

Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia

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Abstract

Estimating minimum viable population and reserve size is a fundamental cornerstone of conservation biology—but these estimates require representative demographic parameters. For example, “Benchmark” Grizzly Bear (*Ursus arctos*) Management Units in British Columbia (BC) are defined as unhunted and naturally regulated populations that can serve as population sources to surrounding hunted areas and provide information on natural population processes. Such benchmarks should have a very small probability of becoming threatened ($N < 100$ animals). The British Columbia Ministry of Environment (BCMOE) recently implemented a plan to establish one benchmark population in each of six different biogeoclimatic zones in the province. How many bears and how large an area for each benchmark remains in question. In this paper I estimate the minimum number of bears and the areal size required to accommodate environmental and demographic stochastic effects that can result in quasi-extinction thresholds of $N < 100$ animals. Demographic data were compiled from six different grizzly bear studies in North America and mean values and standard deviations were entered into a Leslie matrix to conduct a Population Viability Analysis (PVA). I varied initial population sizes from 100, 150, 200, and 250 animals and carrying capacities from $\frac{1}{2}K$, $\frac{3}{4}K$, and K . Results indicated that 200–250 bears were required for a sufficiently small probability ($P < 0.05$) of decline to a quasi-extinction threshold of 27 adult female bears ($N < 100$ animals total) within 20 years and a mean time to extinction > 20 years. Reserve sizes varied from 8556 km² to 17,843 km² depending on population density in each benchmark. These minimum viable populations and reserve sizes would protect approximately 12% of the estimated provincial grizzly bear population and would cover approximately 5% of the landmass of BC. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Determining minimum viable population (MVP) and reserve size is a major objective in conservation biology (Shaffer, 1981; Belovsky, 1987; Ewens et al., 1987; Akcakaya et al., 1999). These estimates are considered critical for grizzly bears (Boyce, 1995) because they are often threatened or endangered and are declining in many parts of their range (Servheen, 1990). Despite these declines, grizzlies (especially adult males) are hunted in many jurisdictions in North America (Alaska, Alberta, British Columbia, Northwest Territories, Yukon) because trophy hunting is believed beneficial or benign for population growth (Dood et al., 1986; Nagy and Gunson, 1990; Smith, 1990; British Columbia

Ministry of Environment, 1995). Many wildlife managers assume trophy hunting results in reduced numbers of competitive or cannibalistic adult males with consequent increases in cub production, survival, and population growth (see review by Miller, 1990). Recent research suggests, however, that hunting adult males may result in reduced cub production (Wielgus and Bunnell, 1994, 2000), decreased cub survival (Swenson et al., 1997, in press), and population declines (Wielgus et al., 2001). In response to these studies and other public concerns, the British Columbia Ministry of Environment (BCMOE) reduced the hunting kill province-wide and instituted a temporary moratorium on hunting grizzlies to census bears and estimate sustainable harvest. The BCMOE also began a program to establish no-hunting “benchmark” populations or Grizzly Bear Management Units (GBMUs) in each of the provinces six biogeoclimatic zones (BC Ministry

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of Environment, 1995). The purpose of these benchmarks are to provide “insurance” against any possible negative effects of hunting, provide population sources for the surrounding hunted areas, and to allow comparison between hunted (anthropogenically regulated) and unhunted (naturally regulated) populations within each biogeoclimatic zone. The benchmarks are defined as unhunted, naturally regulated (little or no human-caused mortality) populations that have a very small probability of becoming threatened. Threatened populations or GBMUs are defined by the BCMOE as GBMUs containing $N < 100$ animals (e.g. < 30 adult females) based on possible severe demographic stochastic effects for such small populations (Boyce, 1992).

How large should each benchmark population be to ensure that the populations remain viable, unthreatened, and naturally regulated (Mattson et al., 1996)? Since each benchmark will be surrounded by, connected to, and part of other viable (albeit hunted) grizzly bear populations, genetic minimum viable populations (MVPs) are not a concern (Lande and Barrowclough, 1987). The concerns for benchmark population viability relate to demographic processes that can result in quasi-extinction threshold population sizes of $N < 100$ animals (e.g. threatened status), related probabilities of the adult female component in each benchmark being subject to extreme demographic stochastic effects (e.g. $N < 30$ adult females; Boyce, 1992, 1995; Caughley and Sinclair, 1994, p. 244), and ability to be naturally regulated (unaffected by human-caused mortalities). The BCMOE has proposed an MVP of 100 animals—just over the threatened threshold (M. Austin, BCMOE, personal communication), but that number was based on deterministic (not stochastic) demographics and an assumed non-variable growth rate R of at least 1.00. However, estimates of such MVPs should include stochastic effects including demographic and environmental variability (Boyce, 1995; Mills et al., 1996).

In this paper I focus on relations between minimum population size, environmental and demographic stochastic effects, and the vital demographic rates that effect population persistence (survival, maternity, age at first reproduction, age at senescence, carrying capacity). The problem remains that these vital rates are unknown for grizzly bears in most of BC, never mind for prospective benchmark areas. I estimate mean vital rates and their variability from six different published papers on grizzly bear demography in North America. I use these average data to estimate minimum viable population sizes for benchmark GBMUs in BC using population viability analysis (PVA; Boyce, 1995; Mills et al., 1996; Boyce et al., 2001). PVA programs such as RAMAS, using empirical data such as mine, have recently been proven extremely robust and accurate in predicting real population trajectories (Brook et al., 2000b). These MVPs could also serve as initial,

approximate guidelines for grizzly bear populations throughout North America where detailed demographic data are not currently available.

2. Methods

2.1. Population data

I reviewed the published literature and obtained six different data sets on grizzly bear population demography. The data sets were: (1) Wielgus et al. (1994) for the Selkirk Mountains in southern BC and northern Idaho; (2) Wielgus and Bunnell (1994, 2000) and Wielgus et al. (2001) for Kananaskis in southwestern Alberta and southeastern BC; (3) Eberhardt et al. (1994) for Yellowstone; (4) Hovey and McLellan (1996) for the Flathead Valley in southeastern BC; (5) Mace and Waller (1998) for the Swan Mountains of Montana; and (6) Pease and Mattson (1999) for Yellowstone. All of these data sets, except Hovey and McLellan, represent demographic data for protected females in unhunted areas and should therefore be representative of protected females in prospective benchmark areas. Hovey and McLellan's (1996) data represented a hunted population, but with very low mortality rates (Table 1). None of these data sets reported annual variability (environmental stochastic effects) in the vital rates separate from measurement errors, however Pease and Mattson (1999) did report variability for all vital rates between mast and non-mast years, therefore their data did provide a measure of the range for environmental stochastic variability.

I calculated means and standard deviations (SDs) for age-specific survival of cubs (S_c), survival of yearlings (S_y), survival of sub adult (2–5 years) females (S_{sf}), survival of adult (≥ 6 years) females (S_{af}), maternity ($m_x = \text{\#female cubs/adult female/year}$), fecundity ($f_x = S_x \times m_{x+1}$; from Jenkins, 1988; and Ebert, 1999), age at first birth (b_x), and age at senescence or maximum age (w) (whichever comes first). I also calculated mean % composition of the populations for offspring (0–1 year olds), sub adult males and females, and adult males and females. Finally, I calculated the mean and SD for finite rate of growth R .

2.2. Population modeling

The survival and fecundity data were entered into a post-breeding, age-class Leslie matrix (Caswell, 1989; Jenkins, 1988; Akcakaya et al., 1999; Ebert, 1999) to estimate mean expected population growth R , stable age distribution, elasticities, reproductive values, probabilities of quasi-extinction, and mean times to quasi-extinction for a hypothetical benchmark population.

I considered two stochastic factors, demographic and environmental stochasticity, in my model because they

Table 1

Demographic parameters including survival of cubs (S_c), yearlings (S_y), sub adult females (S_{sf}), adult females (S_{af}), maternity (m_x), fecundity (F_x), age at first birth (b_x), maximum age (w), composition (% young, % sub adults, % adults) and population growth R for seven different grizzly bear data sets in North America

Demographic parameter	Location of data set								SD
	Flat ^a	YNP ^b	YNP ^c	YNP ^d	Kan ^e	Sel ^f	Swan ^g	Mean	
S_c	0.867	0.845	0.790	0.880	0.780	0.840	0.785	0.826	0.041
S_y	0.944	0.845	0.860	0.910	0.780	0.840	0.906	0.869	0.055
S_{sf}	0.931	0.887	0.845	0.920	0.890	0.780	0.825	0.868	0.054
S_{af}	0.946	0.923	0.860	0.930	0.930	0.960	0.899	0.921	0.033
m_x	0.422	0.328	0.430	0.440	0.230	0.370	0.261	0.354	0.084
F_5	0.392	0.290	0.363	0.404	0.204	0.288	0.215	0.307	0.081
F_{6+}	0.399	0.303	0.369	0.409	0.213	0.355	0.234	0.326	0.078
b_x	6.40	5.75		5.50	5.50	7.30	6.00	6.07	0.68
w	20	20		20	20	20	25	20.83	2.04
% _y	38				16	30	26	28	9
% _{sf}	14				11	11	17	13	3
% _{sm}	13				22	13	9	14	6
% _{af}	22	27			22	32	33	27	5
% _{am}	13				29	14	15	18	8
R	1.085	1.046	0.950	1.070	0.990	1.000	0.977	1.016	0.050

^a Flathead Valley BC, Hovey and McLellan (1996).

^b Yellowstone, Eberhardt et al. (1994).

^c Yellowstone, non-mast years, Pease and Mattson (1999).

^d Yellowstone, mast years, Pease and Mattson (1999).

^e Kananaskis Alberta, Wielgus and Bunnell (1994).

^f Selkirk Mountains ID and BC, Wielgus et al. (1994).

^g Swan Mountains Montana, Mace and Waller (1998).

are likely to exert a major influence on the risk of extinction in relatively small populations (Shaffer, 1981; Goodman, 1987; Belovsky, 1987; Lande, 1993). Catastrophic stochastic effects (Ewens et al., 1987) were not incorporated into the model because none of the data sets demonstrated such effects, data were unavailable for such effects, and because the short-term time horizon of my simulations (20 years) are unlikely to experience such effects. The model is therefore conservative and more likely to underestimate rather than overestimate true quasi-extinction probability (Ludwig, 1999).

Annual variation (separate from measurement error) in vital rates was not available to estimate environmental stochastic effects for the data sets. Therefore, similar to Boyce (1995, p. 49), I used among-population SDs for the vital rates as a surrogate for environmental stochastic variability. These SDs were entered into a standard deviation matrix to estimate environmental stochastic effects (Akçakaya, 1998). This method will likely produce conservative, underestimates of probability of quasi-extinction because variance among population means is usually lower than variance among individual years (Akçakaya, 1998). See Table 1 for evidence that among year SDs for survival and maternity in Yellowstone are larger than among population SDs for the same parameters in grizzly bears. Environmental stochastic effects on fecundity and survival were perfectly correlated (Akçakaya, 1998) because occurrences such as mast, berry crop, and salmon failures or bumper

crops tend to effect survival and fecundity concurrently for grizzly bears (Mills et al., 1996; Pease and Mattson, 1999). Demographic stochastic effects were estimated using the random number generator in RAMAS GIS (Akçakaya, 1998).

My matrix model assumed density independent, exponential population growth up to the ceiling K where growth rate abruptly reduces to 1.0 (Akçakaya et al., 1999) because we do not know how density dependence affects grizzly bear population growth and what form any putative density dependent function should take (McLellan, 1994; Boyce, 1995; Mills et al., 1996). Furthermore, the ceiling model appears consistent with a very high density population observed by Hovey and McLellan (1996), whereby density dependence appears manifested through emigration, not reduced reproduction or survival. Although inappropriate for very strongly density dependent (e.g. cyclical herbivore) species (Chapman et al., 2001), the ceiling model appears well suited for grizzly bears, particularly for short time frames (20 years) such as this (Boyce, 1992; Mills et al., 1996). More recently, Boyce et al. (2001) used a density dependent, not a ceiling, model in their PVA of Yellowstone grizzlies. They found no evidence for density dependent reproduction but did for density dependent survival—therefore they used density dependence in survival only. Bears outside of Yellowstone Park and translocated bears suffered higher mortality than bears inside the park and untranslocated bears (Boyce et al.,

2001). Presumably, as density increased and bears colonized or were translocated to adjacent areas outside the park their mortality also increased. Since I was not interested in estimating population viability outside of protected benchmarks I did not incorporate such a density dependent survival function in my PVA.

Carrying capacity K was fixed and was not subject to environmental stochastic effects because I had no data to estimate environmental variation in K . Similar to exclusion of catastrophes, this method will tend to produce conservative or underestimates of quasi-extinction (White, 2000). By the same token, individual heterogeneity (White, 2000) was not included in the model because I had no data to estimate this heterogeneity. However, lack of individual heterogeneity is more likely to overestimate probability of true extinction ($N=1$) and only at very small population sizes ($N=25$), it appears to have no effect at larger population sizes ($N=100$ – 250) and larger quasi-extinction thresholds ($N=27$) such as these (White, 2000).

I calculated probability of quasi-extinction (P_{ext}) and mean time to quasi-extinction (T_{ext}) for a threshold population size of 27 adult (≥ 6 years old) females because that number of adult females corresponds to an overall population size of 100 or threatened designation in BC (Section 3) and is subject to extreme demographic stochastic effects (Caughley and Sinclair, 1994, p. 244; Boyce, 1992, 1995, p. 64). Brook et al. (2000a) also recommend only modeling the female component of a population to estimate extinction probabilities using RAMAS, because of potential sex ratio variation and underestimation of extinction risk when both sexes are modeled. 1000 simulations were run for each projection to estimate P_{ext} and T_{ext} . Simulations were run for 20 years, the mean maximum age w , observed for these six grizzly populations.

Effects of population size N and carrying capacity K on P_{ext} and T_{ext} were estimated by observing the total number of adult females present during 1000 model runs of 20 years and by calculating quasi-extinction probabilities and mean time to quasi-extinction under stochastic effects. I estimated minimum viable population sizes (MVPs) by varying initial population sizes from 100, 150, 200, and 250 animals and observing the corresponding P_{ext} and T_{ext} . One hundred was chosen as the starting value because this was the MVP for benchmarks initially proposed by the BCMOE.

I incorporated effects of carrying capacity K by running simulations for each population size at K , $\frac{3}{4}K$, and $\frac{1}{2}K$. Simulations for populations at or near K may correspond to prospective benchmark areas that have been protected for a considerable period of time (e.g. established National or Provincial Parks). Those at $\frac{3}{4}K$ may correspond to lightly hunted, newly protected, or relatively inaccessible areas. Those at $\frac{1}{2}K$ may correspond to accessible and currently hunted populations in BC.

Number of females (N_f) in each age class entered into the model at time t corresponded to total population sizes (N_t) of 100, 150, 200, and 250 and were obtained from the mean percentage of females for the six populations (e.g. $N_f = 54\%$ of N_t) and estimates of the stable age distribution for females (Section 3).

This stochastic model assumes population closure for females (no immigration by females)—a not unreasonable assumption given that all six studies observed no female immigration and the generalized paucity of female movements from one area to another (IGBC, 1987; Blanchard and Knight, 1991). Furthermore, any putative density dependent movements or emigrations by females should be from the higher density, unhunted benchmarks to the lower density, hunted matrix—not the other way around. Both empirical and theoretical considerations indicate a closed model is appropriate in this case. Unless otherwise stated, all calculations and simulations were conducted using algorithms in RAMAS GIS (Akçakaya, 1998).

3. Results

3.1. Demographic data and population persistence

Demographic data for the vital rates of the six studies are given in Table 1. Overall, females comprised 54% and adult females comprised 27% of the populations. The mean empirical age distribution of females was 26% young, 24% sub adults, and 50% adults. The mean finite rate of growth R was 1.016 ± 0.050 . The corresponding Leslie matrix and standard deviation matrix for these data are given in Table 2. The resulting geometric finite rate of growth for the matrix was $R = 1.023$ —very similar to the arithmetic mean of the seven data sets. The stable age distribution for the matrix was 27% young, 32% sub

Table 2
Elements for fecundity ($f_x = S_x \times m_{x+1}$) and survival (S_x) in the Leslie matrix

Age class										
	0	1	2	3	4	5	6	7	.	20
0	0.826									
1		0.869								
2			0.868							
3				0.868						
4					0.868					
5						0.868				
6							0.921			
7								0.921		
.									.	
20										0.00

adults, and 41% adults—very similar to the empirical age distribution of females. The sum of the elasticities for F_x was 0.091. The sums for S_y , S_{sf} , and S_{af} were 0.1798, 0.3484, and 0.3818, respectively. The sum of the reproductive values (RV) for young, sub adults, and adults were 2.25, 7.55, and 22.3 respectively.

When the population is at or near K , only at $N_t = 250$ ($N_f = 102$), is the P_{ext} ($N_{af} = 27$) < 0.05 and the $T_{\text{ext}} > 20$ years (Table 3). At $\frac{1}{2} - \frac{3}{4}K$, Nt must be at least 200 to achieve $P_{\text{ext}} < 0.05$ and $T_{\text{ext}} > 20$ years.

4. Discussion

4.1. Minimum population sizes

My results suggest that minimum population sizes for BC benchmarks must be at least 200–250 animals for an acceptably low ($P < 0.05$) probability of decreasing to threatened status within 20 years. The P_{ext} for any N_t increases as Nt approaches K . Likewise the T_{ext} decreases as Nt approaches K because there is little or no room for the population to grow. Most, if not all, proposed grizzly bear benchmark GBMUs are likely to be established on existing protected areas such as provincial parks, so they are likely to be at or near K . If that is the case I recommend a MVP of 250 for benchmarks in BC. If proposed benchmarks are to be established in currently hunted areas ($\frac{1}{2} - \frac{3}{4}K$) then $Nt = 200$ may suffice.

In addition to whether the population is at or near K , it must be remembered that these simulations may be conservative. SDs for environmental stochastic effects on vital rates were obtained from among-population variance. These among populations SDs were similar to observed within-population SDs for survival and maternity (e.g. among population SD for $S_{af} = 0.033$ vs. 0.026, 0.046, 0.043, 0.023, and 0.037 for Hovey and McLellan (1996), Mace and Waller (1998), Wielgus and Bunnell (1994), Wielgus et al. (1994), and Boyce (1995, p. 49), and were very close to the values used by Boyce et al. (2001) in their Yellowstone PVA (SD $F_x = 0.078$ vs. 0.073, SD $S_{af} = 0.033$ vs. 0.037). They were much smaller than those (SD $S_{af} = 0.3$, SD $F_x = 0.30$) used by Mills et al. (1996) in their Yellowstone PVA.

Annual variability within any one benchmark population is likely to be larger than variability among mean values for different populations and this higher variability would result in increased P_{ext} and decreased T_{ext} (Akçakaya, 1998). This can be seen by comparing the among year survival and maternity values for Yellowstone against the same among population parameter values in Table 1. The annual variability in Yellowstone survival and maternity is considerably higher than the variability among populations for those parameters. For example, variability for $Sc = 0.09$ vs. 0.04, var $S_y = 0.05$ vs. 0.05, var $S_{sf} = 0.075$ vs. 0.05, var $S_{af} = 0.07$ vs. 0.03, and var $mx = 0.10$ vs. 0.08. Furthermore, catastrophic stochastic effects, such as recent salmon population collapses in coastal BC, undoubtedly have severe negative effects on small population persistence, but such effects were not modeled here because of the paucity of quantitative data on such effects. Therefore, my recommendation of a minimum population of at least 200–250 animals is just that—a minimum. If data on K are not available, the precautionary principle should be followed and Nt should be set at 250, not 200. Under no circumstances should $Nt < 200$.

Like any other PVA, this analysis contains three potentially subjective parameters (Akçakaya et al., 1999); threshold or quasi-extinction population size, minimum acceptable probability level of decreasing to threshold size, and time horizon or length of simulation run. The first potentially subjective parameter, threshold size, is not subjective in this analysis. The BCMOE defined a threatened population or GBMU as $N_t < 100$ animals. This translates to 27 adult females, based on mean % composition in the published data sets. It makes no sense to designate a GBMU as a viable, naturally regulated benchmark if it has a high probability of becoming threatened in as little as 20 years. Perhaps more importantly, the threshold population size of 27 adult females has a biological and mathematical justification. Adult females are the most important component of the population because only they can contribute directly to fecundity or population growth and persistence. The much higher reproductive values of adult females (sum RV = 22.3 vs. 7.55 and 2.25 for sub adults and young) indicate how important this age

Table 3

Probabilities for quasi-extinction (P_{ext}) and mean time to quasi-extinction (T_{ext} at $P = 0.05$) in years for $N_{af} = 27$ adult females ($N_t = 100$ animals) at varying combinations of initial population size (N_t) and carrying capacity (K)

Initial population size (N_t)	$\frac{1}{2}K$		$\frac{3}{4}K$		K	
	P_{ext}	T_{ext}	P_{ext}	T_{ext}	P_{ext}	T_{ext}
100	1.00	1	1.00	1	1.00	1
150	0.22	3	0.23	3	0.70	2
200	0.01	> 20	0.03	> 20	0.05	19
250	< 0.01	> 20	> 0.01	> 20	< 0.01	> 20

class is. The higher sum of elasticities for S_{af} (0.3818) vs. sum elasticities for S_y and S_{sf} (0.1798 and 0.3484) also indicate the relative importance of adult female survival. At $N_{af} < 30$ the negative effects of demographic stochasticity on fecundity and survival of this sex and age class become pronounced, but at $N_{af} > 30$ the effects taper off very rapidly (Caughley and Sinclair, 1994, p. 244; Boyce, 1992, 1995, p. 64). Therefore $N_{af} = 27$ represents a logical, biological threshold for benchmark GBMUs and other grizzly bear populations.

The second potentially subjective parameter (P_{ext}) is more problematic. At high P_{ext} (e.g. > 0.10) the chances of extinction are deemed too great. At low P_{ext} (e.g. < 0.0001) the required N_t are deemed too great. I settled at $P_{ext} < 0.05$ because this is a scientific standard and is probably deemed acceptable to all. The third potential subjective parameter, is indeed subjective. Some might like to see time frames of about 100 years based on longer-term ecological considerations. Others might like to see time frames of about 5–10 years based on very short-term recreational and economic considerations. I chose 20 years based on lifetime demographic considerations of the bears themselves. Bears live for about 20 years, so the projection time frame was based on that lifetime. Furthermore, longer time frames yield much more variable and uncertain results (Akçakaya, 1998) and assume that demographic parameters will remain the same over the long term. This short-term projection (20 years) should provide much more accurate estimates of quasi-extinction than 100 year projections. This projection horizon was considerably shorter than the 100 years used by Shaffer (1983), Boyce (1995), and Boyce et al. (2001) for Yellowstone bears. However, they also indicate that 100 years was an arbitrary time horizon. Regardless of the inherent subjective nature of the time horizon used in this PVA, it is shorter than most and therefore conservative or more risky in the long term. Longer time horizons typically result in higher P_{ext} (Leigh, 1981; Akçakaya, 1999). Future changes in MVPs and reserve sizes for the longer term (> 20 years) could be enacted through adaptive management (Boyce, 1992; Boyce et al., 2001). Finally, it should be mentioned that the BCMOE proposed an MVP of $N_t = 100$. Larger N_t were believed unnecessary. This analysis resulted in considerably larger N_t than would otherwise be the case and increases the probability of population persistence for benchmarks in BC.

In summary, the recommended MVPs of 200–250 bears for BC benchmark GBMUs are a conservative minimum. These MVPs are smaller than those usually recommended for grizzly bears (Mattson et al., 1996), but other PVAs usually assume genetically isolated, relict populations, whereas this PVA assumes the reserve to be imbedded in and part of a matrix of adjacent hunted populations. I recommend a first approximation MVP of at least 200–250 for grizzly bears in BC and elsewhere in

North America to account for demographic and environmental stochastic effects. Once benchmark areas capable of supporting 200–250 bears have been identified and established, I recommend that population-specific PVAs be conducted for each benchmark. That would allow incorporation of population-specific vital rates, variances, carrying capacities, maximum growth rates and density dependent functions on S_x , m_x , and b_x , if any. Finally, I also recommend that such population-specific PVAs incorporate the effects of habitat, as suggested by Boyce et al. (2001), to allow for effects of habitat change on population growth and persistence.

4.2. Minimum reserve sizes

How large should a benchmark GBMU be in order to protect at least 200–250 animals? That depends on the population density in the proposed benchmark GBMU and associated biogeoclimatic zone. For example, if a benchmark GBMU were to be established in the Flat-head Valley of southeastern BC the required core area size would be 3906 km² based on an estimated density of 6.4 bears/100 km² (McLellan, 1989) at or near K (Hovey and McLellan, 1996) and a required N_t of 250. In south-central B.C. it would be 10,729 km² based on an estimated density of 2.33 bears/100 km² at or near K in the protected, unhunted northern portion of the south Selkirks (Wielgus et al., 1994) and a required N_t of 250.

These reserve sizes will not, however, ensure that all or even most bears in the GBMUs are protected from hunting and naturally regulated—one of the requirements and part of the definition of a benchmark GBMU. The above density estimates, and resulting estimated reserve sizes, were based on the proportional number of bears present in a trapping zone (McLellan, 1989) or on the whole number of bears present in a female composite range (Wielgus et al., 1994). In both cases, male bears (and sometimes females) spent a considerable proportion of their time outside the trapping areas or female composite ranges. Therefore, female and male bears would not be protected and this could have important implications for population persistence (see later).

McLellan et al. (1999) showed that female bears in protected areas often wander out of these areas and are shot on the periphery. Therefore, protected areas must encompass the entire home ranges of all females in the reserve to ensure protection. Furthermore, Wielgus and Bunnell (1994, 2000) and Wielgus et al. (2001) showed that hunting mortality of resident adult males outside of protected areas could have severe negative effects on females wholly inside protected areas. Removal of resident sires can result in increased numbers of potentially infanticidal immigrant males in the protected area. This could result in reduced reproduction (Wielgus and Bunnell, 1994, 2000) and population decline (Wielgus et al., 2001) in the protected female population. Therefore,

even females may not be protected from effects of hunting, and the population would certainly not be naturally regulated, even if all females spent all their time in protected areas. In order to reduce or eliminate such direct and indirect effects of hunting, and to ensure naturally regulated population function in benchmark GBMUs, I recommend placing a “no-hunting” buffer zone around the core GBMU. The buffer zone should be equivalent to half of the mean estimated home range diameter (or radius) of an adult male in the prospective GBMU biogeoclimatic zone. This will protect all females and most or all males that have up to half of their home range outside the benchmark GBMU. That buffer zone should also reduce or eliminate the possibility of anthropogenic-induced infanticide on offspring of protected females residing completely within the benchmark GBMU.

Failure to incorporate a buffer zone around the core will not meet the objectives of establishing a protected, naturally regulated, minimum viable population. For example, the population studied by Wielgus and Bunnell (1994, 2000) was protected in Kananaskis Provincial Park. Hunting of resident males outside of the park resulted in reduced reproduction and population decline by females in the park. That protected population was declining (Wielgus et al., 2001) because of male mortalities outside of the protected area. Such an arrangement cannot serve as a model for benchmark GBMUs.

How large must the core reserve and associated buffer zone be? That again depends on estimated population-specific density and mean male home range size. Assuming a circular configuration and an average home range size of 800 km² for adult males (IGBC, 1987), the home range radius would be 16 km. Assuming a square reserve—if we add this to the Flathead core (3906 km²) we get a GBMU core benchmark and buffer of 8556 km² (e.g. $3906^{0.5} = 62.5$ km core dimension + 15 km per east/west edge + 15 km per north/south edge buffer dimensions = 92.5 km total dimension, $92.5^2 = 8556$ km² total reserve size). Using the same method, for south-central BC we get 17,843 km².

In summary, a system of six such reserves will end up protecting approximately 6 × 250 or 1500 bears. This comprises about 11–15% of the estimated grizzly bear population ($N = 10,000$ – $13,000$) in BC (British Columbia Ministry of Environment, 1995). If very high density populations (similar to Flathead BC) are chosen for these benchmark GBMUs then the total area required would be approximately 51,336 km² or about 5% of the land area of BC.

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References

- Akcakaya, H.R., 1998. RAMAS GIS: Linking Landscape Data with Population Viability Analysis (version 3). Applied Biomathematics, Setauket, New York.
- Akcakaya, H.R., Burgman, M.A., Ginsburg, L.R., 1999. Applied Population Ecology: Principles and Computer Exercises using RAMAS Ecolab 2.0., second ed. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.
- Belovsky, G.E., 1987. Extinction models and mammalian persistence. In: Soulé, M.E. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK, pp. 35–57.
- Blanchard, B.M., Knight, R.R., 1991. Movements of Yellowstone grizzly bears. *Biological Conservation* 58, 41–67.
- Boyce, M.S., 1992. Population viability analysis, 1992. *Annual Review of Ecology and Systematics* 3, 481–506.
- Boyce, M.S. 1995. Population viability for grizzly bears (*Ursus arctos horribilis*): a critical review. Report to the Interagency Grizzly Bear Committee. US Fish and Wildlife Service.
- Boyce, M.S., Blanchard, B.M., Knight, R.R., Servheen, C., 2001. Population viability for grizzly bears: a critical review. *International Association for Bear Research and Management. Monograph Series* Number 4.
- British Columbia Ministry of Environment, 1995. Conservation of Grizzly Bears in British Columbia—Background Report. Ministry of Environment, Lands, and Parks, Victoria, Province of British Columbia.
- Brook, B.W., Burgman, M.A., Frankham, R., 2000a. Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. *Conservation Ecology* 4 (1), 6. Available: <http://www.consecol.org/vol4/iss1/art6>.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akcakaya, H.R., Frankham, R., 2000b. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404, 385–387.
- Caughley, G., Sinclair, A.R.E., 1994. *Wildlife Ecology and Management*. Blackwell Scientific Publications, Boston.
- Caswell, H., 1989. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- Chapman, A.P., Brook, B.W., Clutton-Brock, T.H., Grenfell, B.T., Frankham, R., 2001. Population viability analyses on a cycling population: a cautionary tale. *Biological Conservation* 97, 61–69.
- Dood, A.E., Brannon, R.D., Mace, R.D., 1986. Final Programmatic Environmental Impact Statement: The Grizzly Bear in Northwestern Montana. Montana Department of Fish, Wildlife, and Parks, Helena, MT.
- Eberhardt, L.L., Blanchard, B.M., Knight, R.R., 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology* 72, 360–363.

- Ebert, T.A., 1999. Plant and Animal Methods in Demography. Academic Press, San Diego, California.
- Ewens, W.J., Brockwell, P.J., Gani, J.M., Resnick, S.I., 1987. Minimum viable population sizes in the presence of catastrophes. In: Soulé, M. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, New York, pp. 59–68.
- Goodman, D., 1987. The demography of chance extinction. In: Soulé, M. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, New York, pp. 11–43.
- Hovey, F.W., McLellan, B.N., 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. *Canadian Journal of Zoology* 74, 1409–1416.
- Interagency Grizzly Bear Committee (IGBC), 1987. Grizzly Bear Compendium. National Wildlife Federation, Washington, DC.
- Jenkins, S.H., 1988. Use and abuse of demographic models of population growth. *Bulletin of the Ecological Society of America* 69, 201–207.
- Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142, 911–927.
- Lande, R., Barrowclough, G.F., 1987. Effective population size, genetic variation, and their use in population management. In: Soule, M.E. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, UK, pp. 87–124.
- Leigh Jr., E.G., 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90, 213–239.
- Ludwig, D., 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80, 298–310.
- Mace, R.D., Waller, J.S., 1998. Demography and population trend of grizzly bears in the Swan Mountains, Montana. *Conservation Biology* 12, 1005–1016.
- Mattson, D.J., Herrero, S., Wright, R.G., Pease, C.M., 1996. Designing and managing protected areas for grizzly bears: how much is enough? In: Wright, R.G. (Ed.), *National Parks and Protected Areas: Their Role in Environmental Protection*. Blackwell Science, Cambridge, Massachusetts, pp. 133–164.
- McLellan, B.N., 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. *Canadian Journal of Zoology* 67, 1856–1860.
- McLellan, B.N., 1994. Density dependent population regulation of brown bears. In: Taylor, M. (Ed.), *Density Dependent Population Regulation in Black, Brown, and Polar Bears*. Proceedings International Conference on Bear Research and Management. Monograph Series No. 3.
- McLellan, B.N., Hovey, F.W., Mace, R.D., Woods, J.G., Carney, D.W., Gibeau, M.L., Wakkenin, W.L., Kasworm, W.F., 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management* 63, 911–920.
- Mills, L.S., Hayes, S.G., Baldwin, C., Wisdom, M.J., Citta, J., Mattson, D.J., Murphy, K., 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* 10, 863–873.
- Miller, S.D., 1990. Impacts of increased bear hunting on survivorship of young bears. *Wildlife Society Bulletin* 18, 462–467.
- Nagy, J.A., Gunson, J.R., 1990. Management plan for grizzly bears in Alberta. *Wildlife Management Planning Series No. 2*. Alberta Forestry, Lands, and Wildlife. Fish and Wildlife Division. Edmonton, Alberta.
- Pease, C.M., Mattson, D.J., 1999. Demography of the Yellowstone grizzly bears. *Ecology* 80, 957–975.
- Servheen, C. 1990. The Status and Conservation of Bears of the World. Proceedings International Conference on Bear Research and Management. Monograph Series No. 2.
- Shaffer, M.L., 1981. Minimum population sizes for conservation. *BioScience* 31, 131–134.
- Shaffer, M.L., 1983. Determining minimum viable population sizes for the grizzly bear. Proceedings International Conference on Bear Research and Management 5, 133–139.
- Smith, B.L., 1990. Sex weighted point system regulates grizzly bear harvest. Proceedings International Conference on Bear Research and Management 8, 375–383.
- Swenson, J.E., Sandgren, F., Segerstrom, P., Brunberg, S. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 13 (in press).
- Swenson, J.E., Sandgren, F., Soderberg, A., Bjarvall, A., Franzen, R., Wabakken, P., 1997. Infanticide caused by hunting of male bears. *Nature* 386, 450–451.
- White, G.C., 2000. Population viability analysis: data requirements and essential analyses. In: Boitani, L., Fullers, T.K. (Eds.), *Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University Press, New York, NY, pp. 288–331.
- Wielgus, R.B., Bunnell, F.L., 1994. Dynamics of a small, hunted brown bear *Ursus arctos* population in southwestern Alberta, Canada. *Biological Conservation* 67, 161–166.
- Wielgus, R.B., Bunnell, F.L., 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation* 93, 145–154.
- Wielgus, R.B., Bunnell, F.L., Wakkenin, W.L., Zager, P.E., 1994. Population dynamics of Selkirk Mountain grizzly bears. *Journal of Wildlife Management* 58, 266–272.
- Wielgus, R.B., Sarrazin, F., Ferriere, R., Clobert, J., 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* 98, 293–303.