

Abundance and density of Central Purcell, South Purcell, Yahk, and south Selkirk Grizzly Bear Population Units in southeast British Columbia



¹ Birchdale Ecological
PO Box 920 • Kaslo, BC • V0G 1M0 • Canada • mproctor@netidea.com

² Integrated Ecological Research • Nelson, BC • V1L 5T2 • Canada

³ Conservation Analytics • Edmonton, AB • T6R 2W3 • Canada

⁴ US Fish and Wildlife Service • College of Forestry
and Conservation, 309 University Hall, • University of Montana, Missoula, MT • 59812 • USA

⁵ US Fish and Wildlife Service •
475 Fish Hatchery Road • Libby, MT • 59923 • USA

⁶ Wildlife Genetics International • Nelson, BC • V1L 5T2 • Canada

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Abstract

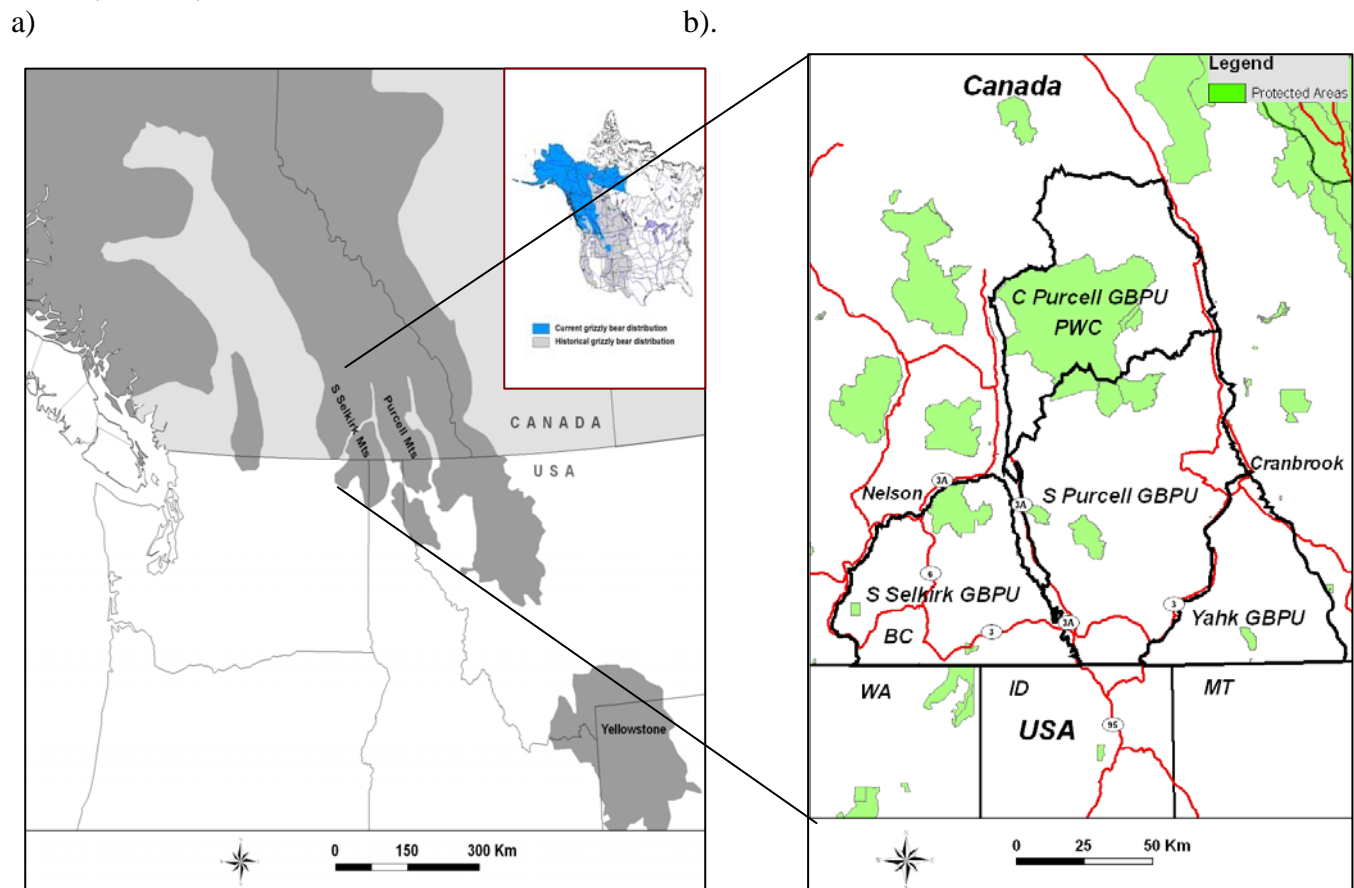
We analyzed DNA survey data for grizzly bears in the Purcell and south Selkirk Mountains of southeast British Columbia and produced population estimates for four Grizzly Bear Population Units (GBPU), the Yahk, South Purcell, Central Purcell, and South Selkirk. As part of a long-term grizzly bear population and ecology study we conducted grizzly bear DNA surveys in 1998, 2001, 2002, 2004, and 2005. Some surveys were designed specifically for population estimation and the remaining were designed for fragmentation, movement, and ecological modeling studies, but all were carried out with the same standardized field design. All surveys used hair-snag techniques as in Woods et al. (1999) with 4 consecutive 2-week hair collection sessions, which was optimal for population estimation. Using meta-analysis techniques we combined all the DNA surveys and generated population estimates for each grid, used GPS radio telemetry to adjust for closure violation where appropriate, and used ecological modeling to extrapolate estimates beyond the grids to the entire GBPU. We estimated the Yahk GBPU to have a density of 7.5 GB / 1000 km² with 20 bears (16 – 24, 95% CI), the South Purcell GBPU to have a density of 13.3 GB / 1000 km² with 92 bears (72 – 119, 95% CI), the Central Purcell GBPU to have a density of 18.9 GB / 1000 km² with 87 bears (67 - 124, 95% CI), and the south Selkirk GBPU to have a density of 14.3 GB / 1000 km² with 58 bears (50-70 95% CI). Our empirically-derived populations were considerably lower than BC Provincial estimates based on extrapolation from other populations.

Introduction

Population estimates can be crucial for setting hunting quotas, particularly for species with low reproductive rates. Grizzly bears exhibit low productivity (Bunnell and Tait 1981) and are susceptible to human-caused mortality other than legal hunting (McLellan et al. 1999; Nielsen et al. 2004a). British Columbia has a legal grizzly bear hunt throughout most of its occupied range and BC Provincial biologists and managers are faced with the challenge of obtaining accurate population estimates to better manage the legal hunt across what is a vast province with varied ecosystems. Due to inherent challenges in sampling grizzly bear populations, estimation of population size has frequently relied on extrapolations of benchmark populations and managerial expertise that rely on habitat or other variables which are not directly affected by changes in grizzly bear abundance. Ten years ago DNA sampling of wild bears was first suggested and demonstrated as a method for rapid (within 1-year) estimation of population size (Woods et al. 1999; Mowat and Strobeck 2000). Since that time over 26 grizzly bear

DNA surveys have been carried out in BC and Alberta (Proctor et al. 2007). Undoubtedly, this method has revolutionized population estimation of bears within Canada, North American, and across the world. Recent surveys have applied improvements in methodology and design that have brought significant improvements in precision and bias (Boulanger et al. 2004, 2005, 2007; Proctor et al. 2007). Methods also have been developed that allow for ecological-based extrapolation of grid estimates. Resource selection function (RSF) models have been used for predicting grizzly bear occurrence and habitat use for many purposes (Mace et al. 1996; Mace et al. 1999, Boyce and Waller 2000; Nielsen et al. 2002; 2004a; 2004b; 2006). We have integrated a variation of RSF modeling to extrapolate population estimates beyond sampling grids to ecosystem boundaries, thus providing biologically realistic estimates of population size by adjusting for habitat condition (Boyce et al. 1999; Apps et al. 2004). Here we report a meta-analysis of 6 such DNA surveys carried out over 5 years in adjacent ecosystems of the central and southern Purcell and Selkirk mountains of southeast BC which represent the Yahk, South Purcell, Central Purcell, and south Selkirk GBPUs (Fig. 1).

Figure 1 a) Current western North American grizzly bear distribution and b) Grizzly Bear Population Units (GBPUs) within the south Selkirk and Purcell mountains.



Methods

We used DNA hair snag methods and mark-recapture study design to estimate population size in 6 grids (Table 1) over an 8 year period for 4 adjacent GBPU's (Fig.2a). We used a meta-analysis within the software program MARK (White and Burnham 1999) to improve precision of individual grid estimates (Boulanger et al. 2002). Field methods were standardized within each grid and followed protocols detailed in Woods et al. (1999) which entailed use of rotted blood and fish scent lure at barb wire hair-snag stations to collect bear hair for eventual DNA "fingerprinting" analysis. Genetic identification of individual bears allows capture histories to generate mark-recapture data from repeated sample collections. All surveys used 4, 2-week hair collection sessions and sites were not moved between sessions. Four grids used 5km x 5km (25km²) cells (1 site / cell) and 1 grid used a sampling intensity equivalent to a 7km x 7km (49 km²) grid while another used a sampling intensity equivalent to a 8 km x 8km grid (Table 1). In the two grids with lower sampling intensities, site selection varied slightly from the strict grid design. We therefore drew convex polygons around the composite sampling area and computed the average area sampled by 1 DNA site. Site selection in all grids used the standard method employed by other grizzly bear surveys of selecting the best available grizzly bear habitat within each cell. Grid estimates were combined, corrected for closure violation using radio telemetry (Boulanger et al. 2004) or core extrapolations (Boulanger and McLellan 2001) and extrapolated based on habitat modeling (Apps et al. 2004) to entire GBPU's. Details of each procedure follow.

Table 1. Study area grids used for DNA surveys of grizzly bears in Purcell and S Selkirk mountains of southeast BC. All surveys were conducted at the same time of the year over 8 weeks between June 10 – Aug 10.

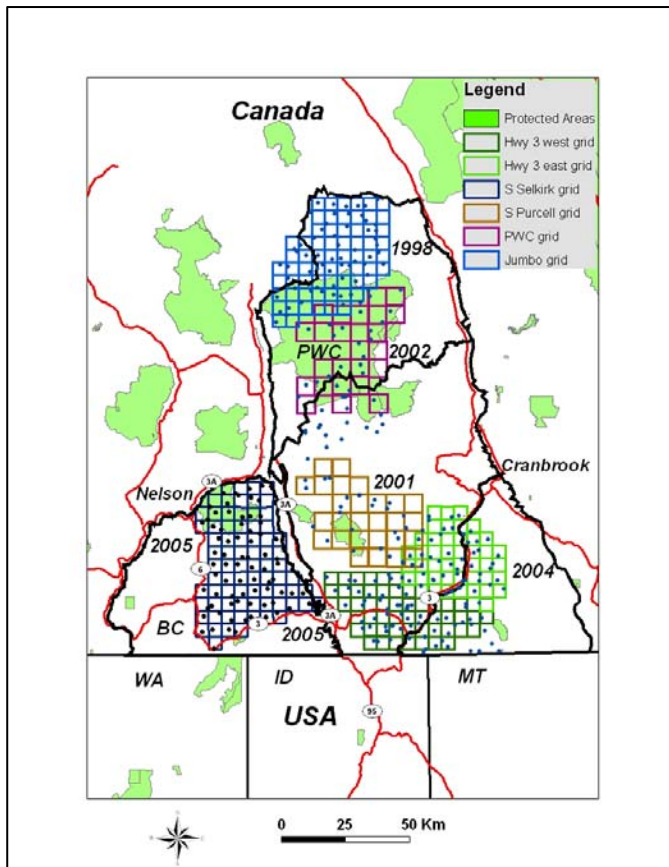
Study area	Year	Area km ²	Cell size km ²	# cells	# sessions
Jumbo	1998	1650	25	66	4
S Purcells	2001	1500	64	24	4
Purcell Wilderness Conservancy	2002	1300	49	26	4
Hwy 3 east	2004	1125	25	45	4
Hwy 3 west	2005	1375	25	55	4
S Selkirk	2005	1950	25	77	4
Total		8900		293	

Genetic analysis

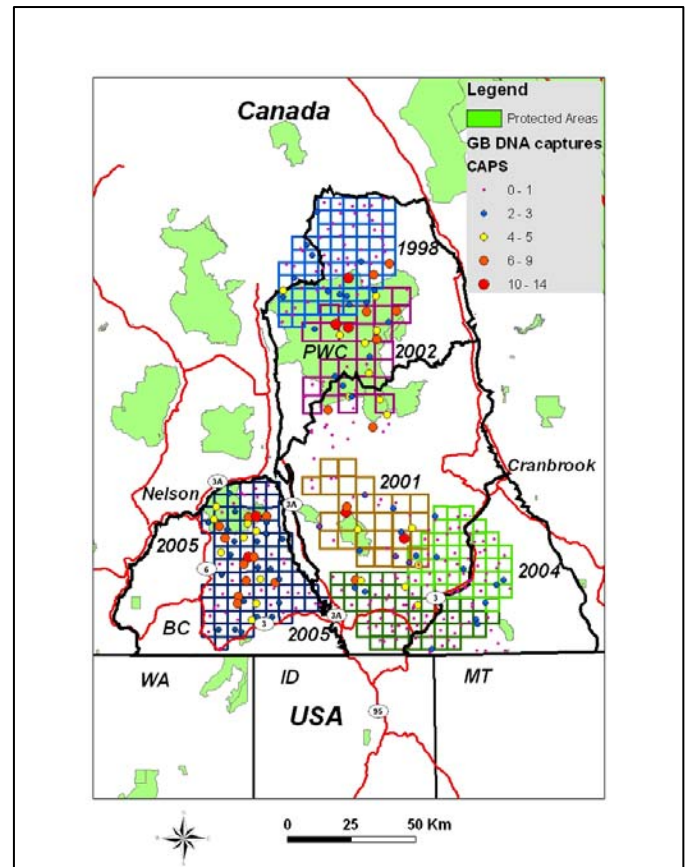
Hair samples collected during surveys were analyzed at Wildlife Genetics International (WGI) in Nelson BC excluding the Jumbo Survey which was analyzed at the University of Alberta by M. Proctor (PhD work). WGI has carried out over 100 bear DNA survey analyses. Lab methods and genotype scoring were standardized between projects and used 6- or 7-locus microsatellite genotypes (DNA fingerprints) for individual identification of bears, with the number of markers depending on the level of genetic variability in a given study area (Woods et al. 1999). Protocols detailed in Woods et al. (1999) and Paetkau (2003) were followed to minimize the risk of genotyping error leading to false individual identifications.

Figure 2. a) DNA grids and sites within the Purcell and Selkirk Mountains of BC and b) DNA captures. DNA sites outside of grids were not used for population estimation but were used for model extrapolation. Green areas are protected areas and red lines are highways.

a)



b)



Population estimation

Huggins (Huggins 1991) closed mixture models (Pledger 2000) were used to estimate population size in the grids where sampling was consistent (5x5 grids) (Boulanger et al. 2002). First, we estimated overall population size for the South Selkirk, Highway 3 east, Highway 3 west, and Jumbo projects. Each of these used a 5x5 km grid cell size. Second, we estimated population size for the South Purcell 2001 and the Purcell Wilderness Conservancy (PWC) surveys. These projects used larger cell sizes. We considered project-specific effects on capture probability as well as the effect of sex on capture probability. In particular, we considered models that allowed the relatively more closed South Selkirk grid to have unique capture probabilities compared to the relatively more open Purcell grids. We considered results from MARK meta-analyses and stand-alone analyses in program CAPTURE (Otis et al 1978) for final population estimates. The meta-analysis approach worked well for the smaller grid cell sized projects whereas stand-alone CAPTURE estimates were used for the larger grid cell sized projects. See appendix I for more details on meta analysis methods.

For purposes of combining the grid estimates in the Purcell Mountains, we divided the overall study area into 2 sections, north and south. We did this for several reasons. In the Purcell south study area (PSA) we ran grids in 2001, 2004, and 2005 and had a reasonable sample of GPS radio collared bears that we could use to correct for closure violation (White and Shenk 2001; Boulanger et al. 2004). The surveys in the north study area (PNA) were conducted in 1998 and 2002 and the closure correction was estimated as a component of the Jumbo/Central Purcell population survey of 1998 (see Boulanger Appendix within Strom et al. 1999). The Jumbo 1998 survey was carried out explicitly to estimate population size and closure violation was adjusted using a core-extrapolated method (Boulanger and McLellan 2001). The second reason was to improve the ecological modeling required to extrapolate population size to the entire GBPU (i.e. habitat-based extrapolation). Habitat characteristics differ considerably between the north and south study areas with the PNA being characterized by rugged mountains with abundant avalanche paths and alpine areas, whereas the southern area was less rugged, lower in elevation, and had fewer avalanche paths.

To estimate density we combined the grid estimates within both the PNA and PSA. In the PSA we first combined the meta-analysis grid estimates for the 2 5x5 grids (Hwy 3 east and Hwy 3 west) because this was the area where we had GPS radio collar data for closure correction. Because adjacent grids had a number of bears captured in each grid, we subtracted this number from the estimate to avoid counting these bears twice. To estimate the proportion of unmarked bears (those not captured but

potentially overlapping in both grids) we used the ratio of marked overlapping bears to the total number of captured bears and applied that to estimate the proportion of unmarked bears in the estimated total population. We also subtracted this estimate of unmarked overlapping bears from the total population. In practice there was a small proportion of overlapping bears between adjacent grids so the magnitude of overlapping unmarked bears was a small relative to the population (1-2 bears). This method of combining estimates in adjacent grids assumes relative population stability over the time period between surveys, and this is a reasonable assumption. Next we used our GPS radiocollar data to generate a closure correction (details below) by estimating the proportion of GPS locations that were on the grids (Boulanger et al. 2004). We combined the Hwy 3 east and Hwy 3 west estimates with the estimate of the S Purcell 2001 grid adjusting for overlapping bears as described above. We applied the closure correction to the overall estimate of the PSA and calculated a density by dividing the closure corrected estimate by the total area of the PSA grids. This process was repeated for the PNA by combining the Jumbo 1998 and the Purcell Wilderness Conservancy 2002 surveys.

Closure correction

Closure violation occurs when bears move in and out of the grid area during sampling. If closure violation exists, population estimates will reflect the “superpopulation” of bears in the sampling grid and surrounding area during the period of sampling (White 1996, Kendall 1999). For estimation of density and comparison between study areas, the average number of bears on the sampling grid at any one time is preferable. With the exception of the south Selkirk grid, all grids were carried out in terrain that was primarily open to bear movements on and off the study areas. Therefore we used two different methods to correct for closure violation. In the PSA we used GPS radiocollar locations from 9 grizzly bears (who were trapped within and across the 2004 and 2005 grids) for the months of the DNA surveys (June and July over 2 years). We determined the average percentage of time these bears spent on the grids and this became our closure correction factor. By multiplying the closure correction factor by the “superpopulation” estimate, we calculated the average number of bears that are on the grid during the study (McLellan 1989; White and Shenk 2001; Boulanger et al. 2004). We combined the estimates of variance from population estimates and the closure correction using the delta method (Seber 1982). Therefore our closure-corrected density and population estimates considered sampling error introduced by both of these components of the estimation process.

For the PNA we used a core-extrapolated method for estimating closure violation and a closure correction factor (Boulanger and McLellan 2001). We used the ratio of the full grid estimate to core-

extrapolated estimate to obtain an estimate of closure violation. Variance of the ratio was estimated by the delta method using the variances from the core and full grid population estimates (Seber 1982). The south Selkirk area was a stand-alone estimate and did not require closure correction because the grid went to natural (Kootenay Lake to the north and east) and anthropogenic barriers (Highways 6 and 3 to the west and south; Proctor et al. 2005). In reality there may have been slight closure violation across the two highways we used as borders, but past radio telemetry data suggests movement is minimal (W. Wakkinen pers. comm.).

Model-based extrapolation

The last step in the process was to use ecological modeling to extrapolate the grid estimates to the entire GBPU (Boyce et al. 1999; Manley et al. 2002; Apps et al. 2004). For modeling purposes (described above) we modeled the PNA which contains the Central Purcell GBPU separately from the PSA which contains the Yahk and South Purcell GBPU and separately from the south Selkirk GBPU. We used multiple logistic regression and a GIS to estimate probability of occurrence of a grizzly bear at any location in the GBPU. Our models were based on relationships between grizzly bear detections (0-absent or 1-present) from DNA surveys to various terrain (terrain ruggedness, slope, elevation), ecological (solar radiation, moisture), land cover (riparian, avalanche paths, alpine, forest cover, forest age, logging history, etc) and human-use (human occurrence points, roads, highway) predictors (Table 2). Variable data was obtained from a variety of sources, including, BC government Ministry of Forest TRIM (Terrain Resource Information Management), BTM (Baseline Thematic Mapping), VRI (Vegetation Resource Inventory data). The highway and human occurrence points (developments) layers were digitized from 1:50,000 topographic maps and ortho-photos, greenness was derived from Landsat imagery using a TasseCap transformation (Crist and Ciccone 1984), and slope, solar radiation, curvature index, and terrain ruggedness were derived from a digital elevation model. Data was modeled at the 100m x 100m pixel size.

Because grizzly bears select habitat and home ranges at multiple scales (Johnson's 1980; Manley 2002; Apps et al, 2004; Nams et al 2005) we modeled each GBPU at 3 scales as defined in Apps et al. (2004). The finest scale (Scale 1) was characterized by averaging each variable over a 2.4 km radius, approximating the average daily movement of a grizzly bear (B. McLellan unpub. data). The moderate scale (Scale 2) averaged each variable over a 6.8 km radius, approximating the female home range. Finally, the coarse scale (Scale 3) was over an 11.2 km radius, approximating a male home range. Our final models considered multiple scales depending on the variable and strength of relationship. For each

scale we assessed collinearity of explanatory variables and removed one of the two correlated variables when Pearson's correlations were >0.7 . Univariate analyses relating the detection of grizzly bears against each explanatory variable were tested and recorded for significance. All significant ($p < 0.1$), uncorrelated variables were considered during multivariate model development. We used the principles of Hosmer and Lemeshaw (1989) for model building where individual variables were added sequentially based on their univariate level of significance (from most significant to least significant), retaining only those variables that were significant ($p < 0.1$) in the multivariate model.

Once multi-variate models were estimated they were used to extrapolate grizzly bear densities within a grid to the entire GBPU. We applied estimates to the same set of variables within our best models to the entire GBPU. In this way, density for the GBPU was estimated and using the GBPU area, the population size is estimated (Boyce et al. 1999). Our best models were used to partition the densities among the Yahk and South Purcell GBPU within the PSA. We have not been able to apply a workable estimate of confidence intervals to this process of model-based extrapolation, and therefore our overall confidence limits will be underestimated. We anticipate this aspect of error estimation will be developed soon due to the popularity of habit modeling.

Model validation

We tested the ability of our models to classify the DNA occurrence results using a confusion matrix (McGarigal et al. 2000). We determined a cut-off probability (a threshold score where the model predicts the occurrence of a bear) using a sensitivity/specificity analysis (Liu et al. 2005). The cut-off probability was then used to classify presences of grizzly bears. A confusion matrix was generated and the overall classification accuracy determined as the ratio of correct classifications (absences and presences) to the total number of classifications.

Because we have radio collared bears in the Purcell south study area, we validated our best multi-scale model using GPS radio location data. Here we used a Spearman's rank correlation test (Sokal and Rohlf 1995) to compare the similarity of our model in predicting DNA captures (that were used to build the model) and independent GPS radio location data for the same area. The correlation test was performed on the two data sets where RSF scores were categorized in equal bins and adjusted for area (Boyce et al. 2002).

Table 2. Predictor variables used in ecological modeling. Abbreviations are for terms used in our multi-variate models presented in Table 5.

	Variables		Variables
Land cover	Alpine Avalanche (aval) Barren Burn Riparian (rip)	Ecological	Elevation Curvature Index (cti) Terrain ruggedness index (tri) Greenness (green) Slope Solar radiation
Forest cover	Forest age (age) % crown closure (cc) Old forest (ofor) Young forest (yfor) Recently logged (rlog) Cedar – Hemlock (ch) Spruce - Sub alpine fir Douglas Fir (dfir) Lodgepole pine (lpine) White pine Deciduous (decid)	Human	Human developments (hop) Highway Roads (road) Parks (park)

Confidence Intervals

The closure-corrected estimates for grid areas had standard errors that considered both the variance estimates from the mark-recapture estimation process and the closure correction process. We calculated log-based confidence-intervals for the average number of bears on the sampling grid estimates using formulas presented in White et al. (2001). These estimates were then extrapolated to the larger GBMU areas using RSF-based extrapolation. No error estimate has been developed for RSF-based extrapolation of population estimates from multi-scale RSF models. Therefore, the variance estimates, and confidence intervals were simply multiplied by the factor of increase/decrease between the closure corrected estimates and the RSF extrapolated estimate. This assumes there is no additive error by the RSF extrapolation process.

Results

The 6 grids used in our meta-analysis covered 8900 km² where we sampled 293 DNA hair-grab sites (Table 1, Fig. 2a). We detected 148 different grizzly bears in 264 capture events (Table 3, Fig 2b). We provide a mismatch distribution from one of our DNA grids (Fig. 3, S Selkirks: others were similar) to demonstrate the low probability that there are erroneous bears in our data set as a result of genotyping

error (Paetkau 2003), and to show that match probabilities were not high enough to create a meaningful negative bias in the population estimates. The capture probabilities for the grid estimates range from 0.27 to 0.47 and averaged 0.35 (Table 3). As discussed further in Appendix 1, meta-analysis results suggested that heterogeneity of capture probabilities existed in all populations, however, behavioural response, or excessive time variation was not detected. The closure correction for the PSA based on the proportion of GPS radio locations occurring within the grid was 0.73 (SE=0.11, n=9 bears) (Fig. 4). In the PNA the closure correction was found to be 0.87 (SE=0.19, n=2 N estimates) (see Boulanger, Appendix I within Strom et al. 1999).

Extrapolation modeling for both the north and south study areas yielded probability of occurrence models that were averaged over 3 scales. The PSA contained both the Yahk and South Purcell GBPU, the PNA contained the Central Purcell GBPU, and the S Selkirk study areas contained the South Selkirk GBPU (Fig. 2a).

Figure 3. Distribution of similar genotypes for 79 mismatching multi-locus grizzly bear genotypes from the South Selkirk Mountains. Extrapolation of the 7-locus distribution yields a prediction of match probability, suggesting ~ 0.1 pairs of individuals with identical genotypes in this area (i.e. very low match probability). The 15-locus distribution has the most power to rule out genotyping errors. The proper interpretation of the 15 locus curve indicates that there is one pair of individuals whose genotypes differs by 3 markers. The likelihood of this occurring through genotyping error is diminishingly low.

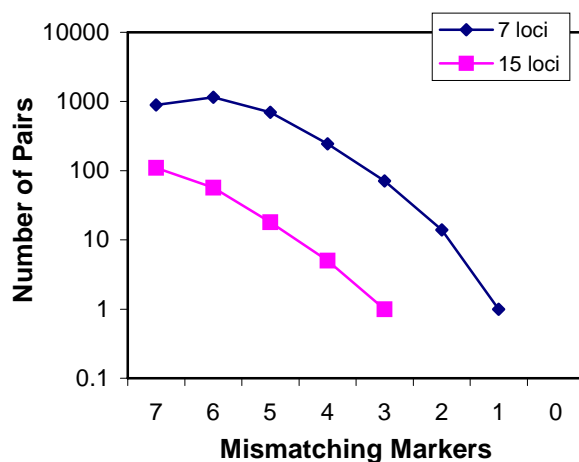
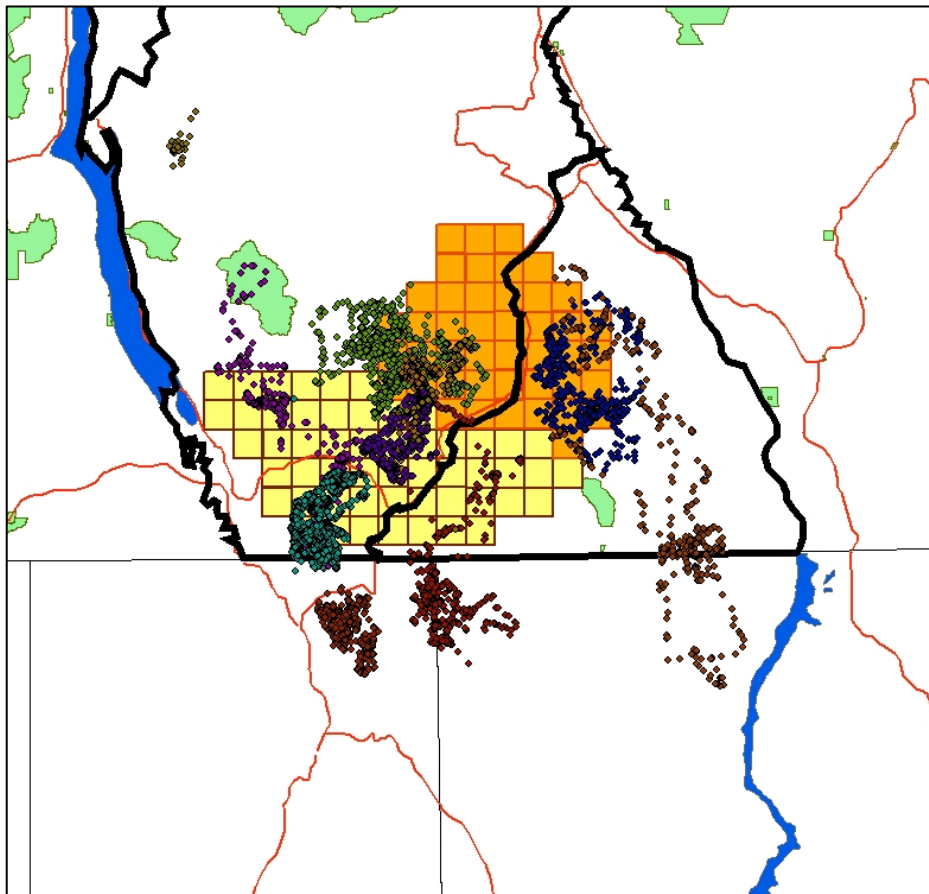


Table 3. Grid areas and meta-analysis derived population estimates. \hat{p} is the capture probability which represent an estimate of the number of bears captured within each session relative to the total population (Boulanger et al, 2002).). Estimates are from Mh (Chao). These estimates of capture probability are most comparable to other studies conducted in the province.

Study area	GB IDs	N	95% CI	\hat{p}
Jumbo	28	37	32-45	0.31
S Purcells	29	45	35-55	0.27
Purcell Wilderness Conservancy	36	53	43-87	0.33
Hwy 3 east	12	16	14-21	0.30
Hwy 3 west	20	23	20-30	0.29
S Selkirk	30	36	32-45	0.47

Figure 4. Map of Closure correction process for the 2004 and 2005 Hwy 3 DNA surveys. Nine GPS radio collared grizzly bears were used in the calculation. 8586 of 11822 locations were found inside the grid in the June-July period resulting in a 0.73 closure correction factor. The West Slope 3 year average closure correction factor was 73% (Boulanger et al. 2004).



We found that habitat associated with grizzly bear detections in our DNA surveys was consistent across study areas. Table 4 summarizes these habitat associations. In June and July bears selected habitats that were higher elevation, rugged terrain, in alpine or avalanche chutes. They also tended to select older forests and forests dominated by Douglas fir (*Tsuga menziesii*) or Englemann Spruce – sub-alpine fir (*Picea englemann* - *Abies lasiocarpa*) stands. They tended to avoid human features such as roads, highways, and human developments (buildings etc.). Bears also avoided cedar-hemlock (*Thuja plicata* - *Tsuga heterophylla*) and lodgepole pine (*Pinus contorta*) forest stands. Interestingly, wet areas, such as riparian and curvature index denoting wet areas (cti) were avoided. This is likely due to their association of wet areas with valley bottom roads. Riparian habitats associated with parks were selected while riparian habitats associated with roads were avoided. Greenness, a variable that represents an overall green leafy index derived from Landsat images (Crist and Ciccone 1984), was selected except when associated with human features such as highways or human development. When recently logged areas were associated with alpine areas, these habitats were avoided in the PNA but selected for in the south Selkirk area. This association may reflect the availability of alternative high quality alpine habitats in the north Purcell areas, whereas the south Selkirk has less high quality high elevation alpine habitat.

Table 4. Significant variables from univariate analyses that indicate grizzly bear selection or avoidance of specific habitat characteristics. These variables were consistently selected or avoided across all study areas within this project and used to build multi-variate models for each study area.

Selection Variable	sign	Avoidance Variable	
		roads	--
elevation	+	highways	--
avalanche	+	human development	--
alpine	+	deciduous forest	--
slope	+	lodgepole pine	--
terrain ruggedness	+	cedar-hemlock	--
old forests	+	young forest	--
Douglas fir	+	curvature - wetness	--
greenness	+	riparian	--
park	+	riparian-roads	--
riparian-park	+	forest age	--
		greenness-human develop	--
		greenness-highways	--

The best models within each study area (Table 5) were combined into multi-scaled models for each GBPU (Fig. 4). Classification accuracy of our models was generally good ranging between 0.67 and 0.84 (Table 6). In the PSA where we had GPS radio telemetry locations, we found that our best DNA-derived multi-scale model predicted the habitat use of radio collared grizzly bears quite well. The binned model scores for the DNA hits and GPS radio locations were highly correlated (Spearman's rank correlation, 0.92).

Table 5. Variables and coefficients for the multi-variate models for each study areas at all 3 scales.

PSA S1			PNA S1			SS S1		
Var	Coef	p	Var	Coef	p	Var	Coef	p
decid	-3.455729	0.051	road	-22.4488	0.004	aval	29.92909	0.022
rlog	3.964161	0.03	lpine	-5.36566	0.061	cti	305.497	0.013
ofor	5.120177	0.013	yfor	7.282218	0.074	cti2	-21.5285	0.014
road x ofor	-76.61629	0.002	yfor2	-15.9006	0.045	cc	0.237233	0.016
green	3.171877	0.018	constant	0.361149		constant	-1092.11	
green2	-0.0105179	0.018						
tri	0.027061	0.014						
constant	-241.3534	0.017						
PSA S2			PNA S2			SS S2		
Var	Coef	p	Var	Coef	p	Var	Coef	p
road	-38.38919	0.006	alpine	92.23757	0.012	ofor	13.13757	0.002
road2	134.7026	0.015	alpine2	-156.334	0.011	dfir	-100.269	0.019
green	4.654343	0.019	age	-0.26971	0.003	dfir2	299.4782	0.01
green2	-0.0155847	0.018	age2	0.003081	0.002	rip-park	406.1594	0.008
hop	-10.94788	0.022	rip-park	124.7762	0.001	green	11.15206	0.061
age	-0.072429	0.012	lpine	-6.03076	0.011	green2	-0.03771	0.065
constant	-340.8867	0.023	constant	-8.23042		constant	-820.451	
PSA S3			PNA S3			SS S3		
Var	coeff	p	Var	Coef	p	Var	Coef	p
age	-0.132973	0	road	-30.3703	0.008	rip	-123.044	0.015
hop	-18.95928	0	lpine	-7.43301	0.081	green	25.31754	0.001
cc	-0.3147559	0.006				green2	-0.08624	0.001
constant	19.69139	0				cti	3.590039	0.011
						dec	61.39468	0.045
						constant	-1880.42	

Figure 4. Population estimates for the South Selkirk, Central Purcell, South Purcell and Yahk GBPUs. The closure corrected and model extrapolated estimates are the bold numbers (58, 87, 92 & 20) and the number below them in parentheses are the BC Provincial estimates, prior to this analysis.

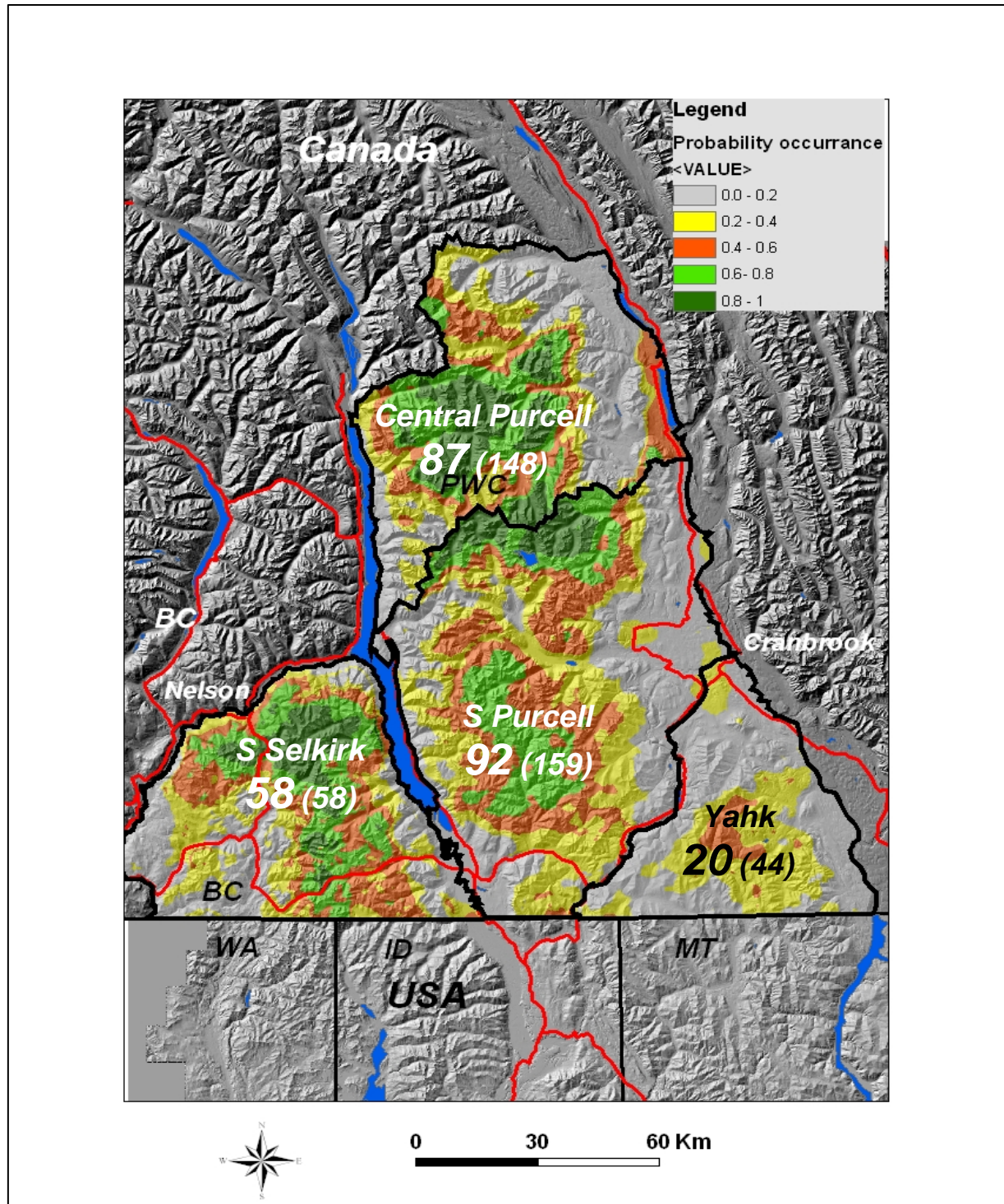


Table 6. Classification accuracy for the “best” models at each of the three scales examined for three study areas. Values represented the proportion of correctly classified bear captures and sites that did not detect bears using cut-off probability thresholds for prediction. For example, in the North study area, the scale 1 (the finest scale) model correctly predicted bear capture locations and sites that did not detect a bear 75% of the time.

Study area	Scale 1	Scale 2	Scale 3
Purcell North study area	0.75	0.78	0.67
Purcell South study area	0.74	0.68	0.71
South Selkirk	0.73	0.85	0.81

The closure corrected and model extrapolated population estimate for the Yahk GBPU is 20 (16 – 24, 95% CI) bears at a density of 7.5 GB / 1000 km² (5.9 – 10.0, 95% CI). The South Purcell GBPU is estimated to hold 92 bears (72 – 119, 95% CI) at a density of 13.3 GB / 1000 km² (10.5 – 17.2, 95% CI), the Central Purcell GBPU, 87 bears (67 – 124, 95% CI) with a density of 18.9 GB / 1000 km² (14.4 – 26.9, 95% CI), and the South Selkirk GBPU, 58 GB / 1000 km² (50-70, 95% CI) at a density of 14.3 GB / 1000 km² (12.2 – 17.1, 95% CI) (Table 7). Our DNA survey-derived abundance and density estimates were considerably lower than official BC Provincial estimates (Hamilton et al. 2004) currently being used to set hunting quotas (Table 8).

Table 7. Closure corrected and ecological model-extrapolated population and density estimates for 4 Grizzly Bear Management Units in southeast BC.

GBPU	Area km²	Density GB / 1000km²	Density 95% CI	Pop Est GB	Pop Est 95% CI
Yahk	2719	7.5	5.9 - 10.0	20	16 - 24
South Purcell	6898	13.3	10.5 - 17.2	92	72 - 119
Central Purcell	4619	18.9	14.4 – 26.9	87	67 - 124
South Selkirk	4070	14.3	12.2 - 17.1	58	50 - 70

Table 8. New population estimates compared to BC provincial population estimates as in Hamilton et al. (2004) and the relationship to capability (how many bears can the GBPU contain under current conditions)

GBPU	Pop Est GB	BC estimate GB	BC capability GB	BC % of Cap	This report % of Cap
Yahk	20	44	101	43%	20%
South Purcell	92	158	198	80%	46%
Central Purcell	87	150	162	93%	54%
South Selkirk	58	58	131	44%	44%

Discussion

Our density estimate for the Canadian south Selkirk GBPU (14.2 GB / 1000 km²) is lower than that estimated by Wielgus et al. (1994) (23.3 GB / 1000 km²). This discrepancy may be explained by the fact that our estimate encompasses the entire GBPU (which includes good and marginal habitat) while those of Wielgus et al. (2004) were limited to a “core” area of higher quality habitat where they radio collared bears. Wakkinen and Kasworm’s (2004) long-term study of population demographics in the international Yahk ecosystem did not provide a density estimate for the Canadian Yahk GBPU (although within their study area) but report an overall declining population trend of approximately 3.7% per year corroborating our low density estimate (7.5 GB / 1000 km²) for the Yahk GB. There are no prior data-based population estimates for the central and south Purcell GBPUs. However, Strom et al. (1999) report a pre-closure corrected population estimate of 45 for the Jumbo DNA survey of 1998. Here we report an estimate of 37 for the same area (Table 3). The reason for this difference is that our more thorough analysis found several genetic errors within that original work that caused the previous estimate to be high.

Our estimates of abundance and density for the Purcell Mt. GBPUs were considerably lower than BC Provincial predictions (Table 8). Historically, BC Provincial estimates were generated from the Fuhr Demarchi (1990) method that relied on qualitative assessments of habitat quality, disturbance, land use changes, and mortality history relative to one of two benchmark populations. More recently, most GBPUs in interior BC are estimated from a province-wide multiple regression modeling exercise with an increased number of benchmark populations (from recent DNA surveys and other research; Mowat et al. 2004) and these include the Yahk, S Purcell, Central Purcell GBPUs (as detailed within Hamilton et al. 2004). In some GBPUs an improved expert Fuhr Demarchi estimate is used (i.e. the south Selkirk

GBPU, Hamilton et al. 2004), and in others direct DNA inventory estimates, as reported here, are used (Hamilton et al. 2004). We suggest that due to the discrepancy between the Provincial estimates for the Yahk, South Purcell, and Central Purcell GBPU's (Table 8) and those reported here, our DNA survey-based estimates should be used (in fact our estimates have been incorporated as official Provincial estimates. G. Mowat, Nelson regional BC Provincial biologist, pers. comm.). Population-specific estimation data is usually preferable to extensive extrapolations. Our estimates result from 5 years of DNA survey effort within the target area where the need to extrapolate based on habitat was minimal. While not all grid estimates were done with population estimation as a primary goal, all surveys were designed to have standardized field methods. The difference among surveys was the sampling intensity and year.

Our results do not suggest that BC provincial population estimates of grizzly bear population size have been systematically too high. Until recently (2004) Provincial estimates were derived from the Fuhr Demarchi (1990) process and hunt quotas for all of BC were set from this process. Boulanger and Hamilton (2001) examined the relationship between grizzly bear population estimates derived from the recently developed DNA survey method (Woods et al. 1999) and the BC Provincial Fuhr Demarchi (1990) method. In a comparison using 9 DNA projects, they found that on average, the estimates from each method were not statistically different even though there were significant differences in specific areas. This suggests that historic population estimates for setting hunt quotas across BC were reasonable, on average.

As mentioned, recently the Fuhr Demarchi (1990) method was generally replaced due to its subjective nature that relied on qualitative estimates by managers (Peek et al. 2004). The method used today across most of the province is the regression-based model that relies on several parameters. We recognize that the model used to generate predictions of GBPU size is dynamic (it evolves). The model presented in Mowat et al. (2004) used 5 parameters (salmon, 10-year mean percent kill, connectivity, precipitation, and human+livestock density) to estimate population densities across the entire province. It assumed one value for each of the parameters for a given GBPU. In cases where a GBPU has heterogeneous landscapes due to anthropogenic disturbance, habitat degradation and fragmentation, and long-term overkill, (i.e. the GBPU's in this study), this model may be challenged to properly characterize these finer scale effects that may have a real impact on local grizzly bear populations. The net result is that estimates from this model may be biased high in GBPU's that have complex, heterogeneous, landscapes due to anthropogenic disturbance. We suggest that regression-based estimates be applied

cautiously especially in southern British Columbia where landscapes and bear mortality history is complex making extrapolation from a broad-scale model challenging, and in GBPUs where solid locally-derived data exist, those estimates should take precedence.

Habitat selection, as determined by our ecological modeling, was found to be similar to that in other habitat modeling efforts for grizzly bears. DNA surveys were primarily conducted in June and July, therefore our modeling results reflect bear habitat use during those months. Apps et al. 2004 working in Columbia Mountains of BC, also modeled habitat in relation to DNA survey results and found avoidance of human features including roads, highways, and human developments with selection for rugged remote terrain, older forests, alpine, and avalanche habitats. Mace et al. (1996) used VHF telemetry data from northwest Montana as a basis for modeling habitat use and found similar patterns, concluding that while bears can persist in areas with roads and human activity, avoidance and mortality will increase as human access and development increase. The Mace et al. (1996) work underpins the US-wide (where grizzly bears persist) legal mandate for access management standards in “recovering” grizzly bear populations. These region-wide patterns that were also found to hold true across our two mountain ranges may hint at the causes for the lower than expected estimates in the Purcell Mountains. However, before firm conclusions can be drawn, more specific work is required on road densities and “core” habitat (habitat away from roads) and their relation to grizzly bear habitat use and mortality risk within these study areas (Nielsen et al 2004a, 2006). Our research team has begun such efforts and several hypotheses will be explored ranging from systemic biases in historic estimates to increased human access to excessive hunting quotas.

The major advantage of our model-based extrapolation used here is that it starts from an extensive dataset of local grizzly bear ‘capture’ events and yields a far more ecological-based realistic extrapolation. The historic alternative of applying densities where surveys took place, often in areas where bears are more abundant, to the edges of GBMUs where abundance is often diminished, especially in populated areas like the Purcell and Selkirk Mountains, is likely to result in an over-estimate of grizzly bear population.

While the DNA grids in this project tended to be small, sampling was intense relative to other Canadian DNA surveys. The average grid size in our study was 1517 km² while the average over 26 surveys in BC and AB is approximately 4000 km² (Proctor et al. 2007). The range of cell sizes across BC and AB is between 25 km² to 100 km². Our cell sizes were predominantly 25 km² with one 49 km² and one 64 km². All our grids were characterized by having relatively high capture probabilities (range –

0.28-0.47. Table 3) well above the 0.2 threshold where model selection is improved from having enough captures and recaptures to detect forms of capture variation and heterogeneity (Boulanger et al. 2002, 2004). The range of capture probabilities across BC and AB is from 0.1 – 0.5 (Proctor et al. 2007). Furthermore, improvements have been demonstrated in our ability to carry out DNA surveys in recent years yielding population estimates that have better precision and minimal bias. (Boulanger et al. 2005, 2006; Proctor et al. 2007).

Meta-analysis had the desirable effect of improving precision for the individual grid estimates. Ideally, the study would have benefited from two large DNA surveys (one in the Purcell and another in the Selkirk Mts.) to minimize closure violation and increase our sample sizes. However, as previously mentioned, population estimation was not the primary goal in several of the surveys. Compensatory advantages can be found in our ability to spread limited financial resources over several years, sample intensively over a large area allowing high capture and recapture rates, and our ability to take advantage of a simultaneous GPS radio collaring effort for a direct measure of closure violation. On balance, we feel that the meta-analysis, closure correction, and ecologically-based model-extrapolation yield an objective data-based population estimate for a large area encompassing 4 GBPU's.

Although our approach was an improvement over other estimates, some limitations should be considered. Our method assumes that populations were relatively stable over the 4 years that surveys were conducted. If they were not, then our estimates represent an approximate average of estimates over the 4 year period weighted by when a study area was sampled relative to the overall trend. However, we suspect that the amount the population potentially changed during surveys was not large given the fact that bear populations do not exhibit extreme fluctuations over relatively short time periods. Also, there was an increased chance in the two larger cell-sized projects (where sampling sites were not moved) in the Purcells that some females were not detectable (i.e. 0 capture probability) potentially creating a negative bias in estimates (Boulanger et al. 2006). However, the degree of bias is unlikely to be high enough to make our estimates of the same magnitude (approximately twice) as the BC Provincial extrapolated estimates. We also assumed that no error was introduced into population estimates by RSF-based extrapolation. In reality, error was introduced with ecological modeling, however, no method to estimate error rates from multi-scale RSF models had been developed. Therefore, the precision of our estimates is expected to be slightly lower than we have indicated. Finally, we assumed that the population size and density of these areas was relatively similar which allowed us to consider estimates from different years.

As detailed in Appendix 1, the meta-analysis approach tested a full range of mark-recapture models. For example, models that allowed project, sex, time-variation, projectXsex specific, and projectXtime variation capture probabilities were introduced into the analyses. In addition, mixture models that allowed undefined heterogeneity variation were tested with the data, therefore potentially accounting for variation that could not be directly parameterized. We then averaged the estimates of these models by their relative support by the data allowing estimates from the full range of models. This provided a comprehensive and objective method of estimating population size for various grid areas that had reasonably standardized methodologies. One interesting result was that models with behavioral response (or sex-specific behavioral response) were not supported by the data. This result is different than the results of Boulanger et al (2006) that suggested male capture probabilities decreased after initial capture (presumably due to trap habituation) when sites were not moved. This difference was potentially due to a lower overall sampling intensity relative to home range and lower test power. However, we also note that a “trap-shy/habituation” behavioural response results in positively biased estimates of population size since the marked population capture probabilities are biased low (causing N to be biased high). The overall effect of behavioral response was minimal with estimates from behavioural response models were only 4% higher than the estimates used in this analysis.

The Yahk and South Selkirk GBPU are considered “threatened” by the BC Province by virtue of being estimated at below 50% of their habitat capability (Hamilton et al. 2004). Current Provincial estimates of the relationship between habitat effectiveness (current bear numbers) and habitat capability (potential bear numbers habitat could contain) for the south Purcell GBPU is 80% while the Central Purcell GBPU is 93%, the Yahk GBPU at 44%, and the Selkirk GBPU is 44% (Table 8). Our population estimates for the Purcell GPBUs suggest these values are considerably lower with the South Purcell GBPU at 46%, the Central Purcell GBPU at 54%, and the Yahk GBPU at 20% (Table 8). Our estimate and the Provincial estimate for the South Selkirks are identical. These numbers are relevant because they underpin the Provincial management approach applied to GBPU. GBPU with values considerably above 50% can typically sustain human-caused mortality and are less likely to be driven to threatened status (below 50% capability; Austin et al. 2004). GBPU with values approaching 50% should be managed more conservatively and may require management designed to increase population size to maximize future hunting quotas. Provincial determination of the conservation status of the South and Central Purcell GBPU should be considered.

Of particular note is that the Purcell GBPU have considerably fewer bears than suspected or expected. These mountain ranges hold peninsular populations within a fragmented regional population (Proctor 2003, Proctor et al. 2005), as shown by the breaks across and between mountain ranges in our probability of occurrence model (Figure 4). The southern tip of the Purcell population south of BC Highway 3 (the Yahk GBPU) has been shown to be fragmented (Proctor et al. 2005) and declining (Wakkinen and Kasworm 2004). The future persistence of the south Purcell and Yahk GBPU (and into the US) is likely reliant on being connected to a healthy grizzly bear population in the Central Purcells. While the PNA was still below expected, the PWC (~2000 km²) has a relatively high density of grizzly bears. This protected area has the potential to act as a source population for the surrounding area and assist in the recovery of the Central Purcell, South Purcell, and Yahk GBPU. This logic follows the stated management intention of the BC MoE to manage for regional source populations (Austin et al. 2004; Peek et al. 2003). The good news is that there is a mechanism to modify rates of human-caused mortality by adjusting hunt quotas.

Our study demonstrates the need to periodically assess the status of hunted grizzly bear populations using methods that are based on local capture data, and not completely rely on correlates of abundance derived from distant times or locations. This need holds true particularly in areas where other human-related pressures are likely to impact bear populations, (high human access, road densities, etc.), and particularly along the fringe of the species range where population fragmentation and decline has led to dramatic loss of range in the past (McLellan 1998). BC is vast and grizzly bears occupy approximately 75% (750,000 km²) of the Province, therefore, not all population can be realistically monitored. However, key areas of the province, where humans and grizzly bears extensively overlap should be considered for periodic surveys of grizzly bear abundance.

Literature Cited

- Apps, C.D., B.N. McLellan, J.G. Woods, and M. Proctor. 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management*. 68:138-152.
- Austin, M.A. , D.C. Heard, and A.N. Hamilton. 2004. Grizzly bear (*Ursus arctos*) harvest management in British Columbia. British Columbia Ministry of Water, Land, and Air Protection, Biodiversity Branch. Victoria, B.C. 9 pp.
- Boulanger, J. and A.N. Hamilton. 2001. A comparison of DNA mark-recapture and Fuhr-Demarchi / stepdown population and density estimates for grizzly bears in British Columbia. BC. Ministry of Environment. Victoria. BC.
- Boulanger, J. and B.N. McLellan. 2001. Closure Violation in DNA-based mark-recapture estimation of grizzly bear populations. *Canadian Journal of Zoology*. 79:642-651.
- Boulanger, J.B., G.C. White, B.N. McLellan, J. Woods, M. Proctor, and S. Himmer. 2002. A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada. *Ursus*. 13:137-152.
- Boulanger, J., McLellan, B.N., Woods, J., Proctor, M.F., and Strobeck, C. 2004. Sampling design and bias in DNA based capture-mark-recapture population and density estimates of grizzly bears. *Journal of Wildlife Management* 68:457-469.
- Boulanger, J., G. Stenhouse, G. MacHutchon, M. Proctor, S. Himmer, D. Paetkau, and J. Cranston. 2005. Grizzly Bear Population and Density Estimates for the 2005 Alberta Unit 4 Management Area Inventory. Report Prepared for Alberta Sustainable Resource Development, Fish and Wildlife Division.
- Boulanger, J., M. Proctor, S. Himmer, G. Stenhouse, D. Paetkau, and J. Cranston. 2006. An empirical test of DNA mark-recapture sampling strategies for grizzly bears. *Ursus* 17:149-158.
- Boyce, M.S. and L.L. McDonald. 1999. Relating populations to habitat using resource selection functions. *Trends in Ecology and Evolution*. 14:268-272.
- Boyce, M.S. and J.S. Waller. 2003. Grizzly bears for the Bitterroot: predicting potential abundance and distribution. *Wildlife Society Bulletin* 31:670-683.
- Boyce, M.S., P.B. Vernier, S.N. Nielsen, F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling*. 157:281-300.
- Bunnell, F.L. and D.E.N. Tait. 1981. Population dynamics of bears - implications. In, T.D. Smith and C. Fowler (Eds.). *Dynamics of large mammal populations*. John Wiley and Sons. New York. pp. 75-98.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. *Biometrics* 45:427-438.

- Crist, E.P. and R.C. Ciccone. 1984. Application of the tasseled cap concept to simulate thematic mapper data. *Photogrammetric Engineering and Remote Sensing* 50: 343-352.
- Fuhr, B., and D.A. Demarchi. 1990. A methodology for grizzly bear habitat assessment in British Columbia. B.C. Ministry of Environment, Lands and Parks, Victoria, Wildlife Bulletin B-67. 28 pp.
- Hamilton, A.N., D.C. Heard, and M.A. Austin. 2004. British Columbia grizzly bear (*Ursus arctos*) Population estimate 2004. British Columbia Ministry of Water, Land, and Air Protection, Biodiversity Branch. Victoria, B.C. 7 pp.
- Hosmer, D.W., Jr. and S. Lemshaw. 1989. *Applied Logistic Regression*. John Wiley & Sons, New York, New York, USA.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725-732.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* 80(8):2517-2525.
- Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28, 385–393.
- Mace, R.D., J.S. Waller, T.L. Manley, L.J. Lyon, and H. Zuring. 1996. Relationships among grizzly bears, roads, and habitat use in the Swan Mountains, Montana. *Journal of Applied ecology*. 33:1395-1404.
- Mace, R.D., J.S. Waller, T.L. Manley, K. Ake, and W.T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in Western Montana. *Conservation Biology* 13:367-377.
- Manly, B.F.J., L.L. McDonald, D.L. Thomas. T.L. McDonald, and W.P. Erickson. 2002. *Resource Selection by Animals*. Kluwer Academic Publishers. Boston. 221 pp.
- McGarigal K. S. Cushman, and S. Stafford. 2000 *Multivariate Statistic for Wildlife and Ecology Research*. Springer. New York. 283 pp.
- 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. 1998. Maintaining viability of brown bears along the southern fringe of their distribution. *Ursus*. 10:607-611.

- McLellan, B.N., F. Hovey, R.D. Mace, J.G. Woods, D.W. Carney, M.L. Gibeau, W.L. Wakkinen, and W.F. Kasworm. 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.
- Mowat, G. and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. *Journal of Wildlife Management*. 64:183-193.
- Mowat, G., DC. Heard, and T. Gaines. 2004. Predicting grizzly bear (*Ursus arctos*) densities in British Columbia using regression model. British Columbia Ministry of Environment. Victoria, BC. 16 pp.
- Nams, V.O, G. Mowat, and M.A. Panian. 2005. Scale dependent habitat selection by grizzly bears. *Biological Conservation* 128:109-119.
- Nielson, S.E., M.S. Boyce, G.B. Stenhouse, and R.H.M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus*:13:45-56.
- Nielsen, S.E., S. Herrero, M.S. Boyce, R.D. Mace, B. Benn, M Gibeau, and S. Jevons. 2004a. Modeling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies Ecosystem of Canada. *Biological Conservation* 120:101-113.
- Nielsen, S.E., M.S. Boyce, and G.B. Stenhouse. 2004b. Grizzly bears and forestry I: selection of clearcuts by grizzly bears in west-central Alberta. *Forest Ecology and Management* 199:67-82.
- Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. *Biological. Conservation*. 130:217–229.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1-135.
- Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology*. 12:1375-1387.
- Peek, J., J. Beecham, D. Garshelis, F. Messier, S. Miller, and D. Strickland. 2003. Management of grizzly bears in British Columbia: a review by an independent scientific panel. BC Ministry of Water, Lands, and Air Protection. Victoria. 90 pp.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed models using mixtures. *Biometrics* 56:434-442.
- Proctor, M.F. 2003. Genetic analysis of movement, dispersal and population fragmentation of grizzly bears in southwestern Canada. PhD Thesis. University of Calgary. 147 pp.
- Proctor, M., B.N. McLellan, C. Strobeck, and R. Barclay. 2005. Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proceedings of the Royal Society, London*. 272:2409-2416.

- Proctor, M., B. McLellan, J. Boulanger, C. Apps, G. Mowat, D. Paetkau, and G. Stenhouse. 2007. Ecological investigation of Canadian grizzly bears using hair-snaged DNA, 1995-2005. *Ursus*. Submitted.
- Seber, G. A. F. 1982. *The Estimation of Animal Abundance*. London: Charles Griffin and Company. 654 p.
- Sokal, R.R. and F.J. Rohlf. 1995. *Biometry*, 3rd Edition. W.H. Freeman and Company. New York. 887 pp.
- Strom, K.B., M. Proctor, and J. Boulanger. 1999. Grizzly bear population survey in the central Purcell Mountains, British Columbia. B.C. Environmental Assessment Office. Victoria, B.C. Canada. 59 pp.
- Wakkinen, W.L., and W.F. Kasworm. 2004. Demographic and population trends of grizzly bears in the Cabinet–Yaak and Selkirk ecosystems of British Columbia, Idaho, Montana, and Washington. *Ursus* 15 Workshop Supplement: 65–75.
- White, G. C. 1996. NOREMARK: Population estimation from mark-resighting surveys. *Wildlife Society Bulletin* 24:50-52.
- White, G. C. 2006. Closed population models and their extensions in program MARK. *Journal of Environmental Statistics* In press.
- White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study Supplement* 46:120-138.
- White, G. C., and T. M. Shenk. 2001. Population estimation with radio marked animals. In: Millspaugh JJ, Marzluff JM, editors. *Design and Analysis of Radio Telemetry Studies*. San Diego, California: Academic Press.
- Wielgus, R.B., F.L. Bunnell, W.L. Wakkinen, and P.E. Zager. 1994. Population dynamics of Selkirk Mountain grizzly bears. *Journal of Wildlife Management*. 58:266-272.
- Woods, J.G., B.N. McLellan, D. Paetkau, M. Proctor, D. Lewis, and C. Strobeck. 1999. Genetic tagging free-ranging black and brown bears. *Wildlife. Society Bulletin* 27:616-627.

Appendix 1-Meta analysis details (John Boulanger, Integrated Ecological Research)

Methods

We attempted to use Huggins (1991) closed mixture models (Pledger 2000) in program MARK (White and Burnham 1999) to estimate population size in two separate meta-(Boulanger et al. 2002) analyses. First, we estimated overall population size for the South Selkirk (2005), Highway 3 east, Highway 3 west, and Jumbo projects. Each of these used a 5x5 km grid cell size. Second, we estimated population size for the South Purcell 2001, Purcell Wilderness Conservancy, and South Purcell 1998 DNA projects. These projects used a 7x7 and 8x8 cell size with 1 site sampled for 4 sessions. We considered project specific effects on capture probability as well as the effect of sex on capture probability.

The meta-analysis was updated for a recent change in parameterization of the MARK Huggins/Mixture models that occurred in late April of 2007. The more recent parameterization is theoretically closer to the original model proposed by Pledger (2000) and therefore its use has been recommended over the previous parameterization (Gary White, Colorado State University, Pers. Comm). However, it is less stable than the previous parameterization for some data set formulations. I evaluated the recent parameterization estimates in comparison with CAPTURE (Otis et al 1978) M_h Chao (Chao 1989) that estimates N for each data set separately. If estimates were less precise then Capture M_h Chao estimates were used instead of the meta-analysis estimates.

Results

Projects with 5x5 km grid cell size

Initial screening of data revealed that the South Selkirk 2005 project had higher capture probabilities than the Purcell projects. This may have been due to less closure violation with this project. Therefore I focused model building where capture probabilities were considered equal for the Purcell projects and different for the South Selkirk project. This base model was more supported than a model with project-specific capture probabilities or H3W, SS, and H3E/Jumbo capture probabilities. Model selection results suggested that a model with Purcell/Selkirk specific capture probabilities, sex-specific capture probabilities, and undefined heterogeneity was most supported (Table 1). A model without undefined heterogeneity was also supported. Models with equal capture probabilities (M_0), time (M_t) and behavioural response (M_{bh}) were less supported.

Table 1: Model selection results for 5x5 km grid cell projects. SS refers to South Selkirk project, PU refers to pooled Purcell projects. Sample size-adjusted Akaike Information Criteria (AIC_c), the difference in AIC_c values between the i th model and the model with the lowest AIC_c value (Δ_i), Akaike weights (w_i), and number of parameters (K) are presented. M_{h2} denotes that a mixture model was used to model heterogeneity. See Boulanger et al. (2002) for more details on meta-analysis terminology

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
$M_{h2} \pi (.) \theta_{1\&2} (PU/SS+SSXsex)$	440.3	0.00	0.201	7	426.0
$M_{h2} \pi (.) \theta_{1\&2} (PU+sex, SS+sex)$	440.5	0.21	0.181	7	426.2
$M_h p(PU/SS+sex)$	442.0	1.67	0.087	3	435.9
$M_{h2} \pi (.) \theta_{1\&2} (PU+sex, SS*sex)$	442.0	1.74	0.084	8	425.6
$M_{h2} \pi (SS) \theta_{1\&2} 2(PU/SS + SS*sex)$	442.4	2.10	0.071	8	426.0
$M_{h2} \pi (SS) \theta_{1\&2} (PU+sex, SS+sex)$	442.6	2.31	0.063	8	426.2
$M_h p(P/S, PU+sex, SS*sex)$	442.8	2.51	0.057	4	434.7
$M_{h2} \pi (.) \theta_{1\&2} (PU*sex, SS*sex)$	442.8	2.54	0.056	9	424.3
$M_0 p(PU/SS)$	442.9	2.58	0.055	2	438.8
$M_{bh} p(PU/SS +sex) c(SS*sex)$	443.6	3.27	0.039	6	431.3
$M_{h2} \pi(SS) p1\&2(PU+sex, SS*sex)$	444.1	3.85	0.029	9	425.6
$M_h p(area+sex)$	445.3	5.02	0.016	5	435.1
$M_{h2} \pi(.) p1\&2(PU) p1\&2(SS)$	445.7	5.38	0.014	5	435.5
$M_0 p(2006)$	445.7	5.40	0.014	2	441.7
$M_0 p(area)$	446.5	6.23	0.009	4	438.4
$M_{h2} \pi (.) \theta_{1\&2}(+SS)$	447.0	6.66	0.007	4	438.8
$M_{bh} p(PU/SS+sex) c(SS+sex)$	447.3	7.03	0.006	6	435.1
$M_{h2} \pi (SS) \theta_{1\&2} (P/S)$	447.7	7.45	0.005	6	435.5
$M_h p(areaXsex)$	449.5	9.24	0.002	8	433.1
$M_h p(sex)$	450.0	9.72	0.002	2	446.0
$M_t p(areaXt)$	453.8	13.54	0.000	16	420.2
M	455.8	15.49	0.000	4	447.7

Model-averaged population estimates for all projects had CV's of less than 20%, a satisfying result given the small number of bears captured ($mt+1$) in some of the projects (Table 2).

Table 2: Model-averaged population estimates (sexes pooled) for 5x5 km cell size projects. M_{t+1} is the number of unique bears identified.

area	M_{t+1}	\hat{N}	SE	cil	cir	CV
H3w	17	23	3.80	20	30	16.4%
H3e	12	16	2.88	14	21	17.7%
Jumbo	27	37	5.03	32	45	13.7%

Projects with 7x7 and 8x8 km cell size

Meta analysis estimates were similar but less precise than the stand-alone CAPTURE M_h (Chao) estimates. Estimates from MARK were 3 bears lower than CAPTURE M_h (Chao) for both study areas. Lower precision was presumably due to the newer MARK mixture model parameterization given that previous analyses resulted in estimates of greater precision. Given this result we decided to use the M_h Chao estimates rather than the MARK estimates (Table 3)

Table 3: CAPTURE M_h (Chao) population estimates (pooled sex) for larger cell size projects

Project	M_{t+1}	\hat{N}	SE	cil	cir	CV
SP01	29	45	10.5	34	81	23.3%
PWC	37	53	10.2	43	87	19.2%