

A comparative analysis of management options for grizzly bear conservation in the U.S.–Canada trans-border area

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Abstract: Grizzly bear (*Ursus arctos*) populations spanning the U.S.–Canada border in the south Selkirk, Purcell–Yaak, and Cabinet Mountains are small, vulnerable, and at the front lines of any further range contraction in North America. Recent genetics work demonstrated that the south Selkirk grizzlies are an isolated population (no male or female connectivity) of fewer than 100 individuals with a 15–20% reduction in genetic diversity and that the Purcell–Yaak population is declining and demographically isolated (no female connectivity) with fewer than 50 individuals. The <25 animals living in the Cabinet Mountains population are likely isolated from both the south Selkirk Mountain and the Purcell–Yaak populations. We recognize these populations need enhanced management. To guide the development of a comprehensive management plan, we explored the effects of 3 actions (population augmentation, enhanced population interchange, and reduced mortality through management actions). We simulated 2 populations of 50 and 100 individuals using population viability analysis (PVA) software (VORTEX). We examined these management actions and combinations of them on population growth rate and extinction probabilities. Our simulations suggest that augmentation had the largest demographic effect on population growth rate over the short-term, mortality reductions had the largest effect in the long-term, and establishing population interchange and reducing mortality had the greatest effect on extinction probability. Enhanced cooperative U.S. and Canadian efforts are required to address the issues facing these small grizzly populations and to build connectivity to existing larger populations and areas of vacant habitat. Our findings apply to recovery and conservation efforts for small populations of all species of bears.

Key words: British Columbia, brown bear, Cabinet–Yaak, demographics, genetics, grizzly bear, Idaho, Montana, population viability analysis, Purcells, Selkirks, small populations, *Ursus arctos*

Ursus 15(2):145–160 (2004)

Population size is one of the most powerful predictors of the likelihood of population persistence (Berger 1990, Shaffer et al. 2000, Reed et al. 2003). Populations with fewer than 50–100 adults are at high risk of extinction (IUCN [The World Conservation Union] 2003). During the past century, fragmentation and excessive mortality were likely responsible for the 98% range contraction of grizzly bears south of Canada (Servheen et al. 1999,

Mattson and Merrill 2002). While historical attitudes toward grizzly bears have experienced a paradigm shift from active persecution toward tolerance and respect (Taber and Payne 2003, Schwartz et al. 2004), forces underpinning range contraction may be still operating, albeit more subtly and less intentionally, resulting in small fragmented trans-border populations at the southern extent of their current North American distribution.

Grizzly bears in this U.S.–Canada trans-border region have been fragmented into habitat peninsulas (Proctor 2003) corresponding to the north–south oriented Rocky, Purcell, and Selkirk Mountain ranges that span the international border. Proctor (2003) found that the south-

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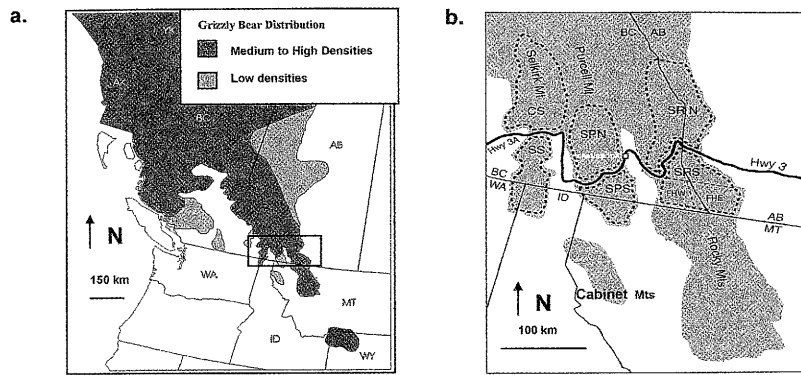


Fig. 1. a. Grizzly bear distribution and intermountain study area in western North America. b. Southern Rocky, Purcell, and Selkirk Mountain study area. Dotted lines outline areas where bears were genetically sampled on both sides of Highway 3 and 3A. Abbreviations: CS = Central Selkirks, SS = South Selkirks, SPN = South Purcells North of Highway 3, and SPS = the trans-border Purcell–Yaak South of Hwy 3. SRS and SRN = South Rockies South and North of Highway 3. FHW (Flathead River West) and FHE (Flathead River East) areas constitute the control area, ecologically within and similar to the southern Rocky system. Map 1a adapted with permission from McLellan (1998), Map 1b from Proctor (2003).

ern tip of the occupied habitat peninsula in the Purcell–Yaak area appeared to have limited female connectivity with adjacent areas across Highway 3, potentially creating a small female island population (Fig. 1). There was evidence of male movement across Highway 3 in this same area, and this appeared to maintain gene flow and genetic diversity; average expected heterozygosity was identical on both sides of the highway (Proctor 2003). In the south Selkirk Mountains, movement of both sexes was restricted across a narrow valley containing British Columbia (BC) Highway 3A, a thin but continuous strip of human development, and a narrow river and lake waterway. The genetic differences detected across this valley were striking considering the small geographic distance (1–5 km). The high genetic distance and the relatively low average expected heterozygosity ($H_E = 0.54$, 15–20% less than in adjacent populations) suggests that genetic interchange with adjacent populations has been limited for at least several generations (Proctor 2003). Long-term radiotelemetry data suggests the Cabinet Mountain population is also isolated (Kasworm et al. 2003).

Systematically-obtained estimates for grizzly bear populations in the south Selkirk, Purcell–Yaak, and Cabinet Mountains are not available, but evidence suggests that these populations are very small as well

as isolated. In the south Selkirk ecosystem, we estimated a population of 105 bears (91–119) by applying density estimates from Wielgus et al. (1994). We applied their U.S. density and their Canadian density to the Canadian portion. The Purcell–Yaak area south of Canada Highway 3 and north of U.S. Highway 2 is estimated to have 35–50 individuals (U.S. portion based on radiotelemetry data from Kasworm et al. 2003; Canadian portion based on Proctor unpublished DNA survey data). The Cabinet population is estimated to be 15 animals (Kasworm et al. 2003). Based on these estimates, it is clear that all three fragmented populations are small and likely have an elevated conservation risk.

Given the current situation of the small and fragmented trans-border grizzly bear populations, we recognized a need to develop and apply enhanced management strategies designed to improve their chances of long-term persistence. As part of the development of a comprehensive management program, we wanted to explore the theoretical benefits and relative value of various management actions. To accomplish this goal we used population viability analysis. We recognize the problems in accurately predicting probability of extinction using PVA modeling (Mills et al. 1996, Boyce et al. 2001, Lindenmayer et al. 2003). Here, we follow recommendations by Boyce (1997) and Lindenmayer et al. (2003) that the best use of population viability analysis is to evaluate alternative management options.

We present simulations on the demographic impacts of alternative management actions and discuss solutions required to increase the probability of long-term persistence of small grizzly populations. Our objective is to examine a comprehensive set of management strategies by integrating the results of population viability analysis.

Study area and methods

We define 3 sub-units within our study area: the south Selkirk Mountain area located south and west of BC Highway 3A spanning the U.S.–Canada border into northeast Washington and northwest Idaho; the Purcell–Yaak area south of Canada Highway 3 to U.S. Highway

Table 1. Simulation inputs into VORTEX. We adapted input parameters from Wakkinen and Kasworm (2004) from the south Selkirks for our isolated population of 100 and from the Purcell-Yaak (Cabinet-Yaak in Wakkinen and Kasworm 2004) for our male linked population of 50. Our hypothetical target mortality values were adapted from Hovey and McLellan (1996) and McLellan (1989a) from the North Fork of the Flathead Valley.

	Baseline data					
	South Selkirk		Purcell-Yaak		North Fork Flathead	
	Input	SD	Input	SD	Input	SD
Adult F breeding (%)	33	10	33	10	37	10
Litter size	2.18	0.53	2.07	0.52	2.67	0.43
Males in breeding pool (%)	100					
Initial population size	100		50			
Stable age distribution	Yes					
Carrying capacity	200	50	100	25		
Mortality rates (%)						
Female						
Cub of year	12.5	5.2	32.1	12.7	13.3	1
Yearling	21.5	9.7	12.5	12.8	5.6	0.6
Subadult	12.2	5.8	22.9	9.1	6.9	0.4
Adult	6.5	1.9	7.1	1.4	5.4	0.2
Male						
Cub of year	12.5	4	32.1	12.7	13.3	1
Yearling	21.5	7	12.5	12.8	5.6	0.6
Subadult	23.5	8	36.8	25	8	0.4
Adult	9.2	3	15.3	5.1	8	0.2

2 extending to the northwest corner of Montana; and the Cabinet Mountains south of U.S. Highway 2 (Fig. 1).

Simulations

We used an individual-based stochastic population viability modeling program, VORTEX (Lacy et al. 2003), to simulate the effects of management actions on 2 hypothetical grizzly bear populations of 50 and 100 individuals. Due to modeling accuracy limitations mentioned above, we do not claim these simulations reflect real likelihoods of extinction for the trans-border populations. Instead, our primary intent was to explore the relative effects of management options (Lindenmayer et al. 2003) and to initiate a longer process of comprehensive, conservation-oriented adaptive management (Boyce 1997). We modeled a baseline, hypothetical, small, isolated population of 100 individuals using reproductive and mortality rates (hereafter vital rates) adapted from means and standard deviations reported for the south Selkirk population (Wakkinen and Kasworm 2004). We also modeled another baseline population of 50 that was connected to adjacent populations by male movement similar to the Purcell-Yaak population (Proctor 2003), using means and standard deviations of vital rates adapted from Wakkinen and Kasworm (2004). We recognize that the estimated parameter values for reproductive and mortality rates for these small pop-

ulations are based on small sample sizes (Wakkinen and Kasworm 2004); this mandates a skeptical interpretation of the absolute values of our simulations.

Additional simulations were designed to evaluate the relative demographic impacts of 3 management options: re-creation or enhancement of interchange with adjacent populations (assumed to occur through creating linkage zones), augmentation (importing bears from elsewhere), and decreases in human-caused mortality. We addressed management to limit human-caused mortality because we were unaware of effective ways to reduce natural mortality. Outputs from our simulations were average growth rate over periods from 10 to 100 years and probability of extinction over 100 years. We defined extinction as the time when only one sex remained during a simulation. Other model assumptions included: polygamous mating; females' first breeding at age 6, males at 9; maximum age of reproduction of 25 years; maximum number of progeny, three; and sex ratio at birth of 50%. Baseline model parameters are given in Table 1. An initial stable age distribution is calculated within VORTEX from demographic parameters provided.

For our augmentation scenarios we modeled the addition of 1-4 three-year-old sub-adult females per year for an initial 10-year period. We chose 3-year-old females for augmentation simulations because natural dispersal begins at age 3 for grizzly bears (McLellan and

Hovey 2001), sub-adults yield the best option for site fidelity after translocation (Maguire and Servheen 1992), and the sub-adult female cohort maximizes demographic benefits while presenting the lowest risk from human–bear conflicts (Maguire and Servheen 1992). We assumed survival of our augmented bears would be equal to that of resident sub-adults. Although we suspect this is optimistic, we have no good estimates of the survival of transplanted bears so have no data on which to base a difference in survival rate. Therefore, we set the mortality of augmented bears and naturally dispersing bears (linkage scenarios) at sub-adult female rates. We conducted sensitivity analyses, simulating a range of ages (3–6 years old) for bears used in augmentation to explore the relative demographic effects of age on our results. We also explored how the length of time for the augmentation effort (5, 10, 15 and 20 years) affected our results.

We modeled 4 scenarios for decreased human-caused mortality. Scenario 1 reflects the age and sex-specific mortality rates estimated by Wakkinen and Kasworm (2004) for the south Selkirk and Purcell–Yaak populations separately. Scenario 4 reflects McLellan's (1989a) and Hovey and McLellan's (1996) rates for an adjacent, healthy, growing grizzly population in the North Fork of the Flathead Valley in southeast BC. Scenarios 2 and 3 were equally spaced intermediate rates modeled for each of four age cohorts (cubs, 0–1 years old; yearlings, 1–2 years old; sub-adults, 3–5 years old; and adults >5 years old; Table 1). For example, for the population of 100 individuals, adult female mortality was incrementally reduced from the initial condition of 0.0650 through 3 equal steps, 0.0617 and 0.0583, to the best case condition of 0.0550 (Table 1). We used Hovey and McLellan's (1996) mortality estimates as the realistic upper limit for age- and sex-specific mortality as a best case scenario to represent how population parameters may look after years of successful management. These estimates represent real, potentially attainable, mortality rates for a grizzly bear population in the interior of North America.

For the demographic effect of population interchange (which we equate here with the concept of linkage, Servheen et al. 2003), we simulated equal interchange of 0.25–2 sub-adult bears (3 years old) per year of each sex, both in and out of each of 2 populations (one with 50 or 100 individuals and the other with 500). A rate of 0.25 bear per year means 1 male and 1 female every four years. The baseline scenario for the hypothetical isolated population of 100 bears using the south Selkirk vital rate and mortality estimates was modeled as an isolated

population (Proctor 2003). The baseline scenario for the population of 50 was modeled with male interchange (Proctor 2003) at a rate of 0.5 males per year (the true rate for the Purcell–Yaak population is unknown and was arbitrarily chosen near the low end of our range). Because linkage zone re-creation and enhancement will theoretically allow animals to move in either direction and there is no way to control the directionality of migrants, we allow equal movement in and out of our simulated populations. Furthermore, male grizzly bears disperse further than females (McLellan and Hovey 2001) and will therefore be more likely inter-population migrants (Proctor 2003). However, females are demographically more influential, and it is for this reason that we included sub-adult females in our simulations of population interchange. Because natural dispersal in grizzly bears in this region is a gradual process that begins at approximately 3 years of age, population interchange would likely occur sometime between the ages of 3 through 6 (McLellan and Hovey 2001). To control for the influence of age, we simulated our population interchange using bears the same age as those added to the population for the augmentation simulations (3 years old). We also conducted sensitivity analyses for age of dispersers through linkage.

We simulated scenarios for initial populations of 50 and 100 bears (1,000 iterations each) for 100 years. Results are for mean population values for the 1,000 iterations. We included a rare catastrophe (2% chance of occurrence in any year) in the baseline and subsequent scenarios that reduced survival and reproduction for 1 year by 30% (baseline \times 70% for a 30% reduction). We did not model density-dependent reproduction or inbreeding depression due to a lack of data to support parameterization. We set 2 times the initial population as an upper limit to population size (Hamilton and Austin 2002).

In addition to the above scenarios for initial populations of 50 and 100 individuals, we ran 1 set of simulations testing short-term effects of augmentation (25 years; same age cohorts as above) for a population of 15 individuals using vital rate data from the Cabinet Mountains (Wakkinen and Kasworm 2004).

Results

Our baseline simulations of a hypothetical bear population of 100 animals generated a 21% probability of extinction within 100 years and a mean annual instantaneous rate of change (r) of 0.018. These values

were based on vital rate estimates reported for the south Selkirks by Wakkinen and Kasworm (2004). The population of 50 animals (using vital and mortality rates similar to those for Purcell-Yaak grizzlies) generated an 85% probability of extinction and r of -0.037 . Although we do not display the error associated with 1,000 iterations, in our simulations of growth rate, the standard errors were uniformly 0.0007. For probability of extinction simulations, standard errors were all <0.02 .

Mortality reduction had the largest effect over the 100-year simulation period and augmentation had the largest effect over the short-term (10 years). Growth rates dramatically increased as a result of augmentation during the 10 years of augmentation (Fig. 2a). The effect of 10 years of augmentation averaged over the 100 years, however, resulted in only slightly improved growth rates and extinction risk (Figs. 2a,b). With an initial population of 15 bears, even low rates of augmentation (1 female per year) reduced the probability of extinction by 33% over 25 years; adding 3 females per year cut the extinction risk in half (Fig. 2c). Sensitivity analyses varying age and length of time for the augmentation effort had little effect on our results. Increasing the age of animals used for augmentation to 6 years lowered the extinction risk by 1%, and increasing the length of augmentation effort to 20 years lowered it by 2%. Growth rates were also only minimally improved by 0.3% and 0.5%, respectively.

Population exchange had a greater effect on reducing extinction risk than on increasing growth rates (Figs. 3a,b). The effects of exchange on growth rates over 10 and 100 years were minimal (Fig. 3a) for the population of 100. Immigration and emigration of 2 bears/year of each sex increased growth rates 1.2% over the baseline (Fig. 3a) in the population of 50 that began with negative growth rates. Population interchange of 1 bear/year of each sex was required to reduce the extinction risk below 10% in the population of 100 individuals (Fig. 3b). Age-specific sensitivity analysis revealed that increasing the age of migrants to 6 years old resulted in a larger reduction in extinction probabilities (than 3 year olds) for the same number of migrants, likely because the model applied higher survival rates and breeding was immediate for this cohort.

Mortality reduction had the greatest positive effect on growth rates over the 100-year period (Fig. 4a), yielding a gain of 3.4% in annual growth rates from the baseline scenario to the best case scenario (Mort 4). These gains were accompanied by equally strong reductions in extinction probabilities with the best option (Mort 4) yielding an extinction probability of 5% (Fig. 4b).

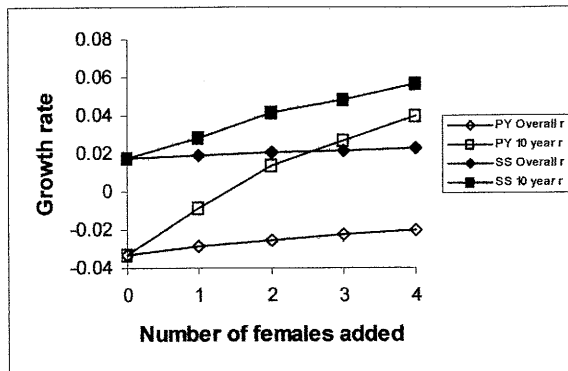
When we examined combinations of management actions over 100 years, mortality reduction had a larger effect on growth rates than population interchange enhancements (Fig. 5a), whereas linkage enhancement and mortality reduction (Fig. 5) had a larger effect on extinction probability than linkage enhancement and 10 years of augmentation measured over the long-term (Fig. 6). Measured over 100 years, mortality reductions were also more effective at improving growth rates and reducing extinction probability than 10 years of augmentation (Fig. 7 a,b). Without population interchange enhancements, mortality reductions were necessary to reduce extinction probability to $<10\%$ (Fig. 7b). Extinction probabilities in the range of 5% were obtained with modest reductions in mortality together with intermediate levels of linkage (Fig. 5b—Mort scenario 2 with 1 migrant/year and Mort scenario 3 with 1 migrant/2 years). Table 2 summarizes the relative net gains of these 3 management actions.

Discussion Simulations

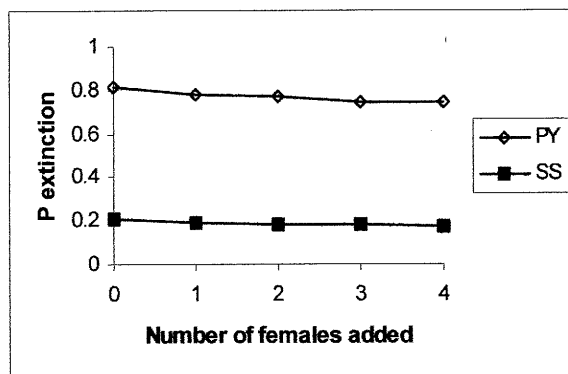
We make no claim that our simulated results on extinction probabilities reflect reality, although they were similar to those of Boyce et al. (2001), who modeled a population similar to the south Selkirk population within a RAMAS GIS (geographic information system) viability modeling exercise and reported a 20% chance of extinction. Many additional factors could have been included in our simulations, such as habitat changes and global warming, which would yield different results. The primary value of our simulations was to contrast the relative effects of management actions to initiate a process of adaptive management for the vulnerable trans-border grizzly populations. Use of population viability analysis to evaluate alternative management options was recommended by Boyce (1997) and Lindenmayer et al. (2003). We agree with Boyce et al. (2001) that the state-of-the-art for population viability analysis has not sufficiently matured for accurate predictions of minimum viable population estimates or probabilities of extinction.

The period of time considered when calculating likelihood of extinction is significant. For instance, when we extended our simulations of the population of 100 individuals to 200 years, extinction risk doubled (42%) over baseline conditions. When considering extinction risk of a long-lived animal with a long generation time such as grizzly bears (10–15 years, Craighead et al. 1995), 100 years is only 7–10 generations. Because of our inability to realistically predict changes in habitat and

a. Growth rate



b. Probability of extinction



c. Probability of extinction

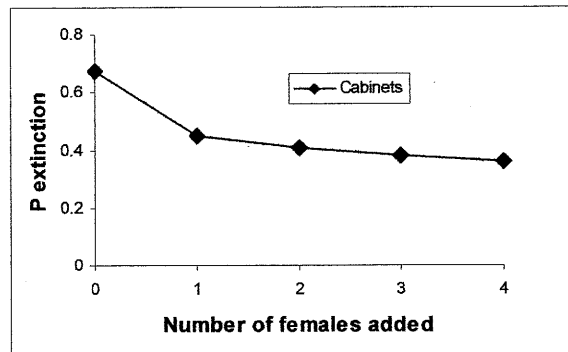


Fig. 2. Average population growth rate and probability of extinction of three small grizzly populations (15, 50, and 100 individuals) in northwest North America as a function of the number of females per year added in augmentation. Augmentation is of sub-adult, 3-year old females over 10 years. Parameter inputs were adapted from estimates for the Purcell-Yaak (50 bears), south Selkirk (100 bears), and the Cabinet Mountain bear (15 bears) populations from Wakkinen and Kasworm (2004). a. Growth rates for 10 years of augmentation (squares) and the entire

other conditions for periods longer than 100 years, we declined to model for longer periods. However, more generations than this are needed to accurately portray extinction risk even in a stable environment.

Our results suggest that management needs to address the demographic issues facing these small populations. Over the short-term, the largest relative demographic benefits can be obtained through augmentation (under our model assumptions). Over the long term, the largest demographic benefits can be obtained through mortality reductions (Table 2). We believe a combination of all 3 management actions is necessary to reduce the likelihood of extinction to acceptable levels over the short- and long-term. In the following sections we discuss the practicality of and challenges associated with implementing population augmentation, enhancing and re-establishing population interchange, and reducing human-caused mortality.

Augmentation

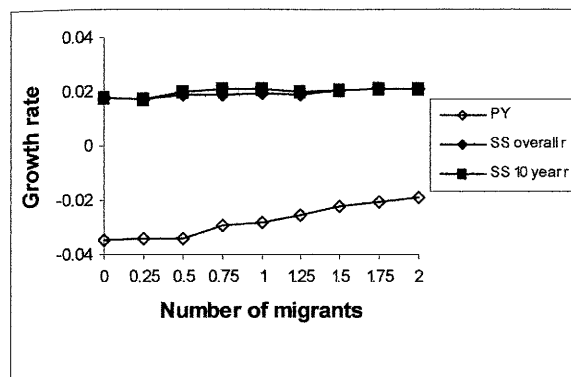
Our results suggest that a modest augmentation effort of up to 4 sub-adult females per year can dramatically increase short-term growth rates. In the population of 15 bears, similar to the Cabinet Mountains, there are likely fewer than 5 breeding-age adult females. The high short-term (25-year) extinction risk is reduced 33% with the augmentation of 1 female per year for 10 years, and it is cut in half by adding 3 bears per year (Fig. 2c). Although augmentation alone will not eliminate this considerable extinction risk, it likely will be necessary while longer-term population interchange and mortality reduction are implemented.

We chose to only model up to 4 females per year for 10 years because longer-term augmentation is not feasible logistically. Additionally, because grizzly bears naturally have slow reproductive rates (Bunnell and Tait 1981) and many jurisdictions value the grizzly bears they currently have, finding a long-term, geographically close source population for an augmentation program would be difficult. Furthermore, augmentation programs for grizzly bears are typically controversial (Servheen et al. 1999, Austin 2004), so these techniques should be used as a temporary measure when necessary to increase the number of reproductive females in small populations while

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100 years (diamonds). b. Probability of extinction for 100-year period with augmentation during the first 10 years. c. Probability of extinction for 25 years for a population of 15 individuals with augmentation during the first 10 years.

a. Growth rate



b. Probability of extinction

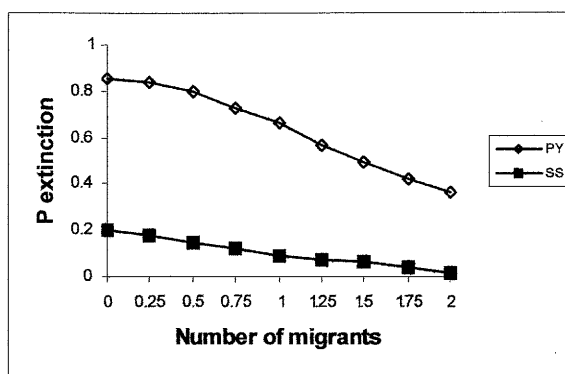


Fig. 3. Average population growth rate (a) and probability of extinction (b) over 100 years as a function of linkage enhancement for grizzly bears in northwest North America. Linkage was modeled by the interchange of 3-year old, sub-adult grizzly bears of both sexes between 2 adjacent populations (one small, with 50 or 100 bears and one large, with 500 bears). For populations of 50 and 100 bears, parameter inputs were adapted from estimates for the Purcell-Yaak and south Selkirk populations, respectively, from Wakkinen and Kasworm (2004). Linkage rates apply to each sex separately (example: 0.25 migrant refers to 1 male and 1 female migrant every four years). Graph a includes a 10-year and 100-year growth curve for the south Selkirk (SS) for comparison to the augmentation scenario in Fig. 2a.

developing long-term solutions (population interchange, minimizing human-caused mortality, and improving habitat where possible).

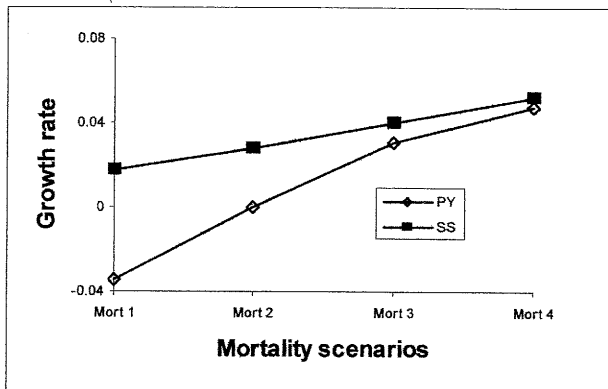
The three most important biological challenges in an augmentation program are survival, site fidelity to the new area, and reproduction within the new population. Mortality rates for dispersing and transplanted bears will undoubtedly be initially higher than that of resident bears (Weisser 2001), although the increase in mortality is unknown. Maguire and Servheen (1992) estimated survival of transplanted grizzly bears at 75% of resident bears. Our models assumed success on all 3 factors (site fidelity, reproduction, and survival), and actual rates of augmentation may have to be increased to achieve the net gains we observed in our models.

Although achieving augmentation success will be challenging, population augmentation has been used as a management tool for grizzly bears in several regions of the world. Several grizzly bears were reintroduced into Austria between 1989 and 1993, and ten years later this very small population had produced 26 cubs, demonstrating success at least reproductively (Rauer et al. 2001). Because of waning public and political support, the population as a whole has not increased beyond 7–20 bears. Several grizzly bears were also reintroduced into vacant habitat in the central Pyrenees

Mountains of France and have reproduced (Quenette et al. 2001), and 3 bears (2F and 1M) introduced from Slovenia have increased to 7–9 bears over 7 years. Four sub-adult females were moved into the vulnerable, small Cabinet Mountain population between 1990 and 1994 (Kasworm et al. 1998). One was shot and the other 3 dropped their radiocollars after one year of monitoring.

These examples illustrate that bears can be translocated into areas where they can survive and reproduce. They also illustrate that without public and political support, augmentation efforts will have trouble succeeding. Public outreach and education, as well as programs to reduce bear-human interactions with rural communities and individuals are an essential part of an augmentation program. None of the examples to date has demonstrated a population-level recovery as a result of augmentation. However, neither have any of the augmented populations gone extinct. Our simulation results suggest that augmentation can contribute significantly to increased viability of small grizzly populations over the short-term. As long as augmentation is not used as a substitute for management actions that will contribute more to viability over the long term, we believe that it is a vitally important component of a program to recover small populations of grizzly bears, and we emphasize the importance of simultaneous application of multiple management efforts

a. Growth rate



b. Probability of extinction

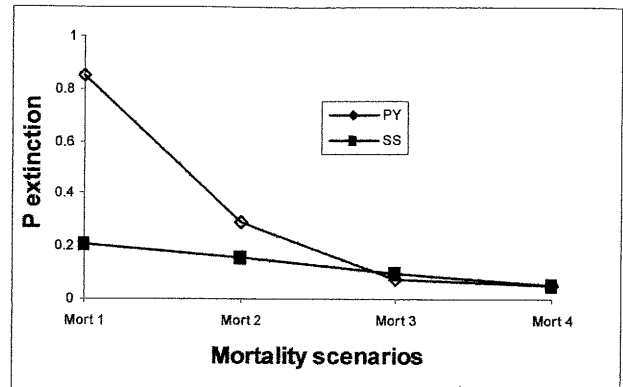


Fig. 4. Average population growth rate (a) and probability of extinction (b) over 100 years as a function of mortality for grizzly bears in northwest North America. Mortality rates were incrementally decreased from rates similar to those estimated for the Purcell–Yaak and south Selkirk ecosystem (Scenario 1, Wakkinen and Kasworm 2004) to realistic target values such as those found in a healthy growing population (Scenario 4, Hovey and McLellan 1996). For the populations of 50 and 100, parameter inputs were adapted from estimates for the Purcell–Yaak and south Selkirk populations, respectively, from Wakkinen and Kasworm (2004).

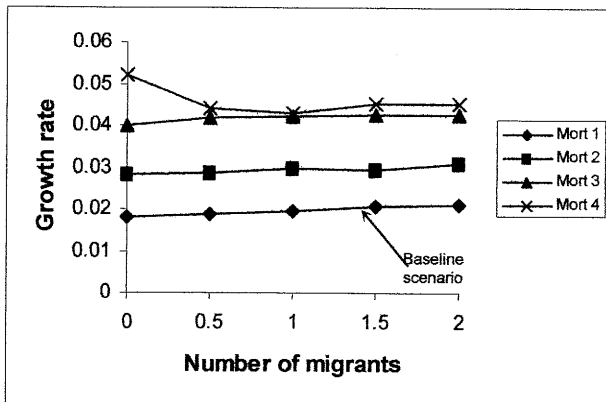
in conjunction with augmentation as part of a comprehensive management program.

Population interchange

Our assumption of population interchange (2-way dispersal) is likely realistic for the south Selkirk population. It has an estimated slightly positive growth

rate, and we therefore assume that if linkage is enhanced through management, bears will move into and out of that population. This assumption is likely responsible for the minimal positive effect that interchange had on growth rates for the hypothetical population similar to the south Selkirks (Fig. 3a). Interchange rates were also a small proportion of the total population. However,

a. Growth rate



b. Probability of extinction

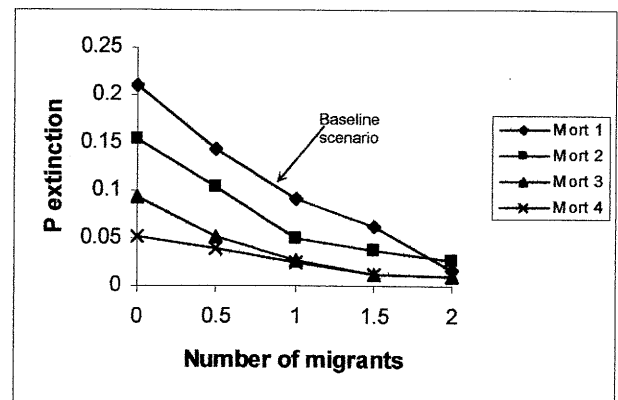


Fig. 5. Average population growth rate (a) and probability of extinction (b) over 100 years for grizzly bears in northwest North America as a function of linkage enhancements and decreasing mortality. Linkage varied according to Fig. 3, and mortality varied according to Fig. 4 for the hypothetical population of 100 individuals only.

a. Growth rate

b. Probability of extinction

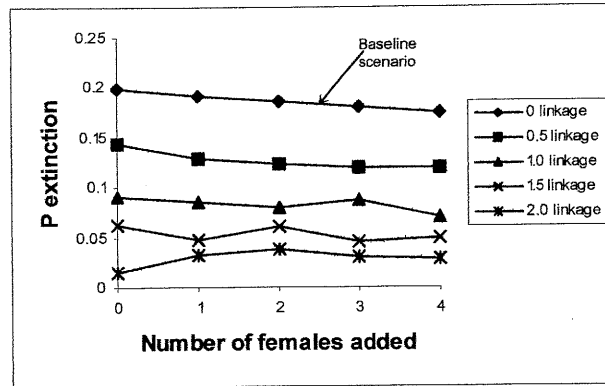
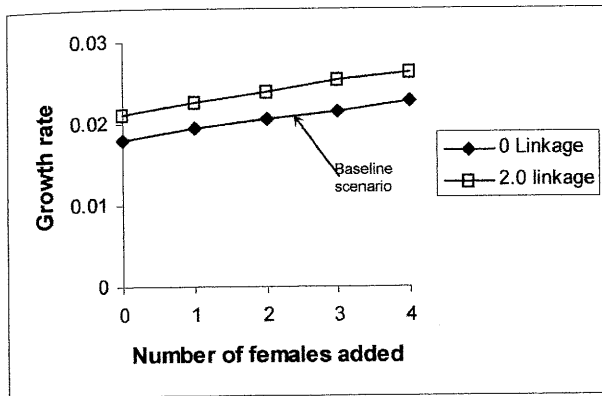


Fig. 6. Simulated changes in population growth rate (a) and probability for extinction (b) for grizzly bears in northwest North America with both augmentation (as per Fig. 2) and linkage enhancement strategies (as per

linkage in this case reduces extinction risk (Fig. 3b), a result of immigration of male and female bears. To lower extinction risk below 10% in the population of 100 bears, immigration of 1 bear/year of each sex was required (Fig. 3b.). This is a relatively high rate of interchange and suggests that linkage accompanied with modest gains in mortality reduction poses a more realistic target (Fig. 5b).

In contrast, the growth rates of the population of 50 (similar to the Purcell–Yaak population) were positively influenced by population interchange (Fig. 3a). This is likely the result of interchange rates that were a higher proportion of the total population (relative to the population of 100). Furthermore, this population was estimated to have a negative growth rate similar to that reported by Wakkinen and Kasworm (2004); therefore,

a. Growth rate

b. Probability of extinction

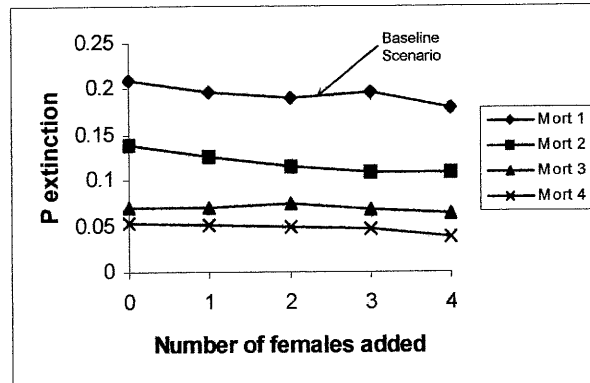
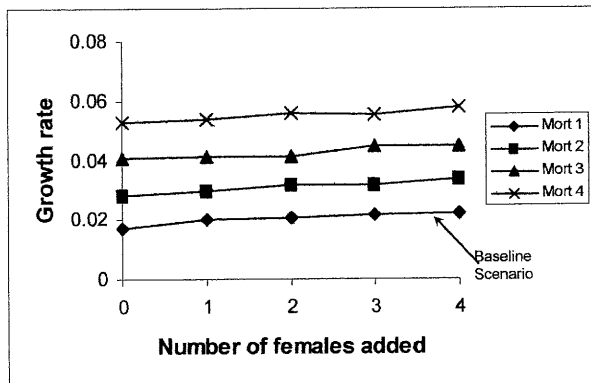


Fig. 7. Population growth rate (a) and probability for extinction (b) for grizzly bear populations in northwest North America as a function of augmentation (as per Fig. 2) and mortality improvements (as per Fig. 4).

Table 2. Net gain in population growth rate as a consequence of simulated management actions on small grizzly bear populations. Net gain was calculated by subtracting the baseline population growth rate from the scenario-specific growth rate for each management action. Parameters for population of 100 (no population interchange) adapted from south Selkirks (Wakkinen and Kasworm 2004). Parameters for population of 50 bears (0.5 male/year population interchange) adapted from Purcell–Yaak (Wakkinen and Kasworm 2004).

Management action	Added bears				
	0	1	2	3	4
Initial population = 100 bears					
10-yr augmentation					
(3-yr old F) 10 yr avg	0	0.0108	0.0233	0.0304	0.0392
10-yr augmentation					
(3-yr old F) 100 yr avg	0	0.0014	0.0026	0.0035	0.0047
Linkage (3-yr old, both sexes)	0	0.0015	0.0033	0.0049	0.0062
Mortality scenario		1	2	3	4
Net gain		0	0.0102	0.0221	0.0341
Initial population = 50 bears					
10 yr augmentation					
(3-yr old F) 10 yr avg	0	0.0251	0.0467	0.0599	0.0731
10 yr augmentation					
(3-yr old F) 100 yr avg	0	0.0044	0.0077	0.0112	0.013
Linkage (3-yr old, both sexes)	0	0.007	0.0016	0.022	0.0024
Mortality scenario		1	2	3	4
Net gain		0	0.0346	0.0655	0.0818

the assumption of 2-way linkage may not hold. Because it may not be realistic (although not entirely unlikely) to expect emigration from a population that is declining at 3.7% per year, higher rates of immigration than emigration may be realized. To the extent that linkage enhancement stimulates asymmetric inter-population movement (e.g. immigration with minimal emigration), the Purcell–Yaak population may receive greater benefit than our simulations suggest. It should also be noted that the positive demographic effects of our interchange simulation are likely exaggerated because we modeled the inter-population movement of males and females. In reality, males are more likely to move between populations than females (McLellan and Hovey 2001, Proctor 2003). A slow influx of male bears will ultimately be of limited demographic value without an influx of females that produce and recruit young.

Re-establishment (or enhancement) of population interchange is not a simple or quick management objective to attain, particularly for females. The distances between the south Selkirks and Purcell–Yaak areas to their nearest neighboring grizzly population are short, usually across a small valley fluctuating between 0.5–2 km wide, well within the average daily movement of a grizzly bear (2.4 km in the Flathead Valley, B. McLellan, BC Ministry of Forests, Research Branch, Revelstoke BC Canada, unpublished data). These valleys usually include varying densities of rural human settlement and busy highways. There are at least

2 ways in which bears may be affected by human presence in linkage zones: avoidance due to human disturbance, and increased mortality risk when bears use linkage zones with human disturbance. These forces require different management strategies to overcome. The challenge will be developing linkage zones that are relevant to grizzly bear habitat needs (reduced avoidance) and minimizing human encounters and therefore mortality. There is evidence that human-caused mortality plays a role in mediating fragmentation; therefore, reductions in mortality are likely part of enhancing connectivity. Using multiple linear regression, Proctor (2003) compared movement rates between 23 adjacent population pairs in southwest Canada and northwest U.S. and found human-caused mortality to be a significant factor in population fragmentation of grizzly bears. Further, radiotelemetry evidence has documented inter-population grizzly movements between the South Selkirk and central Purcell Mountains that all resulted in human-caused mortality (W. Wakkinen, personal observation). Because dispersal in grizzly bears is gradual (McLellan and Hovey 2001), linkage zones need to be designed for bears to spend extended periods in without being killed. It will be necessary to have extensive public outreach programs to minimize human–bear conflicts resulting from mortality associated with linkage because many of the zones will likely include private lands and some areas close to human developments.

Mortality reduction

Wielgus et al. (1994) found the south Selkirk population to be tentatively stable, with growth limited by human-caused mortality. During 1982–2003, there were 41 reported human-caused mortalities in the south Selkirk ecosystem (including 5 hunting mortalities; Wakkinen and Kasworm 2004; BC Ministry of Water, Air Protection files, Nelson, BC, Canada). Twenty-nine (71%) of these mortalities may have been avoided through education (mis-identification by black bear hunters), proper garbage handling and disposal, or more security for livestock. The average reported human-caused mortalities in the south Selkirks is 2.1 bears/year for the past 21 years, 3.3/year for the last 6 years, and 5.0/year in the last 3 years. The average reported human-caused mortalities in the south Purcell–Yaak is 0.9 bears/year for the past 21 years, 1.3/year for the last 6 years, and 1.0 in the last 3 years. Managers may only detect 33% (U.S. Fish and Wildlife Service [USFWS] 1993) to 50% (McLellan et al. 1999) of reported human-caused mortalities. Considering recent rates of human-caused mortality, the unreported portion of total mortality, and the high percent of avoidable mortalities, there is room for reductions through aggressive mortality management.

In the Yellowstone Ecosystem, aggressive mortality management has reduced known human-caused mortality to within the targets established in recovery plans (USFWS 1993, Gunther 1994) and has facilitated geographic expansion (Schwartz et al. 2002, Pyare et al. 2004). Management efforts to reduce mortality have also resulted in increased bear densities and geographic expansion in Sweden (Swenson et al. 1995, 1998).

In addition to efforts to reduce human–bear conflicts and mortality in the human-settled valleys, backcountry security and human access are also important mortality issues (Mattson and Merrill 2004, Apps et al. 2004). Few large protected areas exist within either the south Selkirk or Purcell–Yaak areas, and timber harvest is the dominant activity. In the Selkirk, Purcell–Yaak, and Cabinet Mountains, 29 of 38 (76%) known-location human-caused mortalities occurred within 500 m of a road open to public travel (Wakkinen and Kasworm 2004). Mortality management will have to occur within these extensively roaded, working forests.

Small population size

The size of a population is a reasonable predictor of extinction risk for a wide variety of taxa (Berger 1990, Shaffer et al. 2000, Reed et al. 2003). While there is considerable debate about what a minimum population

size should be to maintain long-term persistence for a species, the IUCN suggests that when the number of mature adults in an isolated species drops below 50 individuals, it is critically endangered. Below 250 adults, a population is classified endangered (IUCN 2003). Wielgus et al. (1994) report that mature adults (>5 yrs old) constitute approximately 41% of the south Selkirk total population. Other studies in the region found similar results (37% adults; McLellan 1989b). With a population estimate of approximately 105 individuals (Wielgus et al. 1994), this suggests there may be only 43 adults in the south Selkirk population. By IUCN criteria, the south Selkirk and Cabinet populations when considered alone are endangered even though the North American population as a whole is not. Furthermore, our assumption of 100 bears for the south Selkirk mountains may be an overestimate because the density estimated by Wielgus et al. (1994) was for core areas that represented the best available habitat in the ecosystem, amounting to approximately a quarter of the total area.

The limiting factors for grizzly reproductive capacity in the south Selkirks and Purcell–Yaak are unknown. Because evidence suggests that the south Selkirk population is isolated and has 15–20% lower heterozygosity (Proctor 2003), inbreeding depression may already be or may soon become a factor. While we have no evidence to suggest that inbreeding depression is negatively affecting the south Selkirk population (or the Cabinet population), small isolated populations are theoretically at risk of the negative effects of inbreeding. Another benefit of augmentation, and over the long-term, population interchange, would be to mitigate and reverse those possible effects. A number of studies demonstrate that inbreeding depression can be reversed through augmentation (Hedrick 1995, 2001; Westemeier et al. 1998; Madsen et al. 1999; Keller and Waller 2002).

Management recommendations

Population augmentation

Our simulations indicate that augmentation of the Cabinet Mountains population should be done to increase the chance of population recovery and to decrease the likelihood of extinction over the short-term (Fig. 2c). This isolated population has an estimated 10–15 bears with fewer than 5 breeding adult females. Even at a 4% rate of increase, this population would take 22 years to double. Wakkinen and Kasworm (2004) report that this population (when included with the Purcell–Yaak area) is decreasing at 3–4% per year. It is likely that augmenta-

tion will be the only hope for a population this small. We also recommend similar augmentation efforts in the south Selkirks because of its isolated status and moderate likelihood of extinction. Human-assisted translocation of bears will mitigate demographic and potential genetic effects while linkage zones are being developed and management actions to reduce mortality are underway. We recognize there is uncertainty associated with the population estimates of the south Selkirk population, the existence and degree of inbreeding depression that may be inhibiting vital rates (now or future), the timing of developing a successful population interchange program, and reducing what appears to be increasing human-caused mortality. It is these uncertainties that argue for augmentation of the south Selkirk population in the interest of caution. Augmentation of the Purcell–Yaak area is also likely required in the near future due to the small size, decreasing growth rate, female fragmentation demographically isolating this population, and subsequent moderate risk of extinction.

We recommend placing 12 sub-adult female bears into the Cabinet Mountains between 2004 and 2010. We also recommend simultaneously placing 20 bears into the Canadian side of each of the south Selkirk and Purcell–Yaak populations during 2004–2010. These numbers were selected based on estimates of availability and assumed public acceptability. We view this as an adaptive process wherein we would place these initial bears, monitor fidelity, survival (radiocollars), and reproduction (DNA surveys), and place additional bears as necessary based on the results of the monitoring. Radio collar monitoring also will provide valuable feedback on causes of mortality and potential linkage zone use.

Origins of the bears placed into these systems can vary depending on availability and capture opportunity. The protocol for placing these bears would call for sub-adult females from similar ecosystems relocated during mid-late summer when natural foods are most abundant (Maguire and Servheen 1992, Servheen et al. 1995).

Reduce current levels of human-caused mortality

Augmentation alone, however, is not a sufficient management response. It is also necessary to address the issues that caused these populations to become threatened. Our simulations and the work of Mattson and Merrill (2004) suggest that human-caused mortality in the Purcell–Yaak and Cabinet ecosystems are limiting population increase and contributing to extinction risk. In the south Selkirks, human-caused mortality is contributing to a moderate extinction risk. This is not

a surprising conclusion as human-caused mortality is a ubiquitous factor in regulating bear populations in the region (McLellan et al. 1999). However in small populations, even with the absence of legal hunting, human-caused mortality dominates (Schwartz et al. 2004), and minimizing it is fundamental to achieving population increases (Gunther 1994, Swenson et al. 1998, Mattson and Merrill 2002). Causes of mortality are diverse (McLellan et al. 1999, Wakkinen and Kasworm 2004) and require interagency cooperation and country-specific strategies to reduce. While our simulation results do not indicate the effectiveness of specific strategies, examination of ever-changing cause-specific mortality is required to develop appropriate and often creative solutions. Common themes include: (1) educating the public to reduce bear attractants to homes, farms, hunting camps, and recreation sites, and (2) hunter education to reduce misidentification kills and minimize attractive ungulate carcasses.

Another area often cited as contributing to grizzly bear mortality is human access, as the majority of human-caused mortality occurs close to roads (Wakkinen and Kasworm 1997; see review in Schwartz et al. 2004). Access management is therefore another avenue often used to reduce mortality risk and should be implemented and tested for effectiveness in these trans-border populations. Although access management is a difficult strategy to implement due to public opposition, motorized access has recently been reduced in U.S. National Forests (Summerfield et al. 2004) and similar actions should be considered in the Canadian portion of these ecosystems. Mortality management also needs to occur inside and adjacent to recovery zones to allow for expansion and inter-population exchange. Within Canada, this may entail lowering the legal harvest in populations adjacent to threatened populations.

Enhance population interchange

Our simulations illustrated that probability of extinction was reduced by population interchange that included females. We therefore recommend that management strategies include female interchange as a goal. Specifically, we recommend the use of GPS (global positioning system) radiotelemetry to identify where bears cross highways and DNA hair-snagging to validate and improve existing, predictive linkage models (Apps 1997, Servheen et al. 2003). These data should be used to identify specific linkage zones that optimize connecting adjacent core areas of the highest local

density while providing secure habitat that minimizes mortality risk within linkage zones.

Besides linkage zone development, we recommend management strategies that consider population productivity in the target populations. If dispersal in grizzly bears is density dependent (Swenson et al. 1998, McLellan and Hovey 2001, Schwartz et al. 2002, Pyare et al. 2004), stimulating population interchange may require growing populations, and this may be mediated through reducing mortality in populations that are the focus of management (e.g., reduction of legal harvest in threatened and adjacent healthy populations).

Within linkage zones, options for management action and testing (adaptive management) include: reducing human-bear conflicts in several arenas (rural settlements, public garbage dumps, and recreational areas), habitat management (cover retention, conservation easements, development restrictions on public land), and access management. Transportation managers need to include linkage zone infrastructure developments into long-term plans, and land management planning should integrate population interchange goals (See Appendix I).

Conclusions

We suggest simultaneous and integrated application of the above actions is needed to address the problems facing the south Selkirk, Purcell-Yaak, and Cabinet Mountain populations (Appendix II). For instance, in the modeled population of 100 bears, only moderate gains in mortality reduction and population interchange are required for reasonable (>90%) chances of long-term persistence. However, realizing that these management goals will be challenging and likely take time, we recommend augmentation to avoid risks of extinction in the Cabinet Mountains and population declines in the South Selkirks while realistic, functional, solutions to long-term problems are implemented. The bears in these populations have dual citizenship; thus international cooperation is necessary. We believe that an effort involving state, federal, provincial, private, county, and non-governmental organization partners and including the simultaneous application of the management actions outlined above will permit the small grizzly bear populations in the trans-border area to recover into self-sustaining viable populations.

Acknowledgments

We thank the L. Claiborne and A. Ortenberg Foundation for their generous contribution to these

trans-boundary grizzly bear conservation efforts. We also thank P. Miller for his advice on population viability analysis and T. Radandt for thoughtful discussions on management recommendations.

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Received: 9 January 2004

Accepted: 28 April 2004

Associate Editor: R.B. Harris

Appendix I

Key grizzly bear management issues on private lands, public lands, and highways within linkage zones (adapted from Servheen et al. 2003).

- On private lands in linkage zones
 - Work gradually one-on-one with community leaders to explain the issue and how they can participate
 - Identify best locations for easements by land conservation non-governmental organizations
 - Stress issues of rural nature, local interest, and maintenance of property value
 - Work with community groups to build understanding and support
 - Use community groups as focus groups on this issue
 - Work with local elected officials as local support is established
- On public lands in linkage zones
 - Consider motorized access control and maintaining visual cover within linkage zones
 - Maintain secure habitat up to private land
 - Work with highway departments to consider highway designs that facilitate wildlife crossings
 - Minimize livestock allotment impacts
- On highway sections in linkage zones
 - Inform highway engineers and biologists on location of linkage areas along highways
 - Develop an understanding by engineers and biologists of what is necessary to enhance the ability for wildlife to cross highways in linkage zones
 - Incorporate wildlife linkage in the construction planning process for Department of Transportation in each linkage zone

Appendix II

Enhanced recovery goals for the south Selkirk (Sel), Purcell-Yaak, and Cabinet Mountain (C/Y = combined Purcell-Yaak and Cabinet Mountain areas) grizzly bear populations, 2004-2010.

	2003 conditions	2010 desired
Known mortalities/yr	C/Y: 1997-2003, avg = 1.9/yr Sel: 1997-2003, avg. = 3.2/yr	C/Y: <1/yr Sel: <1/yr
Augmented bears in the Cabinets and the Canadian portion of the south Selkirks and Purcell-Yaak	4 (since 1990) in Cabinets	12 F in Cabinet 20 F in South Selkirks 20 F in Purcell-Yaak
Linkage management	none	active on public, private, Department of Transportation
Security outside recovery zones	minimal	active outreach with signs, no net increases in road density, sanitation on private lands
Habitat management inside recovery zone	incomplete	motorized access management goals substantially met
Average number females with cubs/yr	1997-2002 avg = 1.7/yr in C/Y	>3.4/yr in each U.S. ecosystem; >3.4/yr in each Canadian ecosystem