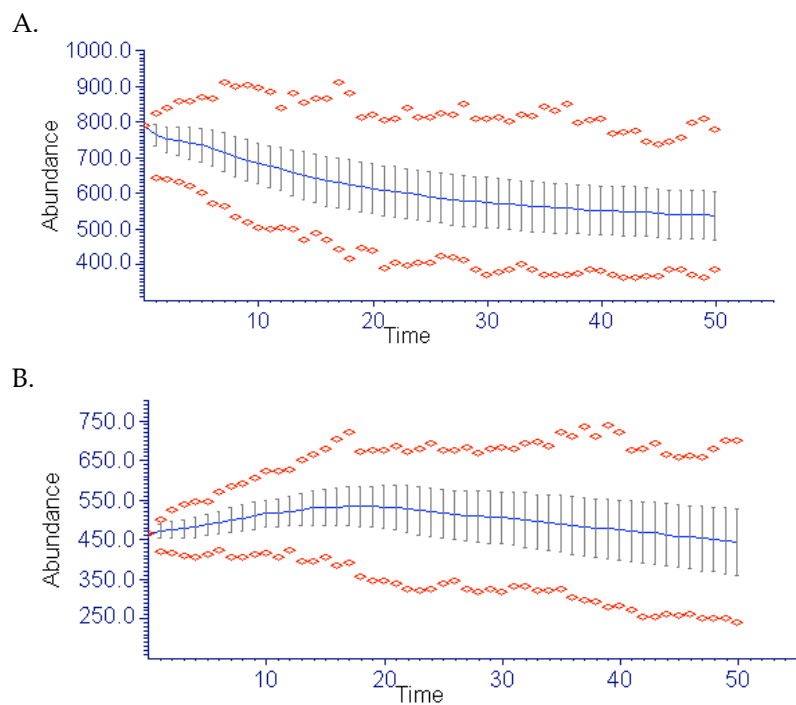


Figure 8. Population trajectories under the base assessment scenario with proportional hunting and dispersal only between the ERM and the BFP populations. A: East-side Rocky Mountain population, B: Boreal forest plateau population.

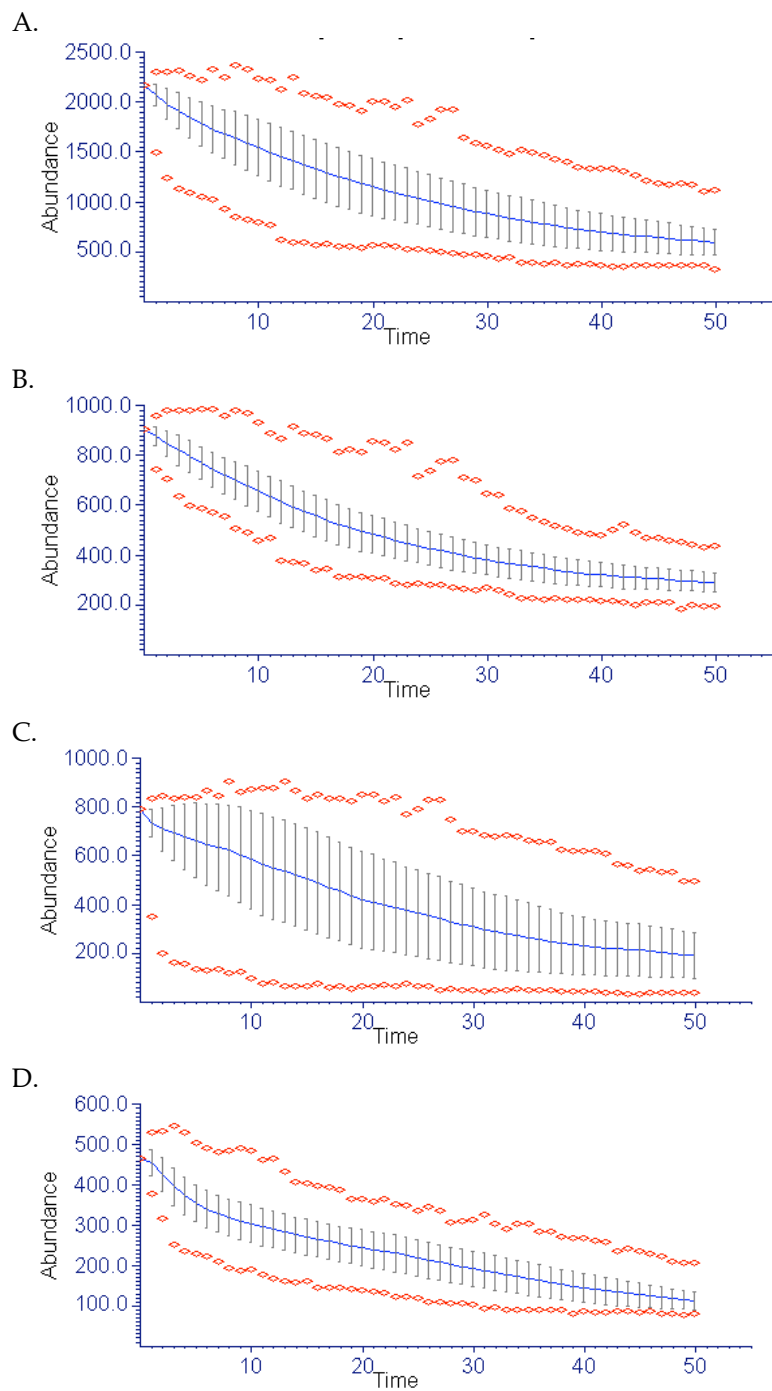


Figure 9. Population trajectories under the parks and protected areas scenario with no hunting applied. A: metapopulation (combined populations), B: West-side Rocky Mountain population, C: East-side Rocky Mountain population, D: Boreal forest plateau population.

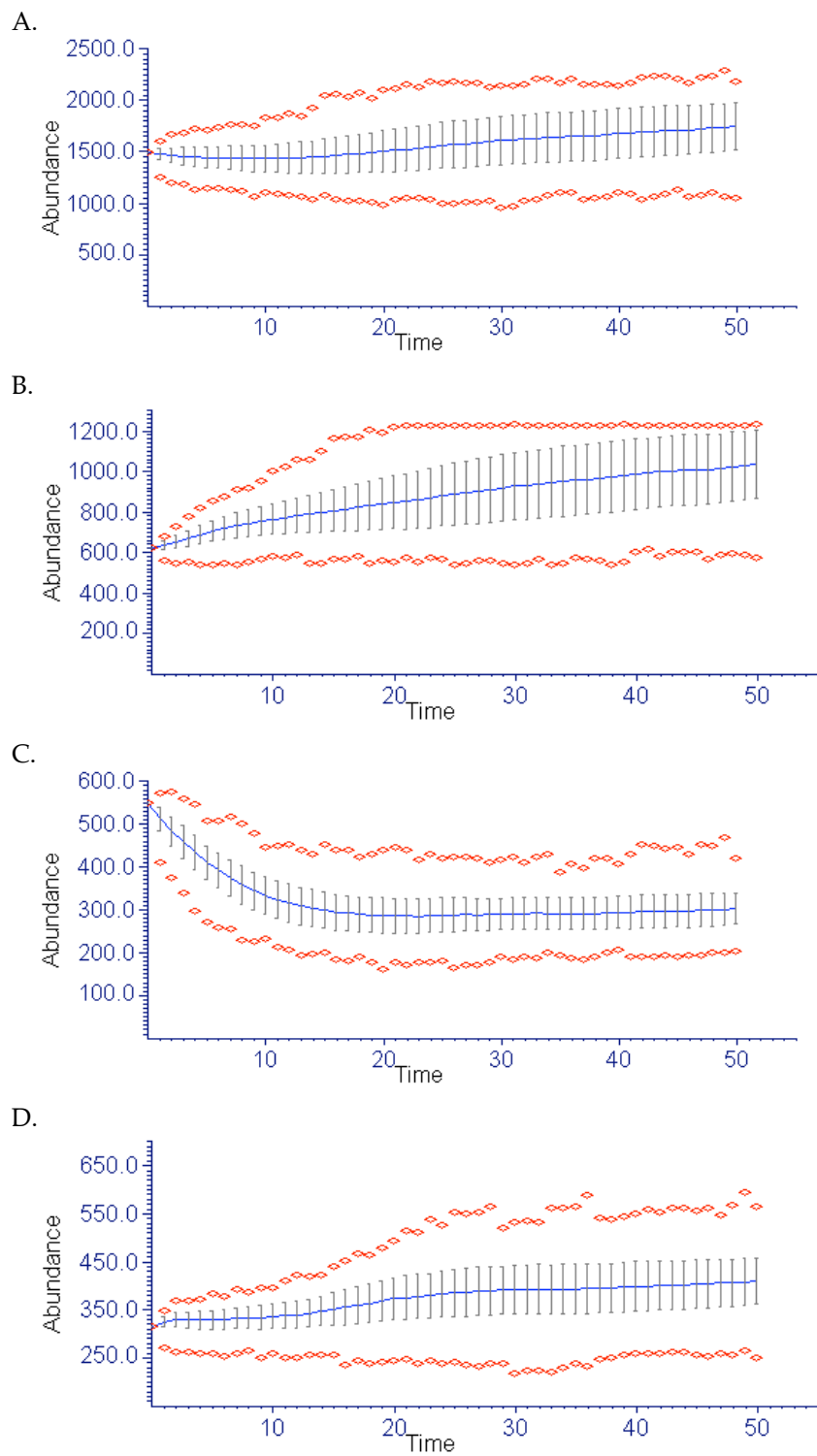


Figure 10. Population trajectories under the MK CAD scenario with no hunting. A: metapopulation (combined populations), B: West-side Rocky Mountain population, C: East-side Rocky Mountain population, D: Boreal forest plateau population.

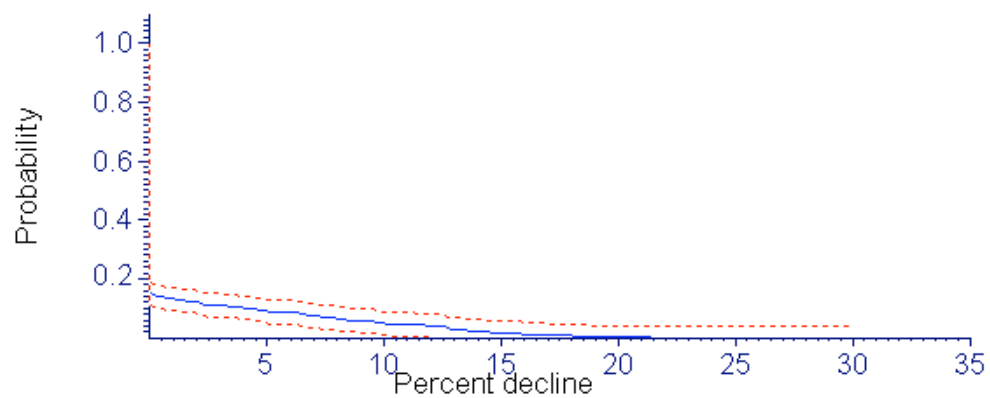


Figure 11. Under the MK CAD scenario with no hunting, the metapopulation has a low probability of declining.

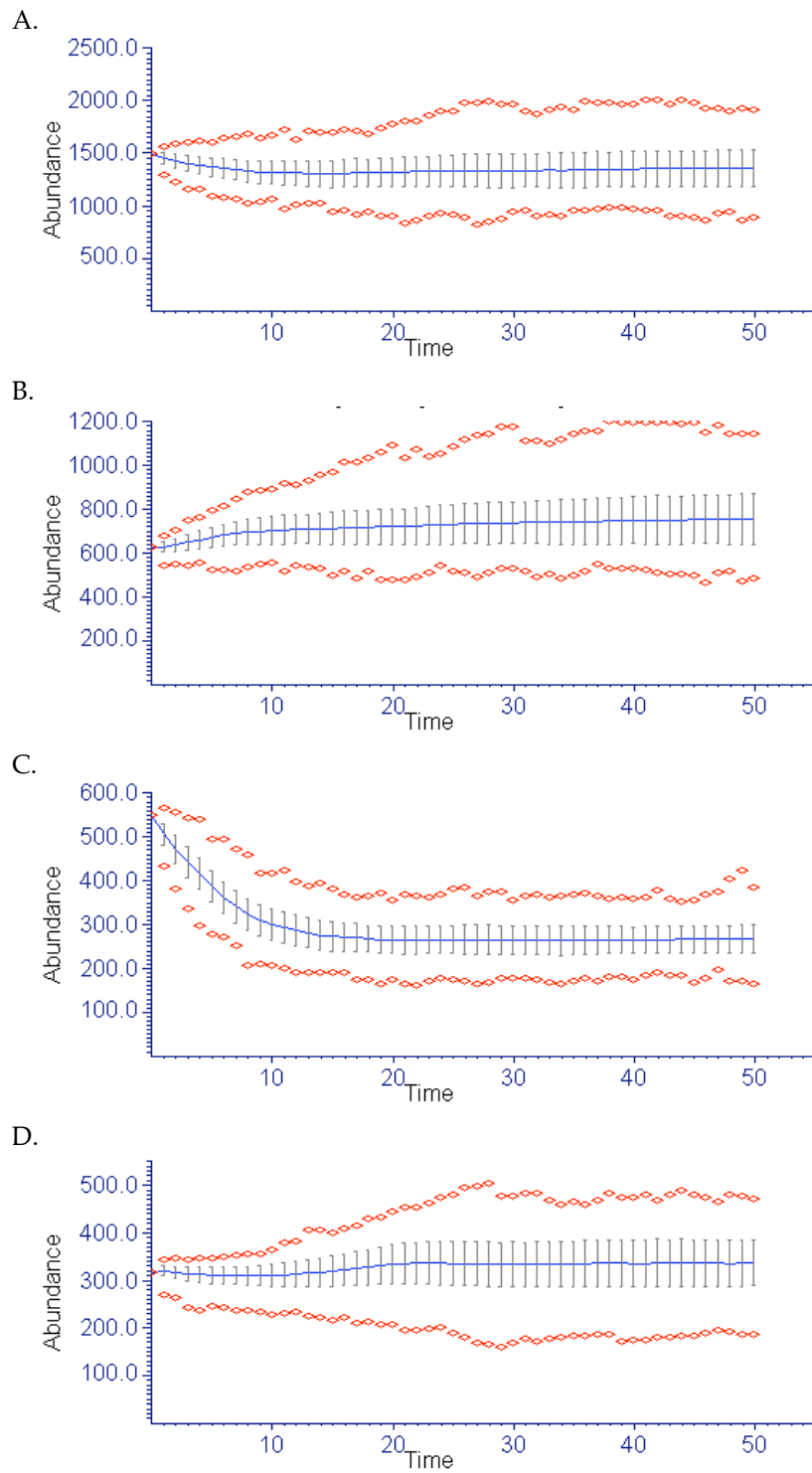


Figure 12. Population trajectories under the MK CAD scenario with proportional hunting applied. A: metapopulation (combined populations), B: West-side Rocky Mountain population, C: East-side Rocky Mountain population, D: Boreal forest plateau population.

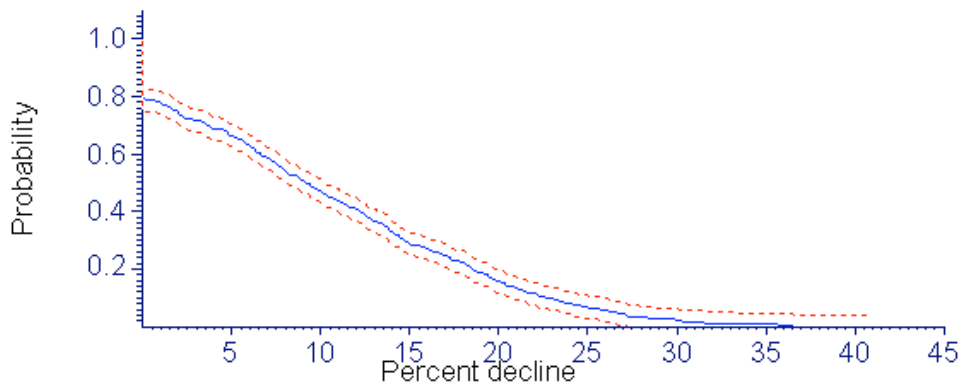


Figure 13. Under the MK CAD scenario with proportional hunting, the metapopulation has a high probability of experiencing of experiencing a decline.

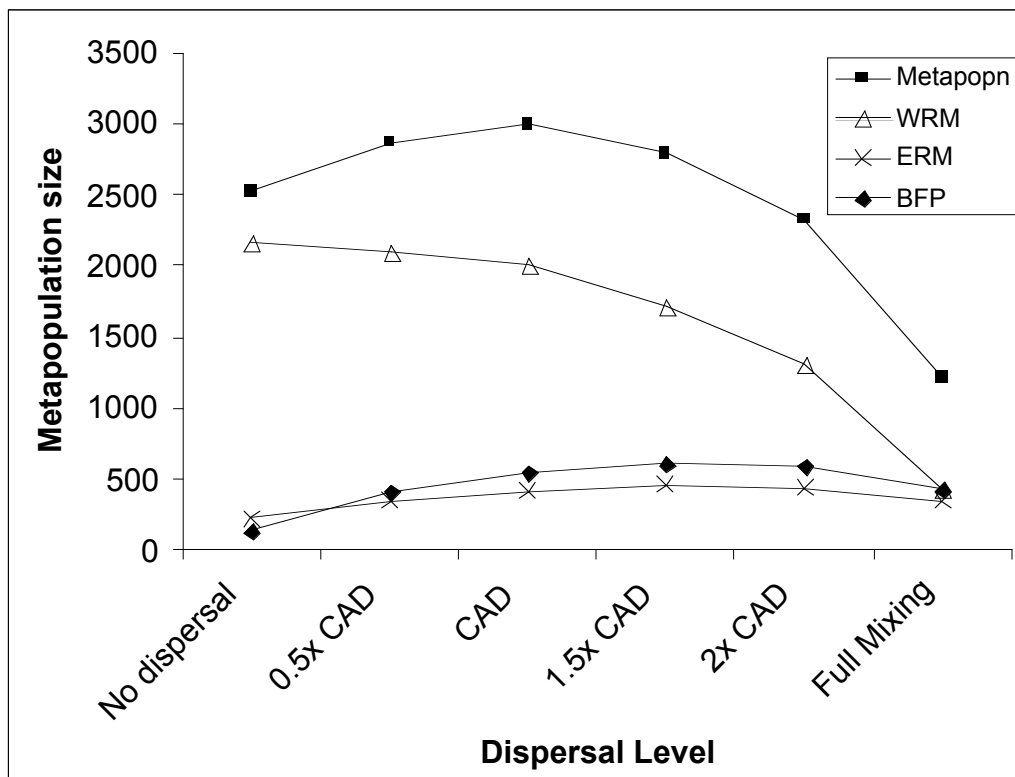


Figure 14. Final population sizes as level of dispersal is varied (and no hunting imposed) from no dispersal to low levels of dispersal (0.5 of MK CAD dispersal estimates) through to very high levels of dispersal (full mixing is assuming .33 dispersal between each population pair).

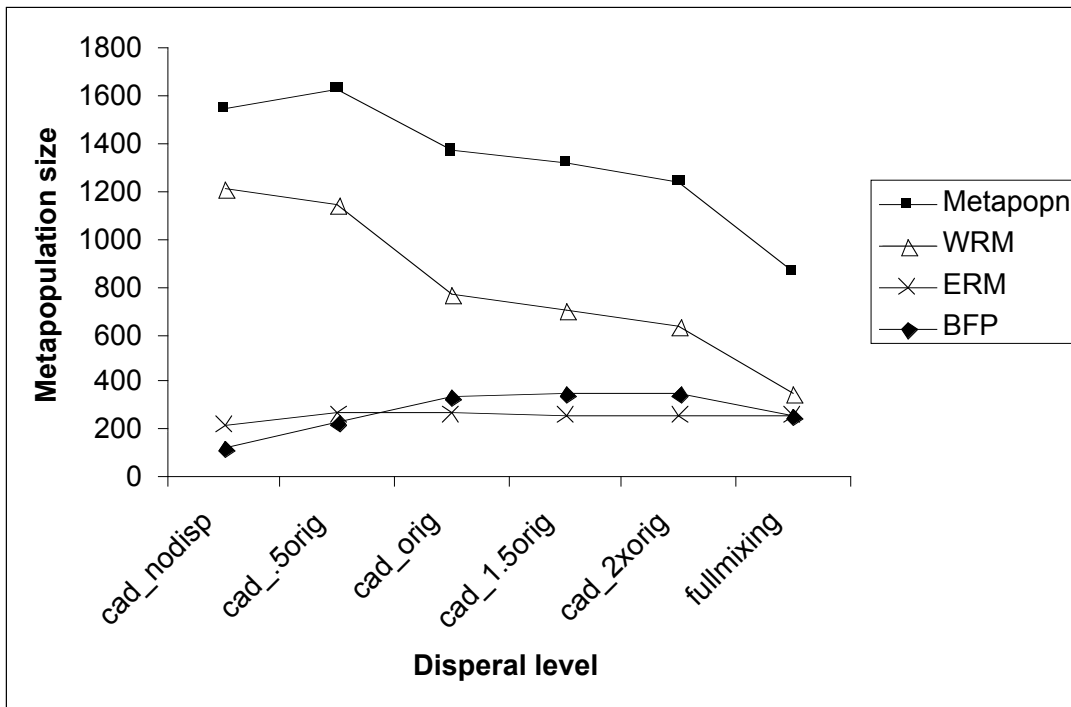


Figure 15. Final population sizes when proportional hunting mortality is imposed and the dispersal rate varied from no dispersal to full mixing (set at 0.33 dispersal rate between each population pair).

8 Appendix A

8.1 *Determining dispersal probability*

We assumed that only subadults would move with any substantial frequency between regions. We estimated the probability of dispersing to an adjacent population based upon dispersal distances reported for subadult male and female grizzly bears in the Flathead region of BC (McLellan & Hovey 2001), the amount of shared boundary between two populations and source population size. A Geographic Information System (GIS) was used to calculate the length of shared borders and to establish distance strata that allowed us to estimate the proportion of the population near a shared border. To calculate the proportion of subadults that would be expected to move far enough to leave a population, we divided each population into sex-specific distance strata based upon the average male and female movement distances. For subadult females, the average movement distance reported in the Flathead region is $9.8 \pm 1.6\text{km}$ ($N=12$); our outer two strata had a total width of 13 km ($9.8 + 2\text{ SD}$) with each strata having equal widths of 6.5km. Subadult males average movement distance in the Flathead study was reported as $29.9 \pm 3.5\text{km}$; our first two strata had a total width of 37 ($30 + 2\text{ SD}$).

We estimated the proportions of the male and female subadult populations likely to move adequate distances to leave each strata as 1- cumulative probability of the midpoint distance of each strata, using a lognormal distribution with the mean and standard deviation of the Flathead male and female subadult movement distances, respectively. For animals interior to the 2 strata, the probability of moving distances sufficient to leave the population was estimated as half the probability of moving 13km and 48km for subadult females and males, respectively, which is the outer boundary of the outer 2 strata.

The proportion of subadults that would move into an adjacent population, Population B, from Population A is based upon the proportion that would move sufficient distance, as described above; the proportion of those that would then also move in the direction of Population B; and the relative adjacency of Population B and Population A. We assumed movement was equally distributed in four directions, and that one direction was towards Population B so that 25% of the available dispersers (i.e., those that would move sufficient distance and were adjacent to Population B) would enter Population B. Final movement probabilities were determined for movement between each population (Table 4) and used to estimate immigration and emigration rates between populations. Due to limitations in the modeling software, dispersal rates used in the population simulations used the subadult male rates, and assumed that subadult females moved at 0.5 this rate, which approximates the calculated rate.

8.2 *Environmental stochasticity*

We built stochastic models which simulate year to year variation in average survival rates. Obtaining estimates of expected annual variation for each population proved difficult, as most variance terms provided for vital rates are overall measures of variation, which include within-year variation, across-year variation and sampling error. The only estimates of year-to-year or process variation we obtained were based upon the Yellowstone data for female and male survival rates (Schwartz et al. 2005); Schwartz and collaborators also estimated process variation for cubs and yearlings. We used the Yellowstone grizzly bear process variation statistics to estimate annual in the survival rates of the other populations by scaling the variance values to each survival estimate. Assuming that survival rates follow a beta distribution (Morris & Doak 2002), it is possible to calculate the maximum expected variation in the survival rate (Morris & Doak 2004). We calculated the *relative standard deviation* for each Yellowstone grizzly bear sex-stage survival rate as the estimated standard deviation/maximum standard deviation. We then used this relative standard deviation to estimate standard deviation for the WRM and BFP survival estimates, given their different mean survival values. These estimates assume that annual variation is proportional to the survival rate, itself and that the proportional relationship found in the Yellowstone population is consistent across the other populations.

8.3 *Vital rates in modified landscapes*

Within all simulations, we assume that undeveloped landscapes support bear productivity as identified in Table 1, but that potentially modified landscapes result in reduced survival rates. We estimate the reduced survival rates using information on population lambda estimates outside of grizzly bear recovery zones in the Yellowstone region (Schwartz, 2005 cite). To estimate the survival rates of sex-stage classes, we used the lower 95% confidence limit of the

Yellowstone cub and yearling survival rate (Schwartz, 2005), and estimated that female survival needed to be 0.86 to obtain the reported lambda of 0.88 (thus, roughly mimicking population productivity outside the Recovery Zone).

Therefore, under protected conditions, female grizzly bears have a “natural” 0.95 survival rate, but in human modified landscapes, this survival drops to 0.86. Assuming that natural mortality rates remain constant and that there is no compensatory response in mortality risks, the additional mortality experienced by bears in modified landscapes can be assumed to be a multiplicative function to obtain the total survival rate:

$$S_{total} = S_{natural} * S_{human-modified}$$

From this simple equation, it is then possible to solve for the human modified survival rate:

$$S_{human-modified} = S_{total} / S_{natural} = 0.95 / 0.88 = 0.90$$

We used this estimate of $S_{human-modified}$ to estimate male and female survival rates outside undeveloped landscapes within each of our scenarios. For simulations involving changes from current conditions (see below), we estimated average sex-stage survival rate for each population as the area-weighted average of the natural survival rate (Table 1) and the human-modified survival rate (Table 5). This assumes that bears move between the undeveloped and developed areas within each population.

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