Evaluating Management Strategies for Grizzly Bears in British Columbia, Canada

by

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Abstract

In British Columbia, The Ministry of Forests, Lands and Natural Resource Operations manages grizzly bear hunting as the most rigid and conservatively managed hunt in the province. However, there has been concern raised in the media and from some members of the academic community over the sustainability of grizzly bear hunting. It is unclear whether the current management strategy effectively incorporates uncertainties in grizzly bear biology and management. My research intends to address these concerns by utilizing a computer model to test the current provincial grizzly bear harvest management procedure, as well as other management options. Here, I developed a model to simulate grizzly bear population dynamics, provincial management, and hunting. Multiple sources of uncertainty were also included in the analysis. The results of this study highlight the potential benefits, challenges, and tradeoffs of three management options for grizzly bears given uncertainty in biological and management parameters.

Keywords: Grizzly bear; carnivore management; management strategy; simulation modelling; hunting; uncertainty

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1. Introduction

In North America and Europe, changing public perceptions allowed many carnivore populations to recover during the mid-20th century after decades of attempted eradication (Linell et al, 2010). However, with the recovery of carnivore populations comes the inevitable habitat overlap due to the ever-growing human-dominated landscape (Fernández-Gil et al, 2016). Carnivore management aims to decrease such conflict, and in many jurisdictions regulated hunting or culling is used to keep population sizes within set limits (Linnell et al, 2010). Such practices are controversial. There is often disagreement amongst conservationists, rural communities, hunters and animal rights activists over the number of animals being killed, as well as whether it is morally sound to kill these animals (Linnell et al, 2010).

Throughout North America, grizzly bears (*Ursus arctos*) are often managed for multiple objectives, with human safety as the highest priority (Peek et al., 2003). Educational programs and effective garbage disposal are useful for reducing human-bear conflict and the risk to crops and livestock (Ordiz et al., 2013; Mowat et al., 2013). In some areas, grizzly bear populations are managed to maintain viable hunts, with quota shared between residential hunters, non-residential hunters, and Aboriginal groups that use grizzly bears for food and ceremonial needs (MOELP, 1995; MOE, 2010; Ordiz et al., 2013). As with many hunts on apex predators, grizzly bear hunting has been controversial and garners concern from conservationists and animal rights advocates (Linnell et al., 2010; Gailus et al., 2010). Such concern is justified since grizzly bears, like most apex predators, are vulnerable to hunting and other anthropogenic sources of mortality due to their low reproductive rates and large habitat requirements (Peek et al., 2003, Artelle et al., 2013).

The current North American range of grizzly bears is limited to British Columbia, Alberta, the Canadian territories, Alaska, and a few small regions in the northwestern United States. Canada is believed to be home to one third of North America's remaining grizzly

bears, where it is listed as a Species of Special Concern by COSEWIC (2012). There is still considerable pressure on the species due to loss of habitat, changing climate, and human-caused mortality related to hunting, car collisions, and human-bear conflict (Peek et al., 2003). Managers are in the difficult position of ensuring grizzly bear populations remain healthy while also considering the demands of multiple interest groups (Linnell et al., 2010). In British Columbia, Canada, grizzly bears are managed to meet multiple management objectives. Politicians are responsible for the decision to hunt, and the role of the Ministry of Forests, Lands and Natural Resource Operations (MFLNRO) is to ensure that the grizzly bear hunt is sustainable (MOELP, 1995; MOE, 2010). The MFLNRO claim the grizzly bear hunt is the most conservative and meticulously managed hunt of all game species in the province, and that safeguards are in place to ensure the hunt remains sustainable (MOE, 2010).

Despite assurance from the MFLNRO that the grizzly bear hunt is rigidly managed, there has been concern raised in the media and from some members of the academic community over the sustainability of the hunt (Artelle et al, 2013; Gailus et al, 2010). One area of concern is the method used most frequently to estimate grizzly bear population size in British Columbia. Estimating the population size of large carnivores is expensive due to the elusive nature and expansive habitat requirements of such animals (Nilsen et al., 2012; Kindberg et al., 2009). As a result, field-based estimates are too expensive to conduct regularly or at large scales (Kindberg et al., 2009). In place of field-based estimates, managers may adopt more conservative methods to assign harvest rates, or use estimates based on indices of the population size (Nilsen et al., 2012). In the case of approximating population sizes for British Columbia grizzly bears, a regression model estimates population density based on habitat and human use (Mowat et al., 2013) and a conservative human-caused mortality limit is applied to this estimate (MOE, 2010; Peek et al., 2003). Some populations throughout the province have been inventoried using DNA based mark-recapture that uses the hair of bears at bait sites (Boulanger et al, 2004) but the majority of GBPUs have not been inventoried directly. Over the years, there have been concerns expressed that MFLNRO harvest rate calculations do not directly incorporate uncertainty in population estimates (Peek et al., 2003; McLoughlin, 2003, Artelle et al., 2013), with some organizations suggesting that government estimates can be off by as much as 100% (Gailus et al., 2010). There have also been concerns raised that the current management strategy

does not directly incorporate implementation uncertainty in harvest results, as well as uncertainties in population vital rates and unknown mortality rates (Peek et al, 2003; McLoughlin, 2003, Artelle et al, 2013). Due to the sensitivity of grizzly bear populations to female mortality, there is concern that the current management strategy may not adequately protect female bears, and at times may result in a female mortality rate that is over the female mortality limit (Peek et al., 2003; Artelle et al., 2013). In a recent study, Artelle et al (2013) suggest that grizzly bear mortality was over government target levels in up to 70% of hunted populations from 2001 to 2011.

The MFLNRO manages grizzly bears in British Columbia through 56 Grizzly Bear Population Units (GBPUs), although all hunted GBPUs are one fully connected population (Proctor et al, 2012; Peek et al, 2003). Of the 56 GBPUs, nine are considered threatened by the province and are not hunted, and approximately 10% of British Columbia's land area was either never occupied by grizzly bears or is no longer occupied due to extirpation (Boyce et al., 2015). The current management strategy restricts the total allowable human-caused mortality (including the estimated unknown mortality) to a maximum of 6% a year, with the limit determined based on a population's productivity. Grizzly bear populations that are estimated to have less than 100 bears, or that have been designated as Threatened are not hunted (MOE, 2010). Using the total allowable human-caused mortality, an annual allowable harvest (AAH) is determined by considering estimates of aboriginal harvest rates, expected unknown mortality rates and reported non-hunting mortality rates. The AAH is then applied over a 5-year allocation period and is used to determine the authorizations for the British Columbia resident's limited entry hunt and the guide outfitter quota that is available to non-residents (MOE, 2010).

There have been previous modelling studies used to determine the sustainable maximum annual harvest rate for grizzly bear populations. Harris (1986) devised a model to provide recommendations to the Montana Department of Fish, Wildlife, and Parks. The individual-based model suggested that grizzly bear populations could persist with a maximum harvest mortality of 6.35%, so long as female mortality did not exceed 3.5% (Harris, 1986). The MFLNRO use these estimates to inform their Grizzly Bear Harvest Management Procedure (Peek et al, 2003). Similarly, Miller (1990) devised a model for grizzly bears in Alaska and estimated that maximum sustainable hunting mortality was 5.7%.

McLoughlin (2003) conducted an analysis to help inform grizzly bear management in British Columbia, with a model that included stochasticity in vital rates, annual variability, and sampling error. Results of the study suggested that populations inhabiting good-quality habitat could endure annual human-caused mortality rates of up to 4.9%, whereas populations living in moderate habitat had a threshold of 2.8%, and populations living in low-quality habitat could not persist in even low levels of human-caused mortality (McLoughlin, 2003). These findings initially suggested that the 6% maximum allowable human-caused mortality rate used by the MFLNRO is unsustainable; however, a shortcoming of this study was that the base or natural survival estimates included human-caused mortality (Schwartz et al, 2006; McLellan et al, 2016). Independent reviewers agree that the vital rates used by McLoughlin (2003) are more conservative than those in the other grizzly bear population models (Peek et al, 2003). Research has recently suggested that some grizzly bear populaitons can sustain higher levels of human-caused mortality than originally thought. Recently, the conservation strategy for grizzly bears in the greater Yellowstone Ecosystem determined that a 7.6% human-caused mortality rate of females and a 15% kill rate of males would be sustainable (USFWS, 2016). McLellan et al (2017) used natural survival rates and hunter records from four study areas in and around British Columbia to address concerns over human-caused mortality limits. The study concluded that the specific grizzly bear populations could sustain a 3.9% to 10.2% total human-caused kill rate (McLellan et al, 2017).

Previous modelling studies of grizzly bears have focused almost exclusively on identifying human-caused mortality thresholds, while research specific to the British Columbia grizzly bear hunt has focused mostly on the shortcomings of the current management strategy. My research intends to address the concerns over the sustainability of grizzly bear management in British Columbia by creating a computer model to test the current provincial management procedure. The MFLNRO's management will also be compared to other management options frequently used for grizzly bear populations. This model will incorporate uncertainties in population parameters in order to estimate potential risks and trends over time. The model's structure was inspired by Management Strategy Evaluation (MSE), which effectively incorporates biological and management uncertainties. MSE is a method popularized in fisheries science that has been gaining traction in terrestrial management (Bunnefeld et al, 2011; Milner-Gulland et al, 2001; Boyce et al, 2012). The

method involves developing three sets of models: the operating model, the observation model, and the management model (Figure 1). The operating model is a simulation of the species' population dynamics using ecological knowledge and data whenever available (Bunnefeld et al, 2011). The observation model and management model simulate the human-side of the system. Estimates of the population, with error and bias, are collected in the observation model. The estimates made in the observation model are then passed to the management model, which applies harvest control rules to calculate quota. Harvests are then removed from the population simulated in the operating model, including implementation uncertainty to occasionally result in under and overharvesting (Bischof et al, 2012).

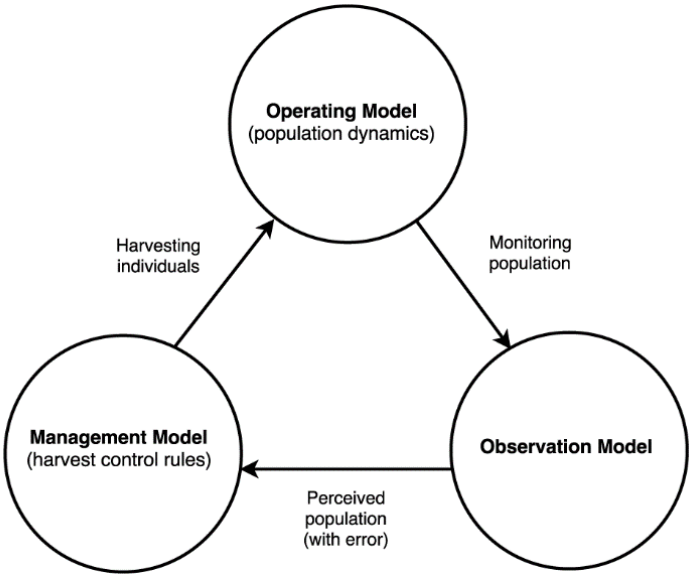

Figure 1. The framework for management strategy evaluation. The operating model produces the population dynamics, while the observation model simulates researchers monitoring and developing population estimates, and the management model applies harvest control rules. Figure adapted from Bunnefeld et al, 2011.

Computer modelling of the harvest management procedure will help quantify the risk that human-caused mortalities would leave populations vulnerable to becoming overhunted. The purpose of this research project is to evaluate the short-term and long-term benefits, challenges, and trade-offs of various grizzly bear management strategies to develop sustainable harvest regulations for grizzly bears in BC, Canada. Since the grizzly bear hunt in British Columbia is a contentious issue, it is important to note that this research will focus

strictly on population level sustainability. This research project does not aim to debate the moral questions or ethics of hunting an apex predator such as the grizzly bear. This research project aims to address just one small portion of the grizzly bear hunting debate, which is whether current practices are sustainable.

2. Methods

I developed a simulation procedure based on MSE that consisted of the following components: 1) an operating model of grizzly bear population dynamics; 2) an observation model to generate population size and carrying capacity estimates, with error and bias; 3) a management model to follow harvest rules and calculations, allocate quota, and implement sources of human-caused mortality. A Monte Carlo algorithm was used to draw survival and reproductive parameters from prior probability distributions to represent the uncertain states of nature.

The first part of the methods section will describe the population data used for this study, followed by how the data was incorporated into prior probability distributions. The second half of this section will describe the model's details, including the operating, observation and management models. The management strategies of interest will be described in full detail in the management model section. The final methods section describes the statistics used to compare management strategies. All described model parameters can be found in Table 1.

Table 1. Descriptions of several of the model parameters and variables referenced throughout this research document.

Symbol	Description
Indices	
t	Year in simulation
s	Sex of an individual bear
a	Age class of individual bear
i	Season of hunt (spring or fall)
Model Parameters	
K	Population carrying capacity
γ_{50}	Sex ratio where reproduction is reduced by 50%
z	Slope parameter of the operation sex ratio effect
S_a^s	Natural survival rate of each age and sex class
R_a	Reproductive rate for females of each age class
v_a	Vulnerability-at-age to harvest

Variables	
$N_{a,t}$	The number of bears of age (a) in year (t) in the population
D_t	Density effect at time (t)
γ_t	Current sex ratio of the population
O_t	Operational sex ratio effect at time (t)
Observations	
$\widetilde{K}$	Estimated population carrying capacity
$\widetilde{N}_t$	Estimated population size at time (t)
r	Estimated population growth rate
Harvest Controls	
y	Year of allocation period (5 years total)
AAM	Annual allowable mortality
$AAFM$	Annual allowable female mortality
$TAHM$	Total allowable human-caused mortality for allocation period
$TAFHM$	Total allowable female human-caused mortality
Al_r	Harvest allocation available to resident hunters
Al_i	Harvest allocation available to non-resident hunters
$\bar{H}_{a,t}$	Average age of harvest data
ρ	Sex ratio of harvest data
$q_{i,t}$	Annual or seasonal quota for resident grizzly bear hunt
$p_{i,t}$	Resident permits issued for the spring or fall hunt of a year
h_i	Hunting success rate for each season
Q_t	Hunting mortality given quota, permits and success rate
$H^s_{a,t}$	Number of bears harvested at time (t) of each age and sex
$\widetilde{M}_Y$	Estimated harvest balance of allocation period
$\widetilde{M}_{F,Y}$	Estimated female harvest balance of allocation period
$\bar{M}_t$	Estimated average annual grizzly bear mortality
$\bar{M}_{F,t}$	Estimated average annual female grizzly bear mortality

2.1. Population Data

I constructed a simulation model to assess trade-offs and consequences of competing management strategies on theoretical grizzly bear populations. I selected vital rate data from the following three grizzly bear populations in and around British Columbia to represent populations living in low, moderate and high productivity habitats (Figure 2): 1) the Flathead GBPU of British Columbia and Montana (McLellan, 2015); 2) Banff National

Park and Kananaskis Country, Alberta (Garshelis et al, 2005); 3) the Selkirk Mountains of British Columbia, Washington and Idaho (Wielgus et al, 1994). I used the 1979-1988 dataset from McLellan's (2015) study on the Flathead GBPU to represent a low productivity habitat. In this region, grizzly bears were hunted in British Columbia, but there was immigration and emigration to and from Montana and Alberta where grizzly bear hunting was not allowed. Low bear density and abundant huckleberry led to optimal conditions ($\lambda = 1.07$) for the Flathead Valley in the 1980's (McLellan, 2015). A study by Garshelis et al (2005) of a grizzly bear population encompassing the unhunted Banff National Park and Kananaskis Country, Alberta was chosen to represent a moderately productive GBPU. Despite low reproductive rates and the region being heavily developed, the study concluded that the grizzly bear population was increasing ($\lambda = 1.04$). The data used for the high productivity habitat originated from a study by Wielgus et al (1994) of grizzly bears residing in the unhunted Selkirk Mountains of British Columbia, Washington and Idaho. The grizzly bear population in the Selkirk Mountains was stable ($\lambda = 1.00$) primarily due to the high human-caused mortality rate of sub-adult females when moving to new home ranges (Wielgus et al, 1994). Survival rates from the three studies were adjusted to remove human-related mortality, but because sample sizes were small in the Selkirk study, some human caused deaths were included to avoid 100% survival rates with no variance for some age and sex classes. When human-related mortalities were removed from each of the studies' survival rates, the three populations exhibited a reversal in productivity. The Selkirk Mountain grizzly bear population became the most productive population with the highest natural survival rates for cubs and yearlings of all three datasets. Similarly, the Flathead grizzly bear population became the least productive of the three populations due to comparatively lower rates of cub and yearling survival. For this reason, the Flathead River Basin study will be regarded as the low productivity population, the Banff National Park study will be regarded as the moderate productivity population, and the Selkirk Mountains study will be described as the high productivity population throughout the remainder of this research paper.

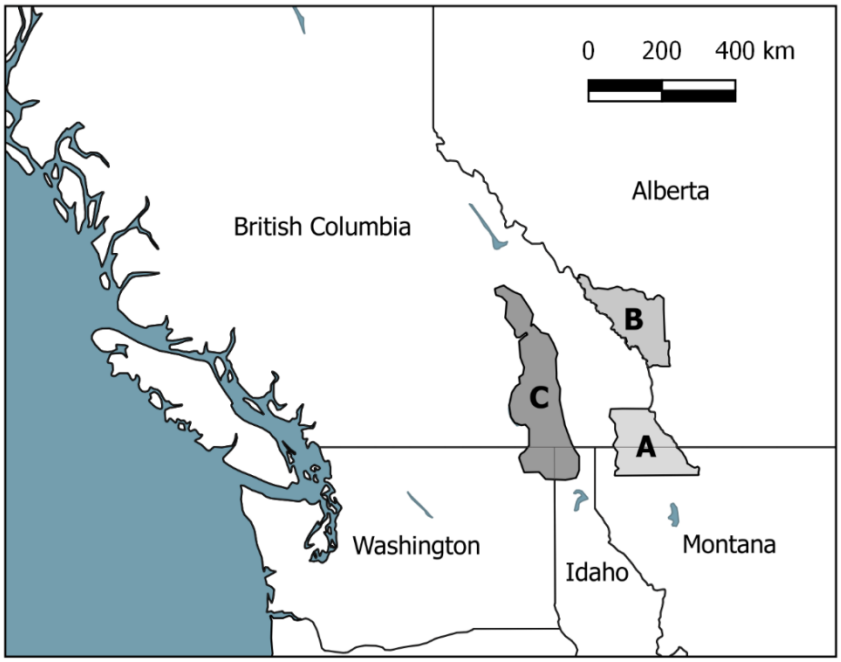

Figure 2. Study sites of the grizzly bear population data used in this study. A is the low productivity population of the Flathead Valley of British Columbia and Montana, B is the moderately productive population of Kananaskis Country, Alberta, and C is the high productivity population of the Selkirk Mountain range.

The above-mentioned studies provided little reproductive or survival rates for individual grizzly bears as they approached and became senescent. To model senescence, Schwartz et al (2003a) meta-analysis was used to identify inflection points in reproduction. The Schwartz et al (2003a) study used female grizzly bear data from Canada, the United States and Sweden, and included all three populations used in this study. Using this model, 25-year-old females were given a reproductive rate of 0.15, while 28-year-old females were considered senescent. Schwartz et al (2003a) also suggest that in the absence of human-caused mortality, grizzly bear survival should parallel the pattern of reproductive maturation. To mirror the inflection points in reproductive maturation, survival rates were subjectively set at 0.60 and 0.30 for 25-year-old and 28-year-old grizzly bears respectively. For detailed information on the vital rates and model inputs used for this study, see Table 2.

Table 2. Model inputs for the low productivity population (McLellan, 2015), moderate productivity population (Garshelis et al, 2005), and high productivity population (Wielgus et al, 1994).

	Low Productivity	Moderate Productivity	High Productivity
Cubs	$\mu = 0.860$, $N = 37$	$\mu = 0.870$, $N = 38$	$\mu = 0.920$, $N = 11$
Yearlings	$\mu = 0.860$, $N = 27$	$\mu = 0.910$, $N = 33$	$\mu = 0.920$, $N = 11$
Female Sub-adults	$\mu = 0.999$, $N = 15$	$\mu = 0.947$, $N = 15$	$\mu = 0.990$, $N = 14$
Male Sub-adults	$\mu = 0.997$, $N = 15$	$\mu = 0.930$, $N = 14$	$\mu = 0.990$, $N = 17$
Female Adults	$\mu = 0.975$, $N = 16$	$\mu = 0.991$, $N = 37$	$\mu = 0.960$, $N = 43$
Male Adults	$\mu = 0.998$, $N = 16$	$\mu = 0.985$, $N = 24$	$\mu = 0.990$, $N = 18$

2.2. Prior Probability Distributions

I used Beta distributions for the survival rate probability distributions for cub, yearling, sub-adult, and adult survival and reproductive rates because these parameters are bounded to the range (0,1) (Artikis & Artikis, 2015). The equation for the Beta distribution is:

(1) $$P(S) = \frac{S^{\alpha-1}(1-S)^{\beta-1}}{B(\alpha,\beta)}$$

where *S* is survival, *B* is the normalization constant, and α and β are shape parameters of the distribution. To determine the shape of the beta distribution, estimates of stage class survival from field studies were used to solve for the α and β parameters by moment matching via the following equations:

(2) $$\alpha = -\frac{\mu\,(\mu^2 - \mu - \sigma^2)}{\sigma^2}$$

(3) $$\beta = \frac{\alpha - (\mu\alpha)}{\mu}$$

The stage class survival mean (μ) and sample size (*N*) were obtained from published population studies (McLellan, 2015; Garshelis et al, 2005; Wielgus et al, 1994). The effective

sample size of each study was approximated by adding the α and β parameters i.e., $N = \alpha + \beta$.

However, before this distribution can be used to generate survival rates, the parameter and environmental uncertainty must be separated from the demographic parameter (White et al, 2002; Taylor et al, 2006). To do this, I solved for the beta distributions variance using the known α and β parameters.

This variance is then partitioned into parameter variance and environmental variance. The MFLNRO often use the computer package RISKMAN, which recommends partitioning 75% of the variance to parameter uncertainty and 25% to environmental uncertainty, since parameter uncertainty has a larger effect on a simulated population (Taylor et al, 2006). For this research, we followed RISKMAN's recommendations of a 25% partitioning to environmental uncertainty for the main analysis, and a range of environmental uncertainty values tested through sensitivity analysis. Equations 4 and 5 show the calculations for parameter and environment variance respectively, where *p* is the proportion of total variance assigned to parameter uncertainty.

(4) $$\sigma^2{}_{parameter} = (\sigma^2{}_{total})p$$

(5) $$\sigma^2{}_{environmental} = (\sigma^2{}_{total})(1 - p)$$

Using the new parameter variance, the α and β parameters are solved for once again to find the beta distribution with 75% of the variance of the original distribution. The mean and parameter variance ($\sigma^2{}_{parameter}$) are used to solve for the α and β parameters.

The new α and β parameters can then be plugged into the beta distribution equation (1) to calculate a range of vital rate probabilities that include less environmental variance. This new beta distribution is used to generate a survival or reproduction mean that will be held constant throughout a simulation run.

The environmental variance ($\sigma^2{}_{environmental}$) is used to generate environmental stochasticity in the model via random normally distributed changes in annual survival and reproductive rates (Figure 3). This environmental effect is auto-correlated both temporally,

and with the environmental effect of other survival and reproductive parameters for different age classes. In doing so, good years and bad years affect each stage class similarly. For each year of the simulation, a random environmental deviate is added to the survival mean or reproductive mean to generate the survival rate ($S_{a,t}$) or reproductive rate ($R_{a,t}$) respectively. This allows the model to simulate environmental stochasticity. Any vital rate over the value of 1 (due to environmental stochastic effect) is replaced with a value of 1; this truncates the survival distribution.

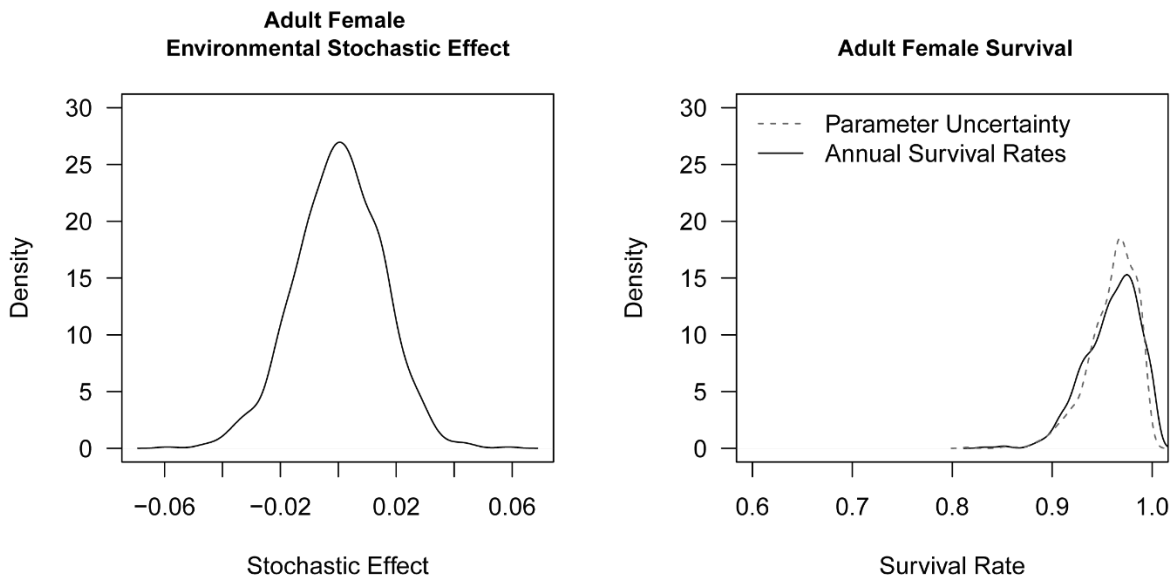

Figure 3. Parameter and environmental survival for adult females of the high productivity dataset (Selkirk Mountains). Left: The annual environmental stochastic effect applied to parameter survival. Right: The dashed line represents adult female survival with parameter uncertainty only. The environmental stochastic effect is added to the parameter uncertainty to obtain the annual survival rates (black line).

2.3. Model Structure

I built an individual-based population model using the computer programs Netlogo (Wilensky, 1999) and R (R Core Team, 2014). The RNetLogo extension (Thiele, 2014) was also used to allow R to send and receive data from the Netlogo console. Individual-based models are considered an appropriate approach to modelling grizzly bear population dynamics, since these models allow for heterogeneity between the traits of simulated individuals, and probabilities to be applied to individuals instead of cohorts (Harris, 1986).

This type of model also provides the complexity required to evaluate a contentious topic such as grizzly bear hunting.

2.3.1. The Operating Model

The operating model simulates the grizzly bear population dynamics. The model begins the year in January (Figure 4). The initial grizzly bear population is determined by assuming a stable age distribution of male and female cubs, yearlings, sub-adults and adults. At the start of each year, the operating model sets new survival and reproductive rates which include an environmental deviate to simulate environmental stochasticity.

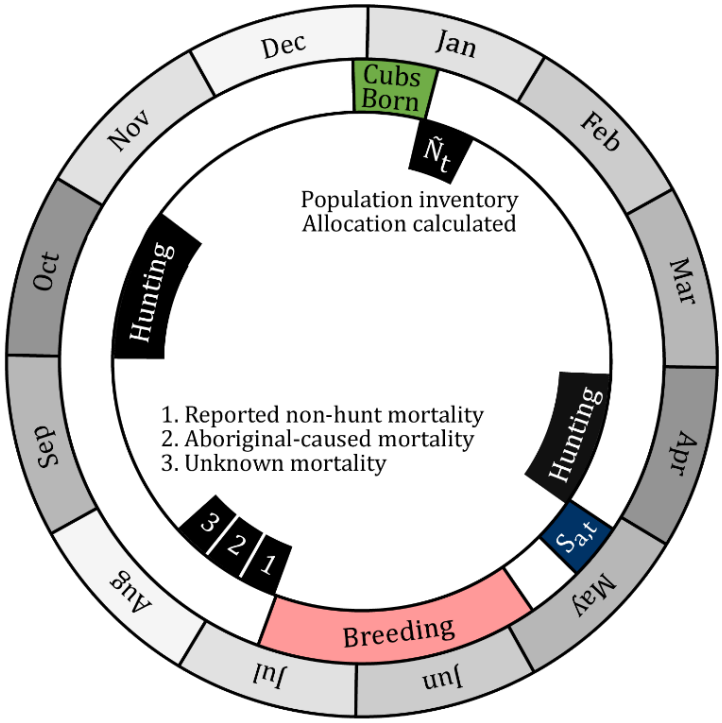

Figure 4. The simplified calendar year used in the model. The year starts in January, when cubs are born in dens. Grizzly bears experience natural mortality in May, followed by breeding season in June and July. The dates associated with human-related mortality and management are seen in black inside the figure. For a real-world version of grizzly bear life history and MFLNRO management events, see Appendix C.

At the beginning of each year, the model increases the age of each grizzly bear by one and adds new cubs to the population for each pregnant female. Female grizzly bears

that had been impregnated in the previous year give birth sometime between January and March (Steyaert et al, 2012). Litter size was modelled using a multinomial distribution, and probabilities were based on the proportions of 1 (0.18), 2 (0.61), and 3 (0.22) cub litters in the Greater Yellowstone Ecosystem (Schwartz and Haroldson 2006). Although 4 cub litters do occur in the wild, such births are rare (Steyaert et al, 2012) and were not included in this model. Density dependence in litter size was modelled via a density effect parameter (D_t) calculated from a threshold-corrected Michaelis-Menton relationship of the form (Taylor et al, 2006),

(6) $$D_t = \frac{\frac{K}{N_t} - 1}{\frac{K}{N_t} - 1 + 0.01}$$

The density effect parameter is used to lower the multinomial litter size probabilities in response to higher population densities. D_t is multiplied by the litter size probabilities and then renormalized to lower the probability of large litters when the population is at high densities. At birth, each cub is assigned a sex based on an unbiased sex ratio of 50:50, which reflects the majority of North American grizzly bear populations (Steyaert et al, 2012). The model also tracks mother-offspring relationships using NetLogo's "link" object, which connects individuals to their mothers at birth. Links remain for two years until offspring become sub-adults and are considered independent. Adult female grizzly bears with links to cubs or yearlings cannot breed; however, should a female lose all her offspring early, all links are deleted and she becomes available to mate once again (Steyaert et al, 2012). Mother-offspring links are also used to model mortality in scenarios where either a mother or a cub is lost. If a mother with dependent offspring dies in the model, each of her cubs and yearlings face additional 80% and 10% mortality rates, respectively. Mother-offspring links also allow the model to identify littermates, which is important in modelling litter survival. The survival of cubs within a litter is considered statistically correlated, especially since a mother's age and experience is a large factor in maternal care (Schwartz and Haroldson, 2006). When one cub in a litter dies, it is common for the rest of the littermates to die as well. Data on this statistically dependent survival of cubs is limited, but I chose a subjective 70% mortality rate to apply to the remaining cubs of a litter with the help of a grizzly bear biologist (McLellan, personal communication, June 3, 2015).

After the operating model adds new cubs to the population, there is the spring hunting season from April to May, followed by the removal of bears due to natural mortality. Natural mortality is applied to the population instantaneously within the model. I chose early spring as the period when modelled grizzly bears experience mortality. This was justifiable because during the late winter and early spring grizzly bears experience the greatest natural stress after overwintering and losing a large proportion of body mass (Schwartz et al, 2003b).

Mating takes place during the period of May to July (MWLAP, 2002). Several factors determine whether a female is fertilized during mating: 1) the annual reproductive rate of that female's stage class, 2) the current ratio of males to females in the population, and 3) the density dependent effect. From our knowledge, sex ratio has not been used to limit reproduction in a grizzly bear model before, but it was included to penalize sex-selective harvests that overexploit the males of the population. Given that the operational sex ratio of grizzly bears is heavily male-biased (Steyaert et al, 2012), it would take a larger change in the sex ratio of the population to see an effect on reproduction. Equation 7 shows how this effect was modelled, where *z* is the slope parameter of the equation, γ50 is the sex ratio in which reproduction is reduced to 50%, and γ is the current sex ratio of the population. The slope parameter (*z*) was set to 20 to allow sensitivity to slight changes in the sex ratio, and the γ50 parameter was determined to be 0.167 based on expert opinion (McLellan, personal communication, Nov 18, 2015). The mating system of grizzly bears is best described as a "scramble polygamous competition" (Steyaert et al, 2012) wherein males and females seek out one another during mating season using scent cues. On average, females mate with three to four males during a breeding season, whereas males range between one to eight mates (Steyaert et al, 2012). McLellan (personal communication, Nov 18, 2015) suggests that the sex ratio at which reproduction drops to 50% below normal would be approximately one male to six females. However, we acknowledge that this is a simplification, since many males in a population do not obtain any mates (Steyaert et al, 2012). Figure 5 illustrates the operational sex ratio effect over a series of potential γ values, which is always a value between 0 and 1.

(7) $$O_t = \frac{1}{1+ e^{(-1*z)*(\gamma-\gamma 50)}}$$

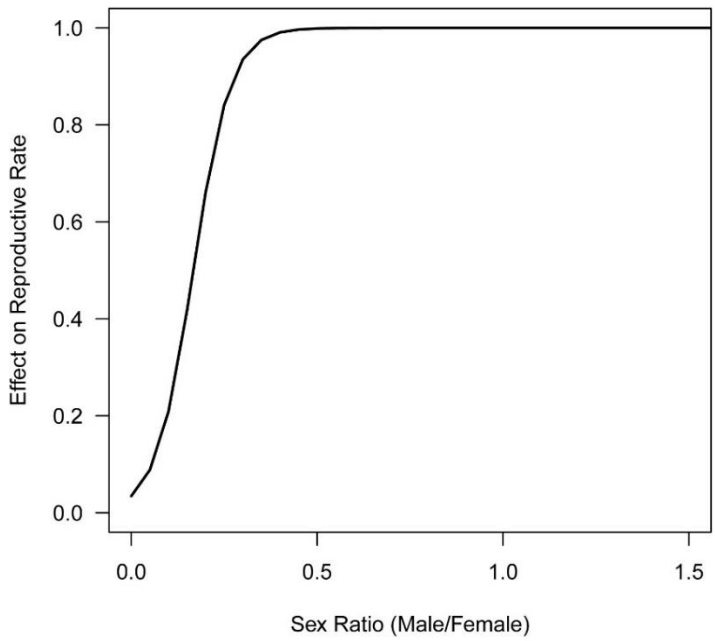

Figure 5. The Operational Sex Ratio Effect (O_t) over a series of potential sex ratio values (γ). At a sex ratio of one male to six females, reproductive drops to 50%.

The density dependent effect (Equation 6) is also a factor that influences the reproduction of a population. If the population is close to or at the population carrying capacity, fewer females will be fertilized during the mating period. Only individual females that do not have dependent offspring are available to mate in this simulation model. When determining whether a female is fertilized, the probability of fertilization is equal to the product of the bear's annual reproductive rate, the operational sex ratio effect and the density dependent effect (Equation 8).

(8) $$P(F) = R_{a,t} O_t D_t$$

The operating model runs through each individual female that is available to mate and determines whether mating is successful. Successful females are recorded within the model to be fertilized and delay birth until the start of the new year. This reflects the delayed implantation that exists in grizzly bears, as fertilized eggs are dormant for several months until November or December (Steyaert et al, 2012; Schwartz et al, 2003a).

2.3.2. The Observation and Management Model

The observation and management model components of the simulation were based on current management in British Columbia, where the grizzly bear hunt is managed in 5-year allocation periods. Early in the first year of the allocation period, the annual allowable human-caused mortality (AAM) for the next 5 years is decided based on estimates of the population and the harvest rules of the specific management strategy (described below). At the start of the simulation, wildlife managers estimate the grizzly bear population's carrying capacity and population size, with bias being log-normally distributed for both estimates. British Columbia's grizzly bear carrying capacity and population size estimates are based on a Multiple Regression Model, which uses habitat qualities such as geography, land cover and human influences to predict grizzly bear densities (MOE, 2011). At the start of each 5-year allocation period, population size and carrying capacity is estimated by managers, with bias modelled as log-normal within the simulation. New population size estimates made every 5 years are autocorrelated with the previous allocation period's estimate. The autocorrelation level was set at 0.9 so that managers are heavily influenced by previous estimates. Wiedenmann et al (2015) described this level of autocorrelation as appropriate for long-lived and lightly exploited species.

For each new 5-year allocation period, a new population size estimate is used to calculate AAM using methods specific to each management strategy. The goal of management is to keep all sources of human-caused grizzly bear mortality within the AAM limit. There are four sources of human-caused grizzly bear mortality that are managed: hunting mortality, reported non-hunt mortality, aboriginal-caused mortality and unknown mortality. Hunting mortality can be further divided into resident and non-resident mortality, which are calculated differently in the quota allocation. Reported mortality includes all sources of non-hunt mortality that are known to wildlife managers including car collisions, railway mortality, illegal killing, and animal control mortalities (MOE, 2010). Aboriginal-caused mortality is a category of grizzly bear mortality designated for the food, social and ceremonial rights of Aboriginal peoples; however, there is uncertainty in the number of bears killed for this purpose. Thus, the aboriginal-caused mortality is another source of unknown mortality estimated by wildlife managers in the quota allocation calculations (Mowat, personal communication, Sep 28, 2015). Unknown human-caused mortalities are any grizzly bear mortalities that go unreported to wildlife officials. For current MFLNRO

management, the unknown mortality rate is estimated for each grizzly bear population and included in the quota allocation calculations (MOE, 2010).

Early in the first year of the allocation period, the observation model determines a population size estimate (with bias) and passes the estimate to the management model. Within the management model, simulated managers apply harvest control rules to determine whether the population meets the conditions required for a hunt. If a hunt is approved, the management model calculates the AAM for each year of the allocation period and incorporates uncertainties in accordance with the management strategy. The AAM is totalled into a total allowable human-caused mortality (TAHM) for the five-year allocation period, and total allowable female human-caused mortality is calculated based on 30% of the TAHM (MOE, 2010; MOE, 2007). The TAHM is then distributed as quota to both resident and non-resident hunters. I used a 64% and 36% distribution of quota to resident and non-resident hunters respectively, since this was a ratio used frequently by MFLNRO (Hamilton, personal communication, November 30, 2015), although these numbers do vary with GBPU. Hunting in the model takes place in both the spring and fall seasons, although there are some areas of British Columbia that are subjected to only a spring hunt. The spring hunt takes place between the births of new cubs and the breeding of adult bears in the population, in the months of April and May. Resident hunting mortality includes implementation uncertainty, wherein the annual quota specified by managers can be missed or exceeded by the hunters. The realized hunting mortality of the spring and fall hunt are determined based on a binomial distribution of the number of hunting permits issued for a season ($p_{i,t}$), the season's hunting success rate (h_i), and a scalar variance (*Var*) used to adjust the level of uncertainty (Equation 9).

(9) $$Bin(p_{i,t}Var, h_i)$$

Hunting success rates, h_i, remained static over time for this study and were based on seasonal success rates documented by the MFLNRO (Hamilton, personal communication, November 30, 2015). Implementation uncertainty also affects the non-resident hunt, although to a lesser extent. It is very rare for the non-resident quota to be surpassed in British Columbia, since the quota and bookings of non-resident hunters is managed through guides. Exceeding the quota for the 5-year allocation period would result in harsh penalties

for guides, as it breaks the rules of the outfitter license and is also against the Wildlife Act (Mowat, personal communication, Sep 28, 2015). Thus, it is rare that the non-resident quota is exceeded. It is more common that non-resident quota is not filled by the end of the 5-year allocation period. This is an issue in northern GBPUs, where there is less of an interest from hunters, and guides struggle to fill more than half of their quota (Mowat, personal communication, Sep 28, 2015). Due to this insight, the non-resident hunting mortality is modelled in one of two ways, 1) as a normal distribution that is biased towards filling the quota as in popular Southern GBPUs, or 2) as a Poisson distribution that centers around filling 50% of the quota, as is seen in the majority of GBPUs. In the case of modelling non-resident quota using the normal distribution, quota may occasionally be surpassed by one grizzly bear mortality, since any more would be unlikely given the heavily managed guide outfitters offices.

Table 3. Management parameters used in the model, including coefficients of variation population estimates. Hunting success rates were based on common rates assigned during MFLNRO's quota calculations.

Parameter	Parameter Value
CV Carrying Capacity	0.4
CV Population Size	0.9
CV Unknown Mortality	0.5
CV Unknown Aboriginal Harvest	0.4
Spring Hunting Success Rate	0.12
Fall Hunting Success Rate	0.25
Variance scalar (Hunting success)	1

Reported non-hunt mortalities, aboriginal hunting mortalities and unknown mortalities all take place during the summer months between the spring and fall hunts. Unfortunately, due to the structure of the model these mortalities are annual events, whereas in nature they occur over the spring, summer and fall seasons. Reported non-hunt mortalities are randomly generated each year based on a Poisson distribution with a lambda value of 0.5, which pulls zero and one most frequently, but occasionally will result in two or three annual non-hunt mortalities. The aboriginal hunting mortalities and unknown mortalities are both generated using a normal distribution centered around the estimated mortality rates of the managers, with a coefficient of variation that can be adjusted by the uncertainty of the manager's estimates. For the purposes of this study, I selected

coefficients of variation with help from a MFLNRO grizzly bear biologist (McLellan, personal communication, June 3, 2015) that would reflect the uncertainties in current management. This also included concerns from the scientific community and the public regarding inaccuracies in population size estimates and unknown mortality estimates. An overview of the management parameters selected for this study can be found in Table 3.

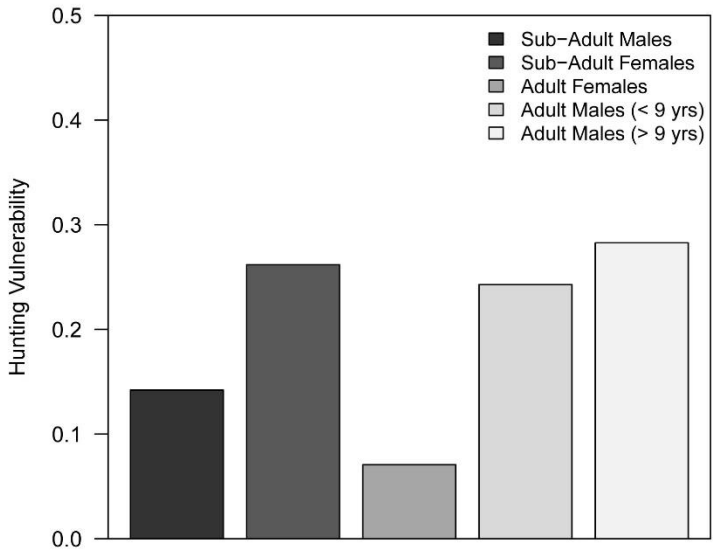

Figure 6. The proportional vulnerability of each stage class to hunting mortality.

The vulnerability of grizzly bears to death varies by age and sex class depending on the type of mortality. The reported and unknown mortality sources are both unbiased mortality rates that affected grizzly bears equally across all ages and sexes. Hunting mortalities, which include the resident, non-resident and aboriginal hunting mortalities, are based on the vulnerabilities of specific sex and age classes to hunting effort (Figure 6) in five classes: sub-adult females, sub-adult males, adult females, adult males under 9 years old, and adult males ages 10 and over. Proportional vulnerability rates of each class were based on harvest vulnerability for the Flathead population in the McLellan et al (2017) study. The hunting vulnerability is 14.20% for sub-adult males, 26.18% for sub-adult females, 7.07% for adult females, 24.28% for younger adult males, and 28.27% for the older and larger adult males. The number of grizzly bears hunted from each of the five classes is determined using a multinomial distribution (Equation 10), given the number of bears harvested (Q_t), and the stage-specific vulnerabilities (v_a).

(10) $$H_{a,t}^{s} \sim Multinomial(Q_t, v_a)$$

Females with dependent offspring do not experience hunting mortality, which is a result of protective legislation making it illegal to harvest a female with cubs or yearlings present. Selected grizzly bears are then removed from the population, and the simulated managers receive data on the age and sex of the reported grizzly bear mortalities, and resident and non-resident hunting mortalities. The unknown and aboriginal-hunting mortalities remain unknown to management.

2.3.3. Management Strategies

I tested three competing management strategies for this study: 1) the current management used by the MFLNRO for grizzly bears in British Columbia (currBC); 2) a management strategy inspired by Alaska's management protocols (quasiAK); 3) a constant hunter kill rate of 6% (cons6%).

The currBC management strategy details can be found in Figure 7. Under the MFLNRO management strategy, a GBPU is only considered viable for a hunt if: 1) it has a population size estimate over 100 bears, and 2) the population size estimate is over 50% of the population's carrying capacity estimate (MOE, 2011). If a GBPU does not meet these criteria, then the population is considered threatened, and no hunting occurs until the population recovers. The MFLNRO management strategy sets a maximum human-caused mortality rate between 4-6%. The designation of this maximum allowable human-caused mortality rate has been described as both a science and an art, and is influenced by the estimated density of the population, the population growth rate, the location of the population, expert opinion, and uncertainties in the population dynamics (MOE. 2011; MOE, 2007). Estimated population density appeared to be the strongest criteria for deciding the maximum human-caused mortality rate in MFLNRO policy, so we modelled the management strategy to designate a 4-6% maximum human-caused mortality based on perceived population productivity (estimated population size divided by estimated population carrying capacity), since our model did not include density. The management strategy then removes the estimated annual unknown mortality rate and the estimated annual aboriginal hunting mortality rate from the maximum human-caused mortality rate to

incorporate the uncertainties that the population faces. This new mortality rate, which incorporates unknown mortality estimates, is considered the corrected AAM (MOE, 2007). Managers then multiply the corrected AAM by 5, the number of years in the allocation period, to determine the TAHM over the entire five-year period. The total allowable human-caused female mortality is calculated as 30% of the TAHM, and any overkills from the previous allocation period are deducted from the TAHM and TAHFM. The predicted reported mortality for the allocation period, which is equal to the reported mortality of the previous allocation period, is also deducted from the TAHM. The managers then distribute the TAHM to both the resident and non-resident hunt; the resident quota is divided into annual quota for each year of the allocation period, whereas the non-resident allocation is distributed to guide outfitters to manage over the 5-year period. The MFLNRO management strategy also has a flag system in place in order to manage AAM on a year to year basis. Hunting is closed if the TAHM or TAFHM are exceeded during the allocation period, but the AAM may be exceeded during some years. In practice, managers track the average annual mortalities each year and compare it to the targeted AAM and AAFM. Flags are issued based on concerns with the annual mortalities of GBPUs. A yellow flag is designated when the average annual mortality or average annual female mortality is 20% below targets or has reached targets (MOE, 2007). In the case of a yellow flag, managers would keep a close eye on the mortality being experienced in a GBPU. A red flag is issued when the average annual mortality or average annual female mortality exceeds the targets set by managers. In practice, if a red flag is issued, managers recommend the reduction of hunting opportunities so that mortalities can fall back to a normal level (MOE, 2007). Within the model, yellow and red flags are issued based on these criteria when managing a population using the currBC strategy. If a red flag is triggered for either AAM or AAFM, the targeted value will be reduced by 80% to lower hunting opportunities for the year. In reality this process is much more flexible and based on subjective judgement, but this is another limitation of this study and using models to simulate management decisions. As the allocation period progresses, AAM and AAFM are monitored year to year and hunting continues so long as the TAHM and TAFHM are not met or surpassed. Any excess mortalities are deducted from the next allocation period's total allowable human-caused mortality or total allowable female human-caused mortality.

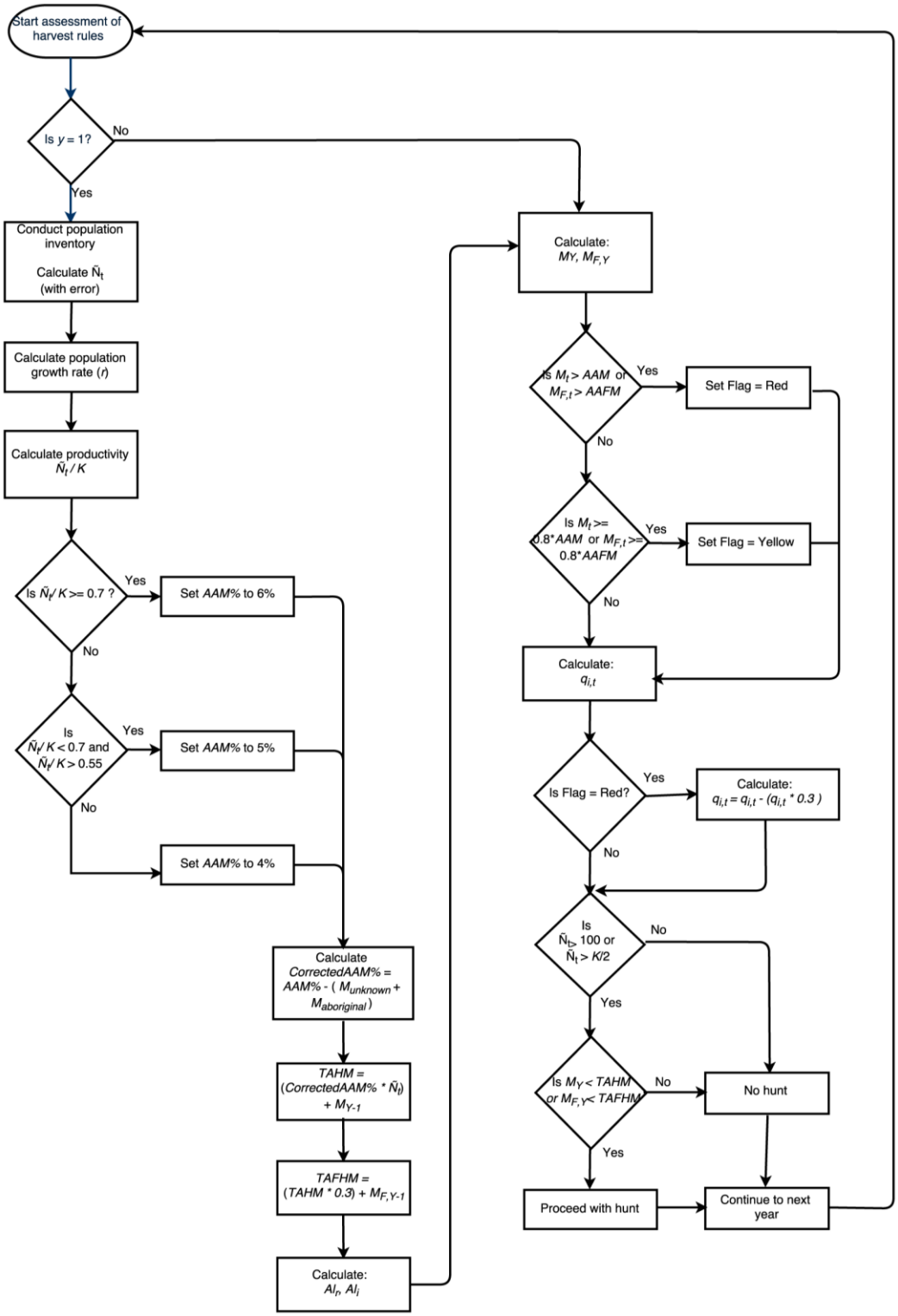

Figure 7. **Flowchart of the currBC management strategy currently used to manage grizzly bears. Note, many of these steps were simplified as they required subjective inputs and expert opinions.**

The second management strategy tested (Figure 8) is based loosely on the management strategy commonly used to manage grizzly bears in the state of Alaska in the United States. Alaskan grizzly bears are managed by the Alaskan Department of Fish and Game, who manage wildlife using 26 game management units (GMU). Management methods and objectives vary between different GMUs (ADF&G, 2011). Some populations are managed by maintaining a constant annual harvest, while other GMUs are managed to maintain a specific targeted population size. One popular management strategy that is used in Alaska, which may be of interest to the MFLNRO, is managing grizzly bears by maintaining a harvest of an average age and sex ratio. The theory behind this method is that a hunt that is selective towards males will display shifts in the age and sex composition of harvest data as the population begins to decline (Harris & Metzgar, 1987). Therefore, by adjusting the harvest rate to maintain an average age and sex ratio in the harvest data, several GMUs are managed without sophisticated analyses. To model the quasiAK management strategy, we devised two linear equations to calculate the percent of the population to be assigned as AAM based on the average age (Equation 11) and the sex ratio (Equation 12) of harvest data from the previous year.

(11) $$\alpha_1 = 1.25\overline{H}_{t-1} - 7$$

(12) $$\alpha_2 = 25\rho - 14$$

Two competing percentages are generated from both equations, where $\overline{H}_{t-1}$ is equal to the average age of the previous year's hunting data and ρ is equal to the sex ratio of the previous year's hunting data. The quasiAK strategy does not allow an AAM over 8% of the population size estimate. Similar to the currBC management strategy, this strategy has safeguards in place to close hunts when the population has been deemed too vulnerable. For a hunt to be open, the population must be greater than 100 bears and cannot be declining by more than 20% in the last 30 years. If a hunt is determined to be open, managers then use Equations 11 and 12 to determine the AAM. The smallest of the two equations is used as the proportion of the population that can be killed due to human causes. This percentage is then multiplied by the population size estimate to calculate the AAM. The AAM is then multiplied by the number of years in the allocation period to determine the TAHM, and the TAFHM is set at 30% of the TAHM. Once the TAHM is calculated, the quota is divided up between resident

and non-resident hunt. Each year of the hunt, total mortality and total female mortality are managed to ensure they do not surpass the maximum allowable levels. However, unlike the currBC management strategy, there is no attempt to incorporate unknown, reported or aboriginal hunting mortality estimates. Exceeded mortalities at the end of the 5-year period are also not accounted for in the next allocation period.

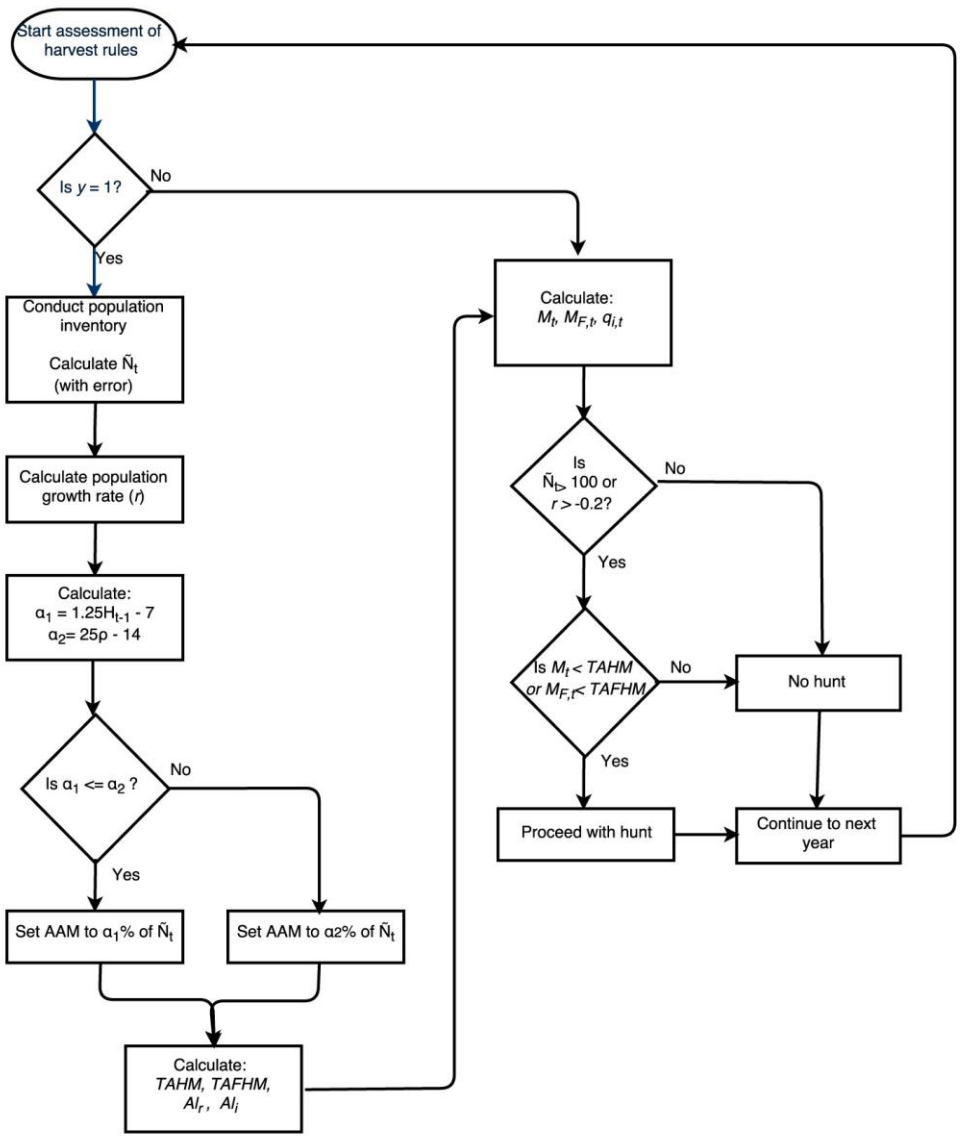

Figure 8. Simplified flow chart for the quasiAK tested in this study, which was heavily inspired by Alaska's use of harvest data to calculate annual mortality rates for several populations.

The cons6% management strategy is a fixed proportional hunter kill rate of 6% (Figure 9). A harvest of 6% population size was chosen because it was considered the maximum sustainable annual harvest mortality for grizzly bears among managers and grizzly bear biologists (Harris, 1986; Miller, 1990). This strategy also requires that the population must be greater than 100 bears and cannot be declining by more than 20% in the last 30 years for the hunt to be open. The AAM is calculated as 6% of the population size estimate, and the TAFHM is set at 30% of this value. Much like the quasiAK management strategy, there is no attempt to incorporate anything other than hunting mortality, and exceeded mortalities are not carried over into new allocation periods.

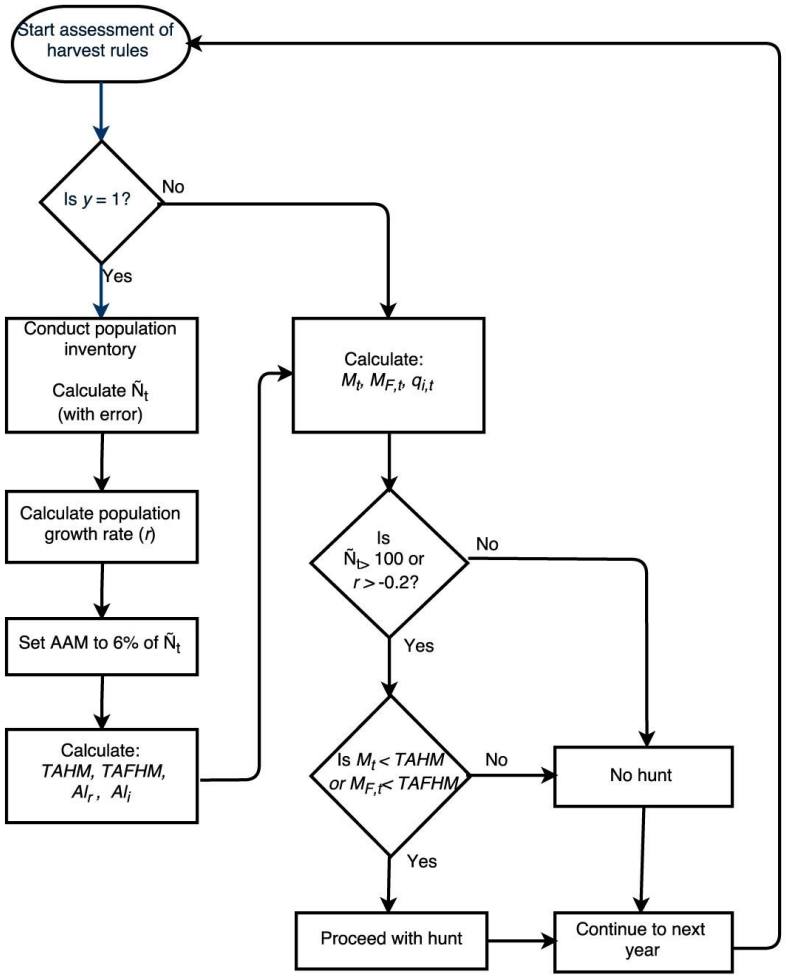

Figure 9. Flowchart of the cons6% management strategy tested in this study, an annual harvest rate of 6% of the population size.

2.4. Model Analysis

The population simulations were run for 100 years each. The first 50 years of the simulation were used to equilibrate the stable state population to a higher level of mortality due to the demographic stochasticity, mother-cub interactions, and human-related causes. The initial 50 years were also a means to eliminate populations that had non-viable vital rates. Due to the small sample sizes from field studies, some runs would pull mean survival or reproductive rates from the lower end of the beta distributions. With several stage classes modelled in this study, some combinations of the mean vital rates were found to not be viable naturally. As a result of the adjustment in the first 50 years of the simulation, extinction events during this phase were not recorded so as not to confuse a non-viable population with the results of an unsustainable management strategy. For the following 50 years, the population was subjected to one of the three management strategies: 1) currBC, 2) quasiAK, and 3) cons6%.

Each of the three different management strategies was tested with each of the three populations of different productivities. For each combination, 1000 Monte Carlo trials were conducted to assess the risk of each management option given the range of vital rate probabilities. The three competing management strategies were tested for their performance managing the three grizzly bear populations of different productivity levels. Management strategies were tested on both unhunted populations and previously hunted populations. The goal of this method was to determine whether there was an increased risk of a management strategy if a population had been previously exploited. For an analysis of unexploited populations, during the initial 50 years of the simulation there was no hunting. As a result, the populations could reach a stable state while only experiencing unknown and reported sources of human-caused mortality. For trials on the hunted population, a 6% constant annual hunting mortality was applied during the initial 50 years of the simulation. Management options were also tested against two different models of filling non-resident quota: 1) a Southern GBPU model that is more biased towards filling non-resident quota, or 2) a model that represents the majority of GBPUs, which centers around filling 50% of the quota. Simulations were also run for each of the three populations in the absence of any human-caused mortality in order to separate the background extinction rate from the effects of unsustainable management.

The trade-offs and risks of each management strategy were evaluated by calculating several population statistics: rate of population extinction, rate of growth, probability of population reaching vulnerable status, cub survival, final population size and average annual harvest. The rate of a population extinction is an empirical rate calculated using the arithmetic mean equation:

(13) $$P(E) = \frac{1}{n}\sum_{i=1}^{n} x_i$$

where n is the total number of simulations, and x_i is the indicator of whether the current simulation resulted in an extinction event.

Equation 14 show how the rate of population growth (r_t) was calculated, where N_t is the population size in year t, and N_0 is the initial population size.

(14) $$r_t = \frac{N_t - N_0}{N_0}$$

This equation was also used to calculate the probability of a management strategy resulting in vulnerable populations. The probability of a vulnerable status was based on the ICUN criteria A2, wherein a population is considered vulnerable if it experiences a 30% decline over 3 generations (IUCN, 2001). A grizzly bear generation is estimated to be between 10-15 years, so a 45-year period ($T = 45$) was used to represent three grizzly bear generations. Equation 13 was then used to calculate the risk of a vulnerable population status. In this case, the variable x_i is an indicator of whether the rate of population growth dropped below 30% throughout any 45-year period during the simulation.

Mean cub survival was calculated using equation 15, where $N_{t,1}^{n}$ is the number of cubs at time t and simulation n, while $N_{t,2}^{n}$ is the number of yearlings at year t and simulation n. The number of yearlings is divided by the previous year's number of cubs to get the cub survival rate over a simulation period. Each simulation's cub survival rate is then averaged

by n, the total number of simulations, to calculate the mean cub survival rate of a management strategy.

(15) $$\bar{S}_0 = \frac{1}{n}\sum_{i=1}^{n}\frac{1}{T}\sum_{t=1}^{T}\frac{N_{t,2}^{i}}{N_{t-1,1}^{i}}$$

The mean final population size was calculated using the arithmetic mean calculation (Equation 13), averaging the final population size at year 50 for all simulations. Mean annual harvest was also calculated using Equation 13, with the sum of the mean annual harvest rates of each simulation divided over n, the total number of simulations.

2.5. Sensitivity Analysis

Several sensitivity analyses were conducted to examine the robustness of the three management strategies to changes in parameter inputs, specifically those that are uncertain due to a lack of information. Single-value sensitivity analyses were conducted for the percent variance partitioned to environmental effect ($\sigma^2{}_{environmental}$), and the auto-correlation coefficient for environmental stochastic effects. Values between 1-25% were tested for the environmental effect as is suggested by RISKMAN software (Taylor et al, 2006), and a range of auto-correlation coefficients between 0.0 and 0.7 were also subject to sensitivity analysis. A bivariate sensitivity analysis was conducted using the *z* and *γ50* parameters, which influences the shape of the operational sex ratio effect. The minimum and maximum plausible parameter values (*γ50*= 3 and 10, *z* = 5 and 30) were tested to determine whether there was a change in risk of any or all management strategies analyzed.

3. Results

3.1. Population Survival in the Absence of Human Mortality

The simulation runs that featured no human-caused mortality demonstrated the expected level of productivity for each of the three locations (Figure 10). The low productivity dataset had a baseline extinction rate of 0.5% over all 1000 simulations and a positive growth rate of 1.30%. The moderate productivity dataset was found to have a background extinction rate of 0.0%, with a slight growth rate of 0.5% over the 50-year period for all 1000 simulations. The dataset representing the high productivity population had no background extinction rate (0.0%), and a rate of growth of 1.27%.

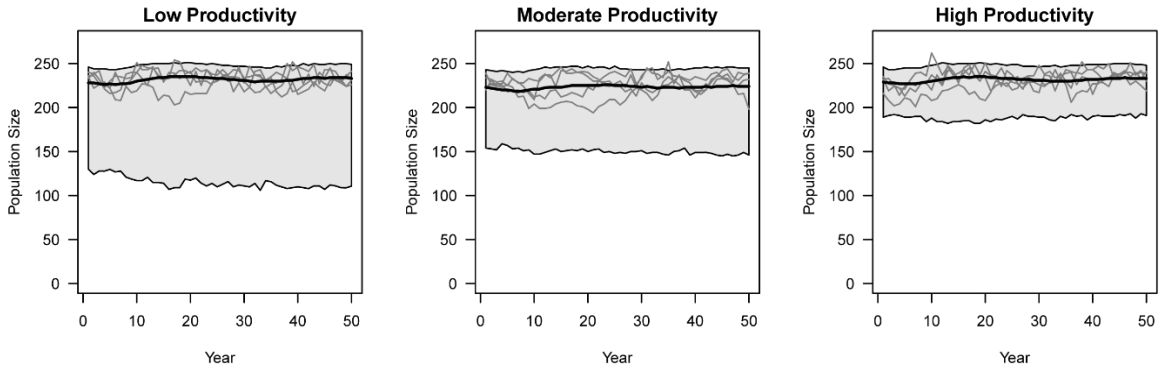

Figure 10. Population simulations the no human-caused mortality case in 1) low productivity (Flathead River Basin), 2) moderate productivity (Banff), and 3) low productivity (Selkirk Mountains). The bolded line is the median population size, and the grey area is the bounds of the 95% confidence interval.

The average population size at the end of the 50 years for the low productivity dataset was 225.10 bears (CI = 110.73-249.00, SD = 34.79), whereas the average population size for the moderate and high productivity datasets was 218.07 (CI = 146.00-245.03, SD= 26.56) and 229.16 (CI= 190.98-248.00, SD= 19.92) respectively. The low productivity dataset had a baseline probability of reaching a vulnerable population status of 2.5%. In contrast, the moderate productivity dataset had a 1.7% probability of becoming a vulnerable population, and the high productivity dataset had a 0.7% probability of being defined as vulnerable. Cub survival was naturally lower for the dataset representing a low productivity population (0.83, CI= 0.70-0.94, SD= 0.09), whereas both the moderate and high productivity datasets had a

cub survival of 0.90 (CI= 0.80-0.97, SD= 0.05) and 0.90 (CI= 0.79-0.97, SD=0.05) respectively.

3.2. Management Strategy Performance with Previously Unexploited Populations

3.2.1. Low Productivity Population

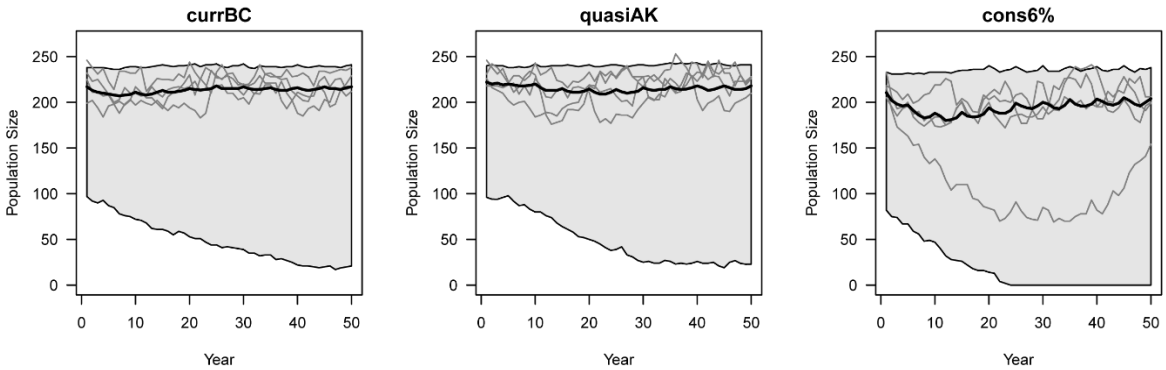

Figure 11. Population projections for 1) currBC management, 2) quasiAK management, 3) cons6% management for the low productivity population (Flathead River Basin). The bolded line is the median population size, and the grey area is the bounds of the 95% confidence interval.

For the least productive population, the currBC and quasiAK strategies performed similarly (Figure 11). The currBC management strategy had a 2.1% rate of extinction over 1000 simulations, whereas quasiAK had a 1.6% rate of extinction. The cons6% management strategy performed the worst with a 5.7% chance of extinction. The currBC strategy had a 9.0% probability of the population reaching the status vulnerable, whereas the quasiAK strategy was slightly worse for population declines, resulting in a 15.1% probability of the population becoming vulnerable. The cons6% strategy had signs of exploitation when compared to natural rates for the low productivity dataset and the other management strategies tested. The simulations under the 6% constant harvest had a 26.6% probability of reaching vulnerable status. All three of the tested strategies had negative rates of growth over the 50 years, with the currBC strategy averaging a -3.05%, the quasiAK strategy averaging a -5.33%, and the cons6% strategy averaging a rate of growth of -13.03%. The average final population sizes were 201.71 bears (CI= 20.88-241.00, SD=48.47), 201.04 bears (CI = 22.83-241.00, SD= 50.18) and 176.10 bears (CI= 0.00-238.00, SD=68.99) for the currBC, quasiAK, and cons6% strategies respectively. Cub

survival was reduced for all management strategies, but was lowest for the cons6% strategy with an average cub survival rate of 0.81 (CI = 0.30-0.94, SD = 0.15). The currBC and the quasiAK management strategies maintained similar cub survival rates, with an average cub survival of 0.83 (CI = 0.64-0.94, SD = 0.11) for currBC and 0.83 (CI = 0.65-0.93, SD = 0.10) for quasiAK. The cons6% strategy provided the most hunting opportunities with an average annual harvest of 6.37 bears (CI = 0.00-10.18, SD=2.93). The currBC strategy resulted in an average annual harvest of 3.13 bears (CI = 0.00-7.50, SD=2.57), whereas the quasiAK strategy provided the least hunting opportunity, with an average annual harvest of 2.62 bears (CI = 0.00-5.38, SD=1.56).

3.2.2. Moderate Productivity Population

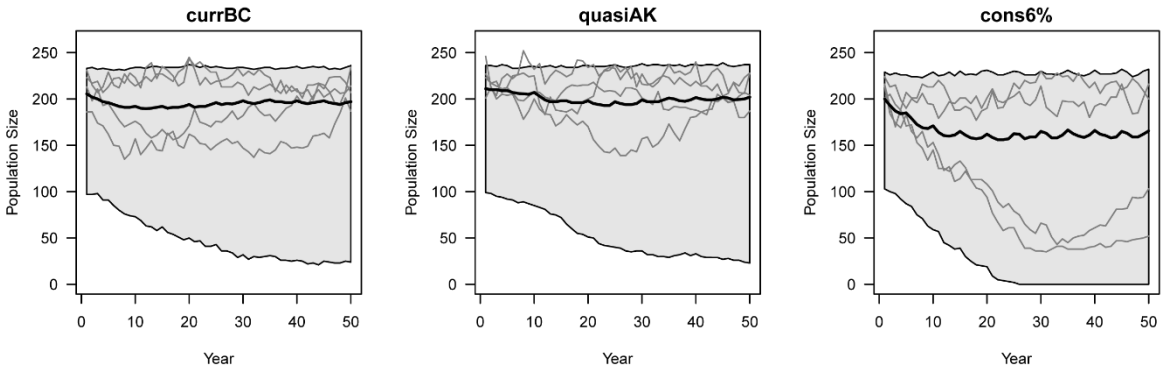

Figure 12. Population projections for 1) currBC management, 2) quasiAK management, 3) cons6% management for moderately productive population (Banff, Alberta). The bolded line is the median population size, and the grey area is the bounds of the 95% confidence interval.

Compared to the management strategies' performances managing the lower productivity population, the simulation runs with the moderately productive dataset reveal increasing population performance (Figure 12). The currBC and quasiAK strategies had probabilities of extinction of 1.4% and 0.9% respectively, while the cons6% strategy had a higher rate of extinction of 9.8%. The currBC management strategy had the lowest probability of the population reaching a vulnerable status, which was 18.5%. The quasiAK strategy had 24.8% of its simulations reach a vulnerable status, while cons6% had 46.0% of simulations reach a designation of vulnerable. The cons6% strategy also had the worst rate of growth compared to the population simulations under the other two management options, with an average rate of growth of -27.99% over all 1000 simulations, while the

currBC and quasiAK strategies had similar average rates of growth of -8.45% and -8.93% respectively. The average population size at year 50 was similar for the first two management strategies. The quasiAK strategy had slightly higher population sizes, with an average of 182.22 bears (CI= 22.98-237.00, SD= 54.86), while currBC management averaged 179.05 bears (CI= 23.98-236.00, SD= 54.29). The third management option, cons6%, had the lowest average population size of 137.90 bears (CI=0.00-232.03, SD=77.66). Average cub survival was the 0.88 for the first two management strategies (CI = 0.68-0.96, SD = 0.09 under currBC; CI = 0.72-0.96, SD = 0.07 under quasiAK). In contrast, average cub survival was reduced to 0.83 (CI= 0.32-0.97, SD =0.16) under the cons6% management scenario. With the highest harvest rates, cons6% provided the highest average annual harvest of 5.45 bears (CI = 0.00-9.26, SD=2.67). The average annual harvest for the currBC strategy was 2.80 bears (CI=0.00-6.62, SD=2.27) and 2.03 bears (CI = 0.00-4.74, SD=1.36) under the quasiAK strategy.

3.2.3. High Productivity Population

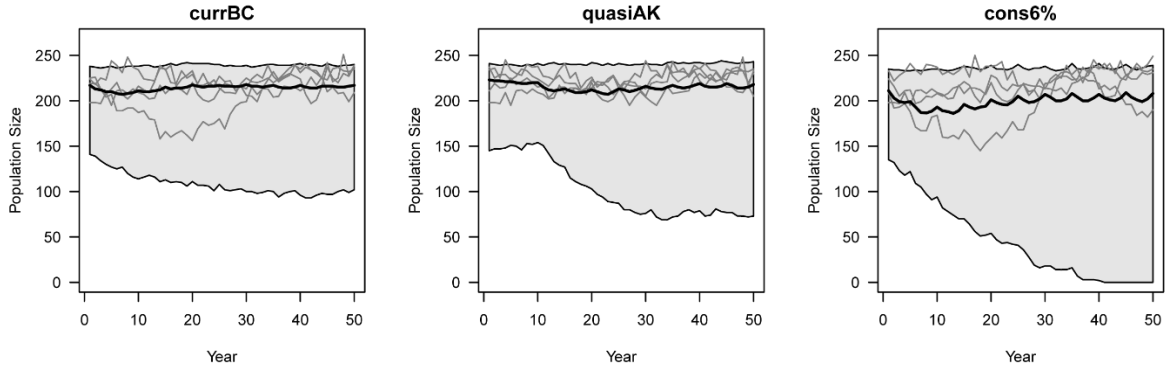

Figure 13. Population projections for 1) currBC management, 2) quasiAK management, 3) cons6% management for the low productivity population (Southeastern British Columbia and northeastern Montana). The bolded line is the median population size, and the grey area is the bounds of the 95% confidence interval.

As would be expected, the simulations for the highly productive dataset were found to have better population performance than the previous two datasets (Figure 13). The probabilities of extinction were lowest for this dataset. The currBC strategy had 0.6% of the 1000 simulations resulting in an extinction event, whereas the rate of extinction was 0.4% from the quasiAK management strategy. The rate of extinction was higher for cons6%, with

3.5% of simulated populations falling extinct. There was a 6.7% probability of populations dropping to a vulnerable status under currBC management, and a 14.1% probability under the quasiAK strategy. The third strategy, cons6%, resulted in 20.1% of all 1000 simulations at one point being designated as vulnerable under IUCN A2 criteria. Under currBC management, the average population size was 207.12 bears (CI=101.95-240.00, SD=36.00), with a rate of growth of -1.96%. Under the quasiAK strategy, the average population size was 205.25 bears (CI=72.98-243.00, SD=40.72), with a rate of growth of -5.51%. Populations under the cons6% harvest rate experienced the greatest decline, with an average final population size of 186.82 bears (CI= 0.00-239.00, SD=58.05) and a negative rate of population growth of -9.85%. Cub survival decreased in all three management strategies, with an average survival rate of 0.89 (CI = 0.80-0.96, SD= 0.07) for currBC management, 0.89 (CI =0.80-0.96, SD=0.06) for quasiAK, and 0.89 (CI= 0.55-0.96, SD=0.10) for the cons6% management strategy. Average annual harvest was once again lowest for the quasiAK strategy, with an average harvest of 2.95 (CI=0.00-5.86, SD=1.68) bears each year. The currBC strategy resulted in an average annual harvest of 3.36 bears (CI=0.00-7.60, SD=2.51), while the cons6% strategy had the highest average annual harvest of 6.55 bears (CI=0.00-10.42, SD= 2.89).

3.3. Management Strategy Performance with Previously Exploited Population

3.3.1. Low Productivity Population

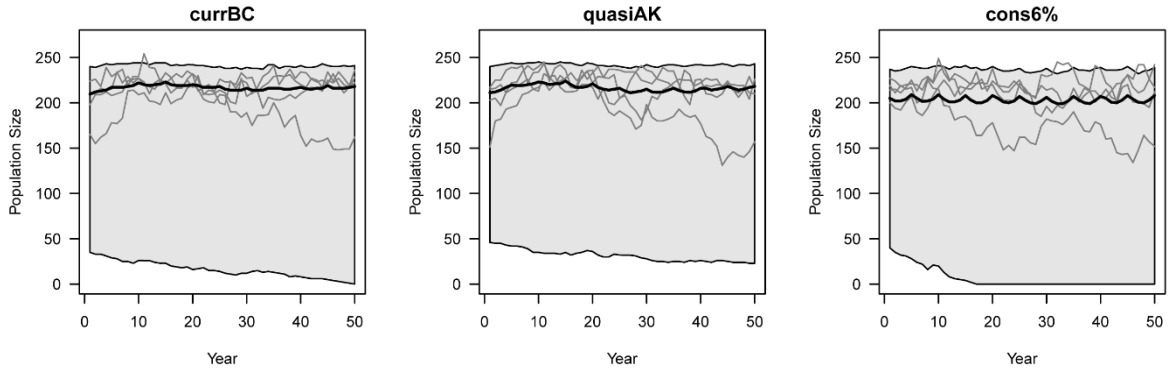

Figure 14. Population projections for 1) currBC management, 2) quasiAK management, 3) cons6% management for the low productivity population (Flathead River Basin) with a 50-year history of hunting. The bolded line is the median population size, and the grey area is the bounds of the 95% confidence interval.

With harvests added to the initial 50 years of each simulation, the rate of extinction rose for all three management strategies, although populations began experiencing increasing growth and lower probabilities of decline. For the currBC management, the rate of extinction throughout all 1000 simulations was 2.6%, whereas the quasiAK and the cons6% strategies experienced extinction rates of 1.9% and 5.9% respectively (Figure 14). The currBC management continued to have a more stabilizing affect on population size, with a 6.4% rate of populations dropping below vulnerable status. That same probability was higher for the other two management strategies, at 10.8% for the quasiAK strategy and 19.2% for the cons6% harvest rate. The final population size under currBC management averaged 203.42 bears (CI= 0.00-241.00, SD=48.90), with a rate of growth of 7.22%. The quasiAK strategy was comparable, with a final average population size of 202.13 (CI = 22.98-243.00, SD=49.39) and a rate of growth of 4.46%. Under the cons6% strategy, average final population size was reduced to 182.11 bears (CI=0.00-239.00, SD=65.61) and the rate of growth was -3.03%. Cub survival was higher for the first two management strategies compared to the cons6% strategy. The currBC management resulted in a cub survival of 0.82 (CI = 0.47-0.93, SD = 0.13), the quasiAK strategy resulted in a similar cub survival of 0.82 (CI = 0.61-0.93, SD = 0.12), and the cons6% strategy resulted in a cub survival of 0.80 (CI = 0.16-0.93, SD = 0.16). Annual average harvest remained highest for the third management option, with an annual harvest 5.84 bears (CI= 0.00-9.74, SD=2.78). In contrast, average annual harvest was 2.58 bears (CI= 0.00-6.90, SD= 2.30) for the currBC strategy, and 2.63 (CI=0.00-5.60, SD=1.60) for the quasiAK strategy.

3.3.2. Moderate Productivity Population

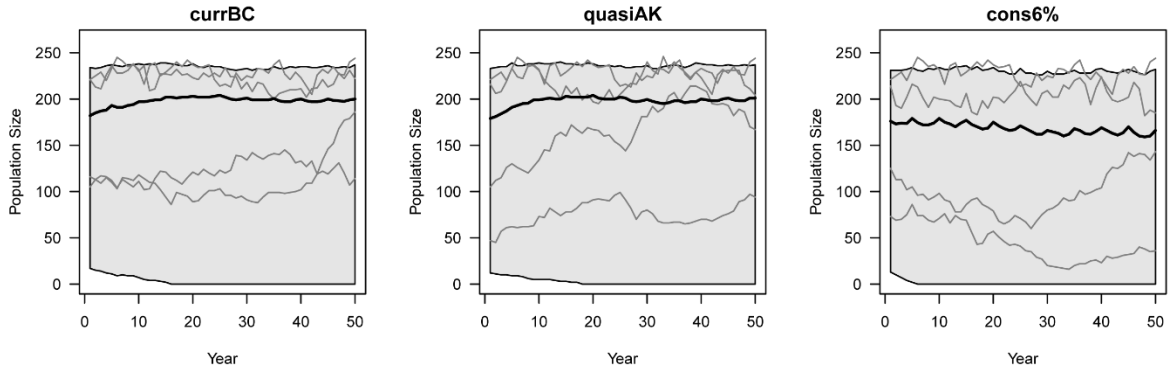

Figure 15. Population projections for 1) currBC management, 2) quasiAK management, 3) cons6% management for the moderately productive population (Banff National Park) with a 50-year history of hunting. The bolded line is the median population size, and the grey area is the bounds of the 95% confidence interval.

For the moderate productivity dataset, population health appeared to decline when compared to the low and high productivity datasets (Figure 15), likely due to naturally lower sub-adult survival. The currBC and quasiAK strategies both resulted in probabilities of extinction of 4.3%. The cons6% strategy had the highest rate of extinction of 12.4%. The currBC management strategy had a 12.6% probability of dropping the population size to a vulnerable status, while the quasiAK and cons6% strategies had a 17.7% and 39.9% probability of resulting in such a decline. The average final population size was 177.60 bears (CI = 0.00-237.00, SD=61.38) under the currBC strategy, with a growth rate of 9.41%. The quasiAK strategy resulted in a comparable average population size of 175.51 bears (CI=0.00-237.00, SD=64.19) and a rate of growth of 10.65%. The cons6% strategy continued to reduce population size for the moderately productive dataset, with an average population size of 138.99 grizzly bears (CI=0.00-232.03, SD=77.86) in the final year, and a rate of growth of -12.20%. Cub survival was strongly affected for the moderate productivity dataset, averaging 0.85 (CI = 0.07-0.96, SD = 0.18) under currBC management. The quasiAK strategy performed similarly, with an average cub survival of 0.85 (CI = 0.08-0.96, SD = 0.18), while the cub survival for the cons6% strategy was even lower at 0.80 (CI = 0.02-0.96, SD = 0.24). Average annual harvest remained highest for the cons6% strategy at 4.72 bears (CI= 0.00-9.00, SD=2.72). Average annual harvest was comparable between the first two strategies, with an average 2.04 (CI= 0.00-6.25, SD= 2.04) and 1.78 (CI= 0.00-

4.54, SD=1.37) bears harvested each year under the currBC and the quasiAK strategies respectively.

3.3.3. High Productivity Population

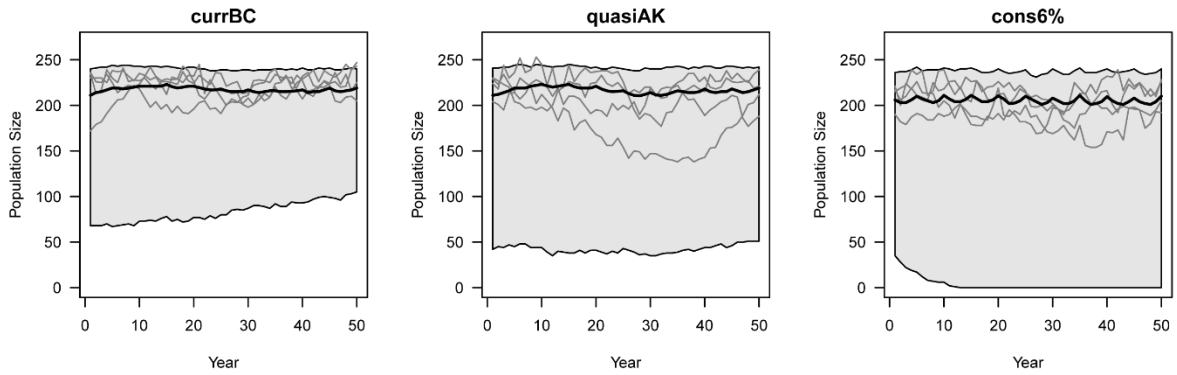

Figure 16. Population projections for 1) currBC management, 2) quasiAK management, 3) cons6% management for the highly productive population (Selkirk Mountains) with a 50-year history of hunting. The bolded line is the median population size, and the grey area is the bounds of the 95% confidence interval.

The highest productivity population showed low rates of extinction for the currBC and quasiAK management options (Figure 16). The rate of extinction was 0.5% for the currBC management strategy, 1.5% for the quasiAK strategy, and 5.8% for the cons6% strategy. The currBC strategy was the least likely to result in a vulnerable population status, with 3.1% of all 1000 simulations experiencing a 30% drop in population size over three generations. The quasiAK strategy resulted in 10.7% of all simulations being designated a vulnerable status, while 16.6% of simulations under the cons6% strategy dropped to vulnerable status. The currBC and quasiAK management strategies averaged positive growth rates of 6.04% and 5.29% respectively, while the cons6% strategy resulted in a decline of -2.23%. The final average population size under currBC management was 209.41 bears (CI = 105.00-240.00, SD= 33.98). The quasiAK strategy resulted in a final average population size of 205.10 bears (CI= 50.95-242.00, SD=44.40), while the cons6% strategy declined the average population size to 186.22 bears (CI=0.00-240.00, SD=62.14). Cub survival averaged 0.89 (CI = 0.80-0.96, SD = 0.07) for the currBC management, 0.88 (CI = 0.75-0.96, SD = 0.11) for the quasiAK management strategy, and 0.86 (CI = 0.12 -0.96, SD = 0.18) for the cons6% strategy. Annual average harvest remained highest for the third

management option, averaging 5.98 (CI=0.00-10.02, SD=2.79) bears annually. In contrast, the currBC strategy averaged an annual harvest of 2.76 (CI= 0.00-7.08, SD=2.39) bears, whereas the quasiAK strategy averaged an annual harvest of 2.89 (CI = 0.00-5.92, SD=1.72).

3.4. Northern GBPU Performance

Northern GBPUs, which tend to fill less non-resident quota, were also tested for this study. Detailed results are available in Appendix A.

3.5. Sensitivity Analysis Results

Two of the parameters tested were found to result in the sensitivity of management strategy performance (please see Appendix B for full analysis).

The degree of environmental autocorrelation was tested through the sensitivity analysis, with values evaluated at 0%, 35% and 70%. All three management strategies were robust to environmental autocorrelation for the rate of population extinction (Figure 20). However, the risk of a population becoming “Vulnerable” was found to result in sensitivity. It was found that the low and moderate productivity datasets experienced increases in the risk of a vulnerable population status over increasing levels of autocorrelation (Figure 21). The effect was slight for the currBC and quasiAK strategies, but the sensitivity was much more pronounced for the cons6% strategy. It appears this management strategy was particularly sensitive to trends of good and bad years, resulting in rates of decline above 30%. This trend is to be expected, since correlated noise causes changes in abundance from year to year (Connors et al, 2014).

Environmental variance ($\sigma^2{}_{environment}$) was also found to result in sensitivity. For all management strategies tested, the moderate productivity dataset was slightly sensitive to environmental variance, resulting in an increased rate of extinction (Figure 22). The low and moderate productivity datasets showed sensitivity for increases in vulnerable population status as environmental variance increased (Figure 23). The sensitivity was slight for currBC and quasiAK strategies, but was more pronounced under cons6% management.

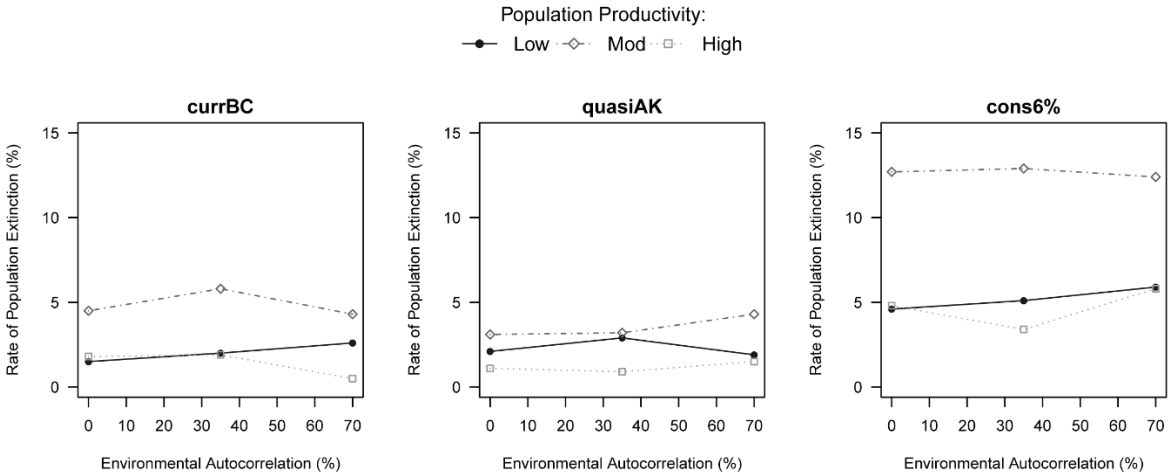

Figure 17. **Sensitivity of high, moderate and low productivity populations to extinction given different degrees of environmental autocorrelation (%). All management options were found to be robust to changes in environmental autocorrelation.**

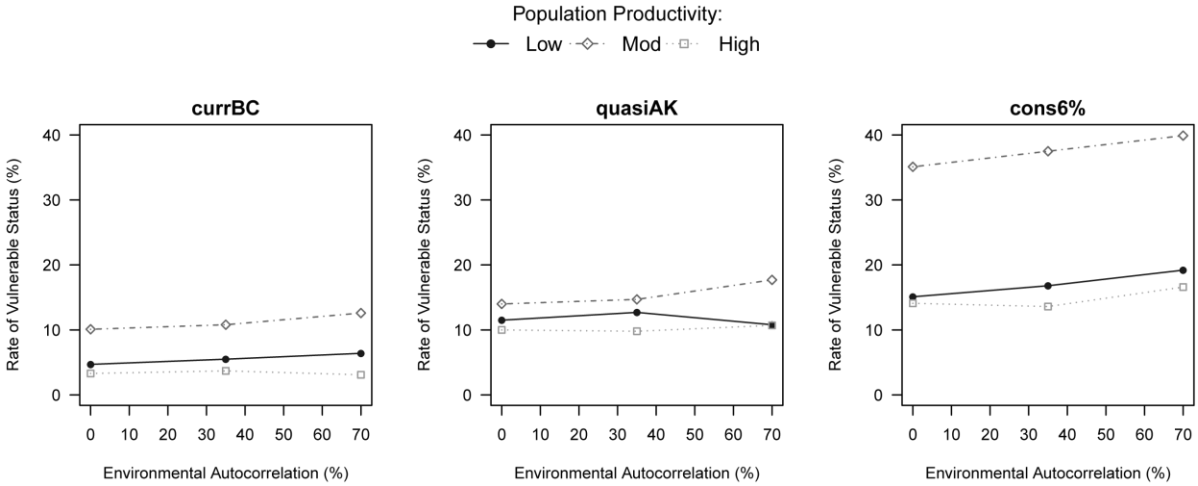

Figure 18. **Sensitivity of high, moderate and low productivity populations to the risk of a "Vulnerable" population status given different degrees of environmental autocorrelation. The moderate productivity dataset (Banff National Park) shows a slightly increased risk of a vulnerable population status as environmental autocorrelation increased.**

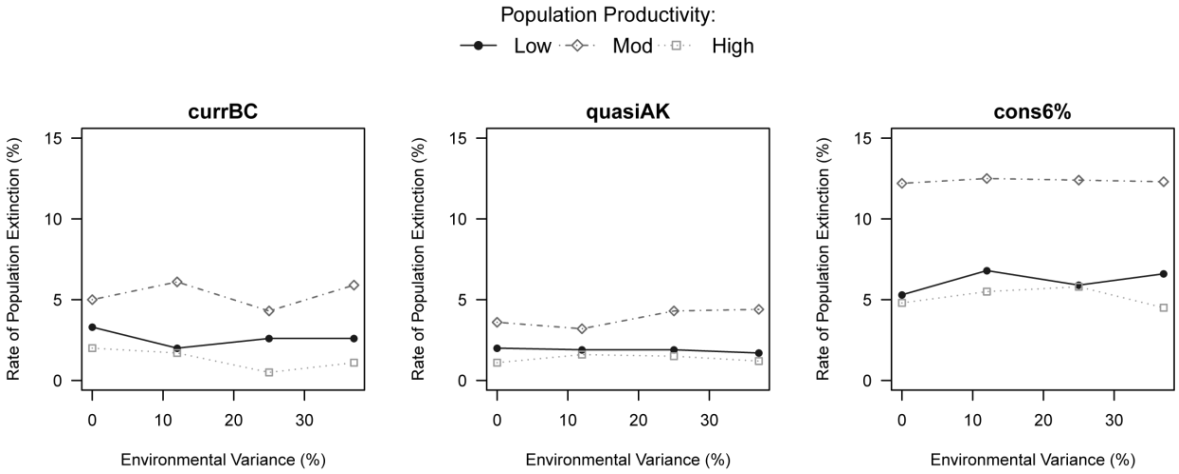

Figure 19. Sensitivity of high, moderate and low productivity populations to extinction given different environmental variances ($\sigma^2{}_{environment}$).

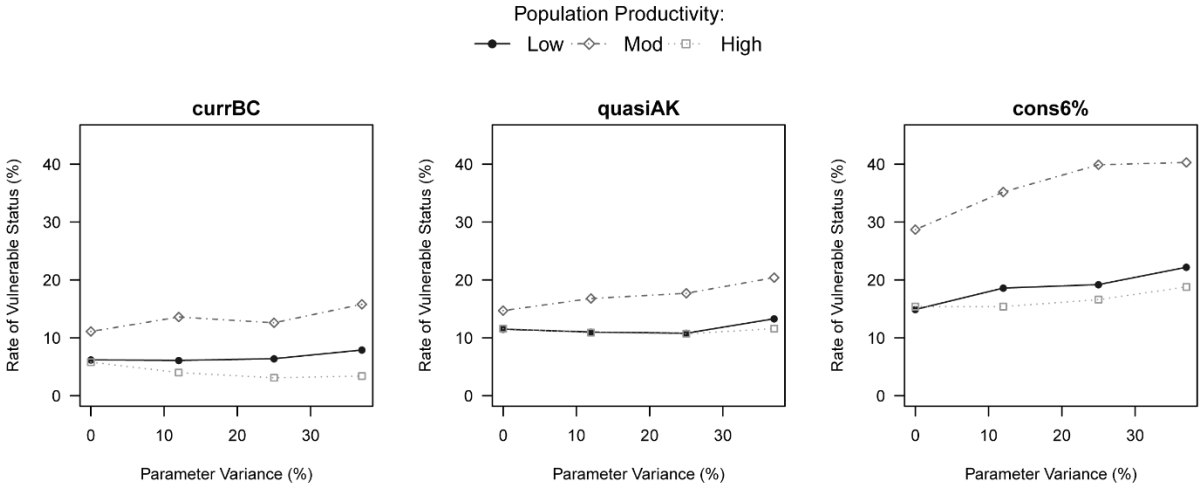

Figure 20. Sensitivity of high, moderate and low productivity populations to the risk of a "Vulnerable" population status given different parameter variance ($\sigma^2{}_{parameter}$). All three management strategies show sensitivity to increases in parameter variance, with cons6% being the most pronounced.

4. Discussion

The purpose of this research was to evaluate competing management strategies on the risks and trade-offs of managing theoretical grizzly bear populations with data sources chosen to reflect the variation seen throughout British Columbia. The general findings of this analysis for selected management criteria can be seen in Table 4. The statistics in this figure reflect simulations that had experienced previous harvest and exploitation, which is the state of most of the grizzly bear populations in British Columbia.

Table 4. Performance of each of the competing management strategies for each of the three theoretical grizzly bear populations. The baseline natural rates are shown for comparison. Population indicators include the rate of extinction, the rate of the population falling to IUCN's "Vulnerable" population status, average cub survival rates (S_0), average population size in the final year of the simulation ($\bar{N}_{50}$), and average annual harvests ($\bar{H}$).

	Rate of extinction	Rate of vulnerable Status	S_0	$\bar{N}_{50}$	$\bar{H}$
High Productivity Habitat					
Baseline	0.0%	0.7%	0.90	229.16	-
currBC	0.5%	3.1%	0.89	209.41	2.76
quasiAK	1.5%	10.7%	0.88	205.10	2.89
cons6%	5.8%	16.6%	0.86	186.22	5.98
Moderate Productivity Habitat					
Baseline	0.0%	1.7%	0.90	218.07	-
currBC	4.3%	12.6%	0.85	177.60	2.04
quasiAK	4.3%	17.7%	0.85	175.51	1.78
cons6%	12.4%	39.9%	0.80	138.99	4.72
Low Productivity Habitat					
Baseline	0.5%	2.5%	0.83	225.10	-
currBC	2.6%	6.4%	0.82	203.42	2.58
quasiAK	1.9%	10.8%	0.82	202.13	2.63
cons6%	5.9%	19.2%	0.80	182.11	5.84

The currBC strategy, which is the simulated version of the MFLNRO's current strategy, performed alongside quasiAK as one of the better options, often with comparable mean cub survival rates, final population sizes and average annual harvests. The currBC strategy was found to be the most stabilizing strategy for the population simulations, with smaller probabilities of population decline. The currBC management strategy also had a higher average annual harvest than the quasiAK strategy, providing more hunting opportunities while avoiding the level of exploitation seen in cons6%. For both unexploited and exploited high productivity populations, the rate of extinction was 0.6% and 0.5% respectively. For the moderately productive population, the rate of extinction was 1.4% for unhunted populations, whereas the rate rose to 4.3% for previously hunted populations. The currBC management strategy has a rate of extinction of 2.1% and 2.6% for unhunted and hunted low productivity populations. The rate of extinction for MFLNRO's management strategy was just slightly higher than the quasiAK management strategy for the low productivity population, but demonstrated less risk in all other situations.

The quasiAK strategy was loosely based off an Alaskan management strategy for grizzly bears that manages the composition of harvest data with little additional input. For a fairly simple strategy with no incorporation of uncertainties, this management option performed on par with, and at times better than, the currBC management strategy for avoiding extinction events. While this management option often had slightly lower risks of population extinction than the currBC strategy, it was more likely to result in population declines. The consequences of this include lower growth rates and a higher occurrence of vulnerable populations when compared to currBC performance. The rate of extinction for high productivity populations under quasiAK management was 0.4% for unexploited populations and 1.5% for previously exploited populations. As with all management options, the highest rate of extinction was for the previously hunted moderate productivity population. The rate of extinction was 0.9% for unexploited populations, and rose to 4.3% for populations with a history of exploitation. For the low productivity dataset, the rate of extinction was 1.6% and 1.9% for previously unexploited and exploited populations respectively.

The cons6% strategy implemented a constant annual harvest of 6% of the grizzly bear population size estimate, with no incorporation of uncertainties. This 6% annual

allowable harvest rate has long been considered the maximum sustainable annual harvest rate for grizzly bears in the academic literature (Harris, 1986; Miller, 1990), and is the upper limit for the MFLNRO's current management strategy. However, this study revealed that a constant harvest of 6%, even with safeguards, may present high risks for populations. The cons6% strategy had the worst performance of all management strategies, with the highest rate of extinction, highest proportion of vulnerable populations, and the lowest rates of growth. This strategy also resulted in the lowest cub survival rates and final population sizes of all the management options tested. However, this strategy had the highest average annual harvest of all management options, often resulting in double the number of bears harvested each year as compared to the other management options. This high harvest rate resulted in significantly higher risks of extinction, with high productivity populations experiencing extinction rates of 3.5% and 5.8% for previously unexploited and exploited populations respectively. The rate of extinction was highest for the moderately productive population, with 9.8% of previously unexploited populations and 12.4% of exploited populations experiencing extinction events during the simulation. For the low productivity population, the rate of extinction was 5.7% for previously unexploited populations and 5.9% for previously exploited populations.

This study provides evidence to support the Alaska-based management strategy of utilizing the sex and age composition of harvest data to set harvest limits. The quasiAK strategy, the Alaskan-inspired management strategy, was found to perform similarly to the currBC management strategy with less inputs and rules. Two linear equations were used in place of subjective input within the model, with both equations designed to maintain an average age of 6.5 and a sex ratio of 3:2 within the harvest data. These targets are the same that are applied for many GMUs in Alaska (ADF&G, 2011). The harvest rate was designed to range from 1% up to a maximum human-caused mortality rate of 8% annually. Considering the low average annual harvests of quasiAK, it is clear this management strategy maintained harvests at a much lower level. The average annual harvests for quasiAK were the smallest of all management strategies; however, harvest pressure on the grizzly bear population can be easily increased by setting different age and sex ratio harvest data targets. Therefore, the performance and sustainability of this management option will be determined by the targets set by managers. There are several shortcomings to this management option. Harvest data will not accurately reflect changes to a population's

composition should: 1) unknown mortality be female biased, and 2) migrant males enter an overexploited population (Harris & Metzgar, 1987). Considering these limitations, strategies such as quasiAK present an easy addition to other management options. Given that this management strategy had minimal inputs, no incorporation of uncertainty, and a robust performance in this evaluation, managers should look to incorporating an analysis of harvest composition data in formal grizzly bear management strategies.

There were several limitations to this study. One of the major limits was the poor availability of population data for grizzly bears within British Columbia. Conducting population inventories to gather precise information regarding population sizes and demographics is costly and time consuming, especially for wide-ranging species (Nilsen et al, 2012). To bypass this issue, we used grizzly bear data from studies in and around British Columbia, but it was difficult to find population studies that existed in areas exempt from hunting. This is likely due to the fact that the presence of hunting creates conservation concerns amongst the public and generates the revenue to fund population inventories (Treves, 2009). In the absence of grizzly bear population benchmarks, this study used expert opinion and information from each study to subjectively remove human-caused mortalities from the demographics used to represent high, moderate and low productivity populations in British Columbia. However, the sources of the population data used in this study are distributed along the southern interior of the province, so the demographics may not reflect northern and coastal grizzly bear populations. However, given the range of population productivities represented in this study, the risks and robustness of the MFLNRO's current management strategy can be applied throughout the province. This study was also limited by the inability to fully simulate the subjective inputs and processes used in decision making. The MFLNRO's management strategy, as well as many of Alaska's grizzly bear management protocols, involve a combination of both science and expert opinion to make decisions regarding harvest rates. As a result, the modelling used for the MFLNRO and Alaska management strategies do not feature the same flexibility and insights that are available in the true management systems. This model also used a constant hunting success rate for grizzly bear hunters, whereas hunting success rates are a dynamic element that is also uncertain and estimated by managers. Another limitation of this study is its scope compared to the real MSE process. Typically, MSE is a long-term process with a great deal of stakeholder consultation to define management objectives and explore harvest rules. Due

to a limited time frame and scope for this project, no stakeholder involvement was possible. Instead, MSE processes were used to inform the methodology of this project, and indicators of population health and resilience were used to assess the competing management strategies. The last noteworthy limitation of the study is that expert opinion was used to inform the shape of the probability distributions used in the Bayesian analysis. These probability distributions represented many of the uncertainties in grizzly bear biology and the management system, with some uncertainties being better understood than others. For this study, coefficients of variation were chosen with the help of biologists to reflect the concerns in current management. The uncertainty in population size estimates and unknown mortality estimates has been a large concern amongst scientists and the public. As a result, the system modelled for this study was biased towards over and underestimation of these parameters based on a coefficient of variation of 0.9 for the population size estimates and 0.5 for the unknown mortality estimates. Therefore, results of this study are likely conservative, and may not be representative of areas where uncertainties are better studied and understood. Due to the scope of this project, we were unable to test other potential states of nature for such uncertainties.

The current grizzly bear management strategy in British Columbia was the strongest performing management option tested during this study. The MFLNRO management protocol was found to effectively incorporate uncertainties when compared to other common management practices, such as using harvest data or the maximum sustainable harvest rate. The current management strategy revealed some risk of extinction and drops in population size to a vulnerable status. However, the level of acceptable risk is left for managers and biologists to consider. It is important to reiterate that the focus of this study is strictly population level sustainability; as researchers, we are not addressing the moral or ethical questions of grizzly bear hunting. The model used in this study is a simple representation of theoretical grizzly bear populations in British Columbia. The social networks within and between populations were not directly simulated so no consideration was given to bears migrating from one GBPU to another. This model is not grounded on a spatial context, therefore, we are not addressing the hunting that takes place on tribal land, which is another part of the ethical debate. This study also does not distinguish between trophy hunting and the hunting for food and other consumptive purposes. We are simply addressing one small portion of the debate on grizzly bear hunting, which is whether it is

currently sustainable in British Columbia. Future research should continue to investigate the conditions under which grizzly bear hunting is a sustainable practice. Upcoming studies should be done to determine the level of human-caused mortality, if any, that weaker grizzly bear populations can sustain. This will be an important target in order to put in place policies that will protect such populations. Future research should also focus on the uncertain conditions in the grizzly bear management system. By identifying which uncertainties can be most easily improved, grizzly bear hunting could become more sustainable by investing in programs. Such efforts could include inventory studies to assist in creating more accurate population size estimates or hunter training to reduce unknown mortality rates.

Resource managers commonly face challenges and trade-offs when managing a species for multiple objectives. Since a large component of grizzly bear mortality is human-caused, decisions by management biologists can have an impact on the long-term viability of grizzly bear populations (Artelle et al, 2013). Considering these management trade-offs and the risks at stake, MSE is an excellent option to assist in decision making (Bunnefeld et al, 2011). A full MSE approach would allow collaboration between resource managers, biologists, economists, sociologist and stakeholders, who would have a shared involvement in the evaluation of potential management options (Bunnefeld et al, 2011). As the human population continues to grow and activities such as resource extraction, agriculture, animal husbandry and housing development continue to remain a priority, grizzly bear populations will become increasingly at risk (Peek et al, 2003). Given the vulnerability of grizzly bears to human-related mortalities, continued evaluation of management practices is necessary to ensure sustainable co-existence into the future.

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Appendix A.

Northern GBPU Performance

Previously Unexploited Northern GBPUs

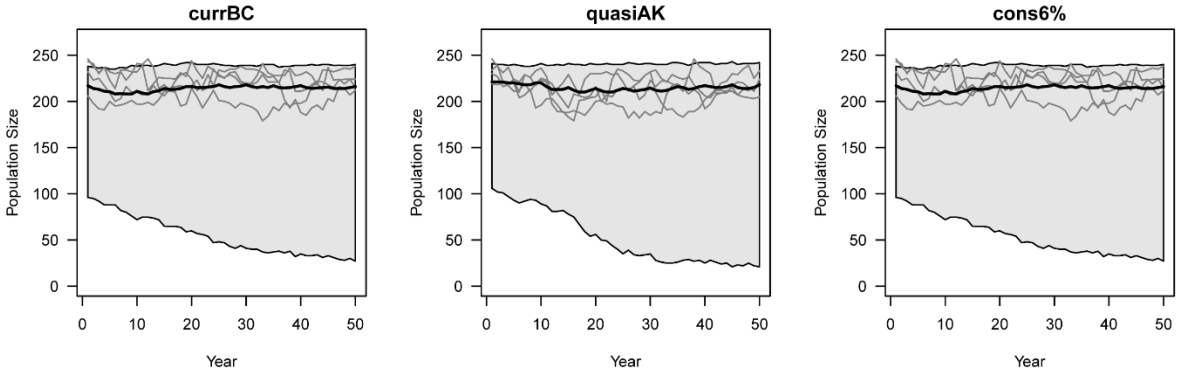

Figure A.1. **Population projections for 1) currBC 2) quasiAK, 3) cons6% for the low productivity population (Flathead River Basin) given a lower rate of filling non-resident quota.**

Table A.1. **Comparison of management risks for the three different management strategies 1) currBC 2) quasiAK, 3) cons6% for low productivity population (Flathead River Basin) given a lower rate of filling non-resident quota and no prior history of exploitation.**

	Mgt 1	**Mgt 2**	**Mgt 3**
Rate of Extinction	1.4%	1.5%	1.4%
% Pops Vulnerable	8.3%	14.3%	8.3%
Cub Survival	0.83 (CI = 0.67-0.94, SD = 0.11)	0.83 (CI = 0.67-0.93, SD = 0.11)	0.83 (CI = 0.67-0.94, SD = 0.11)
Rate of Growth	-3.02%	-5.23%	-3.03%
Average N	202.33 (CI= 27.00-240.00, SD=46.11)	201.36 (CI = 20.98-242.00, SD= 49.52)	202.33 (CI= 27.00-240.00, SD=46.11)
Average Annual H	2.88 (CI = 0.00-6.90, SD=2.29)	2.58 (CI = 0.00-5.16, SD=1.47)	2.88 (CI = 0.00-6.90, SD=2.29)

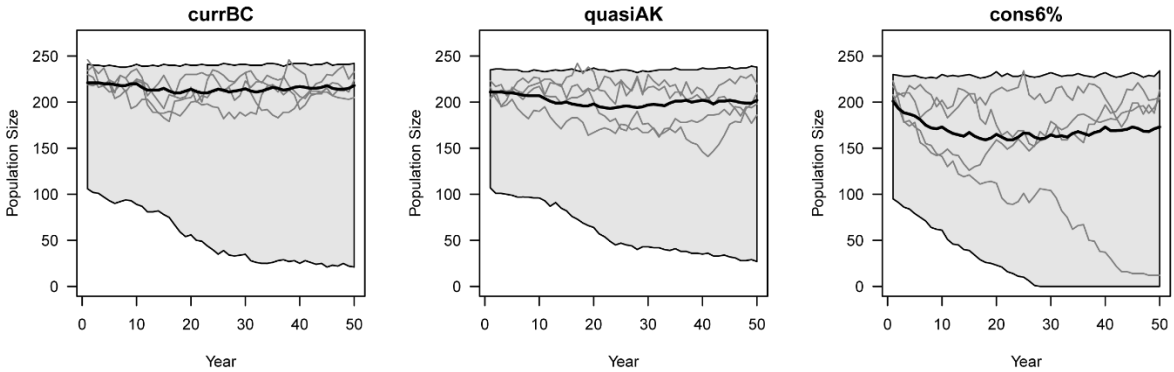

Figure A.2. Population projections for 1) currBC 2) quasiAK, 3) cons6% for the moderately productive population (Banff National Park) given a lower rate of filling non-resident quota.

Table A.1. Comparison of management risks for the three different management strategies 1) currBC 2) quasiAK, 3) cons6% for the moderately productive population (Banff National Park) given a lower rate of filling non-resident quota and no prior history of exploitation.

	Mgt 1	Mgt 2	Mgt 3
Rate of Extinction	1.5%	0.6%	7.5%
% Pops Vulnerable	1.5%	0.6%	7.5%
Cub Survival	0.83 (CI = 0.67-0.93, SD = 0.11)	0.88 (CI = 0.73-0.96, SD = 0.07)	0.85 (CI= 0.37-0.96, SD= 0.14)
Rate of Growth	-5.24%	-8.78%	-24.10%
Average N	201.36 (CI= 20.98-242.00, SD= 49.52)	183.24 (CI= 27.00-238.00, SD= 54.20)	145.12 (CI=0.00-234.00, SD=73.92)
Average Annual H	2.58 (CI=0.00-5.16, SD=1.47)	1.92 (CI = 0.00-4.28, SD=1.23)	5.10 (CI = 0.00-8.72, SD=2.45)

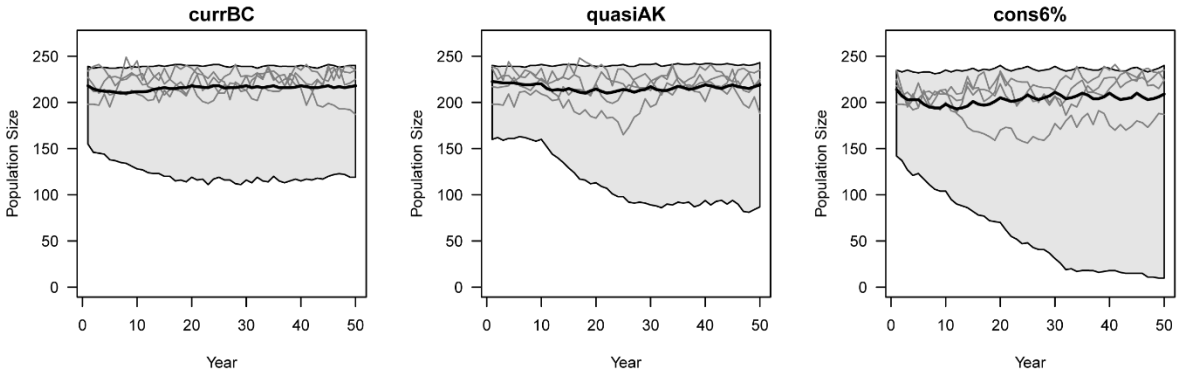

Figure A.1. Population projections for 1) currBC, 2) quasiAK, 3) cons6% for the high productivity population (Selkirk Mountains) given a lower rate of filling non-resident quota.

Table A.2. Comparison of management risks for the three different management strategies 1) currBC, 2) quasiAK, 3) cons6% for the highly productive population (Selkirk Mountains) given a lower rate of filling non-resident quota and no prior history of exploitation.

	Mgt 1	**Mgt 2**	**Mgt 3**
Rate of Extinction	0.2%	0.4%	2.3%
% Pops Vulnerable	4.4%	11.2%	14.9%
Cub Survival	0.90 (CI = 0.81-0.96, SD= 0.05)	0.90 (CI =0.81-0.96, SD=0.06)	0.89 (CI= 0.71-0.96, SD=0.09)
Rate of Growth	-1.78%	-4.49%	-7.94
Average N	210.16 (CI=119.00-240.00, SD=31.15)	207.54 (CI=86.83-243.00, SD=37.85)	192.50 (CI= 9.80-240.00, SD=51.70)
Average Annual H	2.95 (CI=0.00-6.90, SD=2.32)	2.74 (CI=0.00-5.52, SD=1.56)	6.08 (CI=0.00-9.62, SD= 2.55)

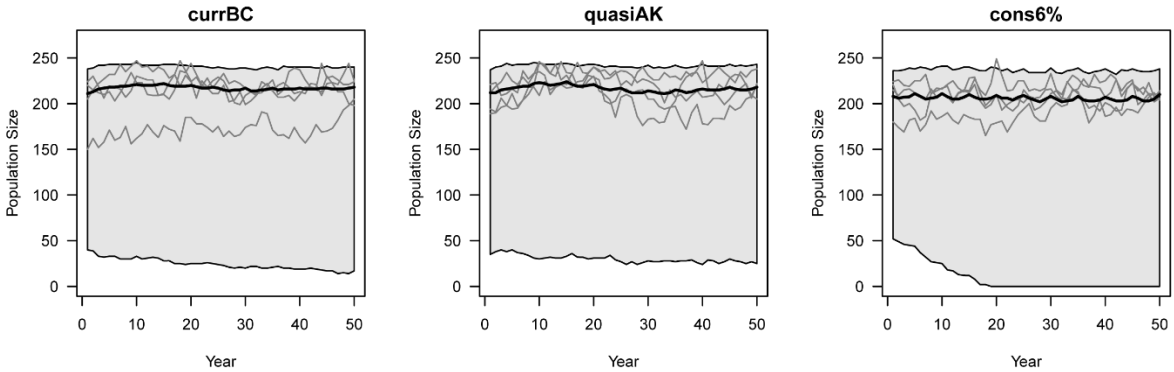

Figure A.2. **Population projections 1) currBC, 2) quasiAK, 3) cons6% for the low productivity population (Flathead River Basin) given a lower rate of filling non-resident quota. Population was exposed to an exploitative 6% harvest rate for 50 years prior to projections.**

Table A.3. **Comparison of management risks for the three different management strategies 1) currBC, 2) quasiAK, 3) cons6% for the low productivity population (Flathead River Basin) given a lower rate of filling non-resident quota and prior history of exploitation.**

	Mgt 1	**Mgt 2**	**Mgt 3**
Rate of Extinction	2.0%	1.3%	4.9%
% Pops Vulnerable	6.2%	10.1%	15.2%
Cub Survival	0.82 (CI = 0.58-0.93, SD = 0.13)	0.82 (CI = 0.63-0.93, SD = 0.11)	0.81 (CI = 0.19-0.93, SD = 0.15)
Rate of Growth	5.47%	4.60%	-2.90%
Average N	204.06 (CI= 16.95-240.03, SD=46.81)	202.99 (CI = 25.00-243.00, SD=48.44)	186.97 (CI=0.00-238.00, SD=60.44)
Average Annual H	2.47(CI= 0.00-6.64, SD= 2.18)	2.54 (CI=0.00-5.22, SD=1.47)	5.34 (CI= 0.00-8.98, SD=2.56)

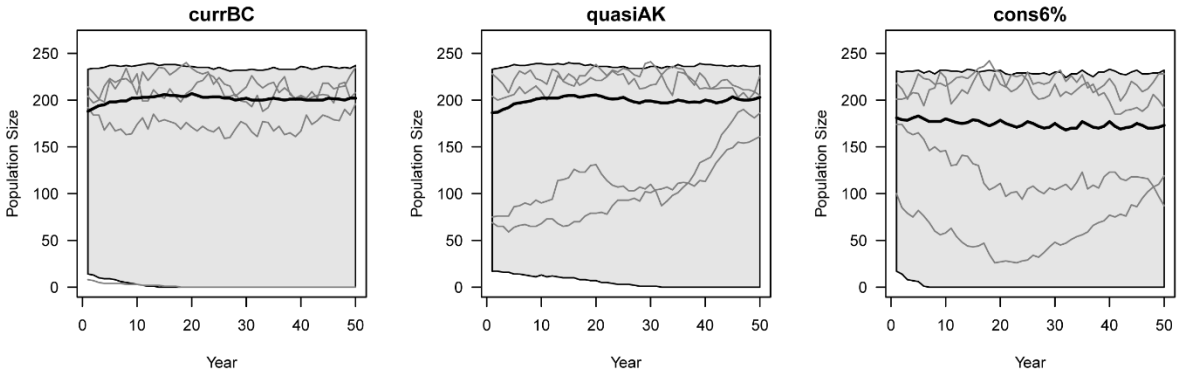

Figure A.3. Population projections for 1) currBC, 2) quasiAK, 3) cons6% for the moderately productive population (Banff, Alberta) given a lower rate of filling non-resident quota.

Table A.4. Comparison of management risks for the three different management strategies 1) currBC, 2) quasiAK, 3) cons6% for the moderately productive population (Banff, Alberta) given a lower rate of filling non-resident quota and prior history of exploitation.

	Mgt 1	**Mgt 2**	**Mgt 3**
Rate of Extinction	4.6%	3.2%	11.8%
% Pops Vulnerable	11.9%	17.3%	36.2%
Cub Survival	0.85 (CI = 0.10-0.96, SD = 0.18)	0.86 (CI = 0.18-0.96, SD = 0.16)	0.80 (CI = 0.03-0.96, SD = 0.24)
Rate of Growth	7.62%	9.16%	-11.61%
Average N	179.21 (CI= 0.00-237.08, SD=61.13)	180.17 (CI = 0.00-237.00, SD=60.44)	142.16 (CI=0.00-232.00, SD=78.04)
Average Annual H	1.86 (CI= 0.00-5.60, SD= 1.90)	1.71 (CI=0.00-4.48, SD=1.31)	4.49 (CI= 0.00-8.56, SD=2.50)

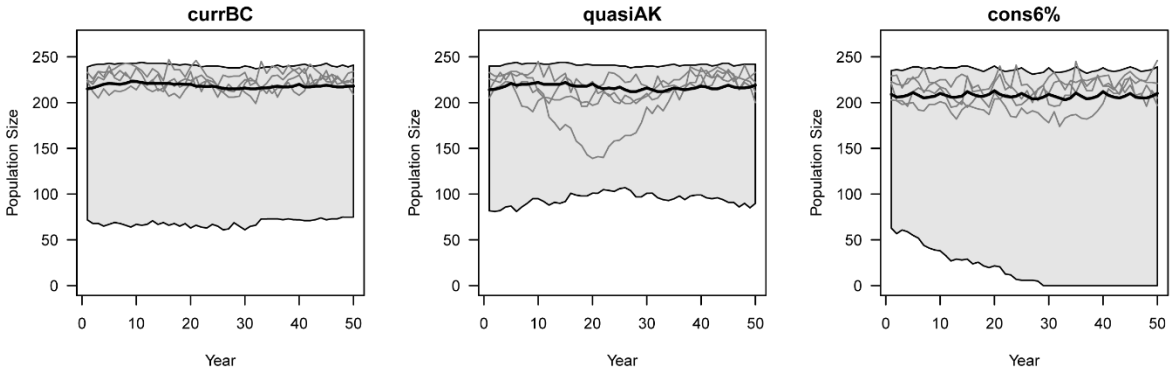

Figure A.4. Population projections for 1) currBC, 2) quasiAK, 3) cons6% for the high productivity population (Southeastern British Columbia and northeastern Montana) given a lower rate of filling non-resident quota.

Table A.5. Comparison of management risks for the three different management strategies 1) currBC, 2) quasiAK, 3) cons6% for the highly productive population (Southeastern British Columbia and northeastern Montana) given a lower rate of filling non-resident quota and prior history of exploitation.

	Mgt 1	**Mgt 2**	**Mgt 3**
Rate of Extinction	1.3%	0.9%	2.9%
% Pops Vulnerable	3.5%	7.8%	13.5%
Cub Survival	0.89 (CI = 0.77-0.96, SD = 0.09)	0.89 (CI = 0.79-0.96, SD = 0.09)	0.88 (CI = 0.30 - 0.96, SD = 0.14)
Rate of Growth	3.71%	3.16%	-1.75
Average N	208.87 (CI = 74.90-241.00, SD= 38.31)	208.05 (CI= 89.93-242.00, SD=38.47)	192.67 (CI=0.00-239.00, SD=52.60)
Average Annual H	2.49 (CI= 0.00-6.68, SD=2.17)	2.80 (CI = 0.00-5.70, SD=1.58)	5.76 (CI=0.00-9.38, SD=2.43)

Appendix B.

Sensitivity Analysis Results

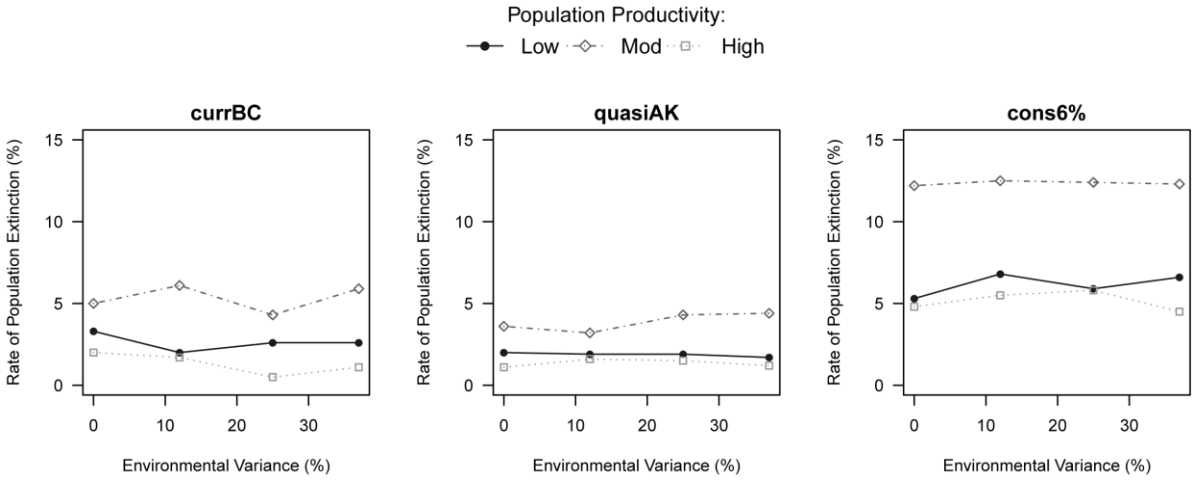

Figure B.1. **Sensitivity of high, moderate and low productivity population to extinction given different environmental variance ($\sigma^2{}_{environment}$).**

Table B.1. **Sensitivity analysis for environmental variance ($\sigma^2{}_{environment}$) on the rate of extinction for the low productivity population (Flathead River Basin)**

Hypothesized Parameter Values	Rate of extinction		
Environmental Variance	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	3.3%	2.0%	5.3%
12%	2.0%	1.9%	6.8%
25%	2.6%	1.9%	5.9%
37%	2.6%	1.7%	6.6%

Table B.2. **Sensitivity analysis for environmental variance ($\sigma^2{}_{environment}$) on the rate of extinction for the moderately productivity population (Banff National Park)**

Hypothesized Parameter Values	Rate of extinction		
Environmental Variance	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	5.0%	3.6%	12.2%
12%	6.1%	3.2%	12.5%
25%	4.3%	4.3%	12.4%
37%	5.9%	4.4%	12.3%

Table B.3. Sensitivity analysis for environmental variance ($\sigma^2{}_{environment}$) on the rate of extinction for the high productivity population (Selkirk Mountains)

Hypothesized Parameter Values	Rate of extinction		
Environmental Variance	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	2.0%	1.1%	4.8%
12%	1.7%	1.6%	5.5%
25%	0.5%	1.5%	5.8%
37%	1.1%	1.2%	4.5%

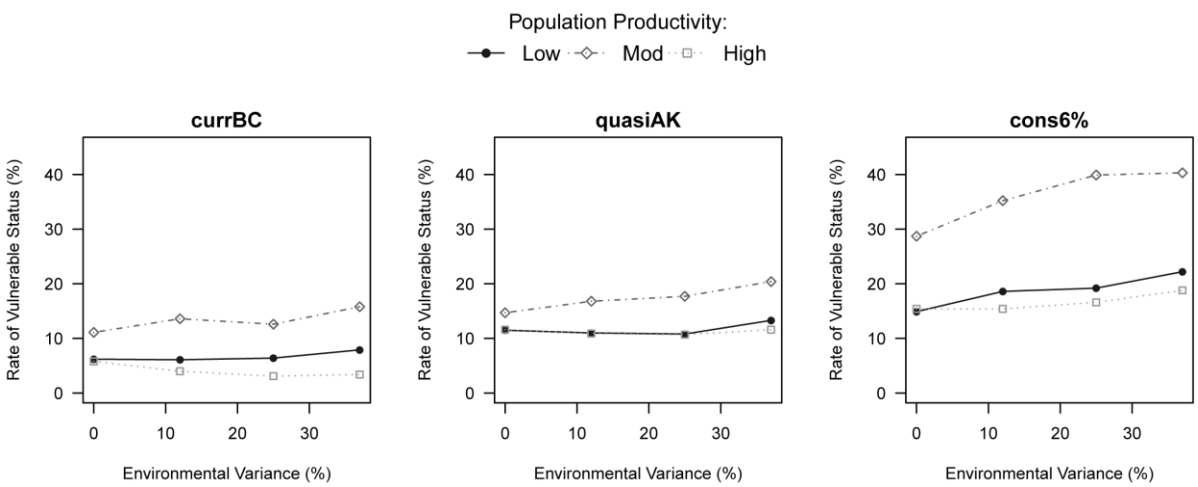

Figure B.2. Sensitivity of high, moderate and low productivity population to the rate of vulnerable population status given different environmental variance ($\sigma^2{}_{environment}$).

Table B.4. Sensitivity analysis for environmental variance ($\sigma^2{}_{environment}$) on the rate of vulnerable status for the low productivity population (Flathead River Basin).

Hypothesized Parameter Values	Rate of vulnerable Population		
Parameter Variance	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	6.2%	11.5%	14.9%
12%	6.1%	11.0%	18.6%
25%	6.4%	10.8%	19.2%
37%	7.9%	13.3%	22.2%

Table B.5. Sensitivity analysis for environmental variance ($\sigma^2{}_{environment}$) on the rate of vulnerable status for the moderately productivity population (Banff National Park).

Hypothesized Parameter Values	Rate of vulnerable Population		
Parameter Variance	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	11.1%	14.7%	28.7%
12%	13.6%	16.8%	35.2%
25%	12.6%	17.7%	39.9%
37%	15.8%	20.4%	40.3%

Table B.6. Sensitivity analysis for environmental variance ($\sigma^2{}_{environment}$) on the rate of vulnerable status for the high productivity population (Selkirk Mountains)

Hypothesized Parameter Values	Rate of vulnerable Population		
Parameter Variance	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	5.8%	11.6%	15.4%
12%	4.0%	10.9%	15.4%
25%	3.1%	10.7%	16.6%
37%	3.4%	11.6%	18.8%

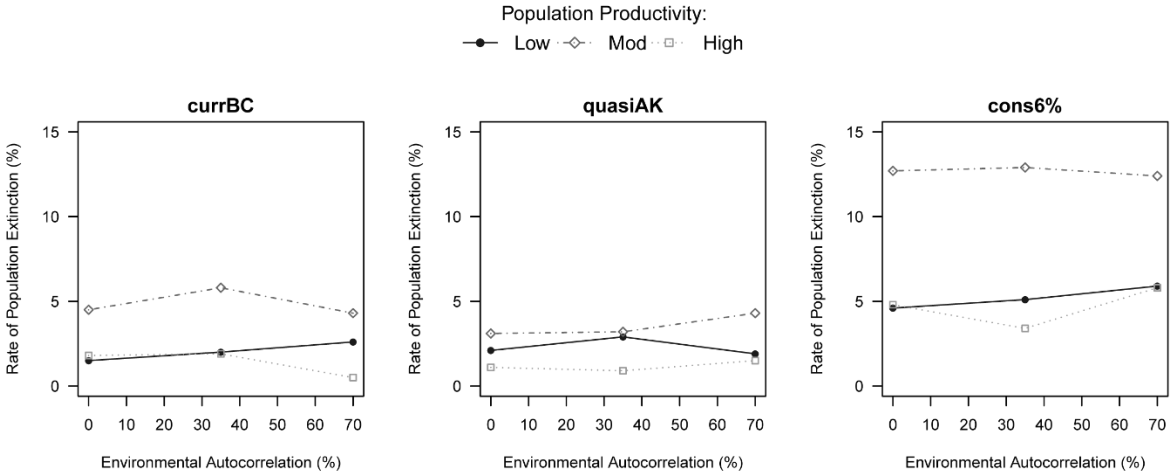

Figure B.3. Sensitivity of high, moderate and low productivity population to extinction given different degrees of environmental autocorrelation (%).

Table B.7. Sensitivity analysis for environmental autocorrelation on the rate of extinction for the low productivity population (Flathead River Basin)

Hypothesized Parameter Values	Rate of extinction		
Environmental Autocorrelation	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	1.5%	2.1%	4.6%
35%	2.0%	2.9%	5.1%
70%	2.6%	1.9%	5.9%

Table B.8. Sensitivity analysis for environmental autocorrelation on the rate of extinction for the moderately productivity population (Banff, Alberta)

Hypothesized Parameter Values	Rate of extinction		
Environmental Autocorrelation	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	4.5%	3.1%	12.7%
35%	5.8%	3.2%	12.9%
70%	4.3%	4.3%	12.4%

Table B.9. Sensitivity analysis for environmental autocorrelation on the rate of extinction for the high productivity population (Selkirk Mountains)

Hypothesized Parameter Values	Rate of extinction		
Environmental Autocorrelation	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	1.8%	1.1%	4.8%
30%	1.9%	0.9%	3.4%
70%	0.5%	1.5%	5.8%

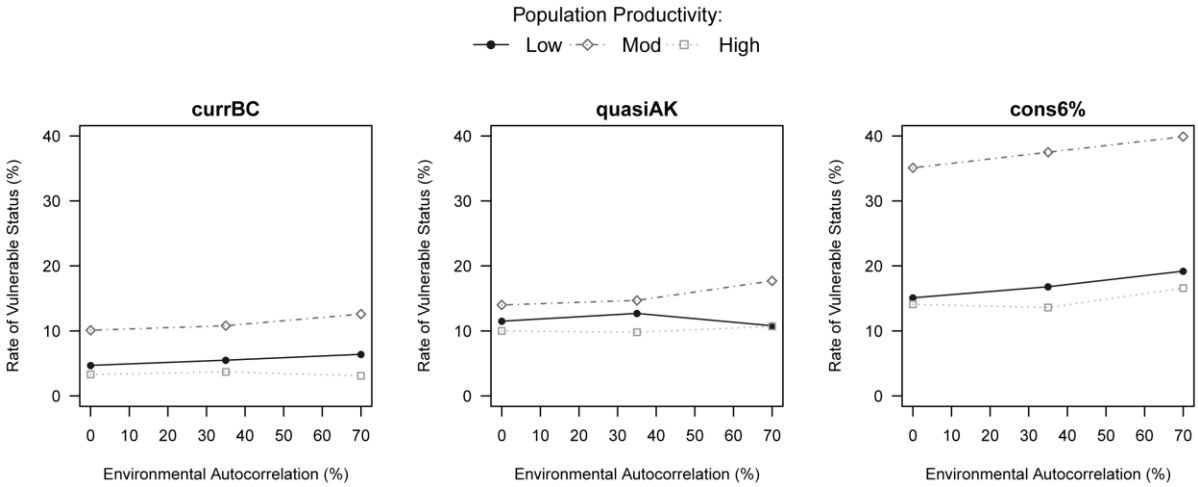

Figure B.4. Sensitivity of high, moderate and low productivity population to the risk of a "Vulnerable" population status given different degrees of environmental autocorrelation.

Table B.10. Sensitivity analysis for environmental autocorrelation on rate of a "Vulnerable" population status for the low productivity population (Flathead River Basin)

Hypothesized Parameter Values	Rate of vulnerable Population		
Environmental Autocorrelation	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	4.7%	11.5%	15.1%
30%	5.5%	12.7%	16.8%
70%	6.4%	10.8%	19.2%

Table B.11. Sensitivity analysis for environmental autocorrelation on rate of a "Vulnerable" population status for the moderately productivity population (Banff National Park)

Hypothesized Parameter Values	Rate of vulnerable Population		
Environmental Autocorrelation	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	10.1%	14.0%	35.1%
30%	10.8%	14.7%	37.5%
70%	12.6%	17.7%	39.9%

Table B.12. Sensitivity analysis for environmental autocorrelation on rate of a "Vulnerable" population status for the low productivity population (Selkirk Mountains)

Hypothesized Parameter Values	Rate of vulnerable Population		
Environmental Autocorrelation	**Mgt 1**	**Mgt 2**	**Mgt 3**
0%	3.3%	10.0%	14.1%
30%	3.7%	9.8%	13.6%
70%	3.1%	10.7%	16.6%

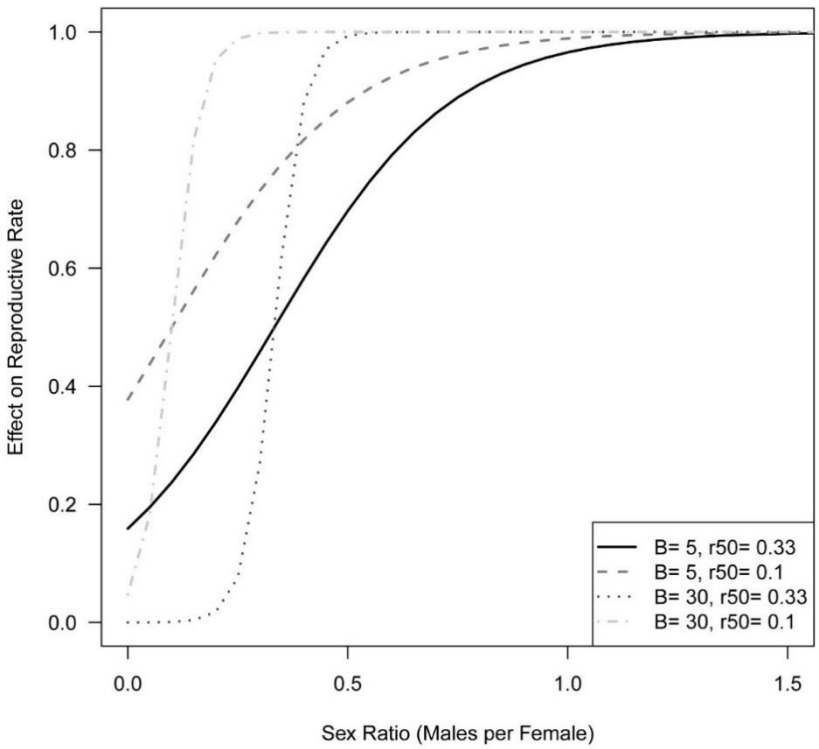

Figure B.5. Four alternative B and r50 combinations tested for the Operational Sex Ratio Effect during sensitivity analysis. Reproduction was not possible in the model if the sex ratio of the population was equal to zero.

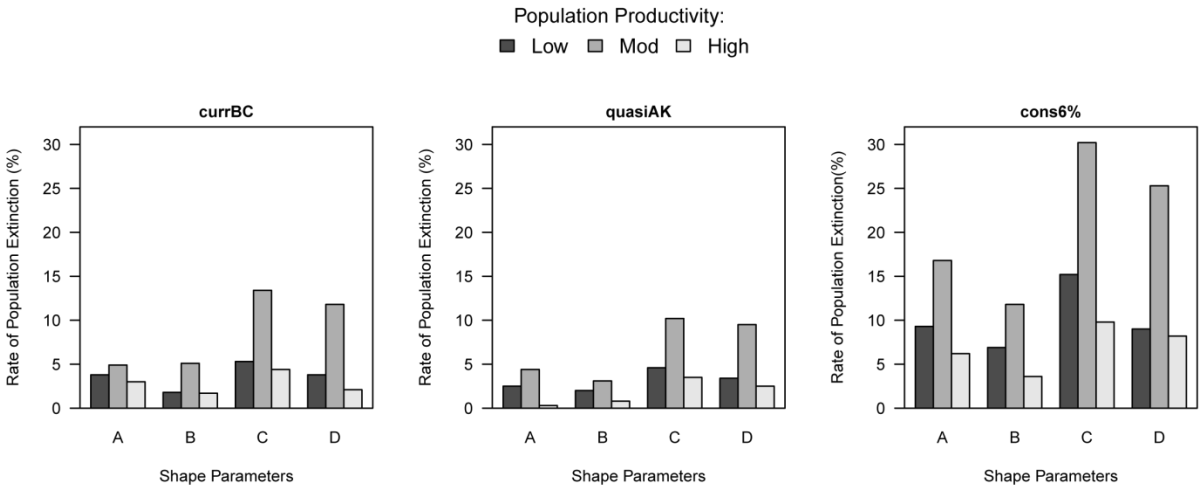

Figure B.6. Sensitivity of high, moderate and low productivity population to the rate of extinction given different combinations for parameters r50 and B of the operational sex ratio effect (Ot). Shape A: r50= 0.10, B= 5; Shape B: r50= 0.10, B= 30; Shape C: r50= 0.33, B= 5; Shape D: r50= 0.33, B= 30.

Table B.13. Sensitivity analysis for parameters r50 and B of the operational sex ratio effect (Ot) on rate of extinction for the low productivity population (Flathead River Basin)

Hypothesized Parameter Values		Rate of extinction		
r50	B	Mgt 1	Mgt 2	Mgt 3
0.10	5	3.8%	2.5%	9.3%
0.10	30	1.8%	2.0%	6.9%
0.33	5	5.3%	4.6%	15.2%
0.33	30	3.8%	3.4%	9.0%

Table B.14. Sensitivity analysis for parameters r50 and B of the operational sex ratio effect (Ot) on rate of extinction for the moderately productivity population (Banff National Park)

Hypothesized Parameter Values		Rate of extinction		
r50	B	Mgt 1	Mgt 2	Mgt 3
0.10	5	4.9%	4.4%	16.8%
0.10	30	5.1%	3.1%	11.8%
0.33	5	13.4%	10.2%	30.2%
0.33	30	11.8%	9.5%	25.3%

Table B.15. Sensitivity analysis for parameters r50 and B of the operational sex ratio effect (Ot) on rate of extinction for the high productivity population (Selkirk Mountains)

Hypothesized Parameter Values		Rate of extinction		
r50	B	Mgt 1	Mgt 2	Mgt 3
0.10	5	3.0%	0.3%	6.2%
0.10	30	1.7%	0.8%	3.6%
0.33	5	4.4%	3.5%	9.8%
0.33	30	2.1%	2.5%	8.2%