

# Ecological investigations of grizzly bears in Canada using DNA from hair, 1995–2005: a review of methods and progress

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**Abstract:** Grizzly bears (*Ursus arctos*) occur across British Columbia and in Alberta in mostly forested, mountainous, and boreal ecosystems. These dense forests make sighting bears from aircraft uncommon and aerial census impractical. Since 1995, we have used genetic sampling using DNA from bear hair collected with barbed wire hair traps to explore a suite of ecological questions of grizzly bears in western Canada. During 1995–2005, we conducted large-scale sampling (1,650 to 9,866 km<sup>2</sup> grids) in 26 areas (covering a combined 110,405 km<sup>2</sup>), where genetic identification of 1,412 grizzly bears was recorded. Abundance estimation was the primary goal of most surveys. We also used DNA from bear hair to examine population trend, distribution, and presence in areas where grizzly bears were rare, as well as population fragmentation in a region with a high human population. Combining spatial variation in detecting bears with that of human, landscape, and ecological features has allowed us to quantify factors that influence grizzly bear distribution, population fragmentation, and competition with black bears (*U. americanus*), and to map variation in bear densities. We summarize these studies and discuss lessons learned that are relevant to improving sampling efficiency, study designs, and resulting inference.

**Key words:** Alberta, British Columbia, density estimation, DNA, fragmentation, grizzly bear, population distribution, trend monitoring, *Ursus arctos*

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The use of DNA has expanded the range and scale of ecological questions that can be investigated in wildlife studies. Besides being a permanent marker of an individual, DNA provides information that can be used to examine a variety of ecological questions, and is particularly useful with sparse and cryptic animals. Higuchi et al. (1988) pioneered the extraction of DNA from human hair. By the early 1990s, obtaining mitochondrial (mtDNA) and nuclear (nDNA) from wildlife hair was accomplished (brown bears [*Ursus arctos*] mtDNA, Taberlet and Bouvet

1992; chimpanzees [*Pan troglodytes*] nDNA, Morin and Woodruff 1992). Taberlet et al. (1993) used nDNA to sex wild brown bears in Europe, and Paetkau and Strobeck (1994) developed the first microsatellites for bears.

Microsatellites are highly informative genetic markers when investigating individual and population level questions (Wooding and Ward 1995, Craighead et al. 1998, Paetkau and Strobeck 1998, Paetkau et al. 1998). To improve our ability to inventory grizzly bears rapidly, and to complement demographic radiotelemetry studies, we applied nDNA-based methods to address questions relevant to the conservation of grizzly bears in western Canada. Using the ability to identify and sex individuals from DNA from hair roots, we surveyed abundance and documented distribution of grizzly

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bears in Alberta and British Columbia, Canada, starting with a pilot study in 1995 (Woods et al. 1999), and followed by mark–recapture surveys.

Our research was stimulated by grizzly bear range contraction over the past 2 centuries (Mattson and Merrill 2002). As of late 2009, grizzly bears in the conterminous states were listed as threatened under the US Endangered Species Act (16 US Code 1531–1544). In Canada, grizzlies were designated of special concern (Ross 2002), but were legally hunted in all provinces and territories where they occur, although there were hunting closures throughout the bear’s Canadian range. The species is legally hunted in Alaska.

Grizzly bears and the biologists who manage them face many challenges, and these become more diverse and intense toward the southern extent of the bears’ distribution (McLellan 1998), where populations are relatively small and occasionally fragmented (Proctor et al. 2005). Because grizzly bear populations are sensitive to excessive human-caused mortality (McLellan et al. 1999), habitat loss, and fragmentation (Proctor et al. 2005), objective estimates of population abundance, status, and trend are needed. There is also a need to extrapolate population estimates over broad and variable landscapes, requiring an understanding of factors that influence abundance, distribution, and fragmentation of bear populations at regional scales. However, in southern Canada dense forests make it difficult to conduct surveys that require observing animals directly (e.g., capture–mark–resight from aircraft, Miller et al. 1997; remote cameras, Mace et al. 1994; counts of females with cubs, Knight et al. 1995, Cherry et al. 2002).

To meet these challenges, we developed methods based on genetic analyses of DNA extracted from the roots of bear hair. These hairs are snagged on barbed wire placed in systematic sampling grids. In this paper, we summarize and describe our methods for estimating abundance and several ancillary applications of genetic data. Data obtained during abundance surveys provide additional information on habitat use, individual movements, and relatedness among individuals, thus creating potential for greater insights into the individual and population ecologies of the animals. We address (1) estimating population abundance and trend within a sampling grid, (2) quantifying ecological and human factors that influence abundance and distribution, and (3) quantifying the degree of population fragmentation, delineating population boundaries, and identifying

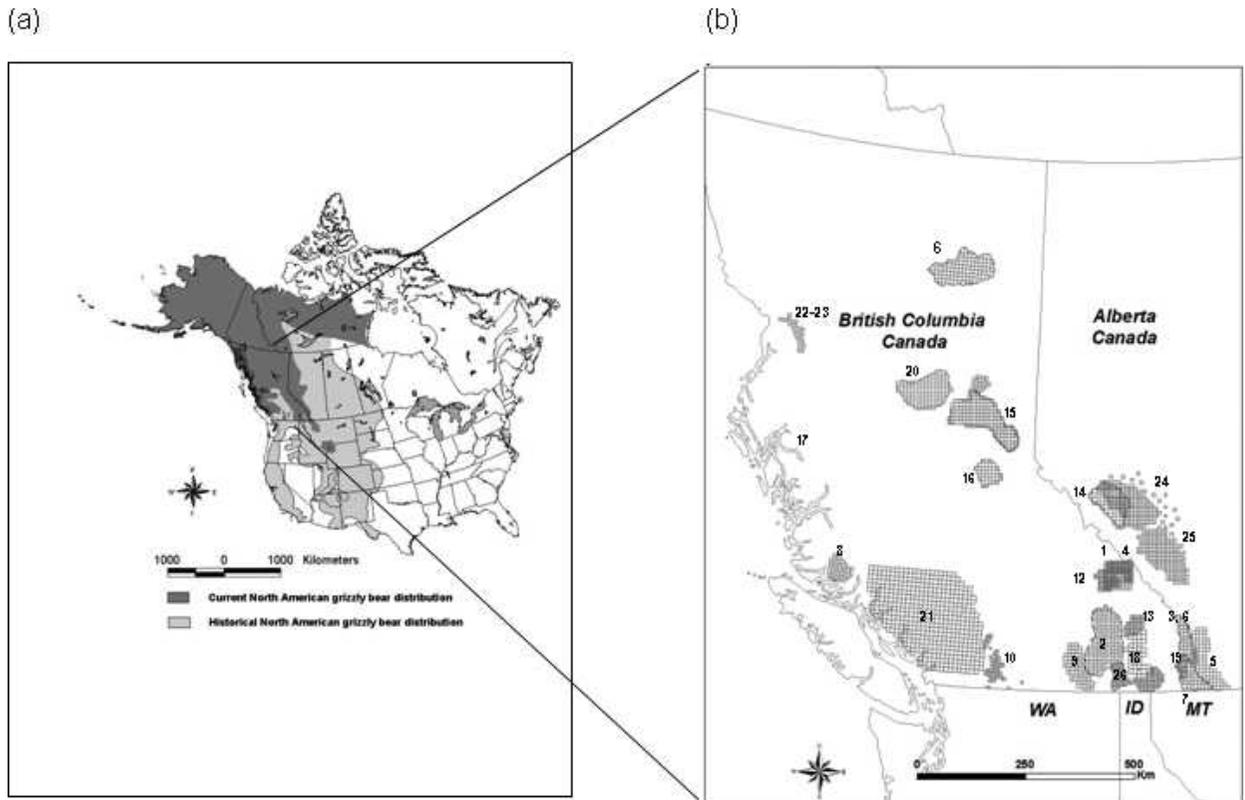
factors, including sex-specific dispersal patterns, that influence this process. We also discuss what we have learned about the ecological applications of the DNA hair-snag technique and suggest possible future uses.

Our cumulative research (26 surveys; 1996–2005) was conducted in British Columbia (BC) and Alberta, Canada (Fig. 1). Grizzly bears occur across approximately 750,000 km<sup>2</sup> of BC and 228,000 km<sup>2</sup> of western Alberta, and our study areas covered 86,822 and 27,679 km<sup>2</sup>, respectively. The terrain is dominated by mountain ranges with north–south orientation separated by valleys and wide plateaus. Variation in precipitation (<30 to >200 cm/yr) and elevation (sea level to 4,000 m) produces a range of ecological conditions: dry grasslands, temperate rainforests, boreal forests, and alpine tundra. Grizzly bear densities vary from 5 bears/1,000 km<sup>2</sup> in drier areas (Boulanger et al. 2005a) to ~80–90 bears/1,000 km<sup>2</sup> in productive areas (McLellan 1989, MacHutchon et al. 1993). Within the current western Canadian grizzly bear range, people live in rural areas and towns of <20,000 residents. Human activities in these areas include forestry, oil and gas development, agriculture, and outdoor recreation, including hunting.

## Field methods

We found that a single string of barbed wire (double-stranded; 4 points per barb; strung ~50 cm above ground) surrounding a scent lure was an efficient method of obtaining hair from grizzly bears in our study areas (Woods et al. 1999). Although we initially hung a scent lure just out of a bear’s reach in the center of a barbed-wire corral (3–6 trees used), subsequent experimentation revealed that pouring 1–2 l of rotted fish and 2–4 l of rotted cattle blood over a central, small (~1 m high) brush pile was as efficient and simpler to construct. We avoided providing edible bait that might act as a reward to bears and increase revisits to traps. Sampling stations were distributed across each study area in a systematic grid of cells with 1 sampling station/cell.

We conducted most sampling during spring when bears were shedding, and scarce food made them responsive to scent lures. We tried to maximize captures by placing snare sites in the best available seasonal habitat within each cell. Hair samples were collected and scent refreshed about every 2 weeks (defined as a sampling session); capture histories over 4 or 5 sampling sessions were used as the basis of



**Fig. 1. (a) North American grizzly bear distribution. (b) DNA-based abundance and distribution survey grids carried out in British Columbia and Alberta Canada, 1996–2005. Number codes are referenced to Table 1.**

mark–recapture population estimates (Woods et al. 1999, Mowat and Strobeck 2000). In some surveys, sampling stations were moved between sessions (“moved sites”); in others, stations remained in the same location over the duration of the survey (“fixed sites”). Alternative sampling patterns were used where terrain and bear habitat use dictated. For instance, when bears concentrated along salmon (*Oncorhynchus* spp.) streams, we placed sampling stations linearly along stream banks (Boulanger et al. 2004a).

### Laboratory methodologies

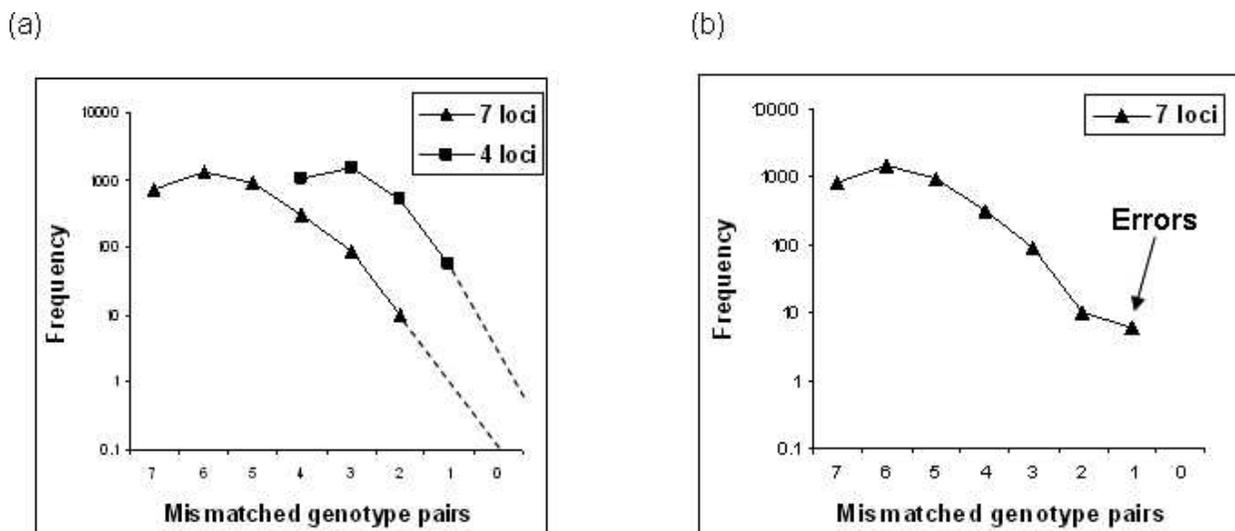
We extracted DNA from snagged hair follicles and used microsatellite genotypes (DNA fingerprints) to identify individuals (Woods et al. 1999). Because hair follicles contain a small quantity of DNA, specific protocols were followed to ensure accurate microsatellite genotypes for individual identification. Additionally, we needed sufficient variability within genetic markers to discriminate individuals. To avoid erroneously considering similar genotypes

from different individuals as a single bear, we required multilocus genotypes to have a low probability of identity. Because close relatives are often sampled, Woods et al. (1999) used the probability of sampling a full sibling with an identical genotype as a threshold for discriminating individuals. Woods et al. (1999) considered the quantity and variability of the markers adequate when this probability was  $<0.05$ . Waits et al. (2001) developed a similar method to deal with this problem by considering the theoretical probability of a sibling genetic match based on population-level allele frequencies. However, the reliability of both these approaches can be challenged in small isolated populations where the proportion of close relatives can be high (Kasworm et al. 2007). Therefore, we began using a system of empirical mismatch distributions (Paetkau 2003). A mismatch between 2 genotypes refers to a non-identical pair of alleles at a given marker (microsatellite locus) within a multi-locus genotype. Using genotypes from live-captured bears (known different individuals), Paetkau (2003)

Table 1. DNA hair-snag surveys from grizzly bear (GB) in British Columbia and Alberta between 1996 and 2005. The superscript number after project name refers to Fig. 1.

Project	Year	Objective: primary secondary <sup>a</sup>	Study area, km <sup>2</sup>	Cell Number of cells	GB IDs	Population estimate	95% CI	SE	CV, %	$\hat{p}^b$	F HR <sup>c</sup> , km <sup>2</sup>	Reference
Upper Columbia 96 <sup>1</sup>	1996	abundance frag, RSF, disp	4,096	64	55	108	78–177	23.8	22	0.16	90	Boulanger et al. 2004b Apps et al. 2004
Central Selkirks <sup>2</sup>	1996	abundance frag, disp	9,866	64	108	258	220–309	23	9	0.09		Mowat and Strobeck 2000, Mowat et al. 2005 Boulanger 1997
Elk Valley <sup>3</sup>	1996	abundance frag, disp	2,560	64	40	100	58–225					
Upper Columbia 97 <sup>4</sup>	1997	abundance frag, RSF, disp	1,900	25	76	55	48–107	9.5	15	0.2	90	Boulanger et al. 2004b Apps et al. 2004
SW Alberta <sup>5</sup>	1997	abundance frag, disp	5,030	64	37	74	60–100	10.1	14	0.16		Mowat and Strobeck 2000 Boulanger 2001
Elk Valley <sup>6</sup>	1997	abundance frag, disp	2,688	64	42	59	129–215	107–427				
Flathead <sup>7</sup>	1997	abundance frag, disp	3,264	64	51	144	91–274				173	Boulanger 2001
Kingcome <sup>8</sup>	1997	abundance frag, disp	2,401	49	58	102	77–163	29.7	20	0.2		Boulanger et al. 2002
Granby <sup>9</sup>	1997	abundance frag, disp	4,480	64	70	38	26–84	16.4	36	0.13		Burwash <sup>d</sup> Austin <sup>e</sup>
Cascades <sup>10</sup>	1998	detection		64								
Prophet <sup>11</sup>	1998	abundance	8,527	81	103	169	140–212	26.2	16	0.17		Poole et al. 2001, Mowat et al. 2005
Upper Columbia 98 <sup>12</sup>	1998	abundance frag, RSF, disp	2,350	25	94	92	71–301	9.5	32	0.12	90	Boulanger et al. 2004b Apps et al. 2004 Proctor et al. 2007
Jumbo <sup>13</sup>	1998	abundance frag, RSF, disp	1,650	25	66	45	39–64	7.1	16	0.26		
Foothills Model Forest <sup>14</sup>	1999	abundance frag, disp	5,352	81	64	77	52–138				250	Stenhouse & Munro 2000, Boulanger et al. 2004c
Parsnip/Herrick <sup>15</sup>	2000	abundance	9,452	64	147	239	314–546	18.2	5	0.12/0.22	143	Mowat et al. 2005
Bowron River <sup>16</sup>	2001	abundance	2,494	64	38	53	63–104	11	14	0.32		Mowat et al. 2005
Owikeno <sup>17</sup>	1998–2002	monitoring	2,494	64	61	123						Boulanger et al. 2004a Proctor et al. 2007
Southern Purcells <sup>18</sup>	2001–2005	frag, link abund, disp, RSF		25	110	50						
Highway 3 – Rockies <sup>19</sup>	2002–2003	linkage		25								
Nation <sup>20</sup>	2003	abundance	7,031	64	117	33	34–49	3.3	8	0.37		Apps et al. 2006a Mowat and Fear 2004 Apps et al. 2006a
South Coast <sup>21</sup>	2004	distribution abund, frag, RSF	9,600	100	90	58						
Stikine River <sup>22</sup>	2004	abundance movement	6,207	256	17	138	87–273	43.3	31	0.13		Mowat (unpub. data)
Iskut River <sup>23</sup>	2004	abundance movement	3,912	256	23	126	105–158	13.3	11	0.15		Mowat (unpub. data)
Foothills Model Forest <sup>24</sup>	2004	abundance frag	8,820	49	108	41	44–80	8.3	16	0.33	250	Boulanger et al. 2005a
Foothills Model Forest <sup>25</sup>	2005	abundance frag	8,477	49	173	41	44–69	3.9	8	0.55	250	Boulanger et al. 2005b
South Selkirks <sup>26</sup>	1999, 2005	abundance frag, RSF, link, disp	1,850	25	75	36	31–43	2.7	8	0.48		Proctor et al. 2007

<sup>a</sup>Frag = fragmentation; RSF = resource selection function; Disp = dispersal; Link = linkage; abund = abundance.  
<sup>b</sup> $\hat{p}$  is the capture probability or the proportion of the total population sampled across the entire grid in each session.  
<sup>c</sup>F HR (km<sup>2</sup>) is the estimated female home range for the areas where it is known.  
<sup>d</sup>M. Burwash, BC Ministry of Environment, British Columbia, Canada, personal communication, 1998.  
<sup>e</sup>M. Austin, BC Ministry of Environment, British Columbia, Canada, personal communication, 1999.



**Fig. 2.** Frequency of mismatches (MM) distributions for grizzly bear microsatellite genotypes generated from a typical hair-snag DNA survey. (a) Exponential decline of mismatched genotypes; the 7-locus curve approaches 1MM and 0MM (dotted line). The 4-locus curve shows that match probabilities would have been excessive had the study been conducted with 4 markers instead of 7. (b) Mismatch distribution before errors have been corrected; the shape of the curve near 1MM depicts the probable errors to correct.

developed the use of an expected mismatch distribution (Fig. 2). Because the frequency of mismatched genotypes is exponentially lower with each additional marker, one can predict how many markers are required to produce a very low probability of observing identical genotypes for 2 individuals (Fig. 2a, termed 0MM by Paetkau [2003] and “shadows” by Mills et al. [2000]). This is best accomplished through a pilot study where a subset of a project’s genotypes is used to develop a mismatch curve similar to Fig. 2a. A similar project-specific curve is used to identify the appropriate number of markers by extrapolating the curve (dotted lines in Fig. 2a) such that we would expect fewer than a specified number (typically 0 or 1) of mismatches. When markers are less variable, more loci must be used to achieve this goal. The example in Fig. 2a demonstrates that 4 markers would not meet this test, but 7 markers would provide enough power to reduce the expectation of 0 mismatches between 2 different animals to  $<1$ .

Errors in genetic results can occur with minute quantities of DNA (Taberlet et al. 1996), and replication in the lab is necessary to ensure accurate genotypes. We expected (and observed) that most errors affected just 1 of the markers being analyzed (Fig. 2b). Although errors at multiple markers are

not strictly independent, the frequency of errors at 2 markers was much lower ( $\sim 10$ – $20\times$ , Paetkau 2003). Woods et al. (1999) approached this problem by re-analyzing pairs of genotypes that mismatched at 1 of 6 markers. However, because of low rates of errors at genotypes mismatched at 2 and 3 markers ( $<1$  occasion per study [100 animals] on average, Paetkau 2003), we began replicating all 1- and 2-mismatch pairs as well as those 3-mismatch pairs that fit the pattern of allelic drop-out, the most commonly observed error when working with minute quantities of DNA (Taberlet et al. 1996).

Inaccurate datasets with erroneous mismatches inflate estimates of abundance by increasing the number of unique genotypes and decreasing the number of recaptures (Mills et al. 2000, McKelvey and Schwartz 2004, Roon et al. 2005, Schwartz et al. 2006). Kendall et al. (2009) recently used blind sample verification ( $\sim 900$  blind samples, 0 errors) and duplicate genotyping to illustrate that the protocol outlined by Paetkau (2003) yielded a near error-free dataset of 563 genotypes. We believe that systems as recommended by Taberlet et al. (1996) and McKelvey and Schwartz (2004) are unnecessary with careful lab work. Kendall et al. (2009) also illustrated that large datasets do not necessarily correspond to higher error rates.

Reporting of error rates will vary with how they are measured. Error rate reporting may compare the final genotype dataset with one of the several stages in the genotyping process. What really matters is some evidence that the final set of genotypes has a very low number of falsely created genotypes from undetected errors. We found that the best approach was to use our genotypes to develop a mismatch distribution (Paetkau 2003, Fig. 2a,b) accompanied by evidence to show that all accepted pairs of individuals with 1 and 2 mismatch pairs had been validated through replication. Our objective was to use a system with a sufficient number of variable markers to ensure that 1 or 2 mismatched pairs were rare. We emphasize that error rates depend on the rigor of the lab, and that expertise and quality assurance protocols are necessary for accurate datasets.

To distinguish between black and grizzly bears, after 2001 we used a microsatellite marker (J locus, Paetkau 2003) rather than mtDNA alleles (Woods et al. 1999). Samples whose amplified PCR had a positive number of nucleotides at the J locus were classified grizzly bear, and those with odd numbers classified black bear. Samples with weak genotyping results in the J-locus species test were discarded without further analysis because they did not yield reliable multilocus genotypes (Kendall et al. 2009).

## Applications of hair-snag derived genetic data

### *Estimation of abundance and trend*

Using mark–recapture methods with DNA fingerprints as marks allowed us to estimate abundance of bears within a single season in forest environments where methods that depend on radiotelemetry or direct observations are difficult. We chose mark–recapture estimators (originally Program CAPTURE; White et al. 1982, later Pradel or Huggins models in Program MARK, White and Burnham 1999) that assumed population demographic closure over the 6–8 week sampling period. We believe that demographic closure over this short period is a reasonable assumption for long-lived animals such as grizzly bears (McLellan 1989). These estimators generate results with better precision and less bias than open models and are appropriate provided that the study is designed to minimize geographic closure violations.

Here, we emphasize 5 analytical and methodological issues that we found to bias or affect the precision of abundance estimates: (1) geographic closure violation; (2) the balance among study area size, sample size, capture probability, and statistical rigor, particularly where densities are low; (3) variation in capture probability between age and sex cohorts; (4) costs associated with surveys, and (5) the estimation of trend.

### **Geographic closure violation**

Grizzly bear DNA-based surveys often have few captures and recaptures, making it difficult to obtain precise and unbiased estimates. We approached these challenges by designing surveys to obtain adequate captures and recaptures while minimizing both capture probability (proportion total population of bears captured in the entire grid within 1 session) variation and movement of bears in and out of the study area during sampling (geographic closure violation). Maximizing closure via appropriate study design helped to ensure adequate recapture rates and minimized variation in capture probabilities, thereby improving precision, and through informed model selection, minimizing bias. Ignoring geographic closure violation can lead to imprecise and inflated population estimates. Our experience suggests that study areas were best located where natural or human features (major highways, human settled valleys) maximized the probability of geographic closure, and high densities of bears were not located near study area boundaries (Fig. 3). Maximizing the size of a study area may help reduce violations of the geographic closure assumption but may not eliminate the problem.

There are several methods to correct a population estimate when geographic closure violation is suspected. Where applicable, we used the distance a capture (or the average of multiple captures) was from the grid edge as a covariate to explicitly model closure violation (Boulanger and McLellan 2001). Using the Pradel model (Pradel 1996) in program MARK (White and Burnham 1999), we estimated a core area where closure violation was unlikely by estimating relative survival and recruitment as a function of distance from the study area edge as indices to full-time occupancy on the grid. We defined a core area where these values remained consistent (reached an asymptote) as distance from edge increased, and used this area to estimate core area density. We then extrapolated this core area

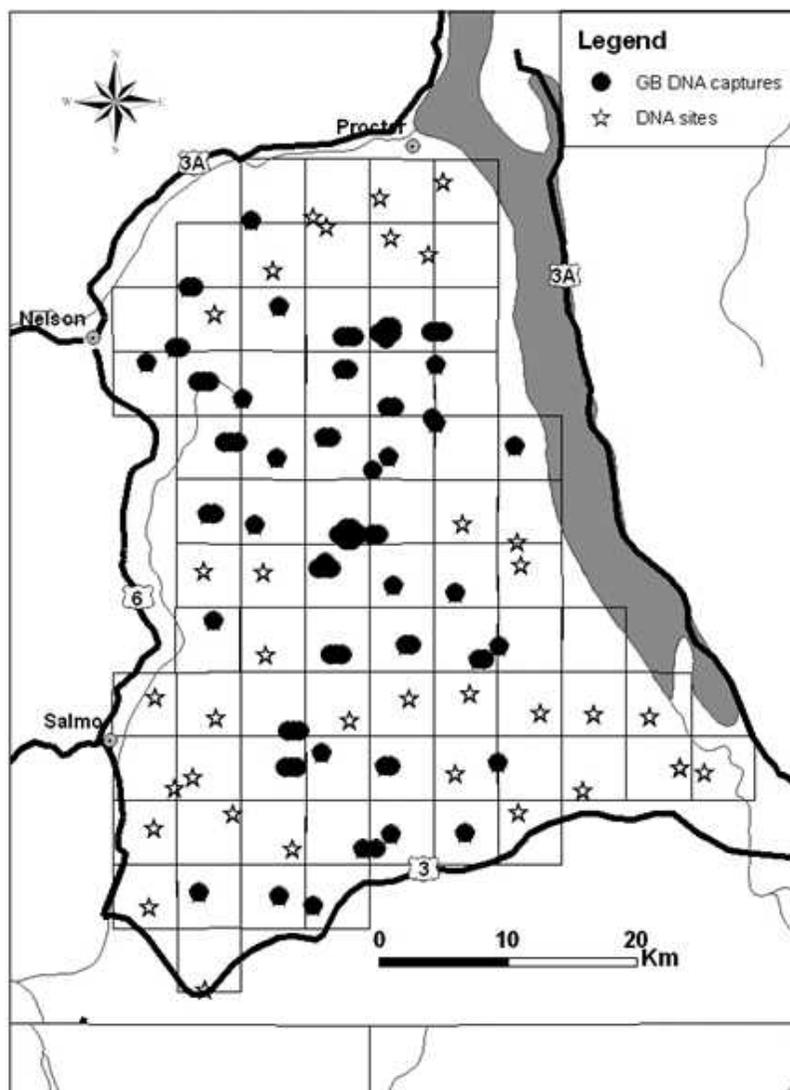


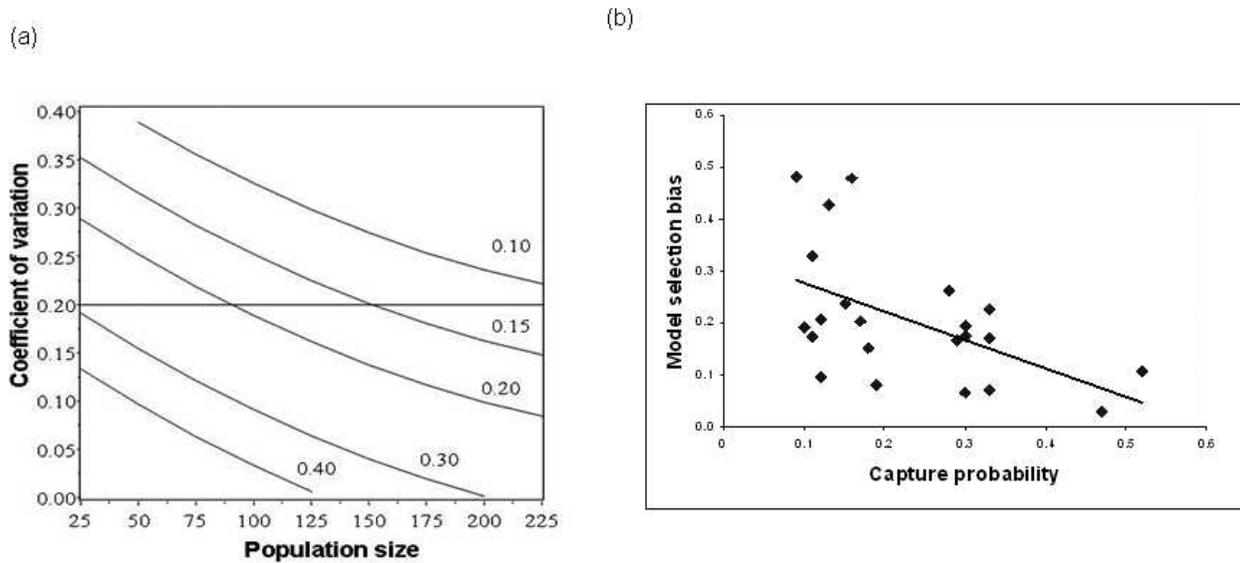
Fig. 3. Spatial pattern of DNA-captured grizzly bears (GB) from a survey in the south Selkirk Mountains in southeast British Columbia (adapted from Proctor et al. 2007). Fragmentation analysis helped define study area boundaries to reduce closure violation by using major highways and a large lake as boundaries: the highest density of captures (solid circles, stars are no capture sites) occurs in the center of the grid.

density to the entire grid under the assumption that densities in core and extrapolated areas were similar (Boulanger and McLellan 2001, Mowat et al. 2005). This extrapolation required reasonably high sample sizes, for example, at least 30 bears with a capture probability of 0.2 (for studies with >50 bears, the capture probability could be reduced to 0.15). When available, we used radiotelemetry to estimate and adjust for closure violation; Boulanger et al. (2004b) used the average percent of time that radiocollared bears spent on the sampling grid during the 2 month

survey as a correction factor for a population estimate.

#### **Balancing study area size, sampling intensity, capture probability, and model selection**

Once a study site has been selected where closure is maximized and bears are expected to have similar life history strategies, we considered sampling strategy. Considerations include size of study area, and thus size of population sampled, and intensity of sampling required. A polynomial regression analysis (Fig. 4a)



**Fig. 4.** (a) Relationship between population size, capture probability (the proportion of the total population captured each session) and precision as represented by the coefficient of variation for grizzly bears in Canada. (CV, the standard error, and population estimate are from J. Boulanger, unpublished data). The isolines 0.1, 0.15, 0.2, 0.3, and 0.4 represent capture probability, and the horizontal line at 0.2 represents a precision often acceptable for management purposes. (b) Relationship between capture probability and model selection bias. We define potential model selection bias from our surveys as the difference in estimates between the null model  $M_o$  and Chao's heterogeneity model (from Program CAPTURE; White et al. 1982) relative to the Chao estimate ( $r^2 = 0.28$ ,  $P = 0.01$ ). All our projects with a capture probability  $>0.2$  have evidence of capture heterogeneity.

using data from our surveys (Table 1) depicts the relationship between population abundance, capture probability (the proportion of the total population captured in each session), and precision (coefficient of variation). Estimator precision increases with population abundance; small populations may generate anomalous densities (Smallwood and Schonewald 1996), so it is advisable to survey populations with at least 50 suspected animals, but  $\geq 100$  is preferable. With intense sampling efforts (5 km  $\times$  5 km grids, Proctor et al. 2007), we have effectively estimated populations with  $<50$  animals. We modeled selection bias (Fig. 4b) as the relative percent difference between the model assuming equal capture probability ( $M_o$ ) and the model assuming variable capture probability ( $M_h$ , Chao) within Program MARK. As capture probability increased, model selection had less potential bias because the spread of estimates among models was minimized ( $r^2 = 0.28$ ,  $P = 0.01$ ). Program MARK has a simulation function that allows researchers to explore their potential study designs and expected and desired results in relation to sample sizes and field efforts.

With resources typically limited, there is often a tradeoff between sampling intensity and study area size. Our study area sizes varied from 1,500 km<sup>2</sup> to 10,000 km<sup>2</sup> (Table 1), and were generally chosen to be large enough to ensure an adequate population size and to further reduce geographic closure violation. If the study area is large enough to capture many animals ( $>200$ ), the coefficient of variation may be small even if capture probabilities are low. We adjusted our sampling intensity approach over the years, initially using 64 km<sup>2</sup> cells with sampling stations moved to different sites within cells during each of 4 or 5 sampling sessions (Woods et al. 1999, Mowat and Strobeck 2000). This cell size resulted in estimated capture probabilities of 0.13–0.18 per session. To increase the probability of capturing bears with small seasonal ranges, we reduced cell sizes (25 km<sup>2</sup>) and fixed sites over 4 or 5 sampling sessions (Boulanger et al. 2004b). This size provided a higher ratio of cell size to home range, thus increasing trap encounter rates without exceeding our budget. This design resulted in capture probabilities of 0.20–0.26, although the population sam-

pled was smaller because the overall grid size was reduced and closure violation was a greater issue. In our most recent surveys, we used 25 km<sup>2</sup> cell sizes with fixed sites where bear home ranges were known or assumed to be small, and 49 km<sup>2</sup> cell sizes and sites moved between sessions where home ranges were larger. These recent surveys achieved capture probabilities of 0.33–0.55 and coefficients of variation <20% (often <10%; Table 1), markedly improving precision and decreasing estimate bias (Mowat and Fear 2004; Boulanger et al. 2005a, 2005b; Proctor et al. 2007). In areas with a history of live bear captures, previously captured bears had a lower capture probability of being sampled by hair snares than naïve bears. Therefore, we recommend that models to estimate abundance consider the history of live captures (Boulanger et al. 2008). Finally, results from all projects suggest that at least 4 sampling sessions are needed to ensure adequate sample sizes and allow use of robust estimation models (although see Future Directions).

We found that maximizing capture probability requires a combination of several factors: using small cell sizes optimal for bear home ranges, using topographic, human fragmentation features, or both to minimize closure violation, having experienced bear biologists select sites, having high quality scent lure (rotted for 6 months–1 year), and having experienced lab technicians able to produce a high percent of successful genotypes from the total sample, thereby missing fewer capture and recapture events.

In an experiment comparing the fixed-site design with the moved-site design, we found that moving sites between sessions captured more female bears/session. It identified more bears than the fixed site design; we also found behavioral responses by males to fixed sites (Boulanger et al. 2006). However, simulations suggested that differences between the designs (fixed versus moved) are insignificant when cell sizes are small enough (5 x 5 km for grizzly bears, J. Boulanger, unpublished data).

Another approach to increasing precision in abundance estimates when sample size is low is to combine data from multiple surveys. Meta analyses can be conducted in program MARK (White and Burnham 1999) when sampling design is standardized. We recommend that the capture data from studies being used in any meta analysis be used in simulations within program MARK to explore estimator robustness of model performance. Simu-

lations can indicate both precision and bias (Boulanger and Krebs 1996; Boulanger et al. 2002, 2004b, 2004c).

### **Heterogeneity in capture probability**

When capture probabilities were <0.20, the majority of bears were captured only once, making it difficult to determine the optimal estimation model (because inference for model selection comes from recaptured bears). When most bears were captured only once, capture heterogeneity (variability of capture probability between groups of bears or individuals) appeared to be absent whether present or not, resulting in a tendency to select a model that assumed equal capture probabilities. If capture heterogeneity was present (which we suspect was most often true), selecting a model that assumed equal capture probability yielded biased population estimates, particularly with populations of <100 animals (Fig. 4b). We found that capture heterogeneity was detected in most DNA-based bear surveys once capture probability exceeded 0.20. Thus, we suggest that heterogeneity models be considered for estimation of population abundance even when heterogeneity is not detected (Boulanger et al. 2002), to minimize model selection bias when sample sizes are low.

Representing potentially >1/3 of the population (McLellan 1989), cubs and yearlings can bias estimates significantly if they are not sampled by the barbed wire. We have evidence that cubs are sampled, although likely at a lower rate than other cohorts (Boulanger et al. 2004b). The use of a second wire failed to increase the number of cubs captured (Boulanger et al. 2006, Mowat and Fear 2004). However, simulations suggested that heterogeneity estimators are robust to lower capture probabilities of cubs, and we conclude that because we do sample cubs, we should include them in our abundance estimates. Kendall et al. (2009) provide a more rigorous example of rates of cubs and yearlings captured by DNA hair-snagging. Their survey captured 44% of 16 cubs and 80% of 15 yearlings known to be on their grid and available for capture through simultaneous radiotelemetry (Mace and Chilton 2007).

### **Survey costs**

Our survey costs varied with accessibility (i.e., road networks), the density of bears in the study area, and whether non-target species were sampled.

Areas with low densities of bears often yield lower numbers of hair samples, minimizing lab costs. Surveys in areas where black bears overlapped with grizzlies incurred the extra lab costs associated with differentiating the species. When our objective was limited to grizzly bears, we were able to visually identify and remove obvious black bear guard hairs (jet black hairs) prior to laboratory analysis with a high degree of accuracy (D. Paetkau, unpublished data), saving extraction and species identification costs. The total cost (field and lab work) per cell per visit for our studies varied from \$500 to \$2,000. We also sub-sampled our hair samples in several ways, saving costs. We documented adjacency of samples as they were found on barbed wires and usually only analyzed the best of a series of 3 adjacent samples (the sample with the most visible roots) under the assumptions that they were from the same bear. In other cases, we applied a variant of this sub-sampling approach, analyzing 2 of 5, 3 of 8, 4 of 11, or similar proportions, with a maximum of 8 samples analyzed/site.

### **Estimating population trend**

Mark-recapture DNA from hair-traps can be used to estimate population trend ( $\lambda$ ) directly using the Pradel model (e.g., in program MARK). For example, Boulanger et al. (2004a) explored factors affecting trend for grizzly bears on coastal salmon streams. The Pradel approach is appealing because trend estimates are robust to heterogeneity of capture probabilities and closure violations, issues that challenge estimation of population abundance and density. Boulanger et al. (2003) and Apps et al. (2005) explored the use of trend monitoring for management purposes, incorporating methods to detect spatial variation in trend and geographic and ecological correlates to these shifts. For example, using simulations, Boulanger et al. (2003) estimated that 3 initial years of sampling, followed by bi-annual sampling, with four 2-week collection sessions would be necessary to detect a trend of  $\lambda = 0.97$  (3% yearly decline) in a population of 100 bears over 10 years with a 95% confidence interval of 10%. Unlike most demographic estimates of  $\lambda$  from telemetry studies, the Pradel model does not estimate survival and reproduction directly, but rather estimates recruitment (which can include immigration) and apparent survival (which includes the complement of emigration). Whether DNA surveys should be used to estimate  $\lambda$  depends on manage-

ment objectives. If changes in population abundance for the exact study area sampled are of interest, then DNA-based estimates can accomplish this goal. If a demographic assessment of a population and cause-specific mortality are desired, a radiotelemetry study is required.

**Future directions.** Our work in BC and Alberta defined a basic study design for DNA mark-recapture projects; recent surveys demonstrated the ability to attain high quality results over reasonably large study areas (Boulanger et al. 2005a, 2005b; Kendall et al. 2009). Study designs are likely to become more standardized to use the power of meta analyses in the newer MARK models that allow multi-data sources to fuel a multi-model analysis integrating capture probability heterogeneity (Pledger 2000). Refined estimates of density for a range of potential study designs are possible (Efford 2004), reducing the requirement for standardization of methods. A meta analysis exploration into predicting geographic closure violation may help guide study designs and provide an objective measurement of a density adjustment if closure is violated. Estimation techniques based on capture frequencies that use information from bears captured multiple times per session (which is ignored in traditional mark-recapture estimators) holds promise to further enhance estimate precision and possibly allow reasonable results with fewer, or even one, sampling session. The Miller et al. (2005) CAPWIRE method offers promise to reduce field collection costs by requiring only one session, assuming adequate recapture rates at different bait stations within that session (Lukacs et al. 2007, Puechmaille and Petit 2007, Robinson et al. 2009). A longer period may be required to let captures accumulate, thus increasing session length. Simulations in the CAPWIRE technique suggest challenges in the confidence intervals containing the simulated population size as populations increase. However, Lukacs et al. (2007) developed an estimator for single sessions that uses Monte Carlo Markov Chain; this methodology is potentially more robust than CAPWIRE, accommodating a wider range of population sizes.

Models that incorporate genetic error rates into mark-recapture estimates are currently being developed which may be useful when low error rates cannot be assumed. Such a situation may occur in populations that have extremely low variability where resolution of individuals is compromised. The method of Lukacs and Burnham (2005) shows

promise in that it uses an information theoretic approach and indirectly tests for the presence and potential significance of genetic error rates by searching for an excess of bears captured only once. It also uses estimates of lab-error rates to correct population abundance estimates.

Kendall et al. (2009) obtained excellent results by supplementing data obtained using survey methods summarized here with hair collected from trees on which bears were known to rub. These supplementary data allowed Kendall et al. (2009) to increase the number of bears captured and recaptured, resulting in tighter confidence intervals (within 10% of estimate). Also, the sex ratio of DNA detections on rub trees approached 50:50 as the season progressed toward late summer and fall, providing evidence that a portion of females thought to have a zero capture probability (due to low representation in spring rub tree surveys) might be better represented and thus more accurately sampled for monitoring. If the rub tree method can be shown to consistently yield sex ratios approaching 50:50 in late summer and fall, there may be potential in that method's use for abundance estimation and population monitoring because all segments of the population will be known to have non-zero capture probabilities (Stetz et al. 2010).

### **Modeling probability of occurrence**

Density of grizzly bears varies across the landscape (Apps et al. 2004, Kendall et al. 2009), and objective quantification of and the ability to predict that variability is a powerful management tool. Spatial analysis of DNA survey results has allowed us to move beyond deriving a single estimate of average abundance within the sampling area to understanding the ecological factors that influence grizzly bear populations across broad regions. Density estimates from DNA-based mark-recapture models have provided us with a foundation for probability of occurrence modeling of grizzly bears at the sub-regional scale (1,600 km<sup>2</sup> to ~10,000 km<sup>2</sup>). Occurrence data from a typical DNA-based survey is well suited to study the ecological and human factors that influence variation in abundance and distribution. Models derived from ecologically representative population-level sampling should provide robust predictions at even the larger regional level (Boyce and MacDonald 1999). We provide a brief overview of this technique and emphasize several issues that we found to influence the quality of inferences about

factors influencing density and extrapolations: (1) scale of inference; (2) extrapolation and bias; (3) model validation; and (4) model quality.

Apps et al. (2004) examined grizzly bear occurrence at 3 spatial scales (daily movement distance, female home range size, male home range) using spatially-explicit ecological variables within a geographic information system (GIS). Those variables covered a range of potential influences including terrain attributes (ruggedness, curvature, slope), landcover types, elevation, solar radiation, human-use variables, and variables derived from remote sensing including greenness and wetness. Variables within GIS were scaled such that values for each cell or pixel were averaged from neighboring cells within a specified radius. Each scale averaged values over a specified movement radius. Apps et al. (2004) developed candidate models to potentially explain occurrence patterns (DNA detections versus no detection) and used logistic regression and information-theoretic methods (AIC, Akaike's Information Criteria, Burnham and Anderson 1998) to select best approximating models to explain grizzly bear occurrence in a 4,000-km<sup>2</sup> area. Models at all 3 spatial scales were integrated and the resulting probability of occurrence model was associated with the pattern of bear density for their study area. They used this model to extrapolate density over the surrounding 11,200 km<sup>2</sup> area. The multi-scaled model was subsequently validated using an independent dataset of radiolocations of grizzly bears in the study area. The output was a predictive map reflecting bear density relative to ecological and human variables across a broader landscape. Apps et al. (2006b) applied similar techniques to explore landscape partitioning and inter-specific competition between grizzly and black bears.

We used predictive outputs of probability of occurrence modeling for grizzly bears to inform industrial and commercial development decisions, prioritize areas for enhanced protection and human access management, and identify linkage habitat in regions where grizzly bear population fragmentation is of concern (Apps et al. 2007, Proctor et al. 2008a, Fig. 5). Spatial predictions at the population-level are also valuable when developing study designs for monitoring long-term population trends and evaluating causal factors. Ecological variables that control population distribution vary with scale of investigation and can differ from those that influence fine-scale habitat selection by individuals. Therefore,

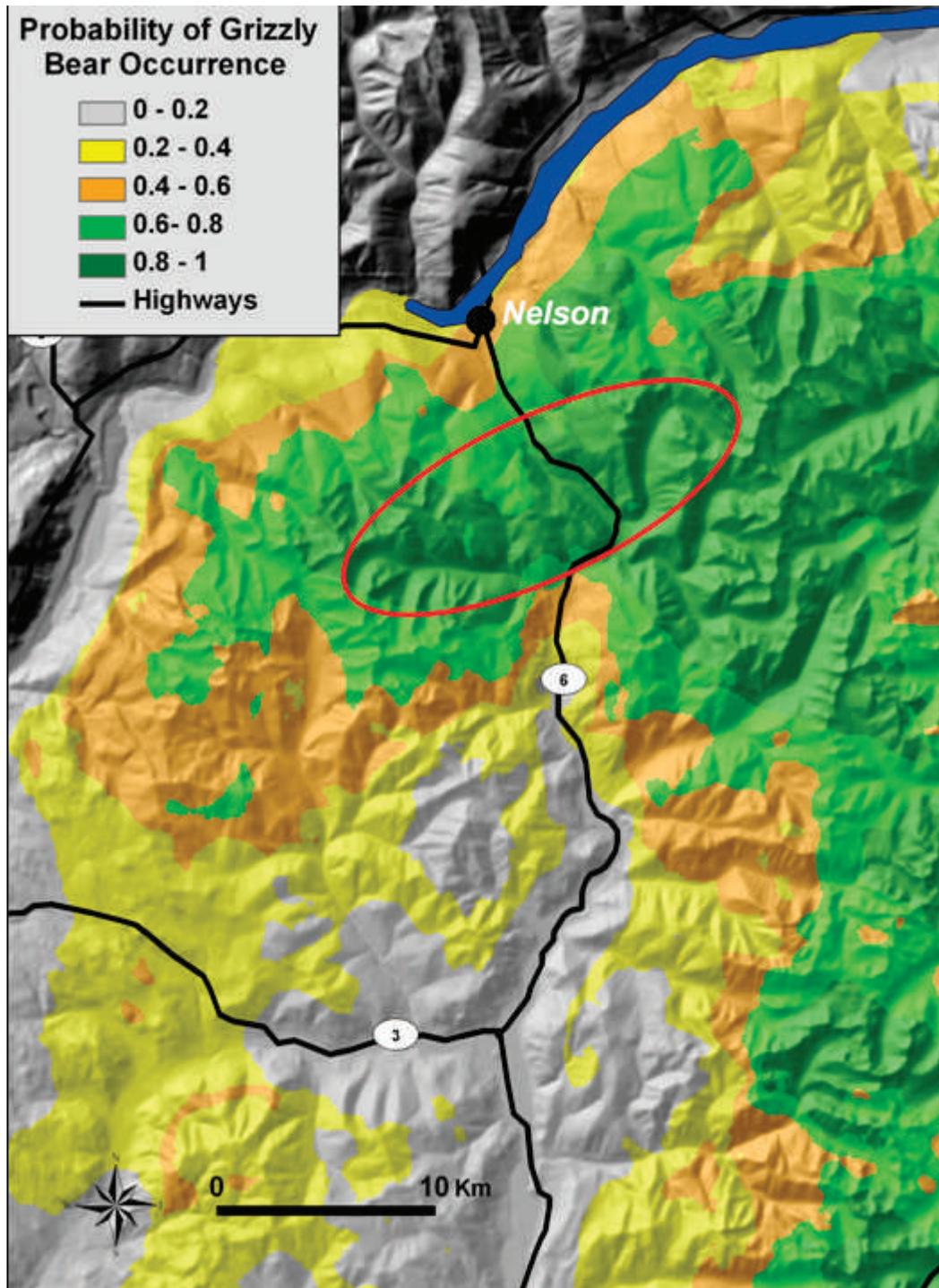


Fig. 5. Example of population core and linkage potential as inferred from a spatial population abundance and distribution model for grizzly bears derived from analyses of DNA-based sampling (from Proctor et al. 2007). The map depicts a high quality habitat linkage zone (red oval) across BC Highway 6 (black line). Highest quality habitat is dark green; lowest quality is grey.

resource selection function (RSF)-like models developed through analyses of habitat selection by individual animals (from, for example, telemetry data) can be inappropriate for predictions of population distribution. Conversely, while occurrence models discussed here are powerful, they need to be applied only at the population level and during seasons when sampling occurred.

Extrapolations may be biased when ecological conditions are significantly different between sampling and extrapolation areas. We found that extrapolation required similar ranges of ecological variables in the source study area and the area where the model is being extrapolated. Our current protocol uses GIS to test for differences in proportions of important habitat types between the sampled and extrapolation areas. We also found it is important when designing a DNA survey where probability of occurrence modeling will be used that sampling sites be in a variety of important habitats. This may require compromises between habitat representation and maximizing bear captures for abundance estimation. One way we accommodated this tradeoff is by moving sites between collection sessions (1 to several times throughout survey) to maximize habitat representation. Model validation is an important step when using probability of occurrence modeling (Boyce et al. 2002, Manly et al. 2002). Using an independent dataset may be the most reliable way to validate models. Where feasible, we used radiotelemetry data in the same area as the DNA survey (Boulanger et al. 2004b, Proctor et al. 2007). Model validation comes in the form of acceptable proportions of telemetry locations in areas with higher probability of occurrence scores.

Model quality and predictability is limited by the quality of input variables. As is typical for interior North American grizzly bear habitat, we did not have GIS layers of foraging patches, so we modeled habitat that supports foraging patches (burned areas that may contain productive berry patches, avalanche chutes that support desirable spring root, herb, and forb communities; Apps et al. 2004, Nielsen et al. 2004, Proctor et al. 2007, Nielsen et al. 2008). Modeling efforts may therefore be limited by the quality of digitized habitat variables available in any particular area. As researchers' knowledge of local bear ecology increases, their ability to model predictive variables will improve. For example, we derived a riparian variable by combining wetland and stream layers with areas of low slopes containing

vegetation typically found in productive riparian layers (Apps et al. 2004, Proctor et al. 2007).

**Future directions.** To date, spatial modeling applications using DNA hair sampling have been inductive, characterizing relationships with variables that are sometimes surrogates for factors directly influencing grizzly bear populations. As suggested by Apps et al. (2004), the mechanisms that influence and control patterns of grizzly bear abundance and distribution will be best explored through meta analyses across a diversity of ecological and human conditions, facilitating a priori testing of hypothetical relationships and wider extrapolation of predictions. This process will require standardized field methods and sampling areas that are locally representative of ecological and human conditions. Most importantly, the number and location of sampling areas should follow a pre-determined stratification that reflects the variety of biophysical and human characteristics on a broad scale. Such analyses may lead to models that can be applied over larger regions, forming the basis for landscape-specific population estimation, harvest management, and long-term population trend monitoring.

Our DNA sampling typically occurred in spring and early summer because bears shed hair then and are attracted to protein-based scent lures. Therefore, our inference about their distribution may reflect this pre-berry season (although our multi-scaled approach captures a component of home range selection that may be multi-seasonal). Sampling techniques that are effective during summer and fall would allow inference less biased by season.

#### **Fragmentation and population delineation**

Genetic samples gathered from mark-recapture surveys can be used to investigate movement patterns and population fragmentation. Population genetics is suited to investigate systems at equilibrium for gene flow and mutation, but this is not the case for recently disturbed systems. Individual-based genetic analysis techniques (Paetkau et al. 1995, Waser and Strobeck 1998, Pritchard et al. 2000, Pearse and Crandell 2004, Manel et al. 2005) can allow exploring individual movement rates in systems that have been recently fragmented and genetic drift has had time to occur. Individual analyses require more than the minimum number of loci for identification (Waser and Strobeck 1998); for example, we found it necessary to expand 6-locus genotypes that were sufficient to identify individuals

to 15-loci to have sufficient power for individual-based population level analyses (Paetkau et al. 1998, 2004; Proctor et al. 2005). We briefly discuss methods we have used to identify inter-area migrants and fragmentation, provide examples, and discuss issues that affect the quality of inference: (1) sample size requirements; (2) differentiating putative from real migrants; (3) identifying source populations; (4) the limits of genetic distances; and (5) the use of fragmentation results in survey study designs.

We and others (Dixon et al. 2006, Haroldson et al. 2010) used DNA from hair snares to test hypotheses about individual movements between adjacent areas based on genetic assignments. Proctor et al. (2005) used assignment methods within program GENECLASS (Piry et al. 2004; Paetkau et al. 1995, 2004) and a model-based clustering method (STRUCTURE; Pritchard et al. 2000) to identify individual migrants between adjacent grizzly bear areas. The GENECLASS assignment method uses area-specific allele frequencies in a likelihood-based assignment test (Paetkau et al. 1995) that calculates the probability of each individual's assignment to an area. The probability of assignment is the cumulative product of each allele's frequency of occurrence in all areas examined. Each individual is assigned to the area with the highest probability of occurrence. The STRUCTURE method clusters individuals into groups through iterative assignments and develops probabilities of area origin for each individual through the cumulative results of those assignments. Individuals that are repeatedly assigned to a group other than that of their capture are considered putative migrants from their source area. The strength of their migrant status is reflected in the resulting probability of their cross-assignment.

For example, analyses by Proctor et al. (2005) revealed several small and isolated grizzly bear populations in BC. Because individual-based genetic analyses provide information about both males and females, measuring sex-specific movement rates is possible. Proctor (2003) and Proctor et al. (2002, 2005) identified sex-specific regional fragmentation in the trans-border area of southern Canada and northwest Montana and Idaho. Using area- and sex-specific movement rates between adjacent areas, Proctor (2003) also used multiple linear regression to explore factors that influenced fragmentation. They found that human settlement, traffic, and human-caused mortality were fragmenting the region's bears into a human-induced meta-population. Fragmenta-

tion was more severe among females than males. Several small subpopulations suffered increased extirpation risk due to the dearth of female interchange with adjacent areas. Offspring production from immigrant females is a critical component of population rescue for small populations. Documenting female movement is therefore important in understanding the nature of fragmentation and its potential solutions.

If sampling is sufficiently widespread, DNA data can also allow estimation of sex-specific dispersal distances. Proctor et al. (2004) used 15-locus genotypes of 97 parent-offspring pairs to estimate male and female grizzly bear natal dispersal in southeast BC. They found male-biased dispersal, with males moving 42 km on average from their natal home range and females moving 14 km on average.

Proctor (2003) and Proctor et al. (2005) were able to detect fragmentation because grizzly bears in their study areas lived at low densities and sometimes in small, isolated populations, allowing genetic drift to drive genetic divergence in a relatively short time (several generations). Grizzly bears in southern BC and southwest Alberta are not long-distance dispersers (McLellan and Hovey 2001, Proctor et al. 2004) and appear sensitive to pressures that create fragmentation (linear developments and human-caused mortality; Proctor et al. 2005). However, power to detect individual movements was variable across the region and was related to the extent of genetic divergence between areas. The genetic and ecological conditions that allowed these inferences may not exist for species that have a greater propensity for long-distance dispersal (e.g., Canada lynx, *Lynx canadensis*, Poole 1997, Schwartz et al. 2002; wolves, *Canis lupus*, Gese and Mech 1991), or where fragmentation is very recent.

To yield adequate inference requires sufficient sample sizes to represent allele frequencies at the population unit. Paetkau et al. (2004) found predicting power to detect migrants may be best estimated by measuring the genetic distance ( $D_{LR}$ , Paetkau et al. 1997) and comparing the amount that distributions overlap in a plot of the individual likelihoods (log of probability) of assignments between 2 compared populations (the less overlap, the more power to identify migrants, see Proctor et al. 2005). Through simulations, they found that sample sizes  $>50$  (in each population) and  $D_{LR}$  values  $>3.0$  between populations were conducive to migrant detection. However, it may be possible to detect migrants in smaller populations using these

methods if a high percent of the population is sampled. For instance, a sample of 20 animals represents 67% of a population of 30 bears, and may be adequate. If DNA samples are gathered through an abundance survey, the sample size can be judged against the resulting estimate.

Program Genetix (Belkhir 1999) may provide another alternative for low sample sizes. Genetix clusters genotypes using principles of allele sharing (increased numbers of shared alleles equates to increased genetic similarity) without the need to estimate allele frequencies. In some instances, this allows inferring genetic origin of just a few samples. For example, we earlier believed that because of geographic proximity, remnant bears in the Cabinet Mountains of northwestern Montana were recently fragmented from the adjacent Yaak population in the southern Purcell Mountains (USFWS 1993). Using Genetix, we demonstrated that 4 animals from the Cabinet Mountains clustered perfectly with bears in the Rocky Mountains in northern Montana rather than with bears from the Yaak (M. Proctor, unpublished data). Program Genetix also allows clustering analyses without a priori assumptions of group membership, adding a level of objectivity when identifying genetic discontinuities.

Recently fragmented populations contain individuals with genotypes that are similar because of shared recent ancestry. It is therefore possible that cross-assigned individuals (assigned to an area other than that of their capture) are not true migrants. We recommend that studies looking for migrants attempt to distinguish true from statistical migrants. Proctor et al. (2005) generated significance levels for individuals assigned to a neighboring area using the simulation routine within GENECLASS 2.0 (Paetkau et al. 2004, Piry et al. 2004). Significance levels were determined by comparing individual genotypes of cross-assigned individuals to a simulated set of 10,000 genotypes that were generated using area-specific allele frequencies. Although several assignment methods determine migrant significance based on simulations (Rannala and Mountain 1997), we recommend the routine developed by Paetkau et al. (2004) because it uses an improved simulation to produce accurate Type I error rates. It mimics natural population processes by generating individuals through uniting gametes. One can develop a pool of migrant candidates and identify migrant individuals in the distribution tails beyond a selected  $\alpha$  error threshold. Individuals beyond the selected

error threshold are likely to be true migrants. When using STRUCTURE, we identify true migrants as those with the highest probability, and very close to 1, of being a migrant, whereas when using GENECLASS, as the lowest probability and very close to 0, of being a resident.

We have also found it important that all possible source populations be sampled. If all possible source populations have not been sampled, it is possible to assign an individual to a false source area with the highest probability only because the real source area has not been sampled and is not tested. We recommend that individual inter-area migrant analysis be carried out, sampling as many adjacent populations as possible within the dispersal distance of the species under study.

We found that patterns of fragmentation may define biological boundaries for populations, allowing better sampling regimes for population census and trend monitoring (Proctor and Paetkau 2004). Population estimates conducted subsequent to delineating population boundaries had higher capture probabilities than estimates done without that analysis, and hence had low closure violation (Table 1, Foothills Model Forest 2004, 2005; Boulanger et al. 2005a, 2005b; and south Selkirks, Proctor et al. 2007). For example, in estimating population abundance in the south Selkirk Mountains (Proctor et al. 2007), preliminary genetics data (from pilot surveys, research bears) suggested fragmentation boundaries (Proctor 2003). The spatial configuration of captures relative to the major settlements and highways that we used as study area boundaries (Fig. 3) was such that the highest density of bears was captured in the center of the study area, contributing to minimal closure violation. Here, 30 bears were DNA-captured 54 times with a capture probability of 0.49; we essentially caught half of the population in each of 4 sessions. Although preliminary genetics data will not always be available for a pre-survey fragmentation analysis, application of the information we now have about potential fragmenting forces for grizzly bears (Proctor 2003, Proctor et al. 2005) can help delineate likely population boundaries for optimal study area design.

**Future directions.** Ecological and human factors that fracture bear populations genetically have now been identified in many parts of BC and western Alberta (M. Proctor, unpublished data), allowing predictions to be made about population boundaries and potential genetic discontinuities in other areas.

Management of connectivity in under-studied areas would benefit from such predictive abilities.

We envision that spatially explicit analyses, similar to that in probability of occurrence modeling, will aid understanding of the causes of fragmentation. Although Proctor (2003) identified human factors that influenced inter-area movement rates, we suspect that further inference can be derived from spatially explicit analyses that incorporate ecological, topographic, and habitat features.

We envision that these methods might be used to monitor movement rates between subpopulations of grizzly bears in the fragmented southern portion of their North American distribution (Proctor 2003, Proctor et al. 2005). Such monitoring can ensure that current movement rates do not decline. It can also document improvements in connectivity that may result from linkage management as well as reproductive success of transplanted individuals (Kasworm et al. 2007).

### **Integration of techniques and future applications**

Where appropriate, genetic techniques using hair can be integrated with radiotelemetry methods to provide more comprehensive understanding than either approach alone can provide. For instance, in the Canada–US border area in southern BC and northwest Montana, we integrated all the methods mentioned above with a long-term radiotelemetry study (Wakkinen and Kasworm 2004) to monitor and inform conservation management of 2 threatened grizzly bear populations. A long-term telemetry effort determined the population trend (Wakkinen and Kasworm 2004). Efforts to examine genetic structure and individual movements using DNA revealed fragmentation lines and delineated sub-population boundaries (Proctor et al. 2005). We used a DNA survey to estimate abundance of bears in the units, and these estimates were combined with reported mortalities to estimate mortality rates (Proctor et al. 2007). Our recent GPS telemetry sample (30 animals since 2004) was used to estimate and correct for closure violation and yield a density estimate (Proctor et al. 2007). Probability of occurrence modeling allowed realistic extrapolation to the entire sub-population units and partitioning of density for more specific management purposes. GPS telemetry was used to develop RSF (Manly et al. 2002) models that identified high quality habitat,

which in turn may be used to manage human access (Proctor et al. 2008b) and to identify linkage zones to re-establish connectivity (Proctor et al. 2008a).

In Alberta, researchers and managers integrated DNA surveys, GPS telemetry, habitat modeling, and remote sensing in province-wide management and conservation of grizzly bears. Inventories of grizzly bears based on sampling grids began several years after they were developed in BC, and a coordinated and comprehensive management and conservation strategy was developed. Proctor and Paetkau (2004) identified management units (MU) based on genetic discontinuities. RSF models based on GPS telemetry data (Nielsen et al. 2002, 2004) were used to help design MU-specific DNA abundance estimates. Franklin et al. (2001) used satellite imagery maps of land cover over the range of grizzly bears in Alberta to illustrate human land-use patterns at a broad scale. DNA survey results, telemetry-driven RSF models, and these landcover maps have been integrated to delineate grizzly bear conservation areas for in Alberta (Nielsen et al. 2008). Research is continuing on possible links between landscape conditions, population size and distribution, and grizzly bear stress levels in Alberta (Stenhouse and Graham 2009). This work will allow development of predictive models for monitoring that can influence land-use decisions across the province (G. Stenhouse, unpublished data).

We recommend that BC, with its estimated 15,000–20,000 grizzly bears over 750,000 km<sup>2</sup>, consider developing an integrated and coordinated research program to guide their management and conservation strategy. BC has digital ecological mapping, forest cover, roads, and elevation models, as well as satellite imagery over the entire province, which would allow the province to be stratified into a number of similar areas. Strategic sampling of the strata with DNA grids (over a representative portion) could enable extrapolation of grizzly bear density over large areas. A province-wide plan would greatly reduce costs compared to the more haphazard approach that has been dictated by short-term, often ephemeral funding.

In summary, abundance estimation techniques can be used to monitor the success or failure of a recovery process through trend monitoring. Assessment of population fragmentation can be used to monitor the effectiveness of connectivity enhancement efforts by documenting inter-population movements and breeding. Finally, DNA-based probability of occur-

rence ecological modeling can be used to guide efforts to protect critical habitat, enhance connectivity, and guide important land-use decisions. We envision that future research in support of wildlife conservation and management will embrace the integration of DNA with other data sources to creatively solve the challenges confronting biodiversity.

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