TR-16-01

Yukon North Slope grizzly bear population estimation and demographic analysis

2016

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Government of Yukon
Fish and Wildlife Branch
TR-16-01

Contributors and Reviewers
A number of Department of Environment and contract staff assisted with the experimental design, field logistics and data collection, including Ramona Maraj, Shelly Marshall, Nicole McCutchen, Al Bear, Kyle Russell, Martin Kienzler, Dorothy Cooley, Todd Shury, Lloyd Freese, Karl Scholz, John Overell, Philip Merchant, Martin Owen, Doug Larson, Spruce Gerberding, Kevin MacLaughlin, Grant McCutchen, John Hechtel, Matt Larsen, Lindsay Staples, Billy Archie, Ian McDonald, Marsha Branigan, Troy Hegel, the Wildlife Management Advisory Council North Slope, the Aklavik Hunters and Trappers Committee, and the Inuvialuit Game Council (apologies for anyone we've missed). We thank Jaylene Goorts and Angela Milani for their work on the telemetry data files and for clarifying aspects of the hair-snare data collection.

We would like to especially thank Murray Efford and John Boulanger for their contributions to those portions of the report that address the genetic data, its analysis and interpretation.

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Suggested citation:

Yukon Fish and Wildlife Branch Report 2016. Yukon North Slope grizzly bear population estimation and demographic analysis. Yukon Fish and Wildlife Branch Report TR-16-01, Whitehorse, Yukon, Canada.

Summary

In 2002, members of the Aklavik Hunter and Trappers Committees (HTC), the Wildlife Management Advisory Council (North Slope) (WMAC (NS)), Government of Yukon and Parks Canada met to discuss needs for managing grizzly bear (*Ursus arctos*) populations in the Yukon portion of the Inuvialuit Settlement Region (ISR). Members of the Aklavik HTC felt that there was a need to update population estimates for the Yukon North Slope (YNS). The *Yukon North Slope Research and Monitoring Plan* and the *Co-management Plan for Grizzly Bears in the Inuvialuit Settlement Region, Yukon and Northwest Territories* also identified the need to update population estimates for grizzly bears so that harvest rates could be reviewed using recent information.

Field work to update population information for bears on YNS was initiated in 2004 and completed in 2010. Our goal was to gather information to estimate population size, reproductive rates, survival rates and the rate of population growth (increase or λ). Specifically, we:

- Estimated the population size using a spatially explicit mark-recapture study design. In 2006 and 2007, we sampled grizzly bear DNA at baited barbed wire hair corrals. DNA data from hair trapping were used to develop spatially explicit individual capture histories for the mark-recapture analysis.
- Collared and tracked 60 individuals and their offspring between 2004 and 2010 and used this information to calculate survival, reproductive and population growth rates.

This research will provide the resource management bodies in the ISR with the information needed to develop appropriate management strategies, including identifying sustainable quotas, and ensuring long-term maintenance of the grizzly bear population in the YNS.

Key findings

- The population estimate for the YNS is given as a range of a ‘low’ and a ‘high’ best estimate: 290 (95% CI=235-358) to 431 (95% CI=349-532) bears, including dependent offspring.
- Population size estimates are based on extrapolations of the data collected in the core study area. They are presented as a range because bear density was not uniform across the study area; rather, density patterns appeared to be driven by ecodistrict (in 2006) or caribou distribution (in 2007). Extrapolating the relationship between bear density and ecodistrict in the core study area to the YNS resulted in the “high estimate” of 431 bears (95% CI=349-532). Extrapolating the relationship between bear density and caribou in the core study area to the YNS resulted in the “low estimate” of 290 bears (95% CI=235-358).
- The population estimate for the core study area was 87 (95% CI=72-106) to 104 (95% CI=85-128) bears. This is the most robust estimate from the study, as it is based on the data collected and not an extrapolation. Extrapolated estimates are really “models” or “predictions” of population size outside of the core study area.

- The grizzly bear population in Ivvavik National Park (INP) was estimated at 69-73% of the total YNS population: 211 (95% CI=173-258) to 298 (95% CI=224-395) bears. It is unknown if the bias towards INP is seasonal or year-round, as the DNA study was limited to only part of the year (June to August) and movement information from collars is limited.
- The estimated sex ratio showed a small but non-significant female bias (54-55% females).
- Using whole litter survival rates for cubs and yearlings, λ was 0.930 (SD=0.091, 95% CI=0.752 – 1.000, in which survival rates were truncated at 1).
- The natural survival rate for adult females was 0.987 (SE=0.013). The natural survival rate for subadult females was 1.0 (no variance). Adult male and subadult male natural survival rates were both 1.0 (no variance). Whole litter cub of year (COY) natural survival rates were 0.462 (SE=0.139) and whole litter young of last year (YOLY) natural survival rates were 0.335 (SE=0.158). For comparison, the individual COY natural survival rates (0.401, SE=0.13) and individual YOLY natural survival (0.340, SE=0.11) were similar to whole litter natural survival rates.
- The earliest age at which a female was recorded to produce a litter was 9. The average age of first parturition for these individuals was 10, although the sample sizes to estimate this were low. Collared females produced 43 cubs in 21 litters. Litter sizes of two were most frequently observed (67%) with a mean litter size of 2.047 (SE=0.196).
- The previous total population size for YNS was estimated as 316 bears (no confidence intervals) (Nagy et al. 1990). However, given differences in study design, variation in the current population estimate, and the amount of time between studies, we cannot conclude that the population has increased or decreased from the 1970s to today. However, trend information (based on survival and reproductive rates) suggests that the population was stable or at carrying capacity in the 2004-2010 period.
- The YNS is an area with few external pressures for grizzly bears, meaning relative risk to the population is low: harvest is below quota and few female bears are harvested, there are few human-bear conflicts and a high percentage of the YNS is protected and has little to no existing development.
- Study results can be used to develop harvest recommendations in collaboration with Aklavik HTC, WMAC (NS), and Parks Canada.

Contents

Introduction

In 2002, members of the Aklavik Hunter and Trappers Committee [herein Aklavik HTC], the Wildlife Management Advisory Council (North Slope) (WMAC (NS)), Government of Yukon and Parks Canada met to discuss needs for managing grizzly bear (*Ursus arctos*) populations in the portion of the Inuvialuit Settlement Region in Yukon (Yukon North Slope or YNS). Members of the Aklavik HTC felt that there was a need to update population estimates for the YNS. The *Yukon North Slope Research and Monitoring Plan* and the *Co-management Plan for Grizzly Bears in the Inuvialuit Settlement Region, Yukon and Northwest Territories* also indicated a need to update population estimates for grizzly bears, so that harvest rates could be reviewed using updated and population-specific information.

At public meetings, some people using the YNS said they were seeing bears more often. Their impression was that grizzly bear numbers had increased since the last estimate of the bear population size obtained for the Barn Mountains in 1972 to 1974 (Nagy 1990). At the start of this study, population estimates and estimates of birth rates and death rates for the region were almost 30 years old. Harvest quotas were based on a combination of these old estimates and estimates from regions in the Northwest Territories. New geographic-specific information on grizzly bears was needed.

We initiated this project to obtain up-to-date estimates specific to the YNS. Our goal was to gather information to estimate population size, reproductive rates, survival rates and growth rate (rate of population increase or (λ). Here, we present results of a seven-year (2004 – 2010) study of grizzly bears on the YNS. This research will provide governments, management bodies, and the Inuvialuit with the information needed to develop appropriate management strategies, including identification of sustainable quotas, and ensure long-term maintenance of grizzly bears-on YNS.

Goals and objectives

The primary goal of this project was to update population information for grizzly bears on the YNS. Our specific objectives were to:

1) Estimate the grizzly bear population size for the YNS based on extrapolation from a hair-based DNA mark-recapture study area.
2) Estimate population parameters (vital rates) on the YNS through the tracking and monitoring of collared bears. This information was used to estimate the rate of population growth (λ) using life table analysis.

This information can be used to identify sustainable quotas in collaboration with Aklavik HTC, WMAC-NS, and Parks Canada.

Previous research

There have been several grizzly bear studies on the YNS. The first bear study on the YNS was conducted in the Barn Mountain area in 1972 to 1975 (Nagy et al. 1983a). This study obtained information on the morphological characteristics of bears, denning habits, and population parameters. Researchers used a direct aerial count of bears to estimate population size. However, no correction factors were applied for distance sightability, or other limiting factors for sightability, such as pelage color and vegetative cover. Not accounting for these biases may have resulted in an underestimation of bear density. Conversely, immigration and emigration were not considered in the estimate, which could have led to an overestimate of bear density. Further, the Barn Mountain study was not considered extensive enough to derive reproductive information for a representative sample of females (Nagy 1990) and the physiographic characteristics of the Barn Mountain Range do not resemble the rest of the YNS. Nagy (1990) also noted that the duration of the study (three years) was not long enough to capture the reproductive cycle of females. As a result of these issues, the majority of the data collected from this study were not used to establish population size. Instead, population parameter estimates were applied to the YNS from other studies throughout the Northwest Territories and neighboring Alaska, resulting in a population estimate of 316 bears with no corresponding confidence interval (Nagy 1990). Nagy (1990) recommended that a five- to ten-year study be conducted to obtain information specific to the YNS.

A two-year intensive mark-recapture study was initiated in the Richardson Mountains in 1992 (Nagy 2003). In 1993, collars were deployed on adult females and these bears were tracked until June 2000. Unfortunately, during spring 1992, prior to the start of the study, a high number of male bears were harvested in the study area. Researchers suspect, based on ratios of marked and unmarked bears, that this high mortality of adult males caused an influx of young males into the area that could have led to inflated population estimates, suppressed reproductive parameter estimates, and resulted in inaccurate sex ratio estimates (Nagy 2003). The Lincoln-Petersen estimate for 1993 was 145 bears $\geq$ 2 years of age and an estimated density of 19 bears per 1000 km^2 in the study area. Due to lack of closure, the estimate was lowered by 10%; however, the results of this study may more accurately represent the changes that occur in population structure following overharvest.

In 1993, a habitat mapping study was conducted in the Firth River corridor (Mackenzie and MacHutchon 1996). This study did not result in any population parameter estimates, but instead investigated habitat suitability along the narrow corridor surrounding the Firth River. Eight bears (five adult females and three adult males) were collared during this study, and observations were made of habitat use, activity budgets, food habits, and movements.

The Brooks Range is continuous with the YNS, though the areas differ physiographically. A grizzly bear study conducted in the Northern Brooks Range, Alaska, prior to 1976 showed that the population there was likely in decline (Reynolds 1980). Nagy et al. (1983a) speculated that, because the reproductive parameters observed in the Barn Mountain population most resemble the Northern Brooks Range population studied by Reynolds (1980), the YNS population was either declining or in long-term equilibrium.

Grizzly bear harvest on Yukon's North Slope

Quotas were established on the YNS in 1994. Eight tags were allotted; three tags for Ivvavik National Park (INP), five tags for the Eastern North Slope, and no tags for Herschel. The quota was increased to nine in 2004 and 11 in 2011 (Table 1). Currently, the Total Allowable Harvest (TAH) for YNS is 13; 11 tags are allocated by Government of Yukon in the Eastern YNS and INP (including Herschel Island Territorial Park) and two tags are administered by GNWT for bears in the NWT Aklavik Hunting area.

In general, harvest has either met or been lower than the quota for YNS and INP (Table 1; Figure 1), has not exceeded eight bears since 1990, and most of the harvest has been comprised of males. Harvest success and activity can be tied to snow conditions and the ability of hunters to access the land. This can cause variability in the total harvest from year to year (WMAC (NS) 2008). Most bears are taken from the harvestable regions close to Aklavik (e.g., Richardson Mountains), along the coast line, and on the eastern side of the YNS (Figure 2).

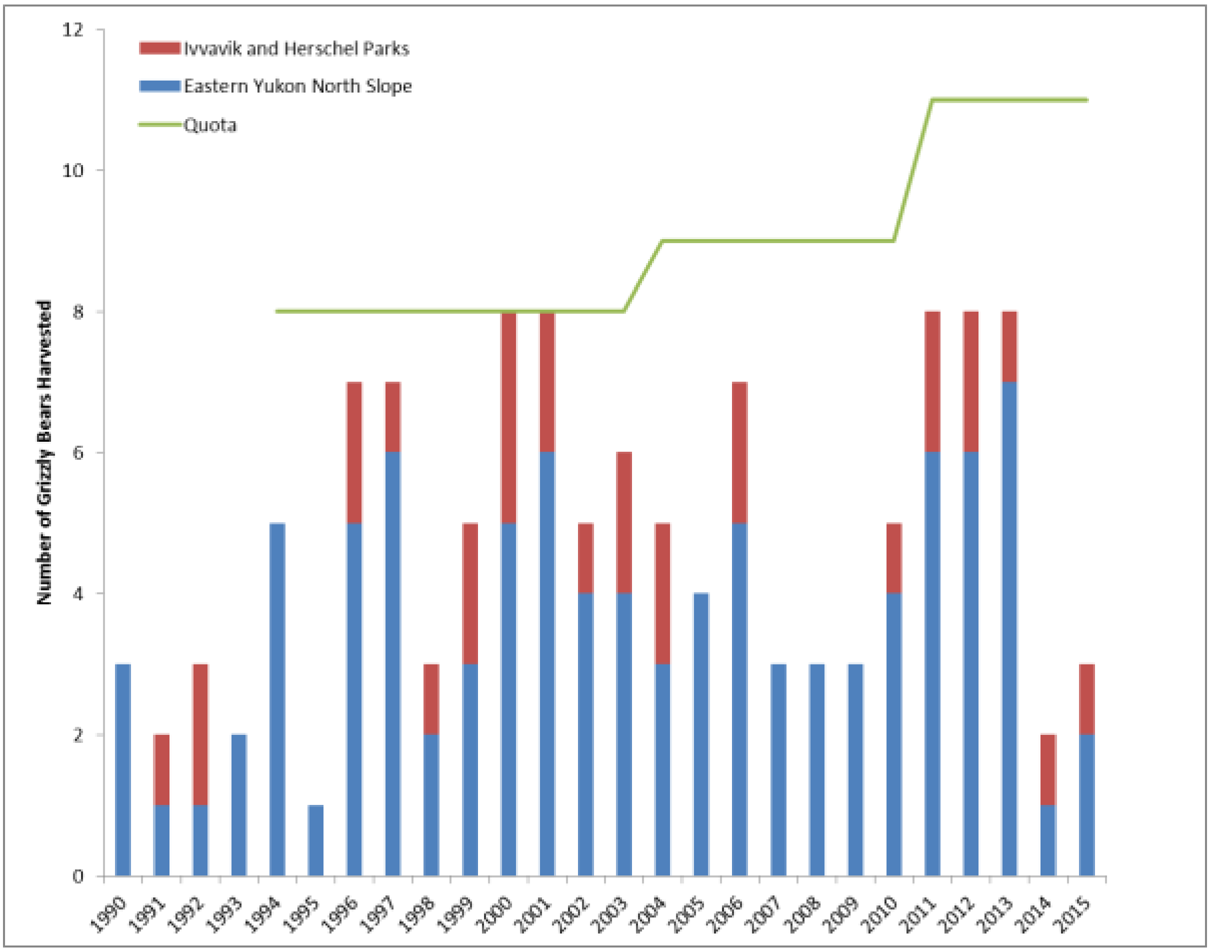

Figure 1. Grizzly bear harvest on Yukon's North Slope between 1990 and 2015.

Table 1. Grizzly bear harvest statistics for YNS. An average of 22% of the harvest occurs in INP. On average, approximately 14% of the harvest is female. On average, 59% of the quota administered by Government of Yukon has been filled since the quota came into effect (currently 11 tags out of the 13 TAH).

Year	Harvest			% harvest in INP	Males	Females	% Females	Quota	% Quota filled
	Eastern YNS	INP	Total						
1990	3	0	3	0%	2	1	33%	--	
1991	1	1	2	50%	2	0	0%	--	
1992	1	2	3	67%	3	0	0%	--	
1993	2	0	2	0%	2	0	0%	--	
1994	5	0	5	0%	5	0	0%	8	63%
1995	1	0	1	0%	1	0	0%	8	13%
1996	5	2	7	29%	5	2	29%	8	88%
1997	6	1	7	14%	5	2	29%	8	88%
1998	2	1	3	33%	3	0	0%	8	38%
1999	3	2	5	40%	4	1	20%	8	63%
2000	5	3	8	38%	6	2	25%	8	100%
2001	6	2	8	25%	7	1	13%	8	100%
2002	4	1	5	20%	3	2	40%	8	63%
2003	4	2	6	33%	4	2	33%	8	75%
2004	3	2	5	40%	5	0	0%	9	56%
2005	4	0	4	0%	4	0	0%	9	44%
2006	5	2	7	29%	7	0	0%	9	78%
2007	3	0	3	0%	3	0	0%	9	33%
2008	3	0	3	0%	2	1	33%	9	33%
2009	3	0	3	0%	3	0	0%	9	33%
2010	4	1	5	20%	4	1	20%	9	56%
2011	6	2	8	25%	7	1	13%	11	73%
2012	6	2	8	25%	6	2	25%	11	73%
2013	7	1	8	13%	6	2	25%	11	73%
2014	1	1	2	50%	2	0	0%	11	18%
2015	2	1	3	33%	2	1	33%	11	27%
AVERAGE	3.7	1.1	4.8	22%	4.0	0.8	14%		59%

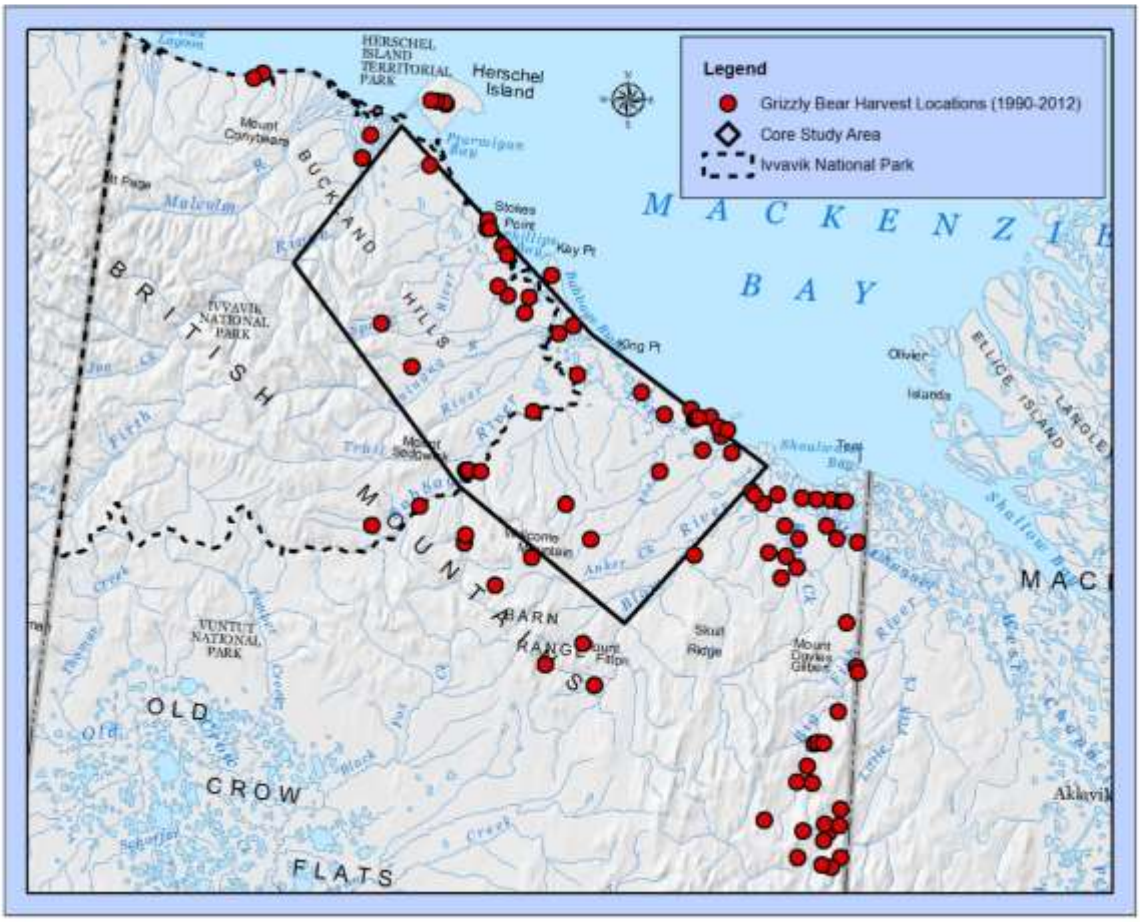

Figure 2. Distribution of grizzly bear harvest over the YNS (1990-2012) in relation to the core study area (see Study Area section for further description) and Ivvavik National Park (INP).

Study area

Our core study area centered on the Babbage River Drainage of the YNS, Canada (Figure 3). The core study area boundary was, in part, selected to maximize geographical closure (i.e., in which movement of study animals in and out of the study area during the sampling period was naturally restricted). The study area was bounded by the Firth and Blow Rivers, providing a moderate amount of geographic closure (the rivers reduced bear movements onto and off of the study area). Mackenzie Bay offered full closure on the north side of the study area. The south was bound by the Richardson, Barn and British Mountains, but it was unlikely that these mountains provided any topographic closure to the study area. The study area included much of the area where Inuvialuit grizzly bear hunting activity takes place.

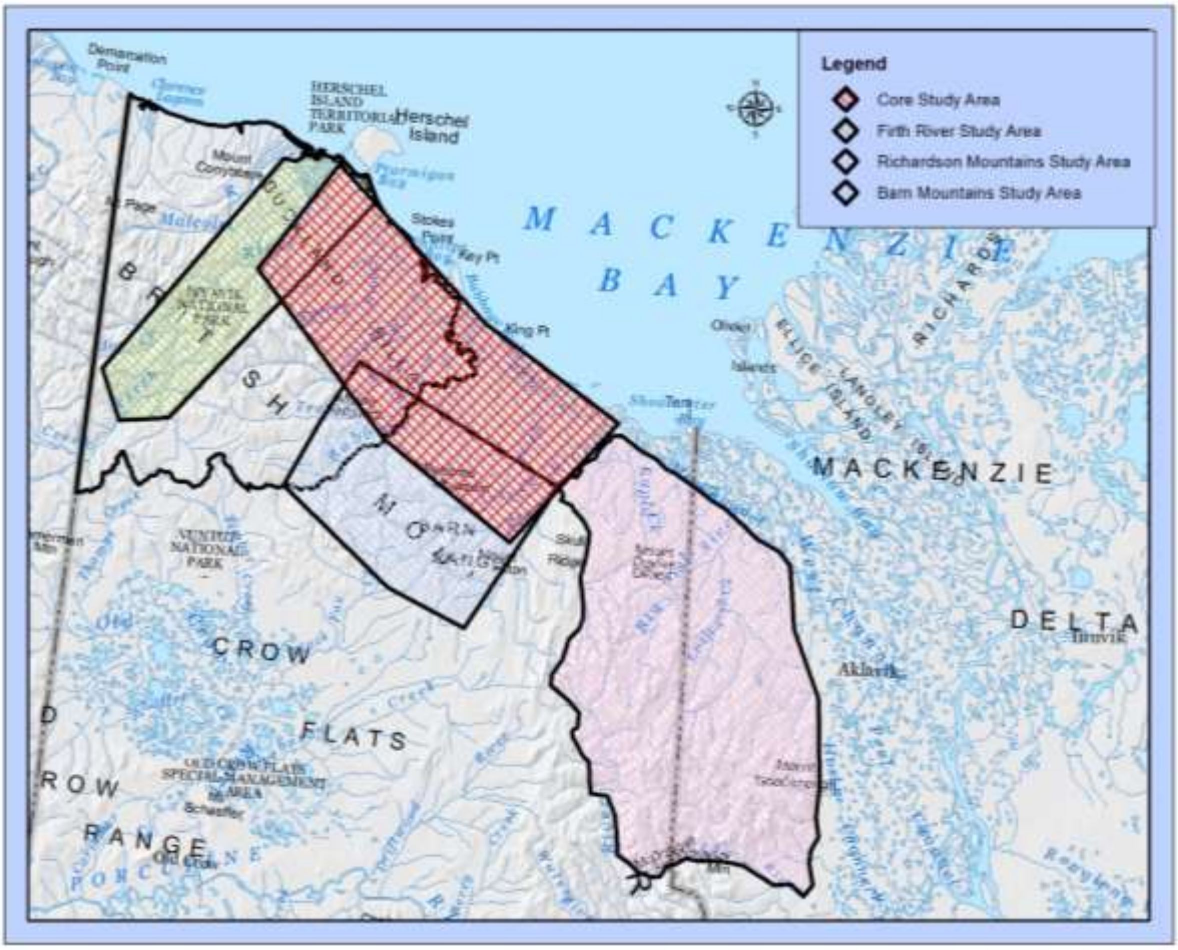

Figure 3. The core study area for the YNS grizzly bear study, Yukon, Canada. The hashed red area was selected as the core area because at the start of this study, it was an area of high harvest pressure, relative to other areas on the YNS. The hashed green, blue and pink polygons represent areas in which other grizzly bear studies have taken place.

The core study area also encompassed portions of INP. This helped us understand the movements of bears across the Park boundary, which will allow management partners to evaluate the harvest quotas inside and outside of the Park. This study was conducted under a partnership arrangement between Parks Canada and the Yukon Government.

We selected our study area to contain portions of three classes of aggregated ecodistricts (Figure 4). We used the ecodistrict classification outlined in the Northern Yukon Ecological Land Survey (Wiken et al. 1981). Based on Nagy et al.'s (1983a) spatial zoning of bear densities, we felt that these aggregated classes of ecodistricts had a good *a priori* basis for significantly different bear densities. Use of these classes also allowed for direct comparison to Nagy et al.'s (1983a) work, comparison to other density estimates in Yukon (which are also based on ecodistricts), and created a convenient unit for extrapolating population estimates. We labeled our aggregated classes Coastal Plains, British Mountains and Barn Mountains and refer to these as ecodistrict groups. More detail on the ecological classifications within the study area is provided in Appendix 1. The geographic area of the YNS was 18 225 km^2. The core study within the North Slope was 5 243 km^2 (Figure 3).

Additionally, the YNS provides important calving habitat for barren-ground caribou. The Porcupine Caribou herd migrates from widely dispersed wintering grounds in Alaska, Yukon, and Northwest Territories onto the Yukon and Alaska North Slopes. Peak calving generally occurs between May 30 and June 8th each year with the long-term average falling on June 2nd (PCTC 2015). Calves are most susceptible to predation by bears during the first few weeks of life (Adams et al. 1985; Reynolds et al. 1987; Porcupine Caribou Technical Committee 1993). .

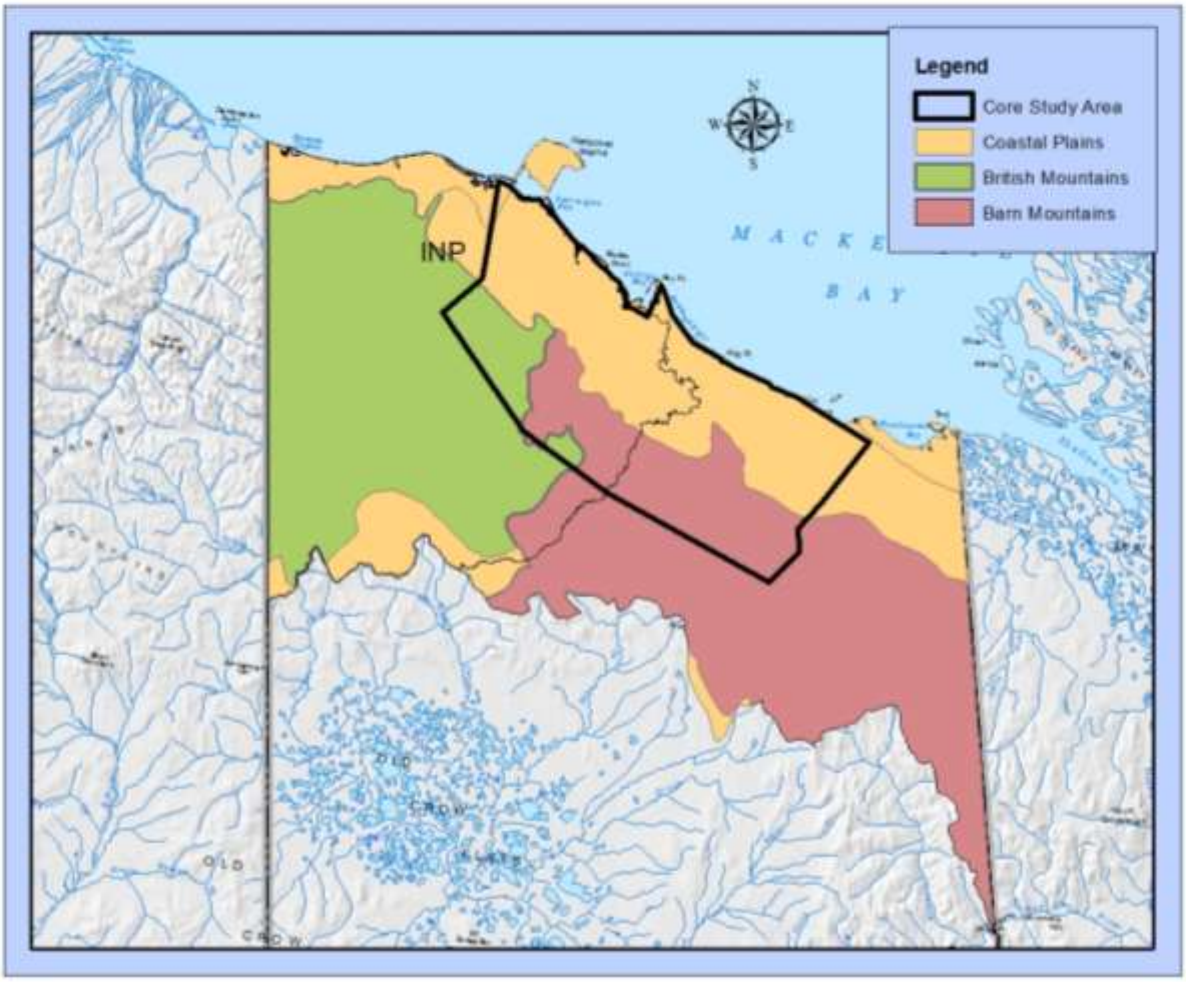

Figure 4. Ecodistrict groups on the YNS used for spatially explicit capture-recapture (SECR) analysis. The colored regions of the ecodistrict groups represent the spatial extent of the YNS or the Yukon portion of the ISR

Methods

Population estimation

Genetic mark-recapture sampling

We collected grizzly bear hair samples for DNA at baited barbed wire hair corrals following Woods et al. (1999). We divided the study area systematically into 107 cells and placed one baited barbed wire hair corral in each 7 km x 7 km cell (Figure 5). We “trapped” for hair in each cell for three consecutive ten-day sampling occasions in each of 2006 and 2007. We used a novel scent in our bait for each sampling occasion. Corrals were not moved within years due to budgetary constraints but were moved between years. All corrals were at least 1 km apart. We installed corrals when the snow melted (June 15) and finished the last check by August 1. Based on information on bear habitat use from previous studies and information about habitat use from bears we had collared and relocated in the study area, we selected sites within cells that had the best potential for bear visitation during the sampling period. Specifically, we navigated to a random location with the cell and placed the corral in an area with the best potential for bear visitation within reasonable proximity to the random location. All hair from each barb was collected, labelled sequentially, and stored in paper envelopes in a cool dry place until they could be genotyped.

Genetic analyses

Hair collected from each barb was treated as a single sample during DNA analysis. All genotyping was performed by Wildlife Genetics International’s commercial laboratory. All grizzly bear samples were genotyped using microsatellite markers for individual identification. They analysed six microsatellite markers (G1A, G10B, G1D, G10M, MU59, G10U) and one loci for gender and assigned an individual identity to a sample when the sibling-match probability was less than 0.05 (Palsbøll 1999, Woods et al. 1999). Error-checking was performed on all samples.

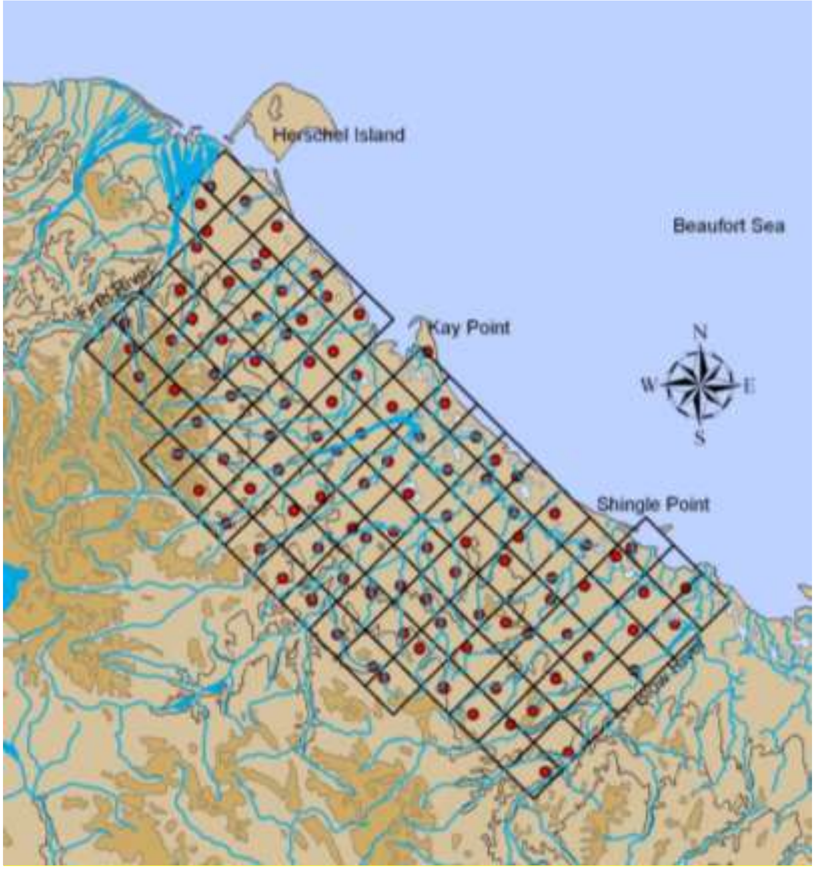

Figure 5. Location of hair snare stations relative to the grid for 2006. Stations remained in the same location for the entire sampling season. Hair trapping stations were moved to different locations in 2007.

Abundance estimation

Mark-recapture is a method commonly used to estimate population size. A portion of the population is captured, marked, and released. Later, another portion of the population is captured and the number of marked individuals within the sample is counted. Since the number of marked individuals within the second sample should be proportional to the number of marked individuals in the whole population, an estimate of the total population size can be obtained by dividing the number of marked individuals by the proportion of marked individuals in the second sample. The method is most useful when it is not practical to count all the individuals in the population.

DNA data from hair traps were used to develop spatially explicit individual capture histories for mark-recapture analysis. We estimated abundance from these data using spatially explicit capture-recapture (SECR) models (Efford 2004, Borchers and Efford 2008, Efford et al. 2009a, b). SECR analysis is a relatively new variation on mark-recapture analysis. One of the issues with mark-recapture studies is the violation of the assumption of population closure (loss or gain of animals either by movement in and out [geographic closure] or through birth and death [demographic closure]) during the capture and marking of animals. This can result in bias in population estimates. SECR models correct for movement bias by incorporating a spatial element to conventional capture-recapture analysis. It is expected that animals whose home range centers are located closer to trap locations are more likely to be detected, and vice versa. SECR combines a model for the spatial distribution of home-range centers (2-D distribution model) with a spatial detection model. It produces a density estimate which can then be converted to a population estimate by extrapolating from the area sampled (Efford and Fewster 2012). Extrapolations to the YNS and INP relied on the assumption that bear densities on unsampled areas were the same as those on sampled areas within the same physiographic units. A technical overview of SECR methods is provided in Appendix 3.

We used two different covariates as potential predictors of grizzly bear density on the YNS: 1) the ecodistricts used to define the study strata; and 2) the geographic variation in caribou density (Appendix 3 and Figure A3 provide definitions for habitat covariates). We also compared both models to one where densities were uniform across the study area. We allowed for sex differences in SECR models. We expected that the spatial scale of detection would be different between sexes given that males often have larger home range sizes than females. We allowed for sex-specific home range sizes using a hybrid mixture-model (Appendix 3).

We assessed terms for a temporal effect, a site-specific learned response, sex-specific spatial scale of detection, and individual heterogeneity in the detection parameters when constructing our detection models. We selected our SECR model by first deciding on a suitable detection model (considering combinations of selected parameters) while assuming uniform density and pooling data across years. We then evaluated the most appropriate density model for each year using the selected detection model.

We fit SECR models to our mark-recapture data (using full likelihood and proximity detectors; Efford et al. 2009b; Appendix 3). We found the best fit model using Akaike's Information Criterion (AIC_c; Hurvich and Tsai 1989).

Bear density estimates were calculated for each density predictor using the fitted density surface from the SECR models. Density estimates were converted to population size within the study grid and extrapolated to the larger INP and YNS. Separate estimates were calculated for 2006 and 2007 for each density model.

SECR models assumed that populations were demographically closed during sampling within years that individuals were accurately identified, that detections of different individuals were independent events, and that animals occupied approximately circular home ranges, the central locations of which were independent of each other and fixed during sampling within years (Efford 2004). We note that while individuals in family groups are typically not detected independently, this underestimates the confidence intervals for population estimates but does not affect the point estimate.

Demographic rate estimation

We collared and tracked 60 individuals and their offspring between June 2004 and May 2010 and used this information to calculated survival rates, reproductive rates and population growth rates. Of the collared individuals, seven were found within the core DNA study area in June and July of 2006 and 2007. Various factors, including collar malfunctions, dropping of collars, and deaths of some collared bears, prevented consistent tracking of all collared individuals over the study duration (Table A8-1).

Capture, handling, and monitoring of free-ranging bears

We used a rotary aircraft to search for bears. Bears were immobilized by aerial darting with Telazol (at 8 mg/kg estimated body weight) or MZT (Telazol 2.5 mg/kg and Medatomidine 0.05 mg/kg estimated body weight). Canadian Council on Animal Care (CCAC) Guidelines were followed during capture and handling operations (Parks Canada Animal Care Committee Protocol Number 1278; Research Permit Number 1278). Capture and handling procedures are outlined in greater detail in Appendix 2. A collar with a GPS or VHF transmitter was fitted to a captured grizzly bear and a premolar was removed for aging after administration of anesthetic. GPS collars were placed on males and females. VHF collars were placed on females only. Overflights were conducted several times a year to record survival information. We attempted to monitor each bear for as long as it remained collared, between den exit and den entrance, over the duration of the study. When collars transmitted in mortality mode, we visited the site as soon as possible to determine whether the bear had died or dropped its collar. For bears that died, we confirmed mortality and attempted to determine the cause of death by examining remains. However, due to the remoteness of our study area it was frequently not possible to get to dead bears in time to establish cause of mortality. We counted litters as early as possible after den emergence to minimize biases introduced by early loss of cubs or entire litters (McLellan 1989a). We collected information on age of first reproduction by monitoring subadult and young adult females for their first litters.

Vital and population growth rates estimation

We used June 15th as time of census for all demographic rates. This ensured that survival rate estimates were specific to an entire active season followed by an entire denning period (generally, bears on our study area emerged from their dens between March 15 and June 15). Furthermore, survival and litter sizes of cub of year (COY), young of last year (YOLY), and 2-yr olds could be confirmed in the spring because visual locations were easier to obtain than at other times of year (e.g., less foliage, snow allows for tracking, etc.).

Survival analysis

We categorized bears into age classes because sample sizes were insufficient to estimate age-specific demographic rates. We categorized bears as COY, YOLY, subadults (2-5 years of age), and adults (>5 years of age). Annual cause-specific survival rates were calculated using methods described by Heisey and Fuller (1985) and Hovey and McLellan (1996). Survival analysis details are provided in Appendix 4.

Reproduction

We calculated age of first parturition (age at which first litter is produced), mean litter size (average number of cubs per litter), and an annual litter production rate across all females within each age category. The age class-specific annual reproductive rates were calculated following Garshelis et al. (1998). We categorized adults into five age classes: >5-year olds, 6-8-year olds, 9-12-year olds, 13-17-year olds, and > 17 years of age. We also calculated the proportion of available females within each age class that produced cubs (m_x; Taylor et al. 1987a). More detail on calculation of reproductive rates is provided in Appendix 5.

Population simulations

We used life table models, as implemented in the freely-available software package RISKMAN (beta version 1.9.9.64, Taylor et al. 2003), to simulate the dynamics of the Yukon North Slope population and to estimate population growth rates from demographic rates (Appendix 6). A life table shows, for each age cohort, the probability that an individual of that age will die before next year (or time of census). From this starting point, a number of inferences can be derived, including the growth rate of a population (lambda or λ). Grizzly bear populations, like most managed wildlife, are age-structured, birth-pulse populations (Caughley 1977). RISKMAN is an age-structured stochastic life table model specifically designed to simulate the growth and harvest of populations of species with multiannual reproductive cycles, such as bears. We used values from the survival and reproductive rates analyses to calculate λ for the population.

Results

DNA-based mark recapture analysis

Genetic mark-recapture sampling

A total of 3154 hair samples were collected from hair snag stations between June and August in 2006, and 1153 between June and August in 2007. We subsampled our hair samples using a cap of four extractions for collection events with eight or fewer samples, a cap of five samples for events with 10 or fewer samples, a cap of six for events with 12 or fewer samples, and a cap of seven for all other collection events. Bears were detected unevenly across the study grid. It was generally observed that the intensity of hair snag events decreased (i.e., fewer hair samples were collected) as you moved across the study grid north-easterly (Figure 6). The majority of hair samples were obtained from the southwestern corner of the study grid, corresponding to the British Mountains Ecodistrict and the westerly portion of the Barns Mountain Ecodistrict within the study area.

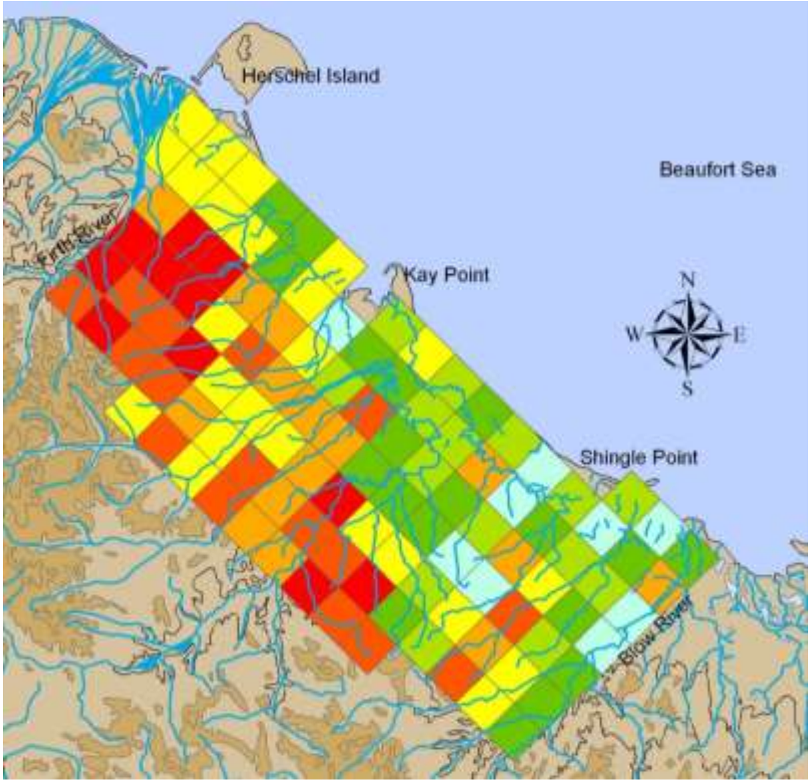

Figure 6. Intensity of hair snag events over the two sampling years (2006 and 2007 combined; spatial patterns of hair snag events between 2006 and 2007 were similar). A hair snag event is when a station was hit by a bear or multiple bears within one sampling occasion (e.g., 10-day sampling period). Red cells indicate six hair snag events over the two years. Dark orange cells indicate five hair snag events, light orange indicates four hair snag events, yellow indicates three hair snag events, dark green indicates two hair snag events, light green indicates one hair snag event, and blue cells indicate no hair snag events.

Genetic analysis

Genetic analysis of 931 hair subsamples from hair traps in 2006 and 2007 identified a total of 177 individual grizzly bears. A total of 110 individual bears were identified in 2006 (53 male and 57 female), and 105 bears identified in 2007 (48 male and 57 female). Sixty-seven of the 105 individuals detected in 2007 were not previously identified in 2006. Further, 144 redetections (repeat detections of the same individual) were recorded in 2006, and 96 redetections were recorded in 2007. Table 2 summarizes the individual detection data. Additional information pertaining to sub-sampling methods for genetic analysis can be found in Appendix 3.

Table 2. Summary of grizzly bear detections on the YNS hair snag grid in the summers of 2006 and 2007. Sampling in each year was divided into three 10-day intervals. Counts are given of the total number of detections of identified bears, the number of distinct individuals recorded in each interval, and the cumulative number of individuals, M(t=1).

Year	Occasion	Total Detections			Individual bears (n)			Cumulative Individuals M(t+1)		
		M	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**
2006	1	41	24	65	31	17	48	31	17	48
	2	49	38	87	32	25	57	45	35	80
	3	44	58	102	32	44	76	53	57	110
	Total	134	120	254	53	57	110			
2007	1	47	31	78	27	26	53	27	26	53
	2	35	32	67	23	24	47	39	39	78
	3	25	31	56	22	29	51	48	57	105
	Total	107	94	201	48	57	105			

Abundance estimation

Detailed results for the SECR analyses are presented in Appendix 3.

Grizzly bear densities were estimated for each of the covariate density models (i.e., ecodistrict, caribou index, and uniform). Densities were calculated for within the study grid (5 243km^2) for 2006 and 2007 and then extrapolated across INP (10 168km^2) and the YNS (18 225km^2), yielding population estimates for the study grid, INP, and the YNS for each density predictor (Table 3).

Comparisons of density models show that the predictor of the best model changed from 2006 to 2007 (Appendix 3 and Table A5), and in both years an inhomogeneous density predictor was preferred over the uniform model. In 2006, ecodistrict was the best predictor of grizzly bear density across the study grid. Conversely, in 2007 the best predictor was the caribou index. We used the estimated density of the best model in each year to estimate the population size, yielding a 'high' and a 'low' estimate, both with corresponding 95% confidence intervals.

Using this method to determine the best estimate, we report the grizzly bear population estimate in the core study area to be 87 (95% CI: 72-106) to 104 (95% CI: 85-128) bears. This estimate is most accurate as it does not require extrapolation. The extrapolated population estimate for INP was determined to be 211 (95% CI: 173-258) to 298 (95% CI: 224-395) bears. For the entire YNS, the population is estimated to be 290 (95% CI: 235-358) to 431 (95% CI: 349-532). All estimates are for pooled sexes and include dependent offspring (Table 3). 69-73% of the total YNS population is estimated to be found in INP.

Using the ecodistrict density model, we also calculated separate densities for each ecodistrict group (Table A6). The density of grizzly bears was highest in the British Mountains (~43-54 bears/1000 km^2), followed by the Barn Mountains (~10-18 bears/1000 km^2) and Coastal Plains (~10-12 bears/1000 km^2). Estimates vary because they differed between the 2 years of the study.

The sex ratio of female to male grizzly bears was biased slightly towards females, though this difference was not significant (2006: 54% female (95% CI: 44-63%); 2007: 55% female (95% CI: 45-64%) (Appendix 3, Table A5). As expected, based on home range sizes, the spatial scale of detection differed between sexes (males sigma$_{EX}$ > female sigma$_{EX}$).

Table 3. Grizzly bear population size inferred from fitted density models. The population size is the expected number of bear activity centers within the relevant polygon. 95% CI in parenthesis. The model that best predicted density changed from 2006 and 2007. The best fit models and corresponding population estimates are highlighted in bold. In 2006 the population size is based on the Ecodistrict density model, and in 2007 the population size is based on the caribou index model. This yields a “high” and a “low” estimate for each area.

Year	Density Model	Core Study Area	INP	YNS
2006	Uniform	95 (80-113)	179 (151-213)	337 (283-400)
	Ecodistrict	**87 (72–106)**	**298 (224–395)**	**431 (349–532)**
	Caribou Index	99 (83–117)	191 (161–227)	304 (254–364)
2007	Uniform	97 (78-121)	183 (148-228)	334 (277-428)
	Ecodistrict	86 (66–111)	361 (266–490)	452 (346–591)
	Caribou Index	**104 (85–128)**	**211 (173–258)**	**290 (235–358)**

Demographic rates

During the study, we collared and tracked a total of 60 individual subadult and adult grizzly bears (41 females and 19 males). The number of bears monitored in each year of the study ranged from 10 to 35.

Survival

The natural survival rate for adult females was 0.987 (SE=0.013). The natural survival rate for subadult females, adult males, and subadult males was 1.0 (no variance) though sample sizes used to calculate these rates were low. Whole litter COY natural survival rates were 0.462 (SE=0.139) and whole litter YOLY natural survival rates were 0.335 (SE=0.158). For comparison, the individual COY natural survival rates (0.401, SE=0.13) and individual YOLY natural survival (0.340, SE=0.11) were similar to whole litter natural survival rates.

During the timeframe we tracked bears (2004 to 2010), one adult female bear was known to die from natural causes. Two subadult bears were known to be killed in defense of life and property but these individuals were not included in analyses of natural survival rates. One adult female bear was killed during capture and handling and one adult male bear was known to be harvested shortly after he dropped his collar, but neither of these bears were included in any survival analyses because research mortality is not considered ongoing in this area and inclusion of uncollared bears can bias survival data. In addition, 10 of 17 tracked YOLY and 16 of 27 tracked COY were known to have died of natural causes.

Reproduction

The earliest age at which a female was recorded to successfully produce a litter was 9 years old. While there were 2- and 3-year old females in the study, we did not track these individuals females long enough to properly assess their age of first parturition. However, we believe we were able to track four individuals that were 4 years or older to their first parturition. The average age of first parturition from these individuals was 10-years old. Collared females produced 43 cubs in 21 litters. Litter sizes of two were most frequently observed (67%) with a mean litter size of 2.047 (SE=0.196). The annual litter production rate across all females within each age category is shown in Table 4. Table 5 shows the proportion of females with litters (m_x values) we used in our RISKMAN analysis.

Table 4. Proportion of litters that occurred in each litter size class for each age class. Standard errors are included. These values were used in the RISKMAN model.

Age	Proportion of 1 cub litters	Proportion of 2 cub litters	Proportion of 3 cub litters	Mean Litter Size (SE)
9-12 years	0.143	0.643	0.214	2.071 (0.103)
13-17 years	0.000	0.667	0.333	2.333 (0.076)
over 17 years	0.250	0.750	0.000	1.750 (0.086)

Table 5. Proportion of females with litters and standard errors.

Age	Proportion with litters (SE)
9-12 years	0.371 (0.134)
13-17 years	0.174 (0.19)
over 17 years	0.222 (0.207)

Population simulations

There were no significant differences among λ values when considering whole-litter survival rates or individual survival rates for cubs and yearlings. Using whole-litter survival rates for cubs and yearlings, our RISKMAN model produced λ of 0.930 (SD=0.091, 95% CI=0.752 – 1.108). When we considered only whole-litter survival of cubs and used individual yearling survival, λ was 0.936 (SD=0.063). Considering individual survival of cubs and yearlings simultaneously produced a λ of 0.920 (SD=0.096). Given the lack of independence of yearling and cub survival, we recommending using λ of 0.930 (SD=0.091, 95% CI=0.752 – 1.108) as the intrinsic (natural) population growth rate for considerations around harvest.

Discussion

Population size

Our analysis indicates that bear density was not uniform over the core study grid; rather, there were clear relationships between bear density, ecodistrict type and the presence of calving caribou. As a consequence, population estimates extrapolated outside of the core study area to the rest of the YNS depended on which spatial density model was used to predict population size (ecodistrict, caribou index, or uniform). The factor that best explained bear density patterns within the core study area was ecodistrict in 2006 and caribou index in 2007, resulting in a range of population estimates for the core study area, YNS, and INP.

Extrapolating the relationship between bear density and ecodistrict in the core study area to the YNS resulted in the "high estimate" of 431 bears (95% CI=349-532). Extrapolating the relationship between bear density and caribou in the core study area to the YNS resulted in the "low estimate" of 290 bears (95% CI=235-358). Using the linear-caribou density model, the estimated population average for the YNS was 127 bears less than the estimated population average using the ecodistrict density model in 2006, and 162 bears less in 2007. The grizzly bear population in INP was estimated at 69-73% of the total YNS population: 211 (95% CI=173-258) to 298 (95% CI=224-395) bears. The population estimate for the core study area was 87 (95% CI=72-106) to 104 (95% CI=85-128) bears. This is the most robust estimate from the study, as it is based on the data collected and not an extrapolation. Extrapolated estimates are "models" or "predictions" of population size outside of the core study area.

The difference in the extrapolated population estimates reflect different relationships between the covariates and bear density. Density estimates predicted in the British Mountains ecodistrict were very high, as many bears were detected in this portion of the study area. Although it only formed a small part of the study area, the British Mountains ecodistrict forms a large portion of INP and YNS, so when the British Mountains density estimate is extrapolated, it results in high population estimates for INP and YNS. The high density in British Mountains is attributed to abundant food sources and low harvest (see the "Population densities" section for more details). Conversely, the caribou index was low in the interior of the core study area, so the caribou model predicted low bear densities there and overall, a lower total estimated population size.

The choice of which spatial population model to use to extrapolate from the core study area to the entire YNS is complicated and ultimately relies on biological judgement. We've made the assumption that the relationship between ecodistrict, caribou, and bear density within the core study area is the same across the entire YNS (including INP), but we don't have the data to confirm this assumption. For example, there may be bear density differences within ecodistricts, not just among ecodistricts. The study grid was comprised of representative proportions of three ecodistricts that were considered ecologically distinct units, had good a *priori* basis for different bear densities, and were convenient units for extrapolation.

Although it was known that the study area could cover areas of high-density calving caribou, the addition of caribou as a covariate was done *ad hoc* in an attempt to explain the high number of bear detections concentrated in the south-westerly corner of the grid (which also happened to encompass the high-density British Mountain ecodistrict). The south-western area of the study is an area that has traditionally seen moderate to large numbers of calving caribou. However, while bears appeared to prefer the south-west corner of the study grid, it *remains unclear* if this was due of the presence of caribou or preferred habitat or both. It is also unclear if the presence of caribou has a short or long term impact on bear density and distribution, given that their presence is seasonally variable. It is also unclear if the majority of the bear population is consistently found within INP (>65% regardless of the extrapolation used). The timing of the DNA study (June-August) and limited collar information means it is not clear if this is a seasonal or year-round trend. Camera work in INP suggests bear use is high in June and July but less so in August (Parks Canada, unpublished results).

The average of the 'high' and 'low' estimates for the North Slope (361 bears) is only 14% higher than was calculated by Nagy (1990). However, both studies have design concerns that make it difficult to draw comparisons between them. Although the average of our high and low estimates is slightly higher than Nagy's (1990) estimate of 316 bears, our 'low' estimate is 9% lower. Additionally, Nagy's (1990) estimate is also uncertain as it was based on a comparison and extrapolation of density estimates from studies in other regions with similar ecotypes, and a calculation of the likely density of female home ranges in the Barn and Buckland Mountains. Furthermore, Nagy et al. (1983a) noted that their estimate of the Barn and Buckland Mountains, where they examined female home range density, is a minimum count because they were unable to account for demographic closure. Given the issues described for both studies, it is difficult to infer the long term grizzly bear population trend on the Yukon North Slope.

Even if we were confident that the differences between Nagy's (1990) population estimate and our own high and/or low estimates were real, we would not be able to discern whether the population had increased/decreased steadily, remained stable, or fluctuated during the time between the two studies because these estimates represent only two, widely-separated (>30 years) points in time, and we have no additional scientific information on population size or trend between the two study periods. Bear population trends in the area are also not clear based on one traditional knowledge study (WMAC (NS) 2008); additional traditional knowledge work in the area may provide further information and clarity.

Population densities

In addition to estimates for the YNS and INP, we estimated population density in each ecodistrict group within the study area to evaluate our *a priori* prediction that bear densities vary between ecodistricts (Appendix 3). We also sought to directly compare our density results to those of Nagy et al.'s (1983a) work. Our density estimates (Table A6) for the Coastal Plains and British Mountains were higher than those found by Nagy (1990), while our density estimate for the Barn Mountains was much lower. Our density estimate for the Coastal Plains was also higher than Reynolds (1980), who found bears at 1.3 bears/1000 km^2; however, Reynolds (1980) and Nagy (1990) speculated that harvest in the eastern

Brooks Range population in Alaska likely resulted in lower bear densities than on the Canadian side of the North Slope.

Densities in the British Mountains are among the highest reported density estimates for an interior grizzly bear population (Miller et al. 1997, Servheen et al. 1998, Mowat et al. 2013) and is commensurate with densities found in coastal populations where bears' diets often include salmon (Miller et al. 1997, Servheen et al. 1998). Our study results suggests the presence of caribou on the study area, particularly during the calving period, contributed to the high bear densities observed in the British Mountains and possibly on the Coastal Plains. Nagy (1990) also speculated that caribou (*Rangifer tarandus*) calving may have influenced population density.

Moreover, during the Nagy (1990) study (1972-1974), the Porcupine Caribou herd was estimated at 135 000 animals (Nagy et al. 1983a). During our study time period (2004-2010), the herd was approaching 169,000 individuals (Porcupine Caribou Technical Committee 2013). It is possible that we observed higher grizzly bear density in the British Mountains and on the Coastal Plains than Nagy (1990) because the caribou herd size increased between study periods and larger aggregations of calving caribou occurred in Yukon. However, we can't conclusively infer a relationship between caribou population size and grizzly bear population size from the data currently available.

We included caribou presence as a covariate in our density predictor models, but the results were only semi-conclusive. Although it appeared that the presence of calving caribou likely has an influence on grizzly bear density, more information is needed to understand the extent of this influence and whether effects are distribution or abundance based. Any future work should consider the size of the caribou herd at the time of the study and temporal variation in the availability of caribou (including multiple temporal pulses of caribou within a given year) as potential correlates of densities, vital rates, and population growth rates of grizzly bears on the YNS.

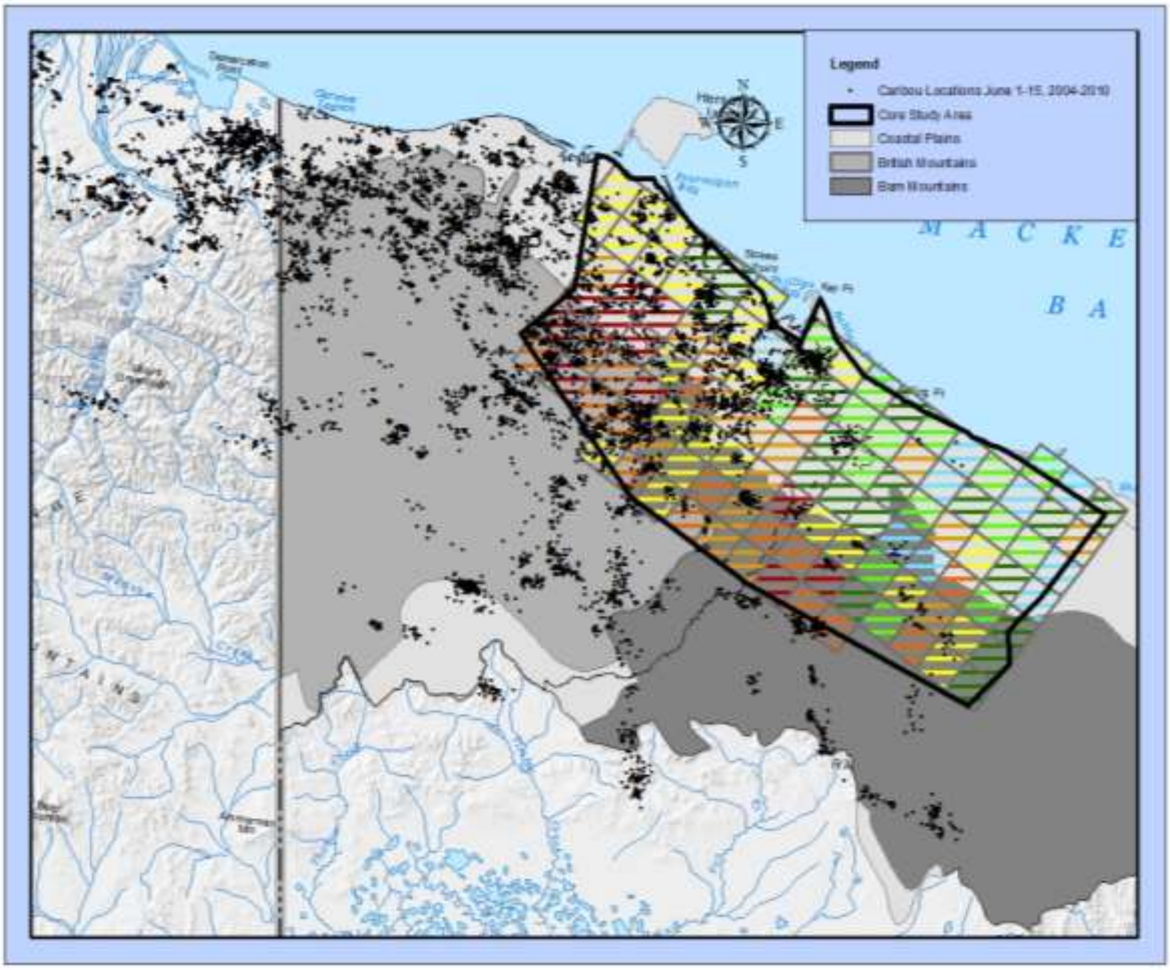

Figure 7. Distribution of collared caribou during and immediately following calving (June 1-June 15) for the study years 2004-2010, in relation to intensity of hair snag events over the two sampling years (2006 and 2007). (Note that caribou relocations do not represent the full annual extent of caribou calving. For full extent of calving see Appendix 7) Red cells indicate six hair snag events over the two years. Dark orange cells indicate five hair snag events, light orange indicates four hair snag events, yellow indicates three hair snag events, dark green indicates two hair snag events, light green indicates one hair snag event, and blue cells indicate no hair snag events.

It is likely that bear density in the western portion of our study area is also influenced by a low to non-existent harvest, minimal human perturbation (minimal development and large protected areas), availability of other protein-based resources (e.g., ground squirrels [*Spermophilus parryii*], dolly varden [*Salvelinus alpinus*], Dall's sheep (*Ovis dalli*), muskox (*Ovibos moschatus*), and moose [*Alces alces*]), good forage production in the valleys, and a mild microclimate relative to other regions of the YNS. This is the only region of the YNS where we found significant patches of soapberry (*Shepherdia canadensis*) and bear flower (*Boykinia richardsonii*). Bear Root (*Hedysarum alpinum*) and horsetail (*Equisetum arvense*), both high in protein, were also more readily available in the British Mountains than in other areas on the YNS (Bostock 1948, Wiken et al. 1981).

Modeling considerations

Unmodelled heterogeneity (e.g., heterogeneity that is not included in a model) is often a problem with mark-recapture population estimates (Boulanger et al. 2004). Some researchers have included models with terms for individual or behavioural heterogeneity in detection parameters in mark-recapture models because bears exhibit heterogeneous probabilities of capture beyond what can be explained by variable exposure to traps (Noyce et al. 2001, Boulanger et al. 2004), and home range sizes of female bears may vary with local differences in habitat quality (Koehler and Pierce 2003, Edwards et al. 2013), or with age and encumbrance status (Alt et al. 1980, Wooding and Hardisky 1994). Innate differences in cautious behavior (Noyce et al. 2001) or differences among bears of different ages or social classes (Miller et al. 1997, Woods et al. 1999, Noyce et al. 2001, Boulanger et al. 2006) can affect the probability of bear's visitation to a trap (independent of spatial effects) and home range sizes of female bears also vary with age and social status (Alt et al. 1980, Rogers 1987, Wooding and Hardisky 1994, Costello 2008). Failing to consider these sources of heterogeneity can result in underestimated population estimates. We assessed terms for a temporal effect, a site-specific learned response, sex-specific spatial scale of detection, and individual heterogeneity in the detection parameters when constructing our detection models. Our chosen model (the best model with the lowest AIC_c) included a site-specific behavioural response and a sex-specific sigma, and compensatory variation in $lambda_0$, although density estimates were largely stable across models.

We did not consider differences in model parameters among sampling occasions in our candidate model set because our radio-tracking data showed no major difference in home range size over each 10-day period within the annual sampling session (Department of Environment, unpublished data). This was likely owing to the homogenous availability of food resources during this timeframe. Further, we deliberately confined our sampling period to the pre-berry season to avoid seasonal home range shifts or variation in movements. An exception to this was during the period in June when the Porcupine Caribou herd calved and then migrated well west of the core study area by the end of the month. In 2006, more calving activity than on average took place in the study area (Arthur 2004, Arthur 2005, Arthur 2006, Arthur 2007, Caikoski 2008, Caikoski 2009, Caikoski 2010). We were concerned that this might violate the assumption of fixed home-range center locations, so we examined the movement rates of collared bears across sampling occasions. Acknowledging low samples sizes, we found that only a few bears had reduced movement rates during the caribou calving period relative to the previous or following occasions (Department of Environment, unpublished data). Consequently, we believe home range centres within each year were fixed over sampling occasions, despite the presence of caribou. Moreover, preliminary analysis suggests male and female home ranges did not universally shift over to areas with high densities of caribou during 2006 and 2007, but available collar data is limited during this period so this assessment should be interpreted with caution (Appendix 8).

Demographic rates

In some grizzly bear populations, the proportion of available females that produce litters annually can approach 1.0 for prime-age adults (Taylor et al. 1987a). However, in our population, the proportion of females with litters was very low. Nagy et al. (1983a) reported similar observations, where he found that the proportion of females with litters on the North Slope was much lower than neighbouring populations. The observed age of first parturition (age 10), while on the high end, was within the range of ages documented for other populations in Yukon and Alaska (5.9 to 9.6; Pearson 1975, Reynolds 1980, Nagy et al. 1983a, Nagy et al. 1983b, McCann 1998). However, this observation may also be the outcome of a small sample size, as only four individuals that were age 4 or over were tracked to their first parturition. The consequence of setting the age of first parturition high would be a calculated reproductive rate that was biased low. We reported the age of first parturition for comparison with other populations but did not use this value, nor the inter-birth interval, to estimate population growth rate to avoid potential associated biases (Appendix 5).

Mean litter size (2.047) in our study area was similar to that in other northern interior Canadian, interior Alaskan, and arctic Canadian and Alaskan populations (1.6 to 2.3 cubs per litter; Pearson 1975, Reynolds 1980, McCann 1998) and is the same as the Nagy et al. (1983a) estimate. We were not able to compare whole litter survival rates across populations as they are sparsely reported for grizzly bears; however, our individual cub survival rates are low in comparison to rates across North America (range 0.66 to 0.85; Bunnell and Tait 1985) and are most similar to the reported rates for the non-hunted populations in Denali National Park or Katmai (0.34; Miller et al. 2003). Yearling survival was also substantially lower than observed in other populations across North America (Sellers and Aumiller 1994, Mace and Waller 1998, McCann 1998, Mace et al. 2011, Miller et al. 2003), while adult and subadult survival rates were high in comparison to other populations (Bunnell and Tait 1985, McLellan et al. 1999, Miller et al. 2003).

The vital rates we obtained were consistent with a population near its carrying capacity (Miller et al. 2003). Miller et al. (2003) speculated the Denali population was at carrying capacity and similarly reported low reproductive rates and cub survival but high adult survival (0.987 for females and 1.0 for males). At carrying capacity, density-dependent competition for food and intraspecific predation are expected to increase mortality rates for dependent offspring, decrease reproductive rates, or both, yet adult survival can be high (Andrewartha and Birch 1954, Caughley 1966, Caughley 1977). Harvest is relatively low and usually focused on subadult or adult males and there is minimal human development or activity in this region. This has been the state of the landscape for decades, inclusive of the years that Nagy et al. (1983a) conducted their research on bears. Indeed, in the 1970s, Nagy et al. (1983a) speculated that, as the population was not hunted and had minimal perturbation, the population was at carrying capacity.

Our analyses do not account for influences that immigration or emigration may play on population dynamics. This limits the interpretation of our demographic data. Given varying vital rates among each group of ecodistricts, future work could examine immigration rates and the underlying meta-population structure, such as through population genetics (e.g., Thiessen 2010). Similar approaches have also been used with polar bears (Cronin et al. 2006).

Population simulations

Although our population simulations suggested the population may have been in slow decline during the study, it is important to note that population stability or slow increase ($\lambda \geq 1.0$) was within 2 standard deviations of the point estimate of λ for all the scenarios we considered, and was within 1 standard deviation of the point estimate in most cases. Given that stochasticity in population simulations reduces mean λ (Boyce 1977, Starfield 1997), and uncertainty around our vital rate and population estimates was relatively high due to small sample sizes and was modelled as 75% parameter uncertainty, slightly negative estimates of λ might be expected even if the population was stable. Furthermore, if the population is near carrying capacity, as we suspect based on our vital rate estimates, and because there was a high percentage of protected area with little to no development, few human-bear conflicts, and minimal harvest of female bears, we may have sampled during a period of relatively low population growth within a longer-term fluctuation in λ around 1.0. For example, the population may decline slowly except following pulses of increased food availability associated with caribou calving on the study area; or, the population might fluctuate regularly around carrying capacity, periodically declining and periodically increasing. Based on all of the available evidence, we suspect that estimates of λ slightly below 1.0 reflect a population near carrying capacity rather than a population in long-term decline. Nevertheless, the low rates of reproduction and population growth for this population could render the population sensitive to, and slow to recover from, external pressures like overharvest, development, climate change, etc.

Conclusion

The information from this study was collected to update the population status of grizzly bears on YNS, which could then be used to make informed management decisions, including those around harvest. Although there is uncertainty around the updated population estimate (namely, the difference between our high and low estimates), we believe the population to be stable or at carrying capacity. External risk to the population is also low at this time: the current pattern of harvest is typically less than (and has never exceeded) the established quota and strongly biased towards males. The population has further benefitted from low rates of development within the YNS, and a relatively large expanse of protected areas both on the YNS (INP in particular) and immediately adjacent (i.e., Arctic National Wildlife Refuge, Vuntut National Park). The uncertainty in our estimate, however, and the seasonal window during which the DNA study was conducted, should be taken into consideration when making management decisions that can impact population size or growth (such as harvesting). In addition, the low numbers of young entering the population, and the general sensitivity of grizzly bear populations to human pressures means we have to be careful about not letting harvest or other human activities lead to a decline. Exercising caution when making management decisions about this population is advised.

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Appendices

Appendix 1: Physiographic description of Yukon North Slope

Most of the study area fell into the Yukon Coastal Plain and British-Richardson Mountain Ecoregions (Smith et al. 2004). The study area contained rugged mountains that were over 1500 m above sea level, the Arctic Plateau between the British and Richardson Mountains, and the Arctic Coastal Plains sloping northward to the Arctic Ocean (Smith et al. 2004, Bostock 1948). The north slopes of these ecoregions were drained to the Beaufort Sea by the Big Fish, Blow, Babbage, Trail, Tulugaq, Firth, and Malcolm Rivers. The Richardson Mountains were drained eastward by several tributaries to the Peel River and Mackenzie Delta. The south facing slopes of the British Mountains were drained into the Porcupine River through the Old Crow Basin. The west side of the ecoregion drained into the Porcupine River.

While open stands of black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam poplar (*Populus balsamifera*) occurred in protected valleys and on some south facing slopes, the majority of the study area was devoid of trees. Dense thickets of willow (*Salix* spp.) were found along river, stream and lake banks. Willows also occurred in shallow depressions at higher elevations where snow patch communities were developed. Higher, well drained areas supported a variety of grasses, herbs and shrubs, most prominent of which were crowberry (*Empetrum nigrum*), blueberry (*Vaccinium* spp.), dwarf birch (*Betula glandulosa*), saxifrages (*Saxifraga* spp.), poppies (*Papaver* spp.), louseworts (*Pedicularis* spp.), vetches (*Oxytropis* spp.), and grasses (*Calamagrostis* spp.).

The climate of the study area was moderated by coastal influences. Mean annual precipitation was approximately 500 mm in the Richardson Mountains; 250-380 mm in the Arctic Plateau and British Mountains; and 125 mm along the Arctic Coast. The mean annual temperature was –10°C to –11°C (Smith et al. 2004). Weather systems moving off the Arctic Ocean resulted in frequent occurrences of fog during the summer (Nagy et al. 1983a).

To remain consistent with Nagy's (1990) analysis, we divided the study area into three ecologically distinctive units, based primarily on ecoregion and ecodistrict breakdown (Smith et al. 2004, Wiken et al. 1981): Coastal Plains, British Mountains, and Barn Mountains. The Coastal Plains ecodistrict group [herein Coastal Plains] was comprised of the Herschel Island, Shoalwater Bay, King Plains, Komakuk Plains, Mount Conybeare, Buckland Basin, Babbage Plains, Running River, and Tulugaq Pediments ecodistricts. These ecodistricts typically had tussocks of cottongrass (*Eriophorum* spp.), interspersed with shrubs and heath. The terrain topographically was flat to gently bevelled and had continuous permafrost underlying a thin active layer. Though not near the coast or the coastal plain, we also included a small portion of the Old Crow Pedimonts ecodistrict (part of the Old Crow Basin Ecoregion) in this unit because the vegetation, soil and topography were closely matched to the coastal plains.

We divided the British-Richardson Mountain Ecoregion into two ecologically distinctive units: the British Mountains and the Barn Mountains. The ecodistricts comprising the British

Mountains unit [herein British Mountains] included the Joe Creek, Upper Trail River, British Mountains, and Upper Trail River ecodistricts. These ecodistricts had high topographical relief but could occasionally be hilly. The British Mountains formed a smooth arc composed of parallel ridges. Alpine tundra and arctic tundra vegetation were predominant in the area with some spruce trees littering the southern portions of the landscape. Permafrost was continuous but the active layer may have been deeper than in the Coastal Plains. The Barn Mountains ecodistricts group [herein Barn Mountains] was comprised of the Mount Sedgwick, Cottonwood Creek, Blackfold Hills, West Barn Range, East Barn Range, Blow Pass, Purkis Creek, and Richardson Folds ecodistricts. The mountains in these ecodistricts were not as rugged as those in the British Range, but rather had widely separated ridges and rounded contours. Like the British Mountains, the permafrost was continuous but the active layer was deeper than the coastal plains. Approximately 11% of the core study area was comprised of the British Mountain ecodistricts, 33% was comprised of the Coastal Plains ecodistricts, and 56% of the study core area was comprised of the Barn Mountains ecodistricts. Approximately 6540 km^2 of the YNS is comprised of the British Mountains ecodistricts, approximately 6855 km^2 is comprised of Barn Mountains ecodistricts, and 4852 km^2 is comprised of Coastal Plains ecodistricts. Approximately 5866 km^2 of Ivvavik National Park was comprised of the British Mountain ecodistricts, 880 km^2 of the Barn Mountain ecodistricts, and 2926 km^2 of the Coastal Plains ecodistricts.

The ecology of the North Slope is highly influenced by the migration of the Porcupine Caribou herd. The Porcupine Caribou migration begins as early as March as caribou gradually drift off toward the northern limits of their wintering areas. The Porcupine Herd follows three major routes to the North Slope from primarily wintering areas in Alaska and the Yukon Territory: the Richardson, Barn, and British Mountains; the Old Crow route, which crosses the Porcupine River near the settlement of Old Crow and continues northward through the Old Crow Flats, over the British Mountains and through the Babbage or Firth Valley; and the Arctic Village/South Brooks Range route which crosses the East Fork of the Chandler River, the Sheenjek, and upper Coleen rivers and follows the Firth River into Canada where it joins the Old Crow route.

The caribou segregate themselves into groups which migrate at different times. Pregnant females along with some yearlings and barren cows are the first to migrate; followed by bulls and the remaining juveniles. In mid-to-late May the pregnant cows arrive on the North Slope, while the others follow a few weeks later either into the British-Barn Mountains or to other areas like the Richardson Mountains or Southern Brooks Range. Peak calving (where >50% of calves are present) generally occurs between May 30-June 8 (PCTC 2015). Calves are most susceptible to predation by bears in the first few weeks following birth (Adams et al. 1985; Reynolds et al. 1987; Porcupine Caribou Technical Committee 1993).

Appendix 2: Capture, handling, and monitoring of free-ranging bears

We used a rotary aircraft to search open areas for bears and/or fresh sign (tracks, scats, and digs). Although these search efforts were limited to open vegetation types where grizzly bears and their tracks can be seen from the air, we suspect that all bears were at risk of capture from aircraft because the majority of the study area was treeless. We dispersed search effort (search time per unit area) evenly throughout the study area. Family groups were not excluded from collaring. Once a bear was located, we used a Bell 206B helicopter for darting and capture. The capture crew determined if the surrounding geography permitted a safe pursuit and capture. Pursuit was stopped if the target bear showed clear signs of fatigue (e.g., stumbling, tongue hanging out), and in all captures, chase times were limited to as little time as possible (e.g., 2-3 minutes). Canadian Council on Animal Care (CCAC) Guidelines were followed during capture and handling operations. Bears were immobilized using a standard rifle system for firing internally charged or air pressurized darts (Palmer darts or Dan Inject darts). Bears were immobilized with Telazol (at 8 mg/kg estimated body weight) or MZT (Telazol 2.5 mg/kg and Medatomidine 0.05 mg/kg estimated body weight). Aerial darting took place from a range of approximately 10 meters.

Once a bear was darted, the helicopter and crew moved away from the bear to reduce stress but maintained visual contact. When the bear showed signs of immobilization, the helicopter landed a safe distance away. Before the capture team approached, the team leader determined the level (and safety) of immobilization by assessment of the bear's response to noise and touch and evaluation of its nervous reflexes (e.g., palpebral, limb withdrawal). Once it was safe to handle the bear, the field crew placed the bear in a sternally recumbent position. Respiratory rate and rectal body temperature were monitored at least every 5 to 10 minutes throughout the handling procedure.

A pulse-oximeter was used to monitor heart rate and percent oxygen saturation in the blood. A full D-cylinder of medical grade oxygen was carried by the capture crew and bears were provided with supplemental oxygen if they began to show signs of hypoxemia (e.g., blue mucous membranes), or if percent oxygen saturation dropped below 85%. Care was taken to ensure that air passages and oral cavities were free and clear to ensure there were no impediments to respiration. All bears had non-medicated ophthalmic ointment applied to their eyes, and blindfolds placed to reduce stress from visual stimulation and reduce the risk of eye injury during collaring. All bears were inspected for signs of previous capture, injury, and/or physical abnormality. Once we finished handling the bear(s), we searched the surrounding area by air to ensure there were no other bears present. Bears found in the area were chased away by helicopter, or when they were persistent in staying in the vicinity of the immobilized bear, we remained with the immobilized bear until it had recovered. In addition, an aircraft overflight was made to check on all captured bears later that same day. The capture crew worked quickly and quietly around bears to minimize stress on the animal.

When locating a family group, we only immobilized the mother, not the dependent offspring (COY, YOLY, or two-year olds) who typically remained within visual distance of the mother throughout the handling duration. Although two-year olds may present more of a human safety issue than COY or YOLY, experience has shown that they are not very aggressive and did not need to be immobilized.

A collar with a GPS or VHF transmitter was fitted to captured grizzly bears, a premolar was removed for aging of bears, lip tattoos were applied, hair and fecal samples were collected for DNA and dietary analysis respectively (scats were also collected opportunistically to supplement dietary information), and blood samples were collected for serum analysis. GPS collars were placed on a random sample of males and females. VHF collars were placed on females only. Locations for bears with GPS collars were recorded a minimum of six times per day (every four hours), providing satellite availability. Overflights were conducted several times a year to get VHF fixes on bears and to record survival information. We attempted to monitor each bear for as long as it remained collared, between den exit and den entrance, over the duration of the study. When collars transmitted in mortality mode, we visited the site as soon as possible to determine whether the bear had died or dropped its collar. If a bear had dropped its collar, we attempted to recapture the individual and put the collar back on. For bears that died, we confirmed mortality and attempted to determine the cause of death by examining remains. However, due to the remoteness of our study area, it was frequently not possible to get to dead bears in time to establish cause of mortality. We counted litters as early as possible after den emergence to minimize biases introduced by early loss of cubs or entire litters (McLellan 1989a). We collected information on age of first reproduction by monitoring subadult and young adult females for their first litters.

Appendix 3: DNA-based mark-recapture analysis

Overview of spatially explicit capture–recapture (SECR)

Spatially explicit capture–recapture (SECR) is a set of mark–recapture methods for estimating the density of a spatially distributed animal population from incomplete samples obtained with known spatial sampling effort, usually by passive sampling at a set of fixed locations ('trap sites') (Efford 2004, Borchers and Efford 2009, Royle et al. 2014).

SECR models combine a model for the spatial distribution of home-range centers with a spatial detection model. Probability of detection is modeled as a decreasing function g(d) of the distance *d* between detectors (hair snag corrals) and the unobserved central locations of individual home ranges (Efford 2004, Gardner et al. 2009). An animal has a high probability of encountering a detector near the centre of its home-range and low probability of encountering a detector in the periphery of its home range. The relationship is described by a simple function (e.g., half-normal or negative exponential) with two or perhaps 3 parameters that are estimated by fitting the model. One parameter sigma (σ) relates to the spatial scale of detection (large σ corresponds to large home range). Another parameter g_0 describes the overall magnitude of detection; it may be thought of as the probability of detecting an individual animal at a detector placed at the individual's activity center (i.e., at distance zero). For technical reasons[1] we choose to use a subtly different model in which $\lambda(d)$ is half-normal, negative exponential etc., where $\lambda(d) = -\log(1- g(d))$ is the expected number of detections or 'cumulative hazard'. The parameter λ_0 replaces g_0 in this formulation.

Animal density *D*, and the detection parameters λ_0, and σ may be described as functions of covariates (Borchers and Efford 2008). Population size (*N*) can be estimated from a fitted SECR model as a derived parameter (Efford and Fewster 2013).

Methods

Model fitting

SECR models were fitted by numerically maximizing the integrated log likelihood in the function 'secr.fit' of R package 'secr' (Efford 2016a). We maximized the full likelihood (i.e. not conditional on *n*, the number caught) as we wished to model habitat-related variation in density (Borchers and Efford 2008). Sampling variances were estimated from the inverse of the observed information matrix, and asymmetric 95% confidence intervals were obtained by back-transforming symmetrical intervals from the log scale (Borchers and Efford 2008).

The model for each parameter (D, λ_0, or σ) was described using a standard formula notation in which ~ 1 indicates the parameter was held constant, and ~t, ~bk, ~h2 represent predefined temporal, behavioural and mixture effects (Efford 2016b). Named covariates may also be introduced, e.g., D ~ caribou for a covariate 'caribou' defined for each mask pixel.

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[1] greater consistency across models for binary and count data, and with models for animal activity measured by telemetry, and compatibility with Royle et al. (2014)

Habitat mask

The home-range centres of bears from which we obtained hair samples were not known precisely, and the locations of undetected bears were entirely unknown. SECR methods allow for this uncertainty by integrating over possible bear locations in a geographic region called the habitat mask (also called the 'region of integration' or 'state space'). The extent of the mask is arbitrary, but if it is too small then it will fail to include the centres of some bears actually detected, causing truncation bias. Increasing the size of the mask beyond a certain point has no direct[2] effect on density estimates. We chose to define a habitat mask with extent equal to the Yukon North Slope, an area large enough to avoid truncation bias that happens to coincide with the area of management interest. We discretized the area as 4559 2-km x 2-km pixels (total area 18236 km^2). The mask was bounded to the north by the coastline of Mackenzie Bay.

Habitat covariates were associated with each mask pixel. We used two different habitat covariates as potential predictors of grizzly bear density (see also Fig. A3):

i. Three habitat strata formed by grouping ecodistricts – nominally Coastal Plain, British Mountains and Barn Mountains – as described in Appendix 1.
ii. An index of geographic variation in caribou density, using all fixes of telemetered caribou accumulated over 2004–2010. The index value for a given mask pixel was the number of fixes within 10 km of the pixel centroid, divided by 100 (values between 0 and 5.97, median 0.44).

Model selection strategy

Each part of a SECR model (the 2-D distribution model and the detection model) requires choices regarding the detailed model structure, use of covariates etc. There are many more permutations than can be fully evaluated. Our strategy was first to decide on a suitable structure for the detection model (parameters λ_0 and σ) while assuming uniform density (parameter *D*) and pooling data across years, and then to seek an appropriate density model for each year using the selected detection model.

Choice of detection model was further broken into two steps: assessment of temporal and other effects on λ_0 and σ, and the choice of shape for the distance-detection function. Models were constructed with a temporal effect (λ_0 ~ t), a site-specific learned response (λ_0 ~ bk), individual heterogeneity in λ_0 and σ (λ_0 ~ h2, σ ~ h2), and inverse variation in λ_0 with respect to heterogeneity in σ (λ_0 ~ a0, σ ~ h2) (cf Efford and Mowat 2014). We compared detection functions in which the cumulative hazard $\lambda(d)$ was related to distance d by half-normal (HHN), negative exponential (HEX) or hazard-rate (HHR) curves (see Efford 2016b). Detection probability was given by $g(d) = 1–\exp(–\lambda(d))$. We used small-sample form of Akaike's Information Criterion (AICc) to choose among models at each stage (Hurvich and Tsai 1989).

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[2] There may be an indirect effect due to increasingly coarse discretization if the software holds the total number of pixels constant – this is the default in 'secr'.

Sex differences

We are interested in the absolute abundance of each sex, and sex may also drive differences in detection. In particular, male grizzly bears have larger home ranges than female grizzly bears (Craighead 1974, Larsen and Markel 1989, McCann 1998, Bjornlie et al. 2014), which leads to larger values of the parameter σ for males.

A simple way to allow for sex differences in SECR models for pooled-sex data is to view the population as a mixture with an unknown mixing proportion (the sex ratio) and mixture-specific values of σ. The estimate of the mixing proportion (parameter 'pmix') is an estimate of the population sex ratio. We selected this using the ‘hcov’ option in secr.fit (Efford 2016b), and specifying ‘h2’ (shorthand for “two mixture classes”) in the formulae for detection models.

The intercept parameter of the detection function (λ_0) is expected to vary inversely with σ (Efford and Mowat 2014), so we also allowed it to vary between sexes, or to follow a fixed inverse relation to σ ($\lambda_0 = a_0 / (2\pi\sigma^2)$, where a_0 is a fitted constant).

Within-season time differences

Bait type was varied simultaneously for all hair snags from one detection interval to the next within a season. This may have caused systematic variation in detection probability, so we included a model with temporal variation in the model set ($\lambda_0 \sim t$). We assumed temporal variation in λ_0 followed the same pattern between years.

Density models

The study area covered only about 28% of the area of interest (YNS). Extrapolation from the study area to the whole YNS required a model for variation in density beyond the study area. In standard SECR, ‘density’ refers to the intensity (expected number per unit area) of the Poisson distribution of activity centres. The simplest model is a uniform density, leading to a ‘homogeneous’ 2-D Poisson distribution.

Density may also be modelled as a function of environmental variables that cause variation from place to place, or are correlated with such variation, and in this case the 2-D Poisson distribution is ‘inhomogeneous’. If we find a strong and credible relationship between density and environmental predictors (‘covariates’) within a study area then it is possible, in principle, to extrapolate density to unsampled areas (in our case the full YNS) for which only the predictors are known. However, the extrapolation may be unreliable, as we discuss later.

In each year we fitted four density models: one with uniform density throughout the YNS, one with uniform density in each ecodistrict group, and two in which density was a function of the pooled 2004–2010 caribou index. The caribou function was either a linear or quadratic relationship between log(density) and the caribou index. Sex ratio was assumed constant across habitats. Detection parameters were sex-specific and included a site-specific learned response as described in the preceding section.

Population size estimation

The estimate of density from a fitted SECR model may be converted to an estimate of the expected number of individuals in a specific area. For uniform density the population size *N* is simply the product of area and density. For a model in which density varies over space, notionally as a density ‘surface’, the expected population size is the volume under the surface, obtained by integration or summation over finite areas (pixels) of uniform density. Calculations were performed with function ‘region.N’ in ‘secr’ for the whole YNS, Ivvavik National Park, and the grid squares of the study area (excluding parts that extended into the sea).

Results

DNA samples

We obtained 3154 hair samples in 2006 and 1553 hair samples in 2007. We subsampled our hair samples using a cap of four extractions for collection events with eight or fewer samples, a cap of five samples for events with 10 or fewer samples, a cap of six for events with 12 or fewer samples, and a cap of seven for all other collection events. This resulted in 931 samples being extracted between the two years (547 in 2006 and 384 in 2007). This produced 177 individuals identified through genetic analysis from the hair traps on the grid study area. Our study area did not have black bears present so no pre-screening was necessary for black bears. Data were binary at the level of each bear, hair snag, and sampling occasion (i.e., repeat detections of the same individual at the same place in one time interval were discarded), so hair snags were treated as binary proximity detectors in ‘secr’ (Efford 2016b).

Summary of capture–recapture data

Tables A1 and A2 summarize the individual detection data. As well as including a large number of individuals, the dataset included a good number of redetections (r = 144 in 2006 and r = 96 in 2007). This is desirable because the precision of SECR density estimates relates to r (RSE($\hat{D}$) $\approx 1/\sqrt{r}$), so we expected RSE($\hat{D}$) ≈ 10% (RSE($\hat{D}$) is sometimes called CV($\hat{D}$)).

Choice of detection model

The ranking of detection models was consistent between sexes (Tables A3, A4). The best model (the model with smallest AICc (Hurvich and Tsai 1989) included a site-specific behavioural response and sex-specific σ, with compensatory variation in λ_0. Using a negative exponential detection function (HEX) resulted in better fit than either the half-normal or hazard-rate functions (Table A5). Despite the large differences in AICc, density estimates were largely stable across models.

These results support a pragmatic choice of detection model: differences in estimated bear density of less than 1 bear / 1000 km^2 are probably not material, given the width of confidence intervals and doubts about extrapolation (main text). We chose to jointly model both sexes with a negative exponential detection function, sex-specific σ_{EX}, compensatory λ_0 and site-specific learned response in λ_0. The final analyses were conducted separately for each year, so estimates of both density and detection parameters were year-specific. Note that the interpretation of the spatial scale parameter depends on the choice of detection function, so we use the symbol σ_{EX} as distinct from σ for the default (half-normal) function.

Our final models for the combined-sex dataset did not allow for unmodelled within-sex heterogeneity in detection parameters. When we included a 2-class mixture model in trials with each sex separately there was only a minor and inconsistent effect on the population estimates (compare sums of sex-specific estimates with estimates from pooled-sex data in Tables A3 and A4).

Density models

The main results are in Table A6 and Fig. A4. A log-linear and log-quadratic caribou models had virtually identical AICc weights and gave similar population estimates (Table A6). For simplicity we refer only to the log-linear model below. Inhomogeneous density models were preferred over the uniform density model, but the density predictor of the best model switched from ecodistrict groups in 2006 to the caribou index in 2007. This switch had a large effect on the extrapolated population estimates.

Both habitat models 'explained' the high density of bears on the inland and Firth River sides of the study grid, but the predictors extrapolated very differently. The caribou index was mostly low in the interior, so the caribou model (Fig. A5) predicted low density of grizzly bears there, and low total population size. The ecodistrict group model (Table A7) attributed a high grizzly bear density to the British Mountains ecodistrict group, as it overlapped a corner of the study grid in which many bears were detected. The British Mountains unit extended over a large part of Ivvavik National Park that was not sampled, leading to high estimates of population size for the Park and for the YNS as a whole (Table 8).

The estimated sex ratio showed a small (and not significant) female bias that did not differ substantially between 2006 (54% female 95% CI 44%–63%) and 2007 (55% female 95% CI 45%–64%) (using the best (lowest-AICc) density model in each year).

Detection parameters

Estimates of detection parameters are shown in Table A9. The spatial scale of detection differed between the sexes as expected (male σ_{EX} > female σ_{EX}). However, the magnitude of the difference is much less than in some other grizzly studies (Efford and Mowat (2014: Table 1) is one example). We parameterized the model to force an inverse relationship between λ_0 and σ_{EX} by holding a_0 constant; the values of λ_0 resulting from each combination of σ_{EX} and a_0 are shown in Table A9.

The fitted 'bk' model implied a positive site-specific learned response (Table A9). We suggest that this effect should be interpreted with caution because the 'bk' effect may be acting as a surrogate for other unmodelled persistent differences among sites. This is a recurring issue in bear studies that has yet to be investigated.

Post hoc assessment of truncation bias

We based our habitat mask on the extent of the YNS.Yukon North Slope. This imposed an arbitrary landward limit on the bear population considered in the analysis, and potentially excluded some distant bears that might have appeared on the study grid. We checked whether this restriction on the region of integration would be expected to cause bias in density estimates by plotting estimates for increasing buffer widths from the three detection functions under a uniform-density model (Fig. A6).

The half normal function (HHN) has a short tail and was nearly asymptotic at 20 km. The negative exponential (HEX) flattens out more slowly, but was essentially asymptotic at 30 km. The hazard-rate function (HHR) does not reach an asymptote and is not recommended. We used HEX, and, as the land boundary of YNS is more than 30 km from the edge of the study area for almost its entire length, we do not expect bias in the density estimate due to truncation of the region of integration.

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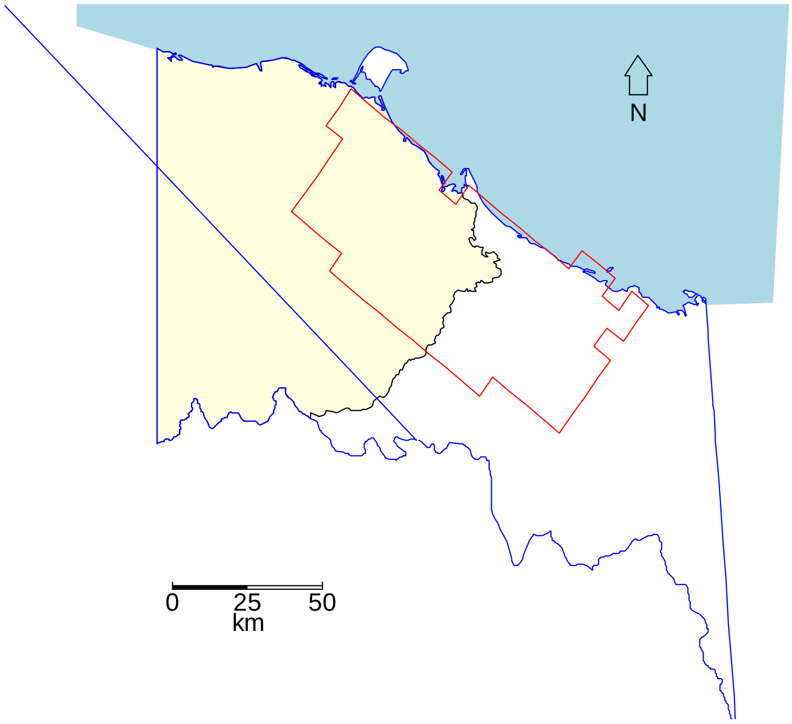


Fig. A1. Relationship of study grid (red outline) to Yukon North Slope (blue outline) and Ivvavik National Park (yellow).

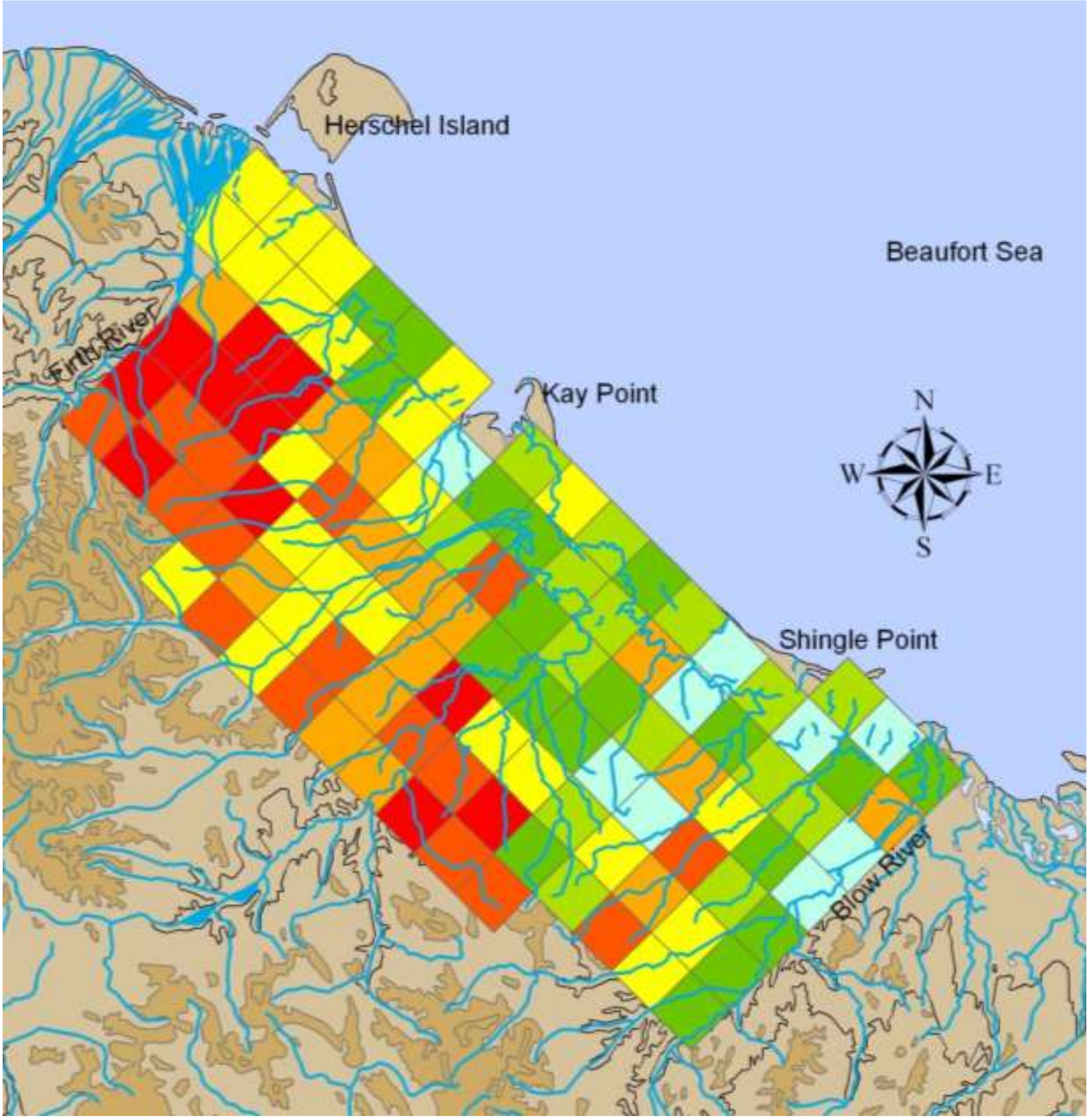


Fig. A2. Intensity of hair snag events over the two sampling years (2006 and 2007 combined; spatial patterns of hair snag events between 2006 and 2007 were similar). A hair snag event is when a station was hit by a bear or multiple bears within one sampling occasion (e.g., 10-day sampling period). Red cells indicate hair snag events in all six sessions over the two years. Dark orange cells indicate five hair snag events, light orange indicates four hair snag events, yellow indicates three hair snag events, dark green indicates two hair snag events, light green indicates one hair snag event, and blue cells indicate no hair snag events.

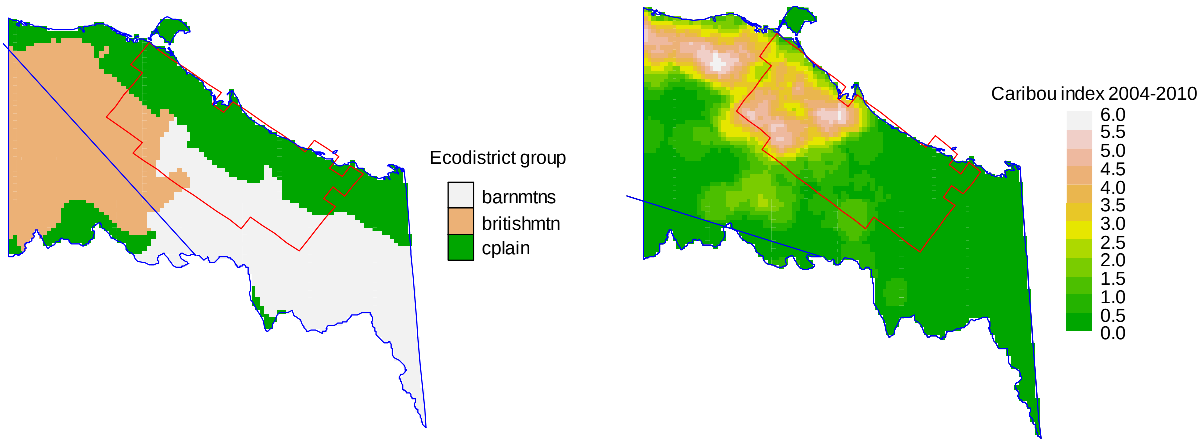


Fig. A3. Habitat covariates used to construct alternative models for grizzly bear density on the Yukon North Slope. Left: strata formed from grouped ecodistricts (Barn Mountains, British Mountains and Coastal Plain). Right: index of caribou distribution formed from the number of telemetry fixes within 10 km of each pixel centroid accumulated over 2004–2010, divided by 100. Red outline indicates extent of study grid.

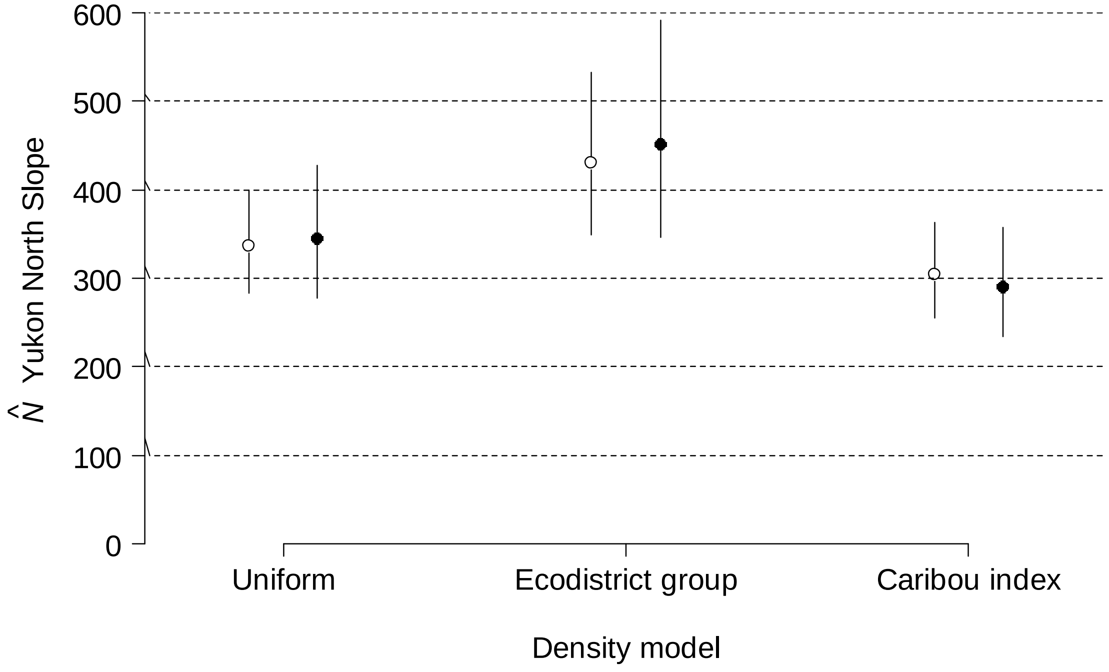


Fig. A4. Estimated number of grizzly bears on Yukon North Slope in 2006 (○) and 2007 (●) under three models for extrapolating density from the intensive study area. Bars indicate 95% confidence intervals.

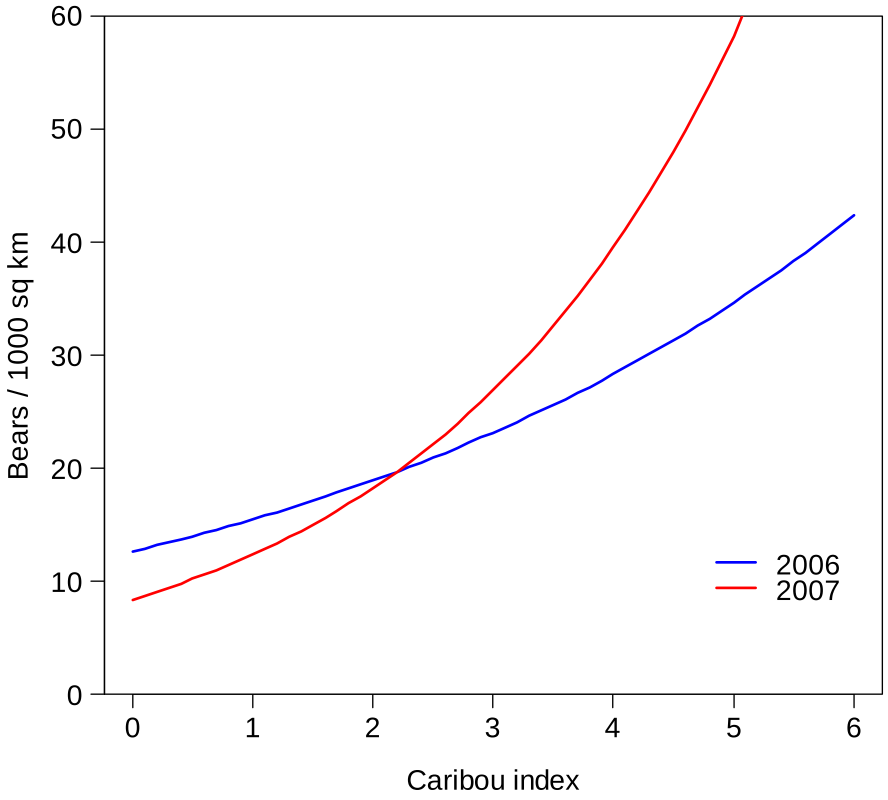


Fig. A5. Fitted log-linear relationship between grizzly bear density and caribou index.

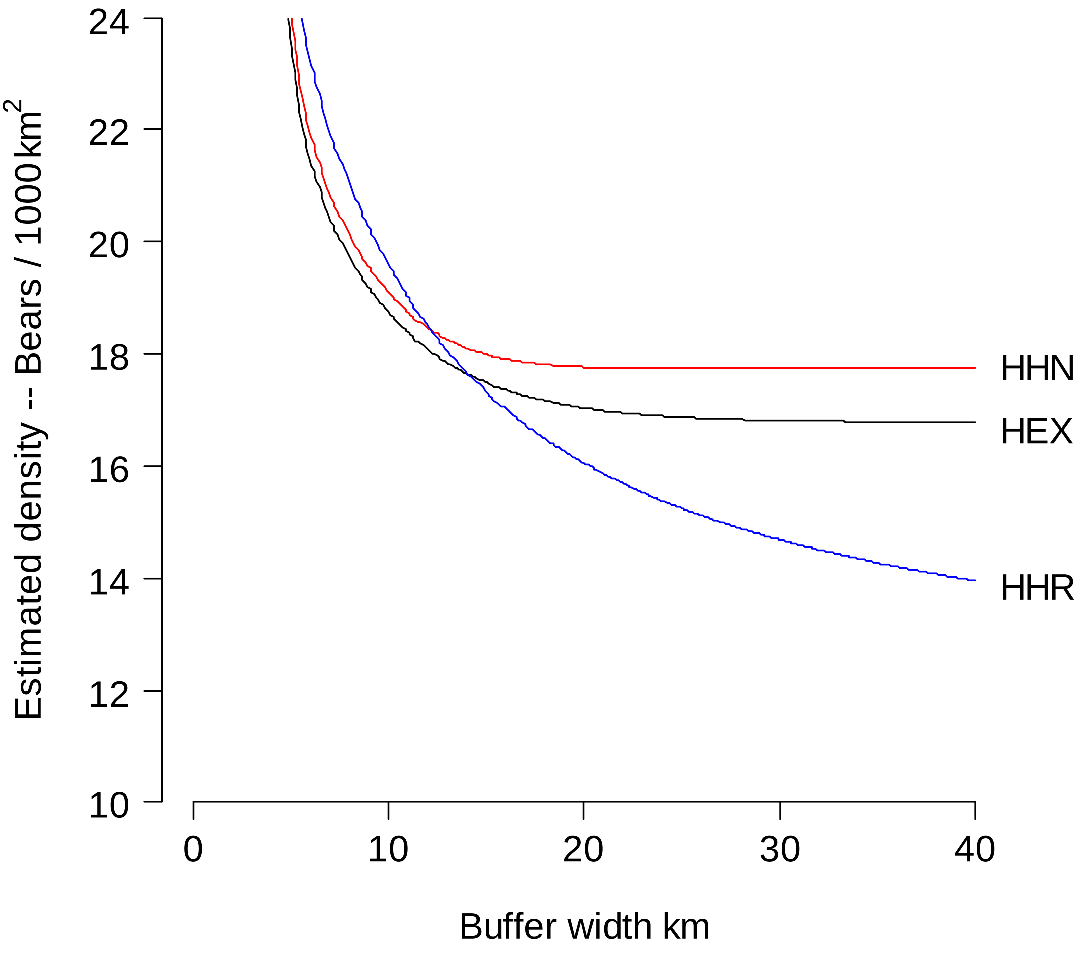


Fig. A6. Effect of buffer width on estimates of grizzly bear density for three shapes of detection function λ(*d*): HHN half-normal, HEX, negative exponential, HHR, hazard-rate.

Table A1. Summary of grizzly bear detections on Yukon North Slope hair snag grid in the summers of 2006 and 2007. Sampling in each year was divided into 3 10-day intervals. Counts are given of the number of distinct individuals recorded in each interval, the cumulative number of individuals, and the number of detections of identified bears.

	2006				2007			
	1	2	3	Total	1	2	3	Total
Female								
Individual bears *n*	17	25	44	57	26	24	29	57
Cum. individuals M(t+1)	17	35	57	57	26	39	57	57
Total detections	24	38	58	120	31	32	31	94
Male								
Individual bears *n*	31	32	32	53	27	23	22	48
Cum. individuals M(t+1)	31	45	53	53	27	39	48	48
Total detections	41	49	44	134	47	35	25	107
Female + Male								
Individual bears *n*	48	57	76	110	53	47	51	105
Cum. individuals M(t+1)	48	80	110	110	53	78	105	105
Total detections	65	87	102	254	78	67	56	201

Table A2. Frequency of detection for individual grizzly bears detected on Yukon North Slope hair snag grid in the summers of 2006 and 2007. Counts refer to the number of individuals detected in 1, 2, or 3 10-day intervals. *N* is the total number of individuals detected at least once. Frequencies do not include detection at multiple hair snags within an interval.

	2006				2007			
	1	2	3	N	1	2	3	N
Female	32	21	4	57	39	14	4	57
Male	22	20	11	53	30	12	6	48
Female + Male	54	41	15	110	69	26	10	105

Table A3. Evaluation of SECR detection models fitted with half-normal $\lambda(d)$ and uniform density to pooled data from 2006 and 2007. 'np' number of parameters, 'logLik' log likelihood, 'dAICc' AICc difference from best model, 'AICcwt' model weight calculated from AICc, $\hat{D}$ estimated uniform density in bears per 1000 km^2.

	model	np	logLik	dAICc	AICcwt	$\hat{D}$ (SE)
Female						
fit.a0bk	D~1 a0~bk sigma~h2	6	–741.9	0.0	1	11.4 (1.2)
fit.a0	D~1 a0~1 sigma~h2	5	–749.6	13.1	0	10.8 (1.3)
fit.h2	D~1 lambda0~h2 sigma~h2	6	–749.3	14.8	0	11.8 (2.4)
fit.bk	D~1 lambda0~bk sigma~1	4	–771.7	55.1	0	11.2 (1.1)
fit.t	D~1 lambda0~t sigma~1	5	–785.6	85.1	0	10.5 (1.0)
fit.null	D~1 lambda0~1 sigma~1	3	–789.8	89.3	0	10.5 (1.0)
Male						
fit.a0bk	D~1 a0~bk sigma~h2	6	–916.2	0.0	1	7.3 (0.7)
fit.bk	D~1 lambda0~bk sigma~1	4	–926.4	15.9	0	7.3 (0.7)
fit.h2	D~1 lambda0~h2 sigma~h2	6	–927.2	21.8	0	8.7 (1.1)
fit.a0	D~1 a0~1 sigma~h2	5	–928.5	22.3	0	7.1 (0.7)
fit.null	D~1 lambda0~1 sigma~1	3	–949.5	59.8	0	7.1 (0.6)
fit.t	D~1 lambda0~t sigma~1	5	–948.2	61.6	0	7.1 (0.6)
Female + Male						
fit.a0bk	D~1 a0~bk sigma~h2	6	–1538.5	0.0	1	18.1 (1.3)
fit.a0	D~1 a0~1 sigma~h2	5	–1558.8	38.5	0	17.3 (1.2)
fit.h2	D~1 lambda0~h2 sigma~h2	6	–1558.0	38.9	0	18.2 (1.5)
fit.bk	D~1 lambda0~bk sigma~1	4	–1571.2	61.1	0	17.8 (1.2)
fit.null	D~1 lambda0~1 sigma~1	3	–1615.0	146.7	0	17.0 (1.1)
fit.t	D~1 lambda0~t sigma~1	5	–1614.6	150.0	0	17.0 (1.1)

Table A4. Evaluation of SECR detection models fitted with negative exponential λ(d) and uniform density to pooled data from 2006 and 2007. 'np' number of parameters, 'logLik' log likelihood, 'dAICc' AICc difference from best model, 'AICcwt' model weight calculated from AICc, $\hat{D}$ estimated uniform density in bears per 1000 km^2.

	model	np	logLik	dAICc	AICcwt	$\hat{D}$ (SE)
Female						
fit.a0bk	D~1 a0~bk sigma~h2	6	–741.5	0.0	0.93	11.5 (1.3)
fit.a0	D~1 a0~1 sigma~h2	5	–745.4	5.7	0.05	11.1 (1.5)
fit.h2	D~1 lambda0~h2 sigma~h2	6	–745.4	7.8	0.02	11.8 (2.5)
fit.bk	D~1 lambda0~bk sigma~1	4	–752.1	16.7	0	11.6 (1.2)
fit.t	D~1 lambda0~t sigma~1	5	–755.9	26.6	0	11.1 (1.0)
fit.null	D~1 lambda0~1 sigma~1	3	–760.5	31.4	0	11.1 (1.0)
Male						
fit.a0bk	D~1 a0~bk sigma~h2	6	–907.3	0.0	1.00	8.2 (1.5)
fit.bk	D~1 lambda0~bk sigma~1	4	–917.0	15.0	0	7.3 (0.7)
fit.a0	D~1 a0~1 sigma~h2	5	–916.0	15.3	0	8.2 (1.5)
fit.h2	D~1 lambda0~h2 sigma~h2	6	–917.1	19.7	0	9.0 (1.2)
fit.null	D~1 lambda0~1 sigma~1	3	–932.2	43.1	0	7.2 (0.7)
fit.t	D~1 lambda0~t sigma~1	5	–930.8	44.9	0	7.2 (0.7)
Female + Male						
fit.a0bk	D~1 a0~bk sigma~h2	6	–1528.2	0.0	1.00	19.3 (2.3)
fit.a0	D~1 a0~1 sigma~h2	5	–1542.0	25.5	0	19.1 (2.5)
fit.h2	D~1 lambda0~h2 sigma~h2	6	–1542.9	29.4	0	20.2 (1.9)
fit.bk	D~1 lambda0~bk sigma~1	4	–1545.4	30.3	0	18.3 (1.2)
fit.null	D~1 lambda0~1 sigma~1	3	–1570.9	79.1	0	17.9 (1.1)
fit.t	D~1 lambda0~t sigma~1	5	–1570.4	82.3	0	17.9 (1.1)

Table A5. Comparison of SECR models with half-normal (HHN), negative exponential (HEX) and hazard-rate (HHR) detection functions fitted to pooled data from 2006 and 2007. Sexes pooled; 'np' number of parameters, 'logLik' log likelihood, 'dAICc' AICc difference from best model, 'AICcwt' model weight calculated from AICc, $\hat{D}$ estimated uniform density in bears per 1000 km^2.

	model	np	logLik	dAICc	AICcwt	$\hat{D}$ (SE)
fit.HEX	D~1 a0~bk sigma~h2	6	–1528.2	0.0	0.99	19.3 (2.3)
fit.HHR	D~1 a0~bk sigma~h2 z~1	7	–1531.8	9.4	0.01	17.2 (1.3)
fit.HHN	D~1 a0~bk sigma~h2	6	–1538.5	20.7	0.00	18.1 (1.3)

Table A6. SECR density models fitted to grizzly bears sampled with an array of hair snags on the Yukon North Slope in 2006 and 2007, and derived estimates of the YNS population size *N* and sex ratio *SR*.

Year	Density model	np	logLik	dAICc	AICcwt	$\hat{N}$ (SE)	$\widehat{SR}$ (SE) %
2006	Uniform	6	–922.3	16.2	0.00	336.7 (29.8)	53.2 (4.8)
	Ecodistrict group	8	–911.9	0.0	0.97	430.8 (46.7)	53.9 (4.8)
	Caribou index - linear	7	–917.0	8.0	0.02	304.2 (27.8)	53.0 (4.8)
	Caribou index - quadratic	8	–916.7	9.6	0.01	298.7 (27.9)	53.0 (4.8)
2007	Uniform	6	–761.5	29.6	0.00	344.4 (38.2)	54.7 (4.9)
	Ecodistrict group	8	–745.0	1.3	0.21	452.1 (62.2)	55.1 (5.0)
	Caribou index - linear	7	–745.6	0.1	0.38	289.8 (31.3)	54.5 (4.9)
	Caribou index - quadratic	8	–744.3	0.0	0.41	278.7 (30.5)	54.5 (4.9)

Table A7. Estimated grizzly bear population density in each ecodistrict group from annual SECR density models stratified by ecodistrict group. Bears per 1000 km^2. Sexes pooled.

Year	Ecodistrict group	$\hat{D}$ (SE)	95% CI
2006	Coastal Plain	10.5 (2.4)	6.8–16.3
	British Mountains	42.5 (7.5)	30.1–59.9
	Barn Mountains	17.9 (3.4)	12.4–25.8
2007	Coastal Plain	12.0 (2.8)	7.7–18.7
	British Mountains	53.7 (9.5)	38.0–75.9
	Barn Mountains	10.1 (3.1)	5.6–18.2

Table A8. Grizzly bear population size inferred from fitted density models. The population size is the expected number of bear activity centres within the relevant polygon. 95% CI in parentheses.

Year	Density model	YNS	Ivvavik NP	Study grid
2006	Uniform	337 (283–400)	179 (151–213)	95 (80-113)
	Ecodistrict group	431 (349–532)	298 (224–395)	87 (72–106)
	Caribou index - linear	304 (254–364)	191 (161–227)	99 (83–117)
2007	Uniform	344 (277–428)	183 (148–228)	97 (78–121)
	Ecodistrict group	452 (346–591)	361 (266–490)	86 (66–111)
	Caribou index - linear	290 (235–358)	211 (173–258)	104 (85–128)

Table A9. Detection parameters for SECR ‘Ecodistrict grouping’ models fitted to data from grizzly bears sampled with an array of hair snags on the Yukon North Slope in 2006 and 2007. ‘bk’ codes the status of a particular bear and hair snag combination: initially all combinations are ‘new’; hair snags become ‘old’ when visited by the bear in question. σ_{EX} is the spatial scale parameter of a negative exponential detection function. Cells are blank where estimates were not stratified by either Sex or bk, and the preceding value(s) apply. The value of λ_0 was derived from the relationship $\lambda_0 = a_0 / (2\pi\sigma_{EX}^2)$ – see Efford and Mowat (2014).

Year	Sex	bk	σ_{EX} (SE) km	a_0 (SE) km^2	λ_0
2006	Female	new	4.6 (0.5)	47.4 (4.7)	0.36
		old		134.7 (30.0)	1.03
	Male	new	6.3 (0.6)		0.19
		old			0.54
2007	Female	new	7.0 (1.1)	37.4 (5.3)	0.12
		old		198.8 (57.1)	0.65
	Male	new	7.9 (0.9)		0.09
		old			0.50

Appendix 4: Details of survival estimation

Sex- and age class-specific survival rate estimates were calculated from the number of days that individuals in each sex and age class were tracked and the number of deaths observed. For bears that dropped their collars and were subsequently recaptured, we did not include the intervening time in the number of days tracked. We divided the survival information for each age class into four seasons: pre-berry season (April 15 to July 31), berry season (August 1 to September 20), post berry season (September 21 to November 30), and winter (December 1 to April 14). Mortality causes were divided into five major categories: natural, legal harvest, poached, control kill (both management agency personnel and private citizens defending life or property), and unknown. We assume mortality for all COY and YOLY of radio-collared females that went missing. No yearlings were collared but we tracked them while they traveled with their collared mothers. Assuming that all yearlings that we lost contact with died may bias yearling survival rates low because yearlings sometimes do separate from their mothers and survive. However, this is more common for grizzly bear population at southern latitudes (McCann 1998). For two-year olds and older dependent bears that went missing we assumed family breakup rather than death.

Using McLellan's (in prep; based on Heisey and Fuller 1985) method, we bootstrapped our records for each individual yearling, subadult and adult until the sample size equalled the number of individuals used for each age class. Because most often entire liters are lost, we also bootstrapped our records for whole yearling litters. For each resampled vector, the daily survival rate per season was calculated by the total number of days individuals or litters were tracked during the season minus the number of individuals or litters that died during that season, divided by the total number of days tracked. The contribution of the daily rate to the annual rate was calculated by raising it to the power of the number of days in the season. The annual survival rate was the product of all seasonal rates. Bootstrapping was conducted 5000 times using POPTOOLS 3.0 (Hood 2010). We estimated 95% confidence limits for the parameter estimate.

The annual survival rate for COY was calculated as the proportion of those recorded when first seen with their radio-collared mother and known to be alive the following spring. We calculated survival rates treating cubs as independent from one another. We also calculated survival rates where we did not treat each cub within a litter as independent, again because most often entire litters are lost. We therefore used entire litters as the sampling unit. The size and number of bears that survived from these tracked litters were then bootstrapped 5000 times. Only COY of mothers that were collared over the entire period (COY first observed to following spring) were used. COY that died before first observation (i.e., in the maternal den or shortly after emergence) were not included. This may bias the estimate of COY survival high; however, this bias is balanced when estimating λ because the corresponding estimate of reproductive rate was likely equally biased low (McLellan 1989a).

Appendix 5: Details of reproductive rates analyses

Four general methods have been used to estimate reproductive rates of grizzly bears (McLellan 1989b, Schwartz and White 2008). Each of these methods presents different biases (Garshelis et al. 1998, Garshelis 2005, Schwartz and White 2008). If the method uses the first age of parturition or interbirth interval, then a negative bias likely exists because bears may drop their collars or die before having their first litter or completing an interbirth interval. Bias would be more severe for species that are late to reproduce or have long interbirth intervals, so these estimates for bears are frequently biased low (Garshelis et al. 1998). Additionally, females with young were less likely to be captured than other adult females, because we frequently chose not to capture these individuals in circumstances where we thought offspring could be put at risk. This could introduce additional biases to reproductive rates (Schwartz and White 2008). For older bears, reproductive rates can be estimated by using probabilities of transition among reproductive states, but this method is problematic for young age classes that include nulliparous females (Schwartz and White 2008). Given the potential for bias, we opted not to use first age of parturition or interbirth interval to estimate population growth rate. However, we report first age of parturition for comparison to other populations.

We calculated an annual litter production rate across all females within each age category (for models run in POPTOOLS 3.0). The age class-specific annual reproductive rates were calculated following Garshelis et al. (1998). We categorized adults into five age classes: >5 year olds, 6 -8 year olds, 9-12 year olds, 13 -17 year olds, and > 17 years of age. We pooled data across years and calculated the average number of cubs produced within each age class, accounting for females that did not produce cubs. The average value was then halved to obtain the proportion of female cubs produced in each year.

We also calculated the proportion of available females within each age class that produced cubs (Taylor et al. 1987a; for models run in RISKMAN). If we tracked individuals for more than one year within an age class they were included more than once. For instance, if a female that was tracked at ages 5, 6, 7, and 8 and had a litter of 1 cub when she was 8, would have 0 cubs when 5, and 0, 0, 1 when in the 6-8 age class. Standard errors around each estimate were calculated using the standard method for binomial proportions. Age class-specific litter sizes were calculated as the mean (and standard error) of the size of litters produced by bears of each age class. All litter production calculations were completed on a spreadsheet and outside of a pre-programmed software package.

Appendix 6: Population simulations

Grizzly bear populations, like most managed wildlife, are age-structured, birth-pulse populations (Caughley 1977). There are two general approaches for modelling the population dynamics of species that reproduce discretely rather than continuously: the Leslie (1945) matrix and the life table (Birch 1948, Cole 1957, Caughley 1977). The main difference between the two is the treatment of the recruitment term (e.g., F_x versus m_x; Taylor and Carley 1988). We used life table models, as implemented in the freely-available software packages RISKMAN (beta version 1.9.9.64 Taylor et al. 2003) and POPTOOLS (version 3.0; Hood 2010), to simulate the dynamics of the North Slope population and to estimate population growth rates from demographic rates.

RISKMAN is an age-structured stochastic life table model specifically designed to simulate the growth and harvest of populations of species with multiannual reproductive cycles, such as bears. The definition of the age-specific recruitment term (m_x) is expanded to account for the fact that females with COY or YOLY are not available to mate (Taylor et al. 1987b, Taylor et al. 1987c). This distinction is important when reproductive rates are estimated from populations not at the stable age distribution, or when simulated populations deviate from the stable age distribution, in which cases annual models with averaged reproductive rates yield inaccurate results (Taylor et al. 1987b). Males are included in RISKMAN simulations to allow more accurate simulation of different harvest scenarios. RISKMAN also allows the user to partition the total variance in demographic rate estimates into sampling error ("parameter uncertainty;" applied at the beginning of each iteration) and temporal process variation ("environmental uncertainty;" applied at the beginning of each year). The model assumed geographic closure (no immigration or emigration).

We parameterized RISKMAN with age class-specific reproductive rates and natural (excluding anthropogenic mortality) survival rates, and population size, estimated as described above. Based on our data and common population parameters for grizzly bear populations (Bunnell and Tait 1985, Taylor et al. 2003), we used the 3-year reproduction model, assumed a 50:50 sex ratio of cubs, set minimum and maximum ages of reproduction to 5 and 25, respectively, and set the maximum litter size to 3. We modeled 75% of the total variance as parameter uncertainty and 25% as environmental uncertainty (Taylor et al. 2009). We conducted 5000 stochastic simulations for each scenario modeled. We considered model scenarios using independent cub and yearling survival rates, whole litter survival rates, and a mix of independent and whole litter survival rates.

We were also interested in calculating population growth rate for each group of ecodistricts. When partitioning survival and reproductive data for smaller areas, we often did not have adequate sample sizes to calculate all the parameters of the RISKMAN model (particularly m_x and rates for males). Therefore, for this exercise we used POPTOOLS, which used data from females only. For each scenario modeled using POPTOOLs, λ was estimated 5000 times for the desired time period using an annual life table model with averaged recruitment rates. For each estimate of λ, simultaneous random samples of records of individual bears (whole litters for cubs) with replacement were used for the nine vital rates calculated as described above under Demographic Rate Estimation: survival rates of COY, YOLY, subadult, and adult females, and reproductive rates of 5 age classes of adult females. A summary of the tracked females with dependent young used for population simulations is presented in Table A6-1.

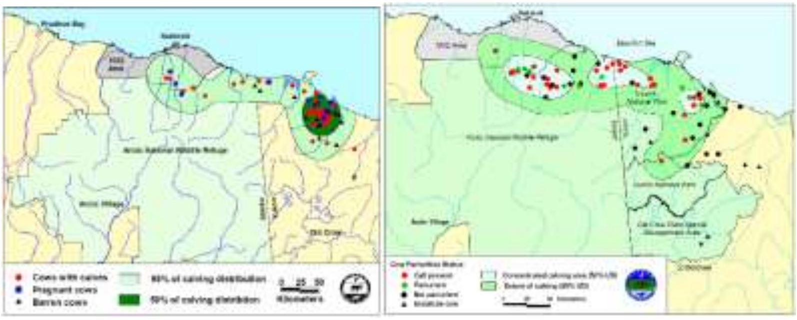
Table A6-1. All adult and subadult females tracked during the study, the number of census years they were tracked for, the number of trackable cubs produced, trackable yearlings produced, and age class when they first entered the study. Bear IDs with a –XX number after represent tracked subadult bears associated with a tracked adult female.

Ecodistrict Grouping	Female	Years tracked	Cubs	Yearlings	Age Class at 1st Capture
Barn Mountains	YT006	4	0	0	Subadult
	YT007	5	0	0	Adult
	YT010	5	2	0	Adult
	YT013	2	0	0	Subadult
	YT023	4	0	1	Adult
	YT032	5	0	0	Adult
	YT034	3	2	0	Adult
	YT047	1	0	0	Adult
	YT048	2	0	3	Adult
	YT053	2	0	0	Subadult
	YT059	2	0	0	Subadult
British Mountains	YT002	1	0	0	Adult
	YT016	5	1	0	Adult
	YT021	4	0	2	Adult
	YT027	2	0	0	Adult
	YT028	2	0	2	Adult
	YT029	2	0	0	Adult
	YT036	1	0	0	Adult
	YT038	3	0	0	Subadult
	YT039	1	0	0	Subadult
	YT044	1	0	0	Adult
	YT045	2	1	1	Adult
	YT046	1	0	0	Adult
	YT050	1	3	2	Adult
	YT051	1	0	3	Adult
	YT054	2	0	1	Adult

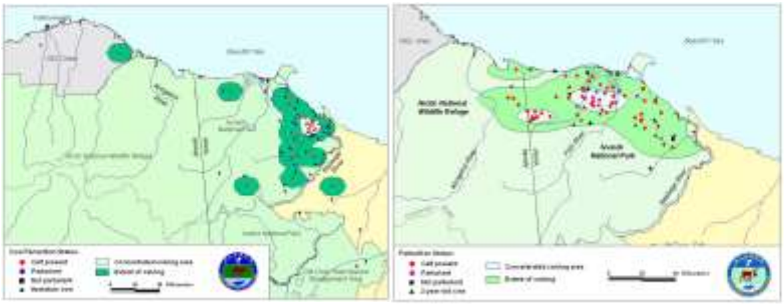
	YT028-3	1	0	0	Subadult
	YT028-4	1	0	0	Subadult
	YT054-36	1	0	0	Subadult
Coastal Plains	YT001	3	2	0	Adult
	YT011	3	2	2	Adult
	YT020	1	0	0	Adult
	YT022	4	4	0	Adult
	YT025	2	0	0	Subadult
	YT026	1	0	0	Adult
	YT031	3	0	0	Subadult
	YT035	4	3	0	Adult
	YT052	2	0	0	Adult
	YT056	1	0	0	Adult
	YT009-29	1	0	0	Subadult
	YT009-30	1	0	0	Subadult
	YT052-34	1	0	0	Subadult
	YT052-35	1	0	0	Subadult
	YT056-37	1	0	0	Subadult
	YT011-45	1	0	0	Subadult

Appendix 7: Caribou calving distribution 2004-2010.

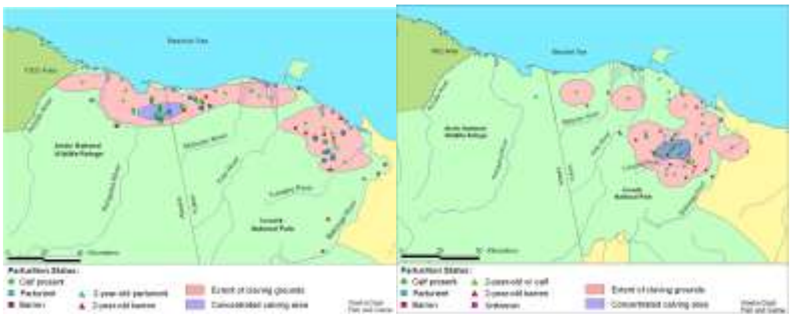
a) 2004 b) 2005



c) 2006 d) 2007



e) 2008 f) 2009



g) 2010

Figure A7-1. Maps were taken from Alaska Department of Fish and Game annual calving survey reports (Arthur 2004, Arthur 2005, Arthur 2006, Arthur 2007, Caikoski 2008, Caikoski 2009, Caikoski 2010). Maps show that the core and extent of calving areas shift annually but have generally encompassed portions of Yukon's North Slope.

Appendix 8: Home ranges of grizzly bears collared on the Yukon North Slope from 2004 to 2010.

Table A8-1. Summary of GPS collared grizzly bears on the Yukon North Slope from 2004 to 2010. Bears with VHF-only collars not included.

Bear ID	Sex	Period collars active
YT001	F	Jun 2004 - Jul 2007
YT002	F	Jun 2004 - Oct 2004
YT003	M	Jun 2004 - Apr 2005
YT004	M	Jun 2004 - May 2005
YT005	M	Jun 2004 - Sep 2004
YT006	F	Jun 2004 - Oct 2008
YT007	F	Jun 2004 - Jun 2005, Jun 2008 - Aug 2009
YT008	M	Jun 2004 - Oct 2005
YT009	M	Jun 2004 - Jun 2005, Jun 2008 - July 2008
YT010	F	Jun 2004 - Jul 2009
YT011	F	Apr 2005 - Jun 2008
YT012	M	May 2005 - Aug 2006
YT013	F	May 2005 - Sep 2006
YT014	M	May 2005 - Oct 2006
YT015	M	May 2005 - May 2006
YT016	F	May 2005 - Jun 2008
YT017	M	May 2005*
YT018	M	May 2005 - Sep 2006
YT019	M	Jun 2005 - May 2007
YT020	F	Jun 2005*
YT021	F	Jun 2005 - Sep 2009
YT022	F	Jun 2005 - Jun 2008
YT023	F	Jun 2005 - Oct 2006, Jun 2008 - Aug 2009
YT024	M	Jun 2005 - May 2006
YT026	F	Jun 2005 - Aug 2005
YT027	F	Jun 2005 - Jul 2006
YT030	M	Jul 2006 - Apr 2007*
YT032	F	Jun 2005 - Jul 2006, Jun 2008 - May 2010
YT033	M	Jun 2005 - Jul 2006

YT034	F	Jun 2005-Jul 2006, Jun 2008 - Sep 2008
YT036	F	Jun 2006 - Sep 2006
YT040	M	Jun 2008 - May 2009
YT042	M	Jun 2008 - Sep 2008
YT057	M	Jun 2008 - May 2009
YT058	M	Jun 2008 - Aug 2008

*MCPs not generated for these bears due to low number of location fixes (<20).

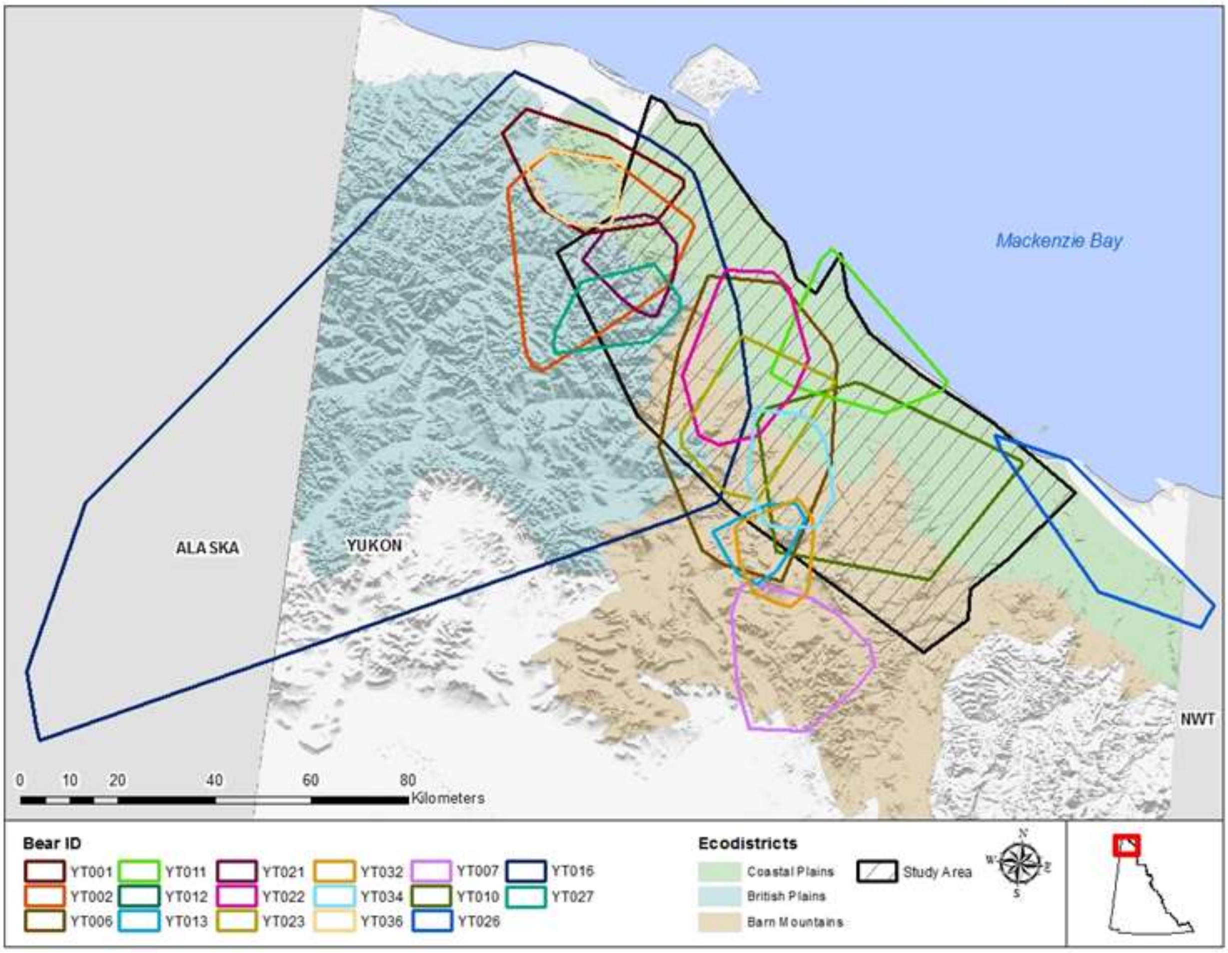


Figure A8-1. Estimates of 100% minimum convex polygon (MCP) home ranges for female grizzly bears in the Yukon North Slope.

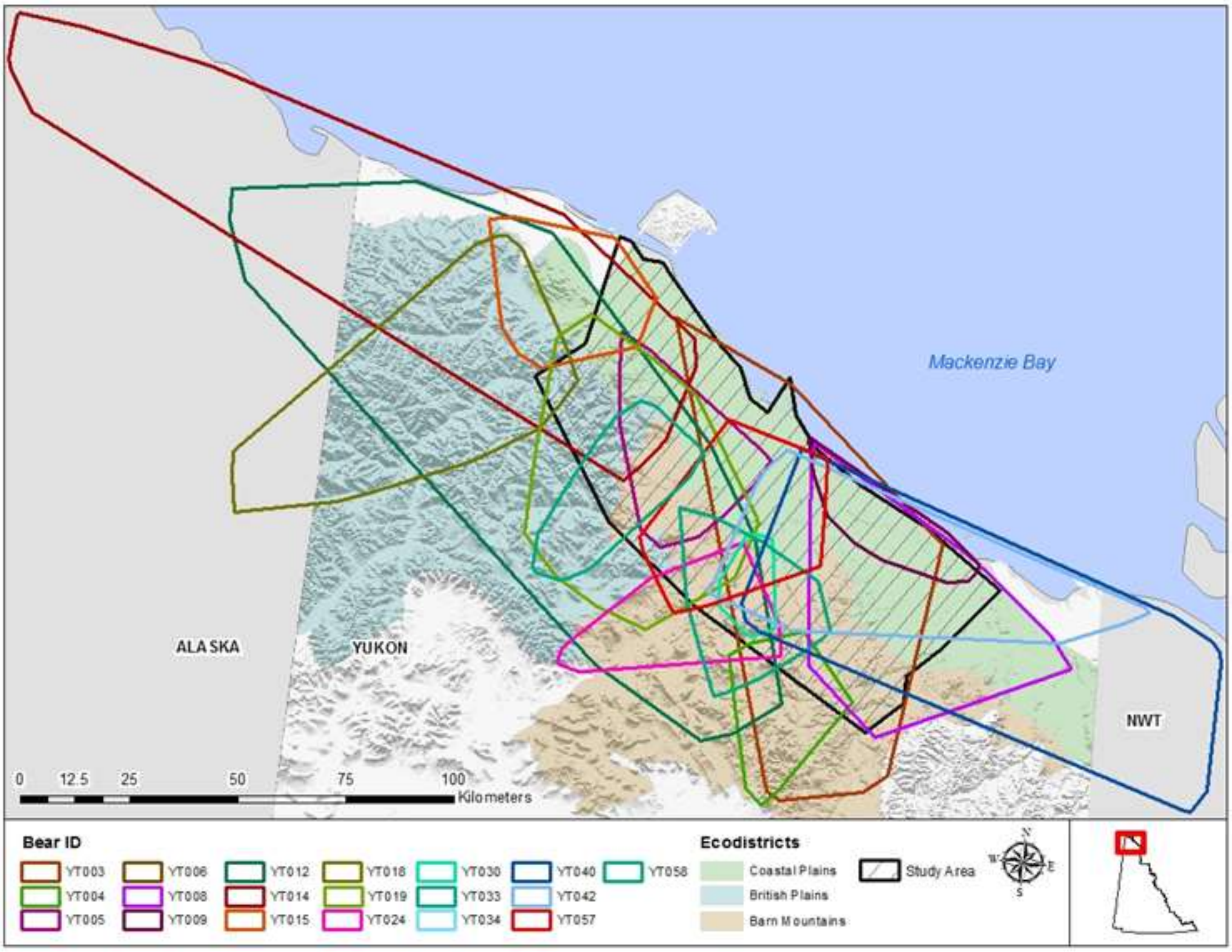


Figure A8-2. Estimates of 100% minimum convex polygon (MCP) home ranges for male grizzly bears in the Yukon North Slope.

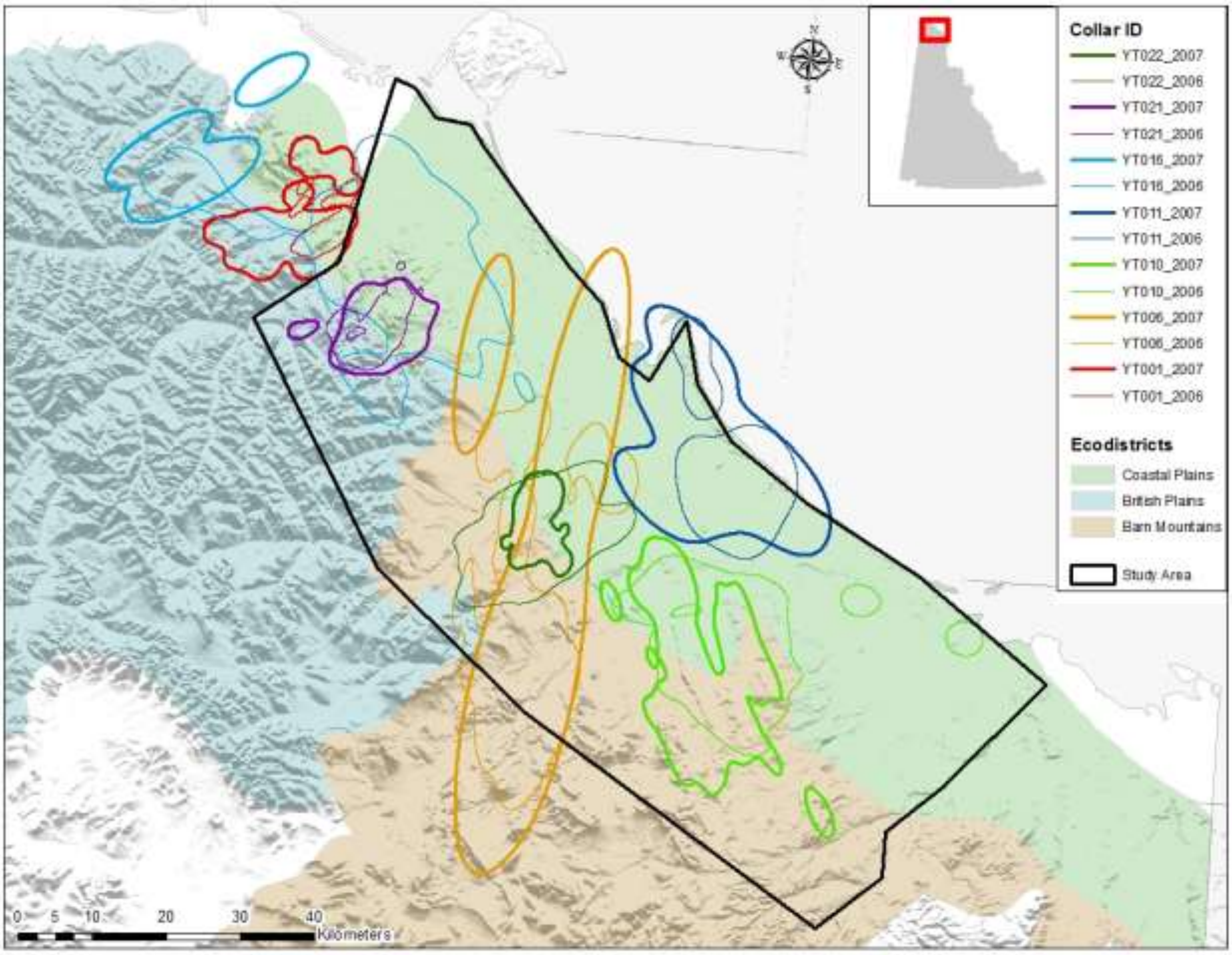


Figure A8-3. June and July ranges of grizzly bears collared in both 2006 and 2007 (*N*=7), on the Yukon North Slope. June/July ranges were calculated in Geospatial Modelling Environment (GME) using a kernel density estimator (KDE, Kernel=Gaussian, Bandwidth=SCV) and mapped as 0.95 isopleths. Number of locations used to generate seasonal ranges (2006, 2007, respectively) are: YT001=351, 144; YT006=207, 18, YT010=350, 191; YT011=27, 24; YT016=239, 12; YT021=359, 122; and, YT022=336, 77.