Chilcotin Coast Grizzly Bear Project:

Grizzly bears in the Tatlayoko Valley and along the upper Chilko River

FINAL REPORT

Prepared for:

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The Wilburforce Foundation, Seattle, WA

December 1, 2013

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Executive summary

This report is the culmination of six seasons of data collection on grizzly bears(*Ursus arctos*) conducted by the Nature Conservancy of Canada (NCC) in the West/ Central Chilcotin region of British Columbia - the area where the Chilcotin plateau meets the Coast Mountain Range - between 2006 and 2012. The dry Chilcotin Plateau is connected to the wet coast of BC by habitat rich, low elevation valleys that transect the Coast Range. These valleys - the western and eastern branches of the Homathko and the Klinaklini, for example - provide interior grizzly bears with valuable spring habitat and potential access to the coast. The Chilcotin region is home to the third largest salmon run in BC, which occurs along the upper Chilko River each fall.

Project goals included estimating the number of grizzly bears using important spring habitats within these low elevation valleys, fall habitats along salmon spawning streams in the region, and to document movement between these habitats. Grizzly bear hair was collected from barbed wire hair traps and analyzed for DNA. Bear hair was collected in the upper Homathko Watershed during four spring seasons in the Tatlayoko Valley and one spring season in the West Branch Valley. Bear hair was collected during six fall seasons along the upper Chilko River and one fall season along the lower Homathko River near Bute Inlet.

Two-hundred-fifty individual grizzly bears were identified over the course of six years of monitoring in the four sampling areas. Sixty-nine grizzly bears (32 females and 37 males) were detected over 4 years in the Tatlayoko Valley during the spring months and 198 grizzly bears (112 females and 86 males) were detected over 6 years on the upper Chilko River during the fall salmon run. Sixteen grizzly bears were detected in the West Branch Valley and 12 grizzly bears were detected in the Scar Creek area of the lower Homathko.

Mark-recapture analysis was used to estimate the *super-population* (the average number of bears located in each study area during the sampling period) of bears in the Tatlayoko Valley and along the upper Chilko River. The Tatlayoko Valley analysis included a full data set and a data set that was reduced to include only sites sampled in all four years. The estimated total number of bears in the Tatlayoko Valley each spring ranged from 28 to 48 +/- 8 (full data set), and 27 to 40 +/- 8 (reduced data set). Despite annual fluctuations in bear numbers, trend analysis suggested that the number of bears utilizing the Tatlayoko Valley in the spring months remained relatively constant. The high density of grizzly bears utilizing the rich early green-up habitat in the Tatlayoko Valley suggests that bears are attracted to the valley from a larger area in the spring much like the salmon stream in the fall.

The mark-recapture estimates for the number of bears along the upper Chilko River varied each fall between 66 +/- 11 (2006), 82 +/- 6 (2007), 113 +/- 17(2008), 94 +/- 18

(2010), 164 +/- 20 (2011), and 142 +/- 14 (2012) bears. Population models suggested bear numbers were related to salmon escapement, and showed more bears returning after a season with greater salmon numbers. Population estimates indicated a general increasing trend, especially in 2011, which correlated with higher bear return after a season with record salmon escapement. Few rivers in the world compare with the upper Chilko River as a source of salmon for grizzly bears. Even rivers with documented fall concentrations of grizzly bears on the coast of BC (the Owekeno River, for example) have not recorded such high grizzly bear numbers. According to the United States National Parks Service statistics, even the Brooks River in Alaska has trouble competing with the Chilko for sheer numbers of bears.

It is important to note that density estimates can only be applied to these specific areas and not extrapolated to the entire region. Fluctuations in “super-populations” of bears does not signify increases or decreases in the overall population and can only be interpreted as variation in the annual use of a particular resource by bears throughout the region.

Forty-two (61%) of the 69 total bears in Tatlayoko were also detected along the Chilko River at least one of the six sampling years. Multi-strata analysis of movement probability (the probability that a bear detected on one grid would be detected on the other grid during the next session) suggested high movement rates from the Tatlayoko Valley study area to Chilko (estimated mean probability was 0.67 +/- 0.13), and lower movement rates from Chilko to Tatlayoko (estimated mean probability was 0.26 +/-0.08). In both cases, male movement rates were higher than female movement rates. Interestingly, multi-strata models consistently detected movement based on salmon availability.

Twenty-eight (17 males, 11 females) detected in the upper Homathko/ Chilko were also detected in grizzly bear DNA projects to the south of our study area. Twelve bears were detected by a grizzly bear survey in the South Chilcotin. Two of these were located near Gold Bridge, BC - over 115 km from their fall locations on the upper Chilko River. Sixteen bears were detected in the Southgate River drainage near the south end of Chilko Lake. Although most of these were located near the headwaters of the Southgate River, one male bear was located where the Southgate River joins Bute Inlet. Interestingly, this bear was located on the coastal inlet in the spring and on the Chilko in the fall which suggests that a “coastal” bear travelled over 100 km to the interior for salmon. *Coastal salmon availability* may be an important variable in determining the annual number of grizzly bears utilizing the Chilko River during the fall months. If this is true, the importance of Chilko salmon for surrounding grizzly bear populations is even more significant than previously thought.

Home range estimates for these 28 bears also detected to the south of our study area were between 2,800 and 10,000 square km which is well above the average published female or male grizzly bear home ranges of 200 – 600 km^2 for females and 900-1800 km^2 for males. The large home range sizes indicate bears are willing to travel great distances for Chilko salmon.

The long distance movements to get to the river, the high movement rates from Tatlayoko to Chilko, and the high number of grizzly bears detected along the river during the salmon run are strong indications of how unequivocally important the upper Chilko salmon are for grizzly bears in the Chilcotin. In fact, the Chilko River salmon run influences an area that reaches over 41,000 square km (calculated by using the maximum detected movement distance as the radius of a circle around the upper Chilko River), which is an area over 4 times the size of Banff, Yoho and Kootenay National Parks combined (9,360 km^2) and over 4.5 times the size of Yellowstone National Park (8,983 km^2).

The West/Central Chilcotin is home to a large, unique and valuable population of grizzly bears. Continued research on bear numbers, movements and important habitats is needed for successful conservation of these populations in the future. In the meantime, the value of identified spring and fall habitats cannot be underestimated and land use planners and local communities must consider the importance of maintaining access for bears to spring habitats in the Tatlayoko and West Branch Valleys, and to fall salmon on the Chilko River to maintain healthy grizzly bear populations in the region.

John Marriott photo

General introduction

Grizzly bears have had a relationship with salmon for thousands of years. One of the places in North America where this relationship is still intact is in the West/Central Chilcotin region of British Columbia where the Chilcotin Plateau meets the eastern slopes of the Coast Range. The West/Central Chilcotin has one of the lowest road densities in southern Canada, and is home to the salmon run of the Chilko River (the 3rd largest sockeye salmon run in BC) where one of the largest seasonal concentrations of grizzly bears in British Columbia congregates on the shores of the river each fall. The dry Chilcotin Plateau is connected to the wet coast of British Columbia by habitat rich, low elevation valleys that transect the Coast Range. These valleys (the Homathko and the Klinaklini, for example) provide interior grizzly bears with valuable spring habitat, as well as potential access to salmon along the coast which may connect them with coastal grizzly bear populations of the Great Bear Rainforest. With few roads, rich habitat and large expanses of inaccessible wilderness, the West/ Central Chilcotin region of British Columbia is home to one of the wildest populations of grizzly bears in Southern Canada and the United States.

Extensive wild areas like the West/ Central Chilcotin are essential for the long-term survival of long-lived, wide-ranging animals like the grizzly bear. The West/Central Chilcotin is part of a 350-mile broad arc of habitat that stretches from the volcanic Itcha Ilgachuz Mountains in the northwest to the Fraser Canyon in the southeast, encompassing over 7.5 million acres of land. The permanent population of people in the area is small (approximately 1,700 east of Bella Coola and west of Williams Lake) and the number of visitors per year is very low, all of which are confined primarily to the Highway 20 corridor. The coastal region (which includes the Great Bear Rainforest) connecting to this extensive wilderness also remains relatively uncompromised. The Great Bear Rainforest, for example, includes 4.4 million acres of undisturbed coastal rainforest.

In contrast, many other wilderness areas that have been identified as refugia for grizzly bears are unlikely to maintain healthy grizzly bear populations in the long term. Banff/Jasper/Kootenay/Yoho National Parks, for example, has a combined area of over 6 million acres. However, over 6 million people travel each year to visit Banff and Jasper National Parks alone. The parks are also major transportation corridors (road and rail) with another several million people moving through annually. Parks Canada recently stated that the grizzly bear mortality rate in the park continues to be well above sustainable levels (Sawaya et al. 2012). Yellowstone National Park (with 2.2 million acres and 3.5 million visitors annually) and the surrounding region currently boasts of a sustainable grizzly bear population but scientists warn that increasing human encroachment may push the population into decline (Merrill 2005).

As wild as the West/ Central Chilcotin region is, it is not without threats for bears. Declines in salmon populations both on the coast and in the Fraser-Chilko may have significant impacts on bear populations in the region. Like everywhere else, humans are steadily infiltrating the area. Settlement, logging, mining, backcountry cattle range use, and recreation are all gradually altering the landscape and compromising this unique wilderness. Taseko Mines, for example, is in the midst of negotiations for approval of a large open pit mine with potential large impacts on the Fraser River and its salmon. Accompanying communities created for workers and their families, and the large numbers of workers onsite will further degrade habitat quality and increase mortality for bears. Bear viewing on the upper Chilko has become increasingly popular with several boatloads of viewers on the river each day – and with it the potential for habituation, loss of access to salmon during the day and increasing human-bear conflict. Global warming is also a threat to the area with its warming waters and changes in run-off for salmon populations in the Chilko River. Changing habitats such as wide-scale pine beetle devastation and corresponding changes in water runoff and extensive salvage logging operations - with accompanying road building and habitat alteration – are also a concern. Long-term protection and management of grizzly bears throughout the West/Central Chilcotin is unlikely to be successful without scientific information about the animals and their needs in a local context.

Recent advances in genetic technology allow identification of species, sex, and individuals without handling bears. DNA is analyzed from bear hair collected along established bear trails and from systematically positioned barbed wire hair traps. The number of individuals identified from surveys yield minimum counts and a baseline index of population size. Bears identified from snagged hair are used in mark-recapture models to estimate population density and trend. DNA data can also be used to estimate movement rates between two areas.

The Chicotin Coast Grizzly Bear Project (CCGBP) expanded on a three year project conducted by NCC between 2006 and 2008 that collected base-line data on grizzly bear numbers and movements in the Chilcotin region using DNA analysis of grizzly bear hair. The CCGBP continued spring and early summer grizzly bear surveys in important low elevation habitat in the Tatlayoko and West Branch Valleys (both part of the upper Homathko watershed) to improve estimates of seasonal grizzly bear population trends and numbers. Surveys were conducted along the upper Chilko River to continue monitoring population trends and numbers in valuable fall habitat and one sampling season was conducted in the Scar Creek area (the lower Homathko River) in hopes of detecting movement between the interior and the Coast.

The following report is a summary of six years of data collected on grizzly bears in the West/ Central Chilcotin between 2006 and 2012. The main objective of this project was to collect baseline scientific information on grizzly bears to ultimately inform grizzly bear management and conservation policy.

Study area

The four sampling areas for this project included the ***Tatlayoko Valley*** as far north as Skinner Creek and south to the Nostetuko River at the south end of Tatlayoko Lake, the ***West Branch Valley*** as far north as Little Sapeye Lake and south to Twist Lake, the ***upper Chilko River*** along 20 km of the river from where it exits Chilko Lake to just downriver of "Henry's Crossing", and the topographical pinch point approximately where ***Scar Creek*** enters the lower Homathko River (Figure 1). The Tatlayoko Valley sampling area was approximately 625 km^2 and the West Branch study area was approximately 325 km^2. Road access to the first three areas is via gravel road from Tatla Lake on Highway 20, 30 km to the north, while access to the Scar Creek area was via helicopter with White Saddle Air.

A portion of the Tatlayoko and West Branch study areas overlaps the Homathko River/ Tatlayoko Protected Area and the upper Chilko River study area borders Tsylos Provincial Park. These three areas include a portion of the Klinaklini-Homathko Grizzly Bear Population Unit (GBPU) where grizzly populations are currently assigned a conservation status of "viable", and the upper Chilko River borders the South Chilcotin Ranges GBPU which is assigned a conservation status of "threatened" (Hamilton et al. 2004).

Tatlayoko, West Branch and the upper Chilko River are in the western portion of the Central Chilcotin Ranges Ecosection (CCR), which is a dry mountainous area in the rain shadow of the Coast Mountains. Highest summits are generally about 3,000 m. The ecosection contains three large lakes including Chilko, Tatlayoko, and the two connected Taseko Lakes. The Homathko River flows out of Tatlayoko Lake, converges with Mosley Creek as it flows out of the West Branch Valley, and transects the coast range to Bute Inlet creating a unique low elevation corridor between the dry interior and the wet BC coast (Figure 2). Scar Creek is in the upper portion of the lower Homathko River and is wet coastal forest. Topography north of Scar Creek is rugged and remote. Scar Creek is near the headwaters of the coastal salmon run and bears feeding or travelling in the Scar Creek area would have easy access to areas further downriver via old logging roads. Many of these roads are decommissioned and human use in the area is low.

The Chilko River eventually flows into the Fraser River and has one of British Columbia's largest sockeye salmon (*Oncorhynchus nerka*) runs. Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*) are also found in the Chilko River. The run occurs annually sometime between late August and October. The spawning beds are located within a few kilometers of Chilko Lake and the run draws large concentrations of bears to the region each year.

Significant human use also occurs along the upper Chilko River during spawning season. Several tourism facilities border the river. In recent years, bear viewing has become increasingly popular, with several boatloads of viewers on the river each day. Cattle and horses graze in the area and numerous trails follow along the river on both sides. Guided and non-guided recreational fishing occurs from shore and in motorized and non-motorized boats. Department of Fisheries and Oceans conducts salmon enumeration in and along the banks of the river, particularly where Lingfield Creek joins the Chilko. Nemiah First Nations (the Xeni Gwet'in) as well as other First Nation individuals fish along the shores and hold gatherings within the area.

The Tatlayoko and West Branch communities (population approximately 100 each) are located in the valley bottoms and include a mixture of ranches and hobby farms. Cattle from ranches at both Tatlayoko and West Branch graze throughout the study area and high into alpine areas both east and west of each valley.

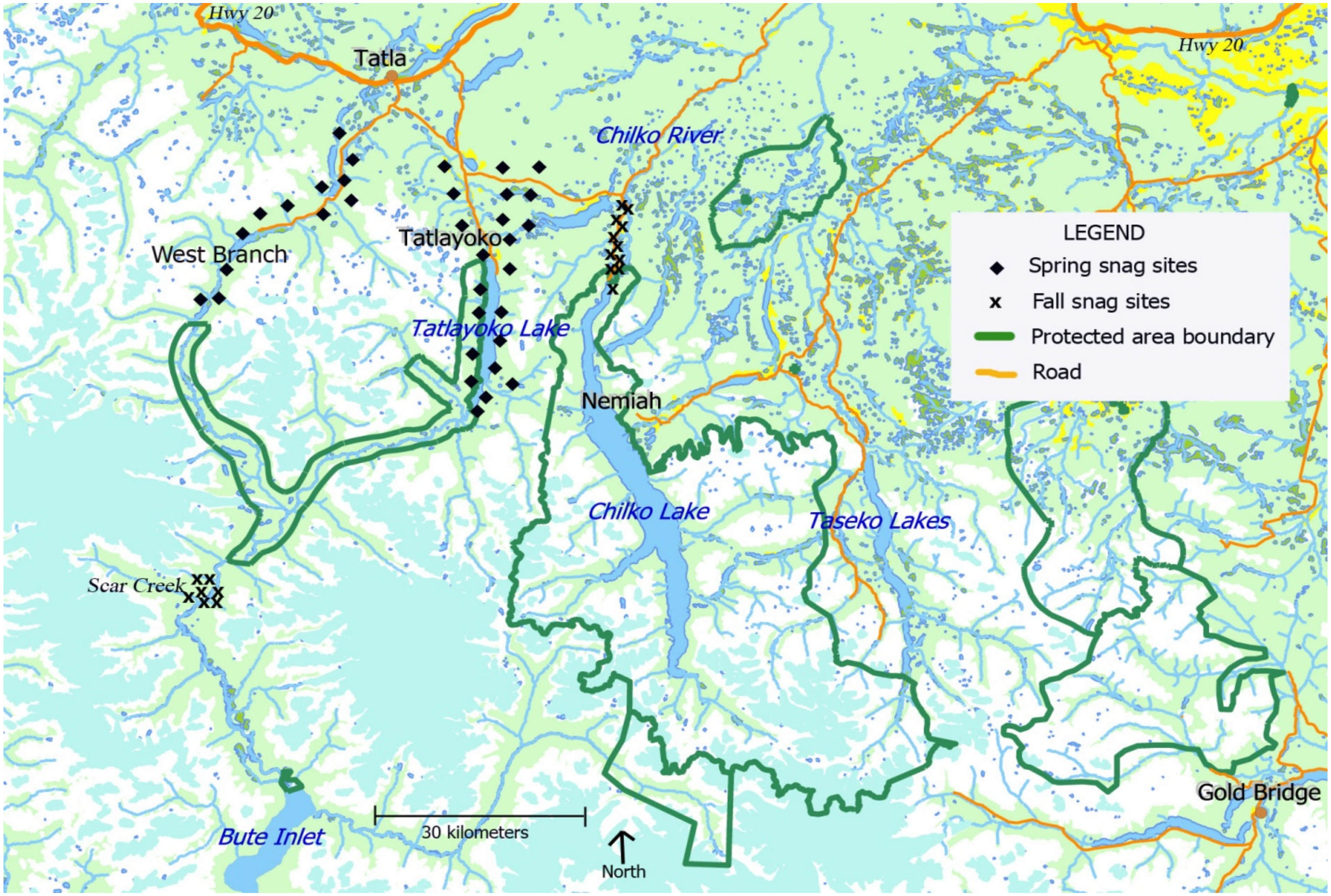


Figure 1. Study area with hair snagging site locations in the West Branch Valley, the Tatlayoko Valley, the upper Chilko and the Scar Creek pinch point.

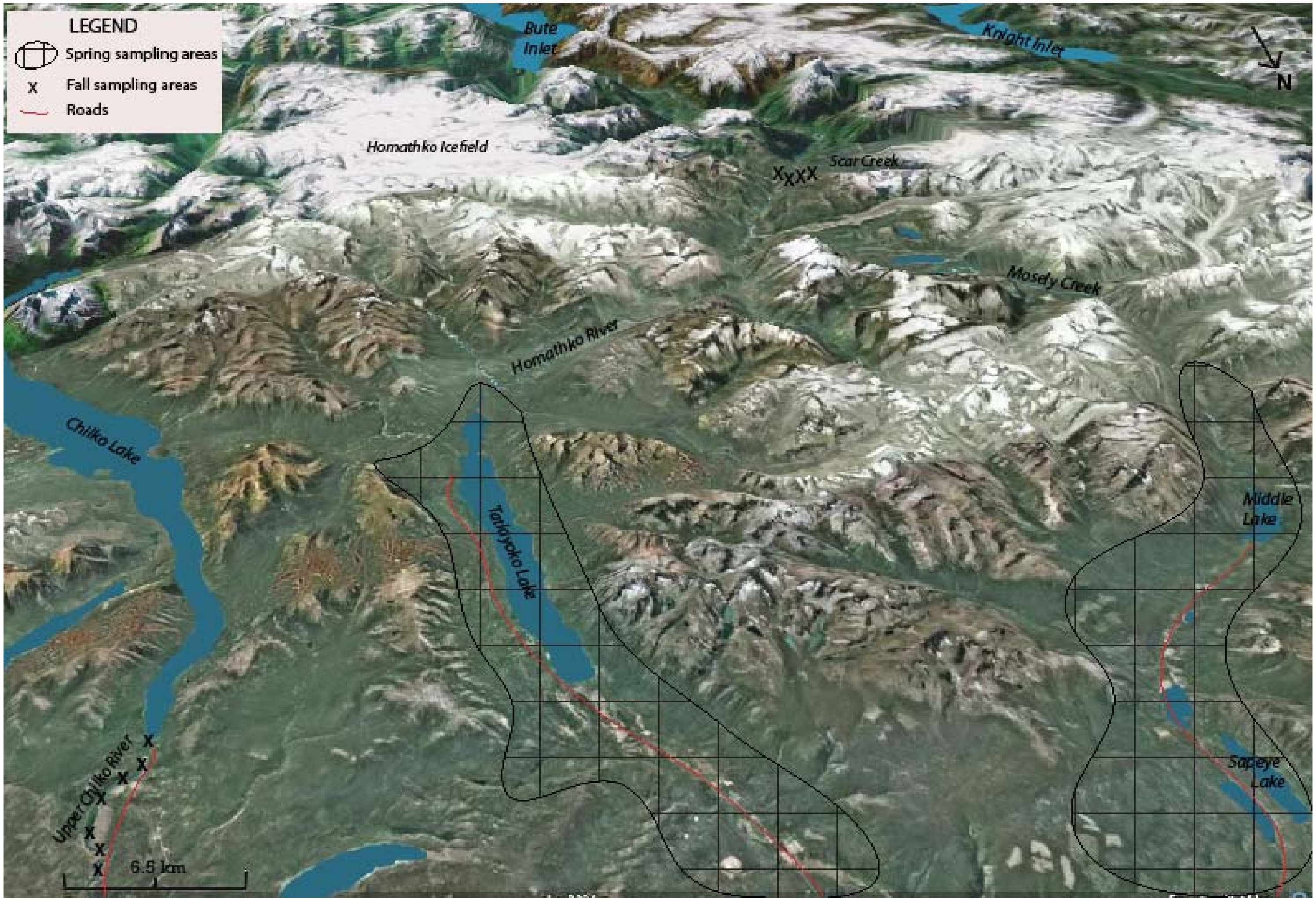


Figure 2. Google Earth image of study area showing the low elevation Homathko River Valley to Bute Inlet. Note this image is looking almost due South.

Goals and Objectives

Project goals and specific objectives are summarized as follows:

Overall Project Goals

- To provide scientific information to help managers make resource and conservation decisions in relation to grizzly bears.
- To enhance eco-regional planning efforts in the region by providing baseline information on grizzly bears in specific habitats and seasons.
- To enhance efforts in protecting and preserving the ecological integrity of the upper Homathko Valleys (Tatlayoko and West Branch) and the upper Chilko River area.
- To increase local knowledge and interest in the status and issues surrounding grizzly bears in the region.

Project Objectives

- To estimate and monitor the number of grizzly bears utilizing the upper Homathko valleys (Tatlayoko and West Branch) during spring/early summer.
- To estimate and monitor the number of grizzly bears utilizing the upper Chilko River during the fall salmon run.
- To detect and monitor movement of grizzly bears between the Tatlayoko and West Branch Valleys and the Chilko River salmon run.
- To detect as many grizzly bears as possible during the fall season within the topographical "pinch point" near the Scar Creek area of the lower Homathko River.
- To detect movement of grizzly bears between the upper (Tatlayoko and West Branch) and lower (Scar Creek area) Homathko.
- To document movement of grizzly bears detected by the CCGBP and a spring/summer grizzly bear population census overlapping with the south Chilko and Bute Inlet area.

Methods

The primary methodology for the Chilcotin Coast Grizzly Bear Project was DNA analysis of grizzly bear hair. DNA hair-snagging is a non-invasive, cost-effective method for collecting scientific information on spatial and temporal trends of grizzly bear populations.

Spring hair sampling

Spring sampling occurred in the upper Homathko Valleys (Tatlayoko and West Branch) between May 1st and June 30th, 2010. Barbed wire sites were located systematically throughout each study area using a grid with one site per each 5x5 km cell. Each hair-sampling site consisted of a small corral-like enclosure of approximately 30 meters of 4-pronged, double-strand barbed wire nailed around 3 to 6 trees at about 0.5 m from the ground. Within each enclosure, a brush pile was built and baited with a non-reward liquid lure to entice bears to enter and leave hair on the wire (Figure 3). The non-reward scent lure for attracting bears to sampling stations was a combination of 3 litres of cow blood and 1 litre of liquid fish per snagging site, per session. The blood and fish was rotted for several months prior to application. Snagging sites were not moved between sessions.

Hair was also collected opportunistically from bear rub-trees and barbed wire range fences throughout the study area. Rub trees that were identified during the sampling period were fitted with crossing pieces of barbed wire to facilitate hair collection.

Following the same protocols as Mueller 2009, bear hair was collected from 21 snag sites during three 12-day sessions in the Tatlayoko Valley. This completed four years of grizzly bear monitoring in the Tatlayoko Valley. Bear hair was collected from 13 hair-snag sites during four 12-day sessions in the West Branch Valley. This was the only year of data collection in the West Branch Valley.

Bear hair was collected from each sampling site at the end of each session. Field crews were comprised of 2 people for safety and sites were accessed by foot, by 4x4 truck along old logging roads, by a 16 foot outboard motor boat along the west side and south end of Tatlayoko Lake, by mountain bike south of Tatlayoko Lake, and by quad in a few harder to get spots on the north end of the lake.

Warning signs were posted at all hair-snagging sites and sites were located in areas of little to no human use. Potential users of areas in close proximity to sites were contacted and informed of snagging locations. Sites were removed at the end of the sampling season.

Figure 3. Grizzly bear checks out a baited debris pile at a hair snag site in the Tatlayoko Valley.

Fall hair sampling

Fall sampling was conducted along the upper Chilko River between late August and early November in 2010, 2011 and 2012. This completed six years of data collection along the upper Chilko following the same protocols as Mueller 2009. Fall sampling was also conducted in the Scar Creek area of the lower Homathko between August 25th and October 25th, 2010.

Chilko

Grizzly bear hair was collected at 13 different snag sites during five 10-12 day sessions along the upper Chilko River. Site locations were consistent with locations from previous years and were chosen based on local knowledge of bear use/travel in the area and put in areas where human disturbance was minimal. Hair was collected from barbed wire stretched across bear trails beside the river and across shorelines by stretching wire to a metal post pounded into the river just off shore (Figure 4). Sampling sites did not include a scent lure. Snagging sites were not moved between sessions. Sites were accessed by a 17-foot canoe from the Tsylos Park campground on the north end of Chilko Lake to Henry's Crossing. Sites were removed at the end of the sampling season.

Scar Creek
Hair was collected from 9 sites during 2 sessions of approximately 30 days each in the Scar Creek area in hopes of recapturing bears from spring sampling areas (Figure 5). Access to Scar Creek was via helicopter from White Saddle Air in the West Branch Valley. Sessions were longer for the Scar Creek area due to access costs.

Steve Ogle photo

Figure 4. Grizzly bear stepping over a snag site and leaving a hair sample along the upper Chilko River.

Steve Ogle photo

Figure 5. A grizzly bear watches hair collection near a shoreline site in the Scar Creek area along the lower Homathko.

Lab analysis

All hair samples were sent to Wildlife Genetics International (WGI) of Nelson, BC, for DNA analysis under the supervision of Dr. David Paetkau.

Prior to detailed genetic analysis, samples were excluded based on quality and visual appearance (i.e. obviously not from grizzly bears). Hair-snag samples from black bears were differentiated from grizzly bears using both visual inspection (for obvious black bears) and a single-locus (the locus is the location of a gene on a chromosome) species test with marker *G10J* to eliminate weak samples and black bear samples.

Every grizzly bear has its own unique genotype. The use of a minimum number of genetic markers (segments of DNA with identifiable physical locations on a chromosome) is required to discriminate among individual grizzly bears with acceptably low error rates (Paetkau 2003). For this study, WGI used the 7 microsatellite markers (repetitive stretches of short sequences of DNA used as genetic markers) that were found to be highly variable for grizzly bears in the area immediately to the south of our study (Apps et al. 2006). This 7-marker locus system had a low enough match probability to ensure accurate individual identification, and minimized the likelihood that too few individuals were identified due to a lack of variability necessary to produce unique genotypes for each individual that was sampled (David Paetkau, personal communication). Once the genotypes were completed and checked for errors, a computer search for identical genotypes was performed and individuals were defined for each unique genotype. To ensure that samples from the same individual did not receive different individual assignments, each individual's genotype had to differ from the genotype of every other individual at a minimum of 2 markers (Paetkau 2003). Each individual grizzly bear was then identified for gender.

Salmon volume and timing

Bear numbers along salmon spawning streams may be relative to salmon availability for bears. Data on Sockeye salmon run volume and timing, and carcass recovery surveys collected by the Department of Fisheries and Oceans (DFO) were summarized for each year of this study.

Population estimates

Grizzly bear population size and trend estimates for this project were derived using mark-recapture analysis. See Appendix 1 for more information on mark-recapture population estimation. Model selection and execution was performed by John Boulanger with Integrated Ecological Research in Nelson, BC.

Grizzly bear population size and trend for the Tatlayoko and Chilko study areas were estimated using the Robust design (Pollock and Otto 1983) Pradel model (Pradel 1996) in program MARK (White and Burnham 1999). Population size and capture probability (p*) were estimated for each year using the Huggins closed population size model (Huggins 1991) and the change in population size (λ) as well as apparent survival (ϕ) and rates of additions between years (f) was estimated using the Pradel model. Apparent survival (ϕ) is the probability that a bear that was on the grid in 2006 would still be on the grid in 2007. It encompasses both deaths and emigration from the sampling grid. Rate of addition (f) is the number of bears on the grids in 2007 per bear on the grid in 2006. It encompasses both births and immigration of bears from outside the grid area between the time in which sampling occurred. Apparent survival and rates of addition are added together to estimate change in population size (λ) for the interval between each sampling occasion. Population rate of change is equivalent to the population size for a given sampling period divided by the population size in the previous sampling period ($\lambda=N_{t+1}/N_t$). Given this, estimates of λ will be 1 with a stable population, less than 1 if the population is declining and greater than 1 if the population is increasing.

In both data sets there was supplementary genotype data from rub trees and opportunistic samples. This data was incorporated as unique sessions (i.e. 1 session for all rub tree data and 1 session for all opportunistic samples in a given year). This approach follows the general methods outlined in (Boulanger et al. 2008, Kendall et al. 2009). The grid size of the Tatlayoko valley changed slightly each year and rub trees were not sampled in 2006. Therefore, an analysis was undertaken with only cells sampled each year and no rub trees included to test the sensitivity of parameter estimates to the inclusion of this data.

Models were introduced into the analysis that tested for sex-specific, session-specific, and year specific variation in demographic and capture probability parameters. It was possible that dead salmon availability and overall escapement influenced demography of bears as well as recapture rates of bears on salmon streams. For example, it was possible that years with high salmon availability would increase fidelity of bears from previous years, and attract new bears to the river areas (Boulanger et al. 2004). On a smaller time scale, increased salmon availability might increase within year recapture rate since bears would be more likely to stay in stream areas. The fit of models was evaluated using the Akaike Information Criterion (AIC) index of model fit. The model with the lowest AICc score was considered the most parsimonious, thus minimizing estimate bias and optimizing precision (Burnham and Anderson 1998). The difference in AICc values between the most supported model and other models (ΔAICc) was also used to evaluate the fit of models when their AICc scores were close. In general, any model with a ΔAICc score of less than 2 was worthy of consideration.

Population size of bears on both grids corresponded to the "superpopulation of bears" that visited sampling areas during the period of DNA sampling given that both grids were relatively open (Kendall 1999).

Movement rate estimates

Another way of using mark-recapture data in projects with multiple study areas is to estimate the probability that an animal will move from one area to another. In this case we were interested in determining the probability that a bear found in the Tatlayoko Valley in the spring would also be found along the Chilko River in the fall, and vice versa. A robust design multi-strata model (Hestbeck et al. 1991, Brownie et al. 1993) was used to estimate movement of bears between the Tatlayoko grid and Chilko River DNA areas. The multi-strata robust design model, like the Pradel model robust design, uses closed models to estimate capture probabilities and population size for a closed sampling session. The Multi-strata portion of the model then estimates apparent survival and movement probabilities (termed transition probabilities as denoted by ψ) of bears from the Tatlayoko grid to the Chilko River and from the Chilko River to the Tatlayoko river grid for the interval between sampling sessions. As with the Pradel robust design, sex and year-specific variation in movement rates was tested and the effect of temporal variation in salmon availability on movement to the Chilko River each fall was considered. See Appendix 3 for more information on the multi-strata analysis.

Home range estimates

Minimum home range sizes were estimated by calculating the area of a circle with the diameter equal to the maximum distance between multiple detections of the same bear.

Remote camera

For interest we collected photos and videos at various hair snag sites with a remote camera during the sampling period.

Community consultation

Consultation with the local community for both community support and cooperation was necessary for successful field seasons. Contact groups included the Xeni Gwet'in First Nation, Homalco First Nation, Friends of Nemiah, the Tatla Lake Resource Association, the Nature Conservancy of Canada, the Department of Fisheries and Oceans, the Chilko Resorts and Community Association, local hunting and tour guides, and local ranchers with cattle ranges that overlapped with the study area. Ministry of Environment and BC Parks were contacted for local permits.

Results

Sampling success

A total of 5066 hair samples were collected over six years. Between 20% and 40% of the hair samples collected each year were grizzly bear samples that were assigned to an individual. The rest of the samples were either excluded due to sub-selection rules, lack suitable material for extraction, were black bear or some other non-grizzly bear species, or somehow failed during the extraction process. Sampling success was consistent with other grizzly bear DNA surveys (Apps 2009, Mueller 2009), with higher than normal success along the upper Chilko and in the Scar Creek area due to the higher concentration of grizzly bears (as opposed to black bears) in both areas during the sampling period. See Table 1 for a summary of the number of hair samples collected in each sampling area each year.

Individual grizzly bears

Between 2006 and 2012, a total of 250 individual grizzly bears were identified. Sixty-nine (average of 25 bears per year over 4 seasons) were captured in the Tatlayoko Valley during the spring, 16 (sampled only one season) in the West Branch Valley, 12 (sampled only one season) in the Scar Creek area, and 198 (an average of 59 bears per year over 6 seasons) along the upper Chilko during the fall. The number of grizzly bears captured and recaptured each year is summarized in Table 2.

Table 1. Number of hair samples collected in each sampling area between 2006 and 2012.

Year	Tatlayoko	West Branch	Chilko	Scar Creek
2006	509	-	344	-
2007	859	-	494	-
2008	659	-	413	-
2010	298	188	247	145
2011	-	-	548	-
2012	-	-	362	-

Table 2. Grizzly bears detected in Tatlayoko, West Branch, the upper Chilko and Scar Creek, 2006 – 2012. Recaptures include all bears captured previously in any sampling area.

	Tatlayoko		**West Branch**		**Upper Chilko**		**Scar Creek**
Year	Individuals	Recaps	Individuals	Recaps	Individuals	Recaps	Individuals
2006	17	0	-	-	41	9	-
2007	33	14	-	-	66	29	-
2008	25	16	-	-	50	30	-
2010	26	19	16	3	39	23	12
2011	-	-	-	-	80	38	-
2012	-	-	-	-	80	53	-
Total*	**69**		**16**		**198**		**12**

**Total numbers do not add up to the grand total due to individual bears being detected in more than one area and in multiple years.*

Black bears

Black bear hair is separated from grizzly bear hair both visually and genetically in the lab. Almost 90% of the genetically detected black bear samples were collected in spring areas and not along the Chilko River nor in the Scar Creek area. This suggests that few black bears are using the salmon as a food resource and may be an indication of inter-specific (between species) competition.

Bear movement between spring and fall sampling areas

Many bears were captured in both spring and fall sampling areas. Close to two thirds (61%) of all the bears (42 of 69 bears) detected in Tatlayoko between 2006 and 2010 were also detected along the upper Chilko during the salmon season at least one of the sampling years between 2006 and 2012 (Table 3). Two out of the 16 bears detected in the West Branch Valley were also detected in Chilko. Twelve new bears were identified in the Scar Creek area. None of these were recaptures from spring sampling areas, therefore no movement was detected between the upper Homathko Valleys and the lower Homathko (Scar Creek).

Table 3. Number of bears captured on Chilko, Tatlayoko, and both areas 2006 - 2012.

Movement	F	M	Totals
Tatlayoko only	9	18	27
Chilko only	89	67	156
Both grids	23	19	42
Totals	121	104	**225**

South Chilcotin/ Southgate

Twenty-eight (17 males, 11 females) detected in the upper Homathko/ Chilko were also detected in grizzly bear DNA projects to the south of our study area.

12 individual bears were detected in the South Chilcotin Grizzly Bear Project between 2006 and 2007 (Apps 2009). The furthest of these was located 115 km as the crow flies from the Chilko River. Sixteen bears detected along the upper Chilko were detected in the Southgate Grizzly Bear Project study area between June 26th and August 10th 2010. The majority of these were located near the headwaters of the Southgate River but one male bear was located where the Southgate River joins Bute Inlet (Figure 6). Interestingly, this bear was located in Bute Inlet in the spring and along the upper Chilko in the fall which suggests that a "coastal" bear might have travelled to the interior for salmon. Data was provided by Clayton Apps, Aspen Wildlife Research Inc.

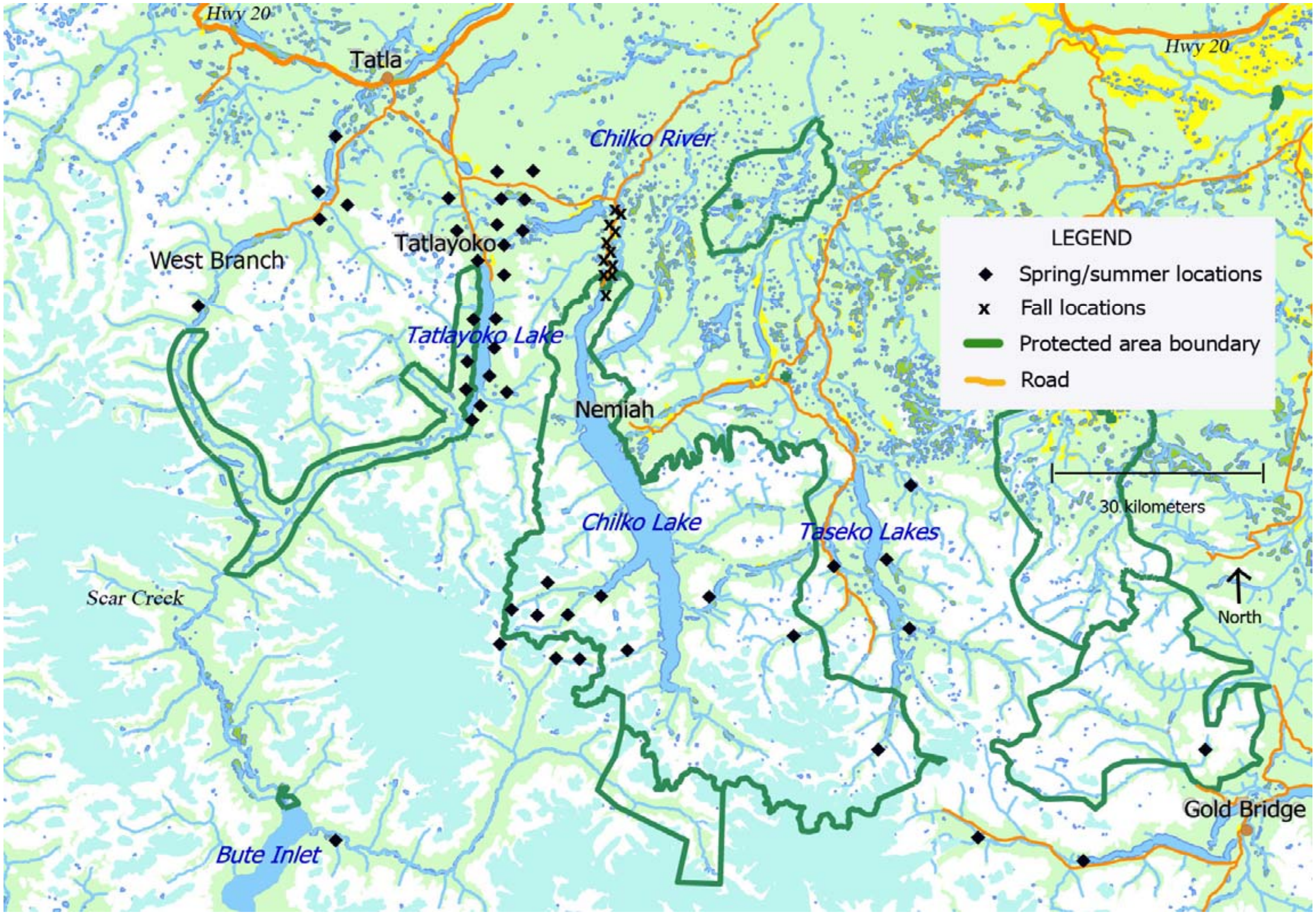


Figure 6. Spring locations of grizzly bears that were also located in fall on the upper Chilko River (including bears detected in the South Chilcotin study area and the Southgate study area) between 2006 and 2011.

Salmon escapement

Sockeye salmon escapement in the upper Chilko River and Lake fluctuates each year. The 2010 sockeye escapement estimate for the Chilko area was the largest on record at nearly 2.5 million fish (Figure 7). This is more than double the previous record of just over 1 million sockeye set in 1991. The 2011 sockeye escapement estimate for the Chilko was recorded at 919,254, with the 2012 run being significantly lower with less than 250,000 sockeye (Table 4).

Table 4. Summary of Sockeye escapement for the upper Chilko River and Lake, for grizzly bear sampling years 2006 – 2012.

Year	Total escapement
2006	469,504*
2007	306,707
2008	250,583
2010	2,462,975
2011	919,254
2012	246,602

******Department of Fisheries and Oceans near final escapement estimates (www.dfo-mpo.gc.ca)*

Remote camera

The remote camera recorded several photos of grizzly bears, black bears and birds at each hair snag site (Figure 8). One video clip recorded a grizzly bear stepping carefully "on" the wire rather than over it. Another video clip shows two young grizzly bears leaping over the wire. Clearly not all bears in the area are detected with the barbed wire sampling methods. Fortunately mark-recapture population modelling takes this fact into account. Unfortunately, the video file sizes are too large to include and send with this report.

Figure 7. Carcasses accumulate on the shoreline after a record sockeye run on the upper Chilko River.

Figure 8: Female and cub negotiate a wire hair snag site.

Mark-recapture analysis

Tatlayoko Valley

The number of bears detected per session varied between sessions and year with the highest number of detections in the 2nd year (Figure 9). In general, temporal variation in detections for each session was non-directional.

The Tatlayoko valley analysis was reduced to include only sites sampled in all years and without rub trees that were only sampled in years 2, 3 and 4. Rub tree detections were modeled as a separate parameter so inclusion or exclusion should have not affected estimates greatly, however inclusion of extra sites in later years may have affected population and demographic estimates.

Model averaged population size estimates from the full and reduced data sets were similar except for larger estimates for males in 2007 with full data set compared to the reduced data set. The reduced data set suggested a slight increasing trend in estimates whereas the full data set suggested an increase then decrease in males and variable estimates for females (Figure 10). The estimates in Figure 10 are also given in Table 5. Precision of estimates was marginal for sex-specific estimates but improved for pooled estimates.

Inspection of demographic parameters revealed that estimates from the full data set suggested population was decreasing each year whereas the reduced data set suggested a slight increase (λ greater than 1). However, these differences should be interpreted in terms of estimate precision, and population estimates, in which case the difference is negligible (Figure 11 and Table 6). More interesting is the relative contribution of apparent survival (deaths and emigration) and additions (births and immigrants) to trend which suggests lower apparent survival but reasonably higher rates of addition resulted in the positive lambda estimate (Figure 11 and Table 6).

Of the two data sets, the reduced data set provides a more reliable trend estimate since it will not be affected by changes in study area size, and used more consistent sampling methods. Of notable interest in the inclusion of rub trees for the full data set in later years given that this may have also affected trend estimates if the rub trees were targeting a different segment of the population than hair snags.

More details on Mark-recapture analysis for the Tatlayoko Valley can be found in Appendix 2.

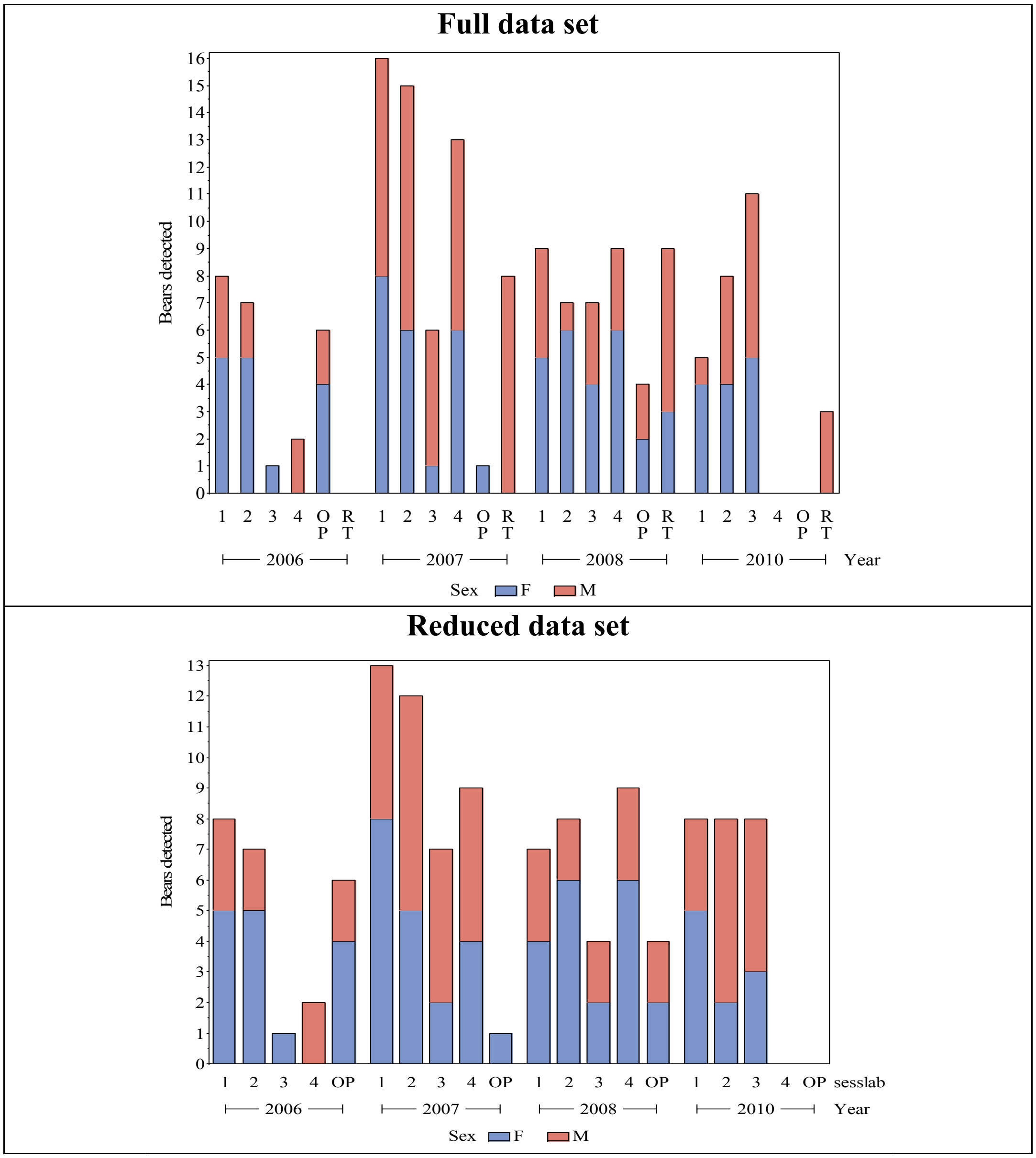


Figure 9: Summary bears detected with the full and reduced data sets from Tatlayoko Valley

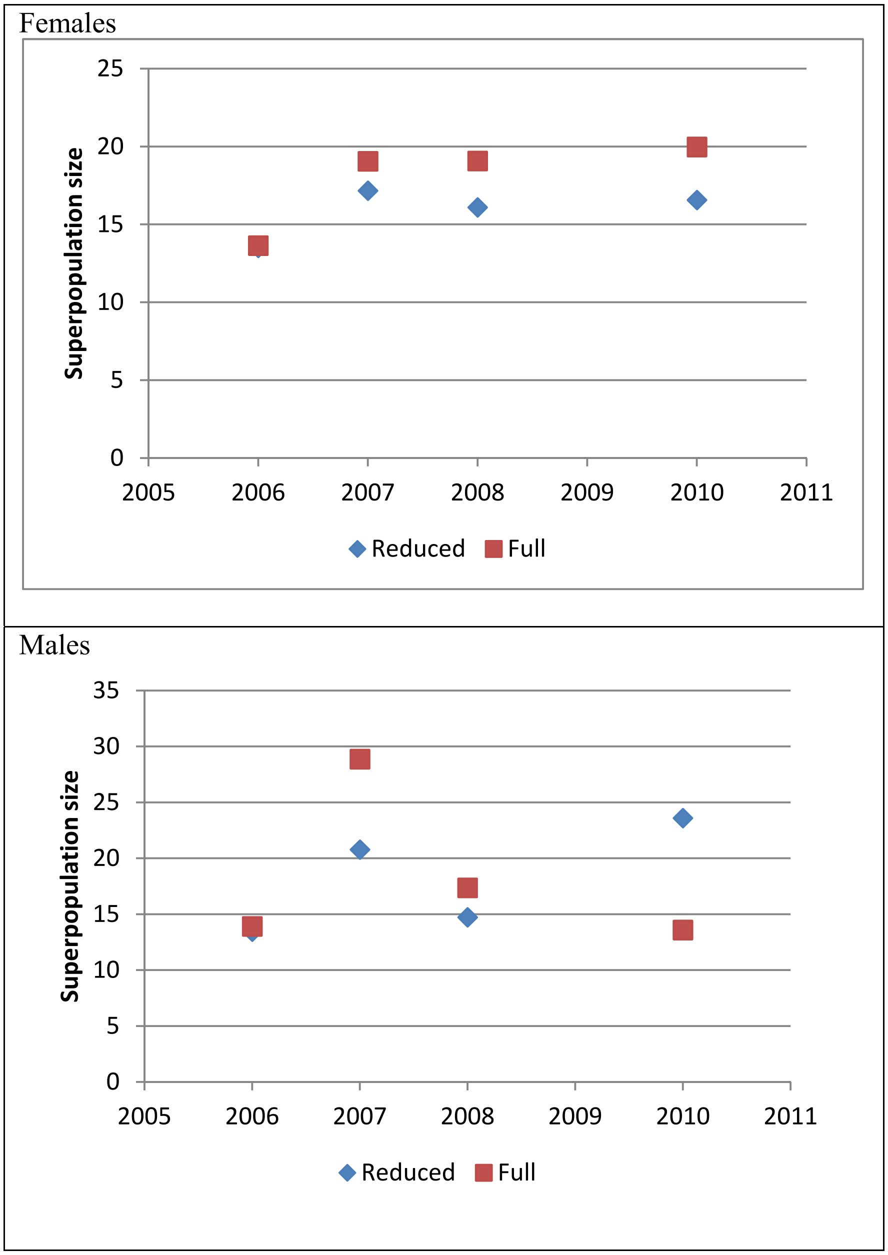


Figure 10: Comparison of full and reduced data set population estimates for the Tatlayoko grid.

Table 2: Model averaged population estimates for the Tatlayoko Valley grid from the full and reduced data set

sex	year	M_{t+1}	Estimate	SE	LCI	UCI	CV
Full data set							
2006	Male	8	14	4.28	10	29	30.7%
2007	Male	20	29	4.80	23	44	16.6%
2008	Male	12	17	3.41	14	29	19.6%
2010	Male	8	14	3.61	10	26	26.6%
2006	Female	9	14	3.56	10	27	26.1%
2007	Female	13	19	4.09	15	33	21.4%
2008	Female	13	19	4.08	15	33	21.4%
2010	Female	11	20	5.55	14	38	27.8%
2006	Pooled	17	28	6.95	20	51	25.2%
2007	Pooled	33	48	6.89	39	68	14.4%
2008	Pooled	25	36	6.13	29	56	16.8%
2010	Pooled	19	34	8.81	24	62	26.2%
Reduced data set							
2006	Male	8	13	4.53	9	31	33.7%
2007	Male	13	21	5.25	15	39	25.3%
2008	Male	9	15	4.21	11	30	28.6%
2010	Male	11	24	8.43	15	53	35.7%
2006	Female	9	14	3.91	10	29	29.0%
2007	Female	12	17	3.53	14	29	20.6%
2008	Female	11	16	3.66	12	29	22.8%
2010	Female	9	17	5.31	11	35	32.1%
2006	Pooled	17	27	6.95	20	51	25.8%
2007	Pooled	25	38	6.89	30	59	18.2%
2008	Pooled	20	31	6.13	24	50	19.9%
2010	Pooled	20	40	8.81	29	66	21.9%

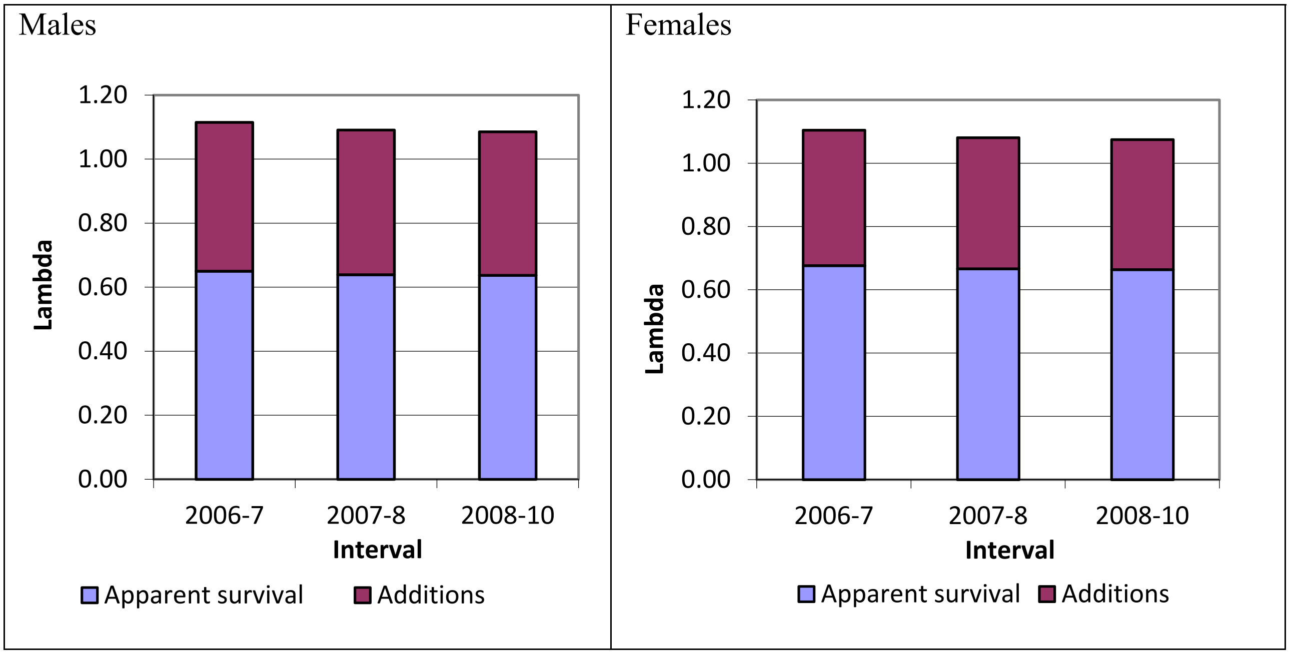


Figure 11: Model averaged estimates of apparent survival and rates of addition (added to equal lambda) for the reduced Tatlayoko data set.

Chilko River

The number of bears identified per session each year varied with increasing (2006, 2007, and 2010), decreasing (2008) and peaking (2011 and 2012) trends in the number of bear captures. Rub tree captures were low in most years.

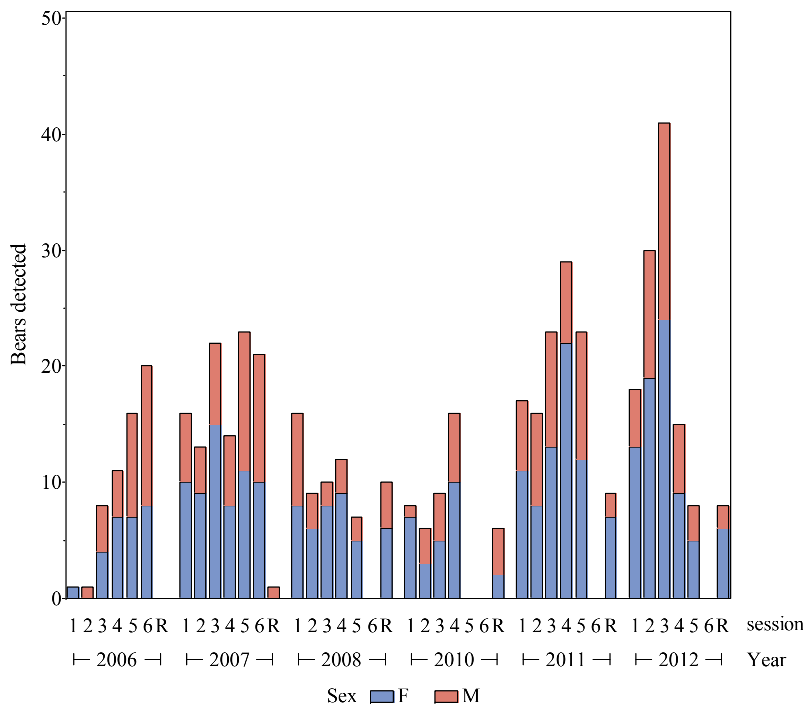


Figure 12: Summary of the number of bears detected on the Chilko for each year, season, and session. Numbers indicate hair snag sessions and R indicates rub tree detections (pooled across sessions). Rub tree sampling was not conducted in 2006.

The first step in the Mark-recapture analysis was to attempt to build a satisfactory base model to explain the *within* year variation in detection rates for bears along the Chilko River (Table 6). A model that considered linear or quadratic trends in detection rates (model 9) was more supported than models that used unique detection rates for each session. Next, sex-specific and temporal variation was considered in apparent survival (deaths and emigration) and additions (births and immigrants). A model with year specific variation in additions (f) (model 4) was more supported than a model with year-specific variation in apparent survival (phi) (model 17) or year-specific variation in both apparent survival and additions (model 7). Furthermore, all models were more supported then models with no year specific variation (model 10) or only sex-specific variation (model 15).

Table 6: Model selection for Chilko River analysis. Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (Δ_i), Akaike weights (w_i), number of parameters (*K*) and model deviance are presented. Deadsalmon are covariates from dead sockeye counts , escapement is mean annual escapement estimate, meandead; mean dead salmon count, maxdead-peak dead salmon count. HS denotes hair-snag detection probability model, RT denotes rub tree model. A T denotes a linear trend in detection probabilities whereas T^2 denotes a quadratic trend.

No	Model	AICc	ΔAICc	wi	K	Deviance
1	Phi(sex+escape) f(sex+year) RT(.) HS(sex*yr*session(T), T^2(2012))	3302.9	0.00	0.300	24	3252.4
2	Phi(sex+meandead) f(sex+year) RT(.) HS(sex*yr*session(T), T^2(2012))	3303.1	0.22	0.269	24	3252.6
3	Phi(sex+maxdead) f(sex+year) RT(.) HS(sex*yr*session(T), T^2(2012))	3304.1	1.21	0.164	24	3253.6
4	Phi(sex) f(sex+year) RT(.) HS(sex*yr*session(T), T^2(2012))	3304.8	1.90	0.116	23	3256.5
5	Phi(sex) f(sex+year) RT(.) HS(sex*yr*session(T), T^2(2011&2))	3306.4	3.46	0.053	24	3255.9
6	Phi(sex) f() RT(.) HS(sex*yr*session(T), T^2(2012))	3308.3	5.44	0.020	18	3270.9
7	Phi(sex+year) f(sex+year) RT(.) HS(sex*yr*session(T), T^2(2012))	3308.3	5.44	0.020	27	3251.2
8	Phi(sex+escape) f(sex+meanescape) RT(.) HS(sex*yr*session(T), T^2(2012))	3309.3	6.41	0.012	21	3265.4
9	Phi(sex) f(sex) RT(.) HS(sex*yr*session(T), T^2(2012))	3309.6	6.75	0.010	19	3270.1
10	Phi(.) f(.) RT(.) HS(sex*yr*session(T), T^2(2012))	3310.1	7.19	0.008	17	3274.8
11	Phi(sex) f(sex+escapement) RT(.) HS(sex*yr*session(T), T^2(2012))	3310.5	7.60	0.007	20	3268.8
12	Phi(sex) f(sex+meandead) RT(.) HS(sex*yr*session(T), T^2(2012))	3310.7	7.85	0.006	20	3269.0
13	Phi(sex) f(sex+maxdead) RT(.) HS(sex*yr*session(T), T^2(2012))	3310.8	7.95	0.006	20	3269.1
14	Phi(sex) f(sex) RT(.) HS(sex*yr*session(T), T^2(2011&2))	3311.2	8.29	0.005	20	3269.4
15	Phi(sex) f(sex) RT(sex) HS(sex*yr*session(T), T^2(2012))	3311.3	8.43	0.004	20	3269.6
16	Phi(sex) f(sex) RT(sex) HS(sex*yr*session(T), T^2(2012))	3311.3	8.46	0.004	19	3271.8
17	Phi() f() RT(.) HS(sex*yr*session(T), T^2(2011&2))	3311.6	8.71	0.004	18	3274.2
18	Phi(sex+year) f(sex) RT(.) HS(sex*yr*session(T), T^2(2011&2))	3315.9	13.03	0.000	24	3265.4
19	Phi(sex) f(sex+year) RT(.) HS(sex*yr*session(T), T^2(2012)+deadsalmon)	3329.5	26.62	0.000	23	3281.2
20	Phi(sex) f(sex+year) RT(.) HS((sex*yr)+deadsalmon)	3365.3	62.40	0.000	17	3330.0
21	Phi(sex*yr) f(sex*yr) RT(yr) HS (sex*yr*session)	3384.7	81.82	0.000	92	3159.2

The effect of salmon covariates (availability) to explain *across* year variation in detection rates was then considered. The salmon covariates are all correlated however given that they were slightly different we chose to try all three rather than choose one. Covariates were assigned for the latter year of the interval since it was most likely that this year would affect bear attraction to the river. For example, for the 2006 to 2007 interval, escapement for 2007 was used to model temporal variation in apparent survival which basically tests the hypothesis that bears were more likely to return and stay on the river if salmon escapement was high. In addition, salmon covariates tested whether new bears were more likely to appear during years of higher salmon escapement. Of models considered (Table 6), models with apparent survival varying as a function of escapement (model 1), mean dead salmon (model 2) and max dead salmon (model 3) were more supported than similar models that tested associations with additions (models 11-13). All the salmon covariate models for apparent survival (models 1-3) were supported as well as models with constant apparent survival were supported as indicated by ΔAICc of less than 2.

The model selection suggests that salmon escapement (as indicated by the various indicators) influence population trend by making it more likely that bears will show up again from the previous year. A plot of the relationship between escapement and apparent survival reveals that escapement increases apparent survival of bears. In other words, bears are more likely to return to the river during years of high escapement (Figure 13).

Estimates of apparent survival and additions add up to equal lambda (year to year trend). First, trend is determined by how many bears from the past year show up again (apparent survival: deaths and emigration) and how many new bears arrive (additions: births and immigrants). Changes in either one of these will cause the population to go up or down. The bar charts (Figure 14) show how apparent survival and additions add up to trend (lambda). If lambda >1 then the population increases, is 1 it is stable, and if <1 it decreases. This relationship is shown in Figure 14 which suggests that variation in additions drives changes in trend more than apparent survival. Apparent survival was highest for the 2008-10 interval which was associated with high escapement in 2010. Super-population estimates for males and females increased (especially for males) over the course of the study. Coefficients of variation were variable for both sexes with higher precision for the pooled sex estimates (Table 8). A plot of the estimates for males and females reveals a general increasing trend especially in 2011 which is also reflected in higher rates of addition for this year (Figure 15).

Table 7: Estimates of apparent survival (θ), rates of addition (f) and resulting λ for the Chilko River.

parm	sex	Year interval	Estimate	SE	LCI	UCI
Phi	M	06 to 07	0.75	0.07	0.60	0.85
Phi	M	07 to 08	0.72	0.08	0.54	0.85
Phi	M	08 to 10	0.89	0.07	0.65	0.97
Phi	M	10 to 11	0.80	0.05	0.68	0.88
Phi	M	11 to 12	0.72	0.08	0.55	0.85
Phi	F	06 to 07	0.86	0.05	0.75	0.93
Phi	F	07 to 08	0.84	0.06	0.70	0.93
Phi	F	08 to 10	0.94	0.04	0.79	0.99
Phi	F	10 to 11	0.89	0.03	0.81	0.94
Phi	F	11 to 12	0.84	0.06	0.70	0.93
f	M	06 to 07	0.51	0.28	0.11	0.90
f	M	07 to 08	0.53	0.19	0.20	0.83
f	M	08 to 10	0.09	0.09	0.01	0.44
f	M	10 to 11	0.73	0.29	0.14	0.98
f	M	11 to 12	0.07	0.11	0.00	0.67
f	F	06 to 07	0.44	0.25	0.10	0.85
f	F	07 to 08	0.45	0.16	0.18	0.75
f	F	08 to 10	0.08	0.07	0.01	0.39
f	F	10 to 11	0.63	0.23	0.20	0.92
f	F	11 to 12	0.06	0.10	0.00	0.63
lambda	M	06 to 07	1.26	0.28	0.71	1.81
lambda	M	07 to 08	1.25	0.20	0.86	1.64
lambda	M	08 to 10	0.98	0.10	0.00	1.00
lambda	M	10 to 11	1.53	0.28	0.98	2.08
lambda	M	11 to 12	0.80	0.14	0.41	0.96
lambda	F	06 to 07	1.30	0.25	0.81	1.79
lambda	F	07 to 08	1.30	0.17	0.97	1.62
lambda	F	08 to 10	1.02	0.08	0.87	1.17
lambda	F	10 to 11	1.52	0.23	1.07	1.97
lambda	F	11 to 12	0.91	0.11	0.40	0.99

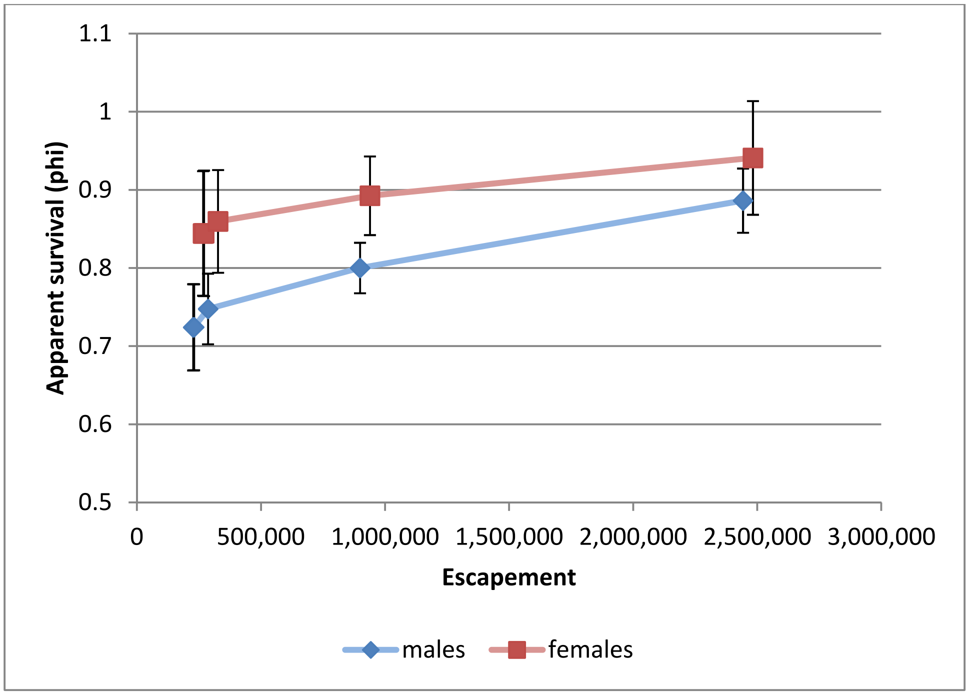
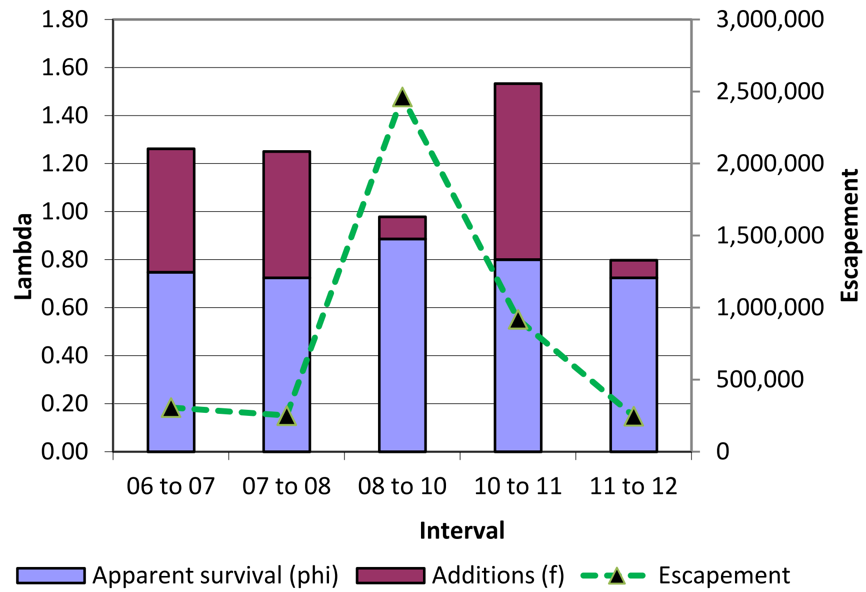


Figure 13: Estimated relationship between salmon escapement and apparent survival. Error bars are 1 standard error. Points are staggered around mean escapement value.

Males



Females

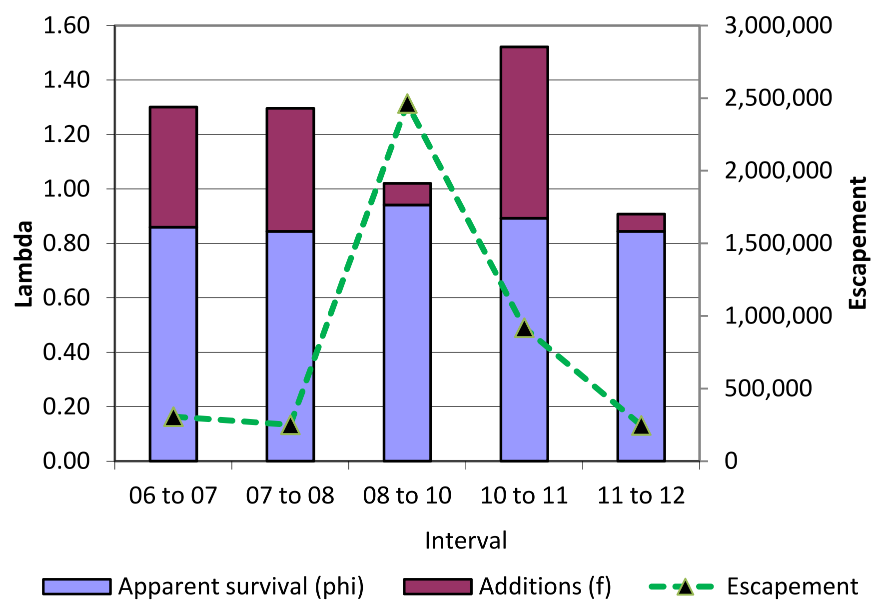


Figure 14: Trends in apparent survival, additions and lambda as related to escapement levels for the latter year of each interval.

Table 8: Population estimates for Chilko River. M_{t+1} is the number of unique bears detected each year.

Sex	Year	M_{t+1}	N-hat	SE	CI		CV
M	2006	20	32	6.4	25	52	20.0%
	2007	26	33	3.5	29	44	10.7%
	2008	17	38	8.3	27	61	22.1%
	2010	16	36	9.6	24	65	26.6%
	2011	34	71	11.7	54	102	16.5%
	2012	30	52	7.4	42	72	14.2%
F	2006	21	34	6.7	26	55	20.0%
	2007	39	49	4.4	44	62	8.9%
	2008	34	75	13.0	57	109	17.3%
	2010	23	58	12.9	40	94	22.3%
	2011	46	94	14.0	73	130	15.0%
	2012	50	90	10.3	74	116	11.5%
P	2006	41	66	11.3	52	99	17.2%
	2007	65	82	6.1	74	99	7.4%
	2008	51	113	17.5	87	157	15.5%
	2010	39	94	18.1	68	142	19.3%
	2011	80	164	20.9	132	216	12.7%
	2012	80	142	14.3	120	177	10.1%

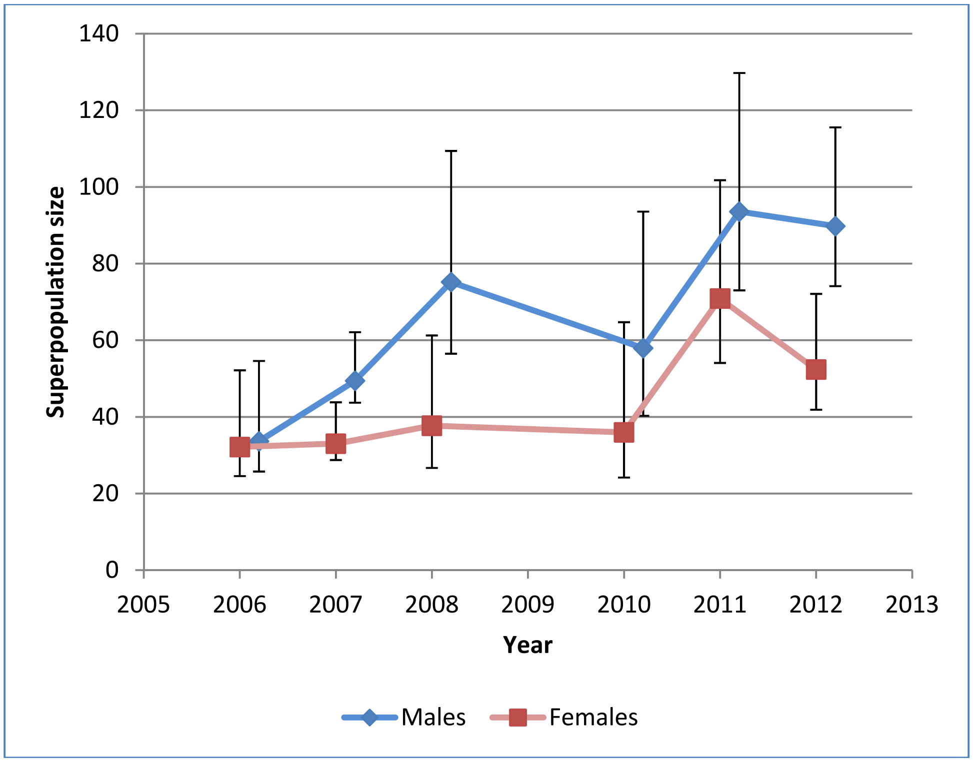


Figure 15: Super-population estimates for male and female bears on the Chilko River

Multi-strata analysis

<u>Bear movement between Tatlayoko and Chilko</u>

Summary of individuals detected each year at Chilko River, Tatlayoko Lake or both areas (Table 9) demonstrates that movements did occur between the 2 areas for both males and females.

Table 9: Summary of unique bear detections for male and female bears on the Chilko Lake and Tatlayoko sampling areas.

Year	Females			Males		
	Chilko	Tatlayoko	Both	Chilko	Tatlayoko	Both
2006	17	5	4	15	3	5
2007	33	7	6	20	14	6
2008	32	11	2	15	10	2
2010	20	8	3	14	6	2
Totals	102	31	15	64	33	15

For the multi-state analysis, a base model was developed that captured the main sources of variation for detection probabilities based on the individual analyses of the Chilko and Tatlayoko data sets. Using this base model, sex-specific and year-specific variation in movements between Chilko River and Tatlayoko were considered. Of model considered, a model with no variation in movements between areas was most supported (Table 10, Model 1). In addition, salmon availability covariates were considered for movement from the spring Tatlayoko grid to the Chilko River in the following fall. The hypothesis being tested was that bears would be most likely to be detected on the Chilko River in years of higher salmon availability. Models with associations of mean dead salmon counts (Model 3), maximum dead salmon counts (Model 4) and escapement (Model 5) were all weakly supported by the data as indicated by delta AICc values of less than 2.

A plot of model averaged estimates of movement further shows the general relationship between movement from Tatalyoko Valley to Chilko River and salmon availability (mean dead salmon count) (Figure 16). Highest movements were observed during the years of highest salmon availability in this case. Male and females displayed similar movements.

A plot of bear movement from Chilko to Tatlayoko suggests similar yearly rates with males having higher movement probabilities than females (Figure 17).

Table 10: Model selection for robust design multi-state model of movements between the sampling grids. Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (Δ_i), Akaike weights (w_i), number of parameters (*K*) and model deviance are presented.

No	Movement probabilities		Model fit				
	Tat to Chilko	Chilko to Tat	AICc	ΔAICc	wi	K	Deviance
1	constant	constant	2360.56	0.00	0.15	16	2327.28
2	constant	sex	2360.61	0.05	0.14	17	2325.16
3	dead	constant	2360.67	0.10	0.14	17	2325.22
4	maxdead	constant	2360.73	0.16	0.14	17	2325.28
5	escapement	constant	2360.77	0.21	0.13	17	2325.32
6	dead	sex	2360.80	0.23	0.13	18	2323.17
7	sex	sex	2362.77	2.21	0.05	18	2325.15
8	sex+dead	constant	2362.84	2.27	0.05	18	2325.21
9	year	constant	2364.28	3.71	0.02	19	2324.47
10	year	sex	2364.36	3.79	0.02	20	2322.35
11	year	year	2364.45	3.89	0.02	21	2320.24
12	sex+year	sex	2366.56	5.99	0.01	21	2322.35
13	sex+year	sex+year	2367.59	7.02	0.00	23	2318.93

[A] A base model S(sex) Chilko (RT(.) HS(sex+yr), Tatlayoko (Opp(.) RT(sex) HS(sex)) was used for all models

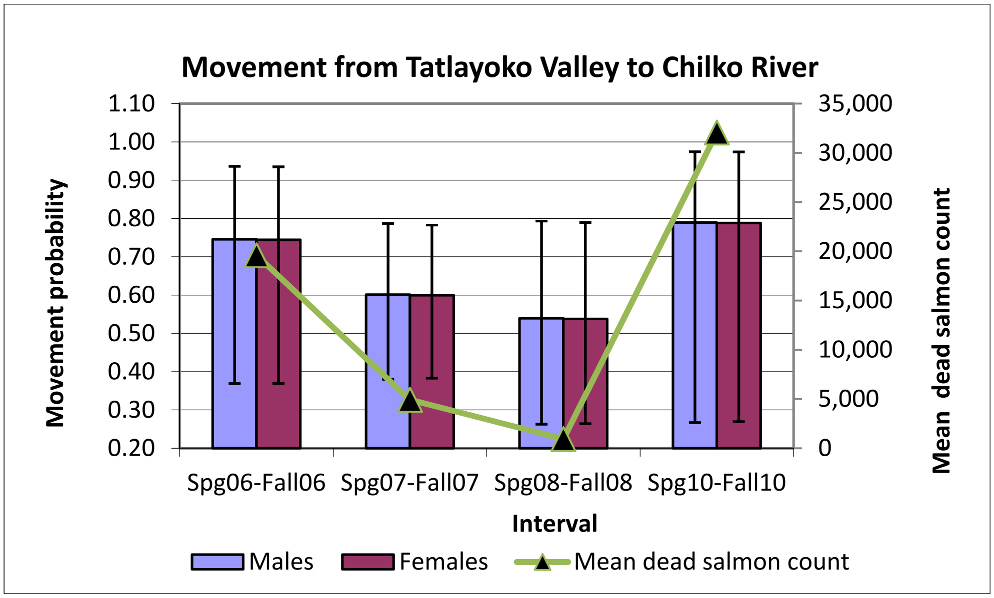


Figure 16: Estimates of yearly movement probabilities from Tatlayoko to Chilko River based on model averaged values from models in Table 10. The mean dead salmon count is shown for reference on the right axis.

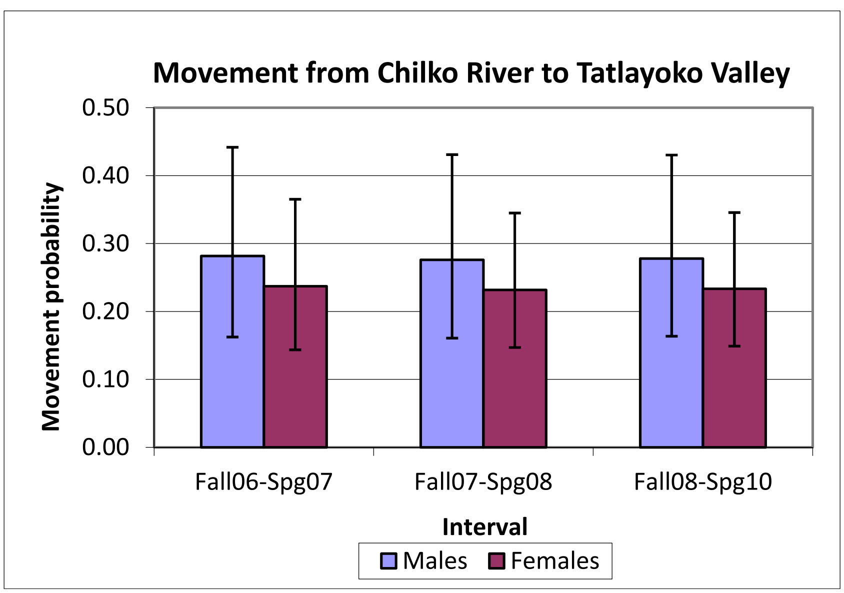


Figure 17: Estimates of yearly movement probabilities from Chilko River to Tatlayoko spring sampling grid based on model averaged values from models in Table 10.

Home range estimates

Minimum home range sizes were estimated by calculating the area of a circle with the diameter equal to the maximum distance between multiple detections of the same bear. Calculated home ranges varied in size from 7 km^2 to 1,000 km^2. Actual home range sizes are undoubtedly significantly larger. Home range estimates for the 28 bears that overlapped with the South Chilcotin and Southgate grizzly surveys ranged between 2,800 and 14,000 km^2.

Area of influence of the Chilko River salmon

The Chilko River salmon run influences an area of over 41,000 square kilometers (Figure 18). This was calculated by using the maximum detected movement distance as the radius of a circle around the upper Chilko River.

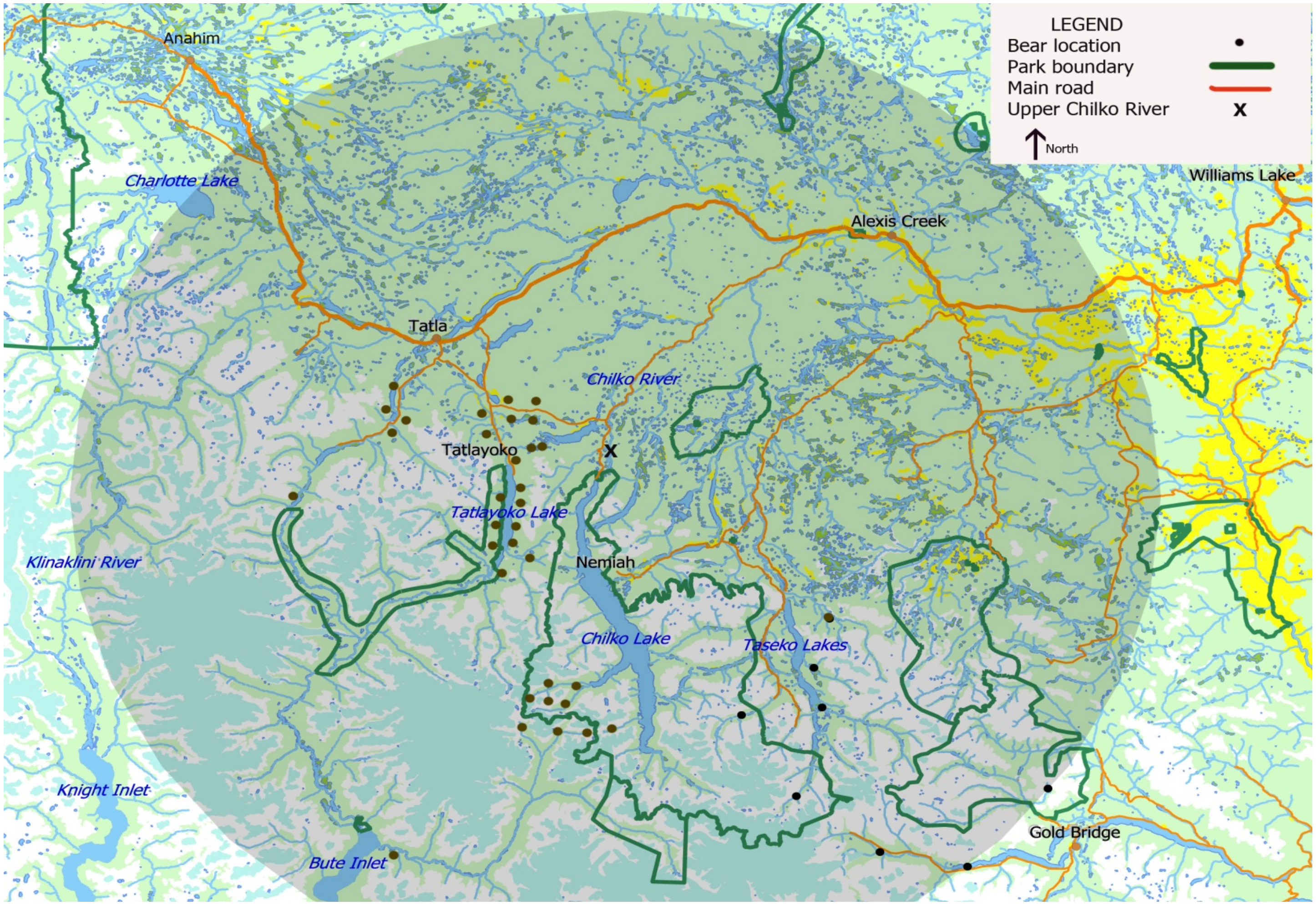


Figure 18: The circle of influence includes an area of over 41,000 square km. Calculated using the largest movement distance as the radius of a circle with the upper Chilko at the center. Map shows spring locations of grizzly bears that were also detected on the upper Chilko during the fall salmon run.

Discussion

Tatlayoko Valley spring population estimates

With mark-recapture population estimates of 36 (annual range 28 - 48) grizzly bears per year, results from this study continue to show a high density of grizzly bears in the Tatlayoko Valley during the spring months. Despite annual fluctuations in bear numbers, trend analysis suggested that the number of bears utilizing the Tatlayoko Valley in the spring months remained relatively constant. These results support the conjecture that early green-up, rich spring habitat in the Tatlayoko Valley attracts bears from a larger area much like the salmon stream in the fall.

The Tatlayoko Valley study area is located in significantly higher quality habitat than the surrounding area (low elevation, valley bottom, agricultural areas, as opposed to higher elevation, mountainous, forested, dry plateau) therefore bear density estimates from this study cannot be extrapolated for the surrounding region. These population estimates only apply to the Tatlayoko Valley and only for the spring season as grizzly bears tend to move to higher elevations for the summer season and to richer food source areas (i.e. salmon streams) for the fall season.

Our data does not give an indication of how far bears will actually travel to access this spring habitat. However, Neilson (2011) found that source areas (or areas with high grizzly bear density and low mortality risk) are often irreplaceable on the landscape, making any loss of those areas a significant impact on the overall grizzly bear population. Even without further research land use planners and local communities must consider the importance of maintaining spring habitats for bears if we are to maintain healthy grizzly bear populations in the region. It may in fact be the current behavior of the local communities that has enabled grizzly bears to use the rich, early green-up vegetation of the agricultural lands in the Tatlayoko Valley. Changes in local behavior - including, for example, the reopening of a spring grizzly bear hunt - may dramatically change how bears perceive humans and therefore how they use habitats in proximity to humans, effectively reducing accessibility to important spring habitats.

West Branch Valley grizzly bears

Sampling in the West Branch Valley was limited to one season. However with a sampling area almost half the size of the sampling area in Tatlayoko, the number of grizzly bears detected was relatively high. Spring habitat values in the West Branch Valley are similar to those in Tatlayoko with low elevation, early green-up, valley-bottom mixed with rich agricultural land.

Scar Creek grizzly bears

Unfortunately none of the 12 bears detected in the Scar Creek area of the lower Homathko were captured previously so our question as to whether bears travel between the upper and lower Homathko to access salmon remains unanswered.

Chilko River fall population estimates

The mark-recapture estimates for the number of grizzly bears along the upper Chilko River varied each fall with an estimated average of 110 (annual range 66 – 164) bears each year. Population models indicated bear numbers were related to salmon escapement, and showed more bears returning after seasons with higher salmon availability. Population models indicated a general increasing trend, especially in 2011, which correlated with higher bear return after a season with record salmon escapement.

If grizzly bear populations are reliant on salmon, then it would be expected that the number of grizzly bears found along salmon streams would be associated with salmon availability levels. Hilderbrand et al. (1999) states "We conclude that the availability of meat, particularly salmon, greatly influences habitat quality for brown bears at the individual and population level". It is important to note, however, that a population may appear to be fluctuating, when it is really just responding to spatial or temporal shifts in resources, not necessarily changing the absolute numbers of bears.

A DNA study in the Owikeno area of BC also found significant fluctuations in grizzly bear numbers using salmon streams that correlated with salmon availability. DNA mark-recapture estimates from 1998-2002 showed there were 43 (annual range 3-26) bears using the Chuckwalla/ Ambach area, 52 (4-28) in the Neechanz/Genesee area, and 28 (0 – 16) bears in the Washwash/Inziana area (Boulanger et. al 2004).

The Brooks River, in Katmai National Park, Alaska, has an average annual salmon escapement of 1.8 million fish (1989 to 2008) and is quoted as being "one of the greatest seasonal concentrations of brown bears anywhere on earth" (National Park Service www.nps.gov). Between 2004 and 2008, a total of 53 – 80 individual grizzly bears were identified on the river during the summer spawn and 45 – 59 bears in the fall, with "the time of year along with salmon densities and spawning activity dictating when, where and how bears feed along the river".

Few rivers in the world compare with the upper Chilko River as a source of salmon for bears.

Fluctuations in salmon numbers

Salmon escapement on the Chilko often varies wildly from one year to the next. For example, 2010 was a record breaking sockeye salmon run in the Fraser River that sent the upper Chilko over 2.5 million fish – 1.5 million more than the previous record on file. Locals were calling it a one hundred year run. Compare this with around 250,000 sockeye that spawned in 2012 and we get an idea of how different a year or two can be in terms of salmon availability for bears in the area. In October 2012 fish were almost non-existent along the river banks they were being eaten up so quickly. Even the Department of Fisheries crew had to find fish mid- river and pull them off the bottom to collect their annual samples, whereas in October 2010 there was a carpet of carcasses along the shorelines and no place to step without putting your boot on a slippery fish.

In 2012, grizzly bears along the Chilko appeared to be more visible than usual and more active during the day, particularly family groups of females and cubs. This is likely a result of the reduced availability of fish and the desire to avoid large male bears who were probably fishing during times of reduced human activity (i.e. at night). A study in southeastern Alaska concluded that social dominance was much more important in determining intake rates among bears than salmon densities. Dominant bears visited the stream more often and foraged for longer periods than subdominant bears. They found that subdominant bears were more vigilant, used a smaller fraction of each stream, and carried salmon much farther into the forest prior to consumption, presumably to minimize interactions with other bears. This study concluded that social dominance may play an important role in regulating reproductive success when salmon densities are low and may have important implications for managers in bear-viewing areas (Gende and Quinn 2004).

Human activity can significantly affect bear access to salmon. A study comparing grizzly bear temporal and spatial activity in three coastal areas of BC found that during periods when bears were fishing for salmon, grizzly bears were more active during the night in the area of high human use than in the area of low human use. They also found that sub-adult (sub-dominant) grizzly bears were detected more frequently in the area of high human use and they tended to be more active during the day (Machutchon et al. 1998).

With increasing human activity along the upper Chilko during the salmon season, in particular with the rapid increase in bear viewing activity in recent years, the implementation of a human management plan (human activity levels, timing and protocols) during the salmon run may be essential to maintain adequate access to salmon for bears and to ensure low levels of human/bear conflicts in the area (BC Parks 2011).

Bear movement to the upper Chilko

Forty-two (61%) of the 69 total bears in Tatlayoko were also detected along the Chilko River at least one of the six sampling years. Multi-strata analysis of movement probability (the probability that a bear detected on one grid would be detected on the other grid during the next session) suggested high movement rates from the Tatlayoko Valley study area to Chilko. Male movement rates were higher than female movement rates. Interestingly, multi-strata models consistently detected movement based on salmon availability.

Twenty-eight (17 males, 11 females) detected in the upper Homathko/ Chilko were also detected in grizzly bear DNA projects to the south of our study area. Twelve bears were detected by a grizzly bear survey in the South Chilcotin. Two males were located near Gold Bridge, BC - over 115 km from their fall locations on the upper Chilko River and one female travelled from southeast of Taseko Lakes approximately 90 km away. Sixteen bears were detected in the Southgate River drainage near the south end of Chilko Lake. Although most of these were located near the headwaters of the Southgate River, one male bear was located where the Southgate River joins Bute Inlet. Interestingly, this bear was located on the coastal inlet in the spring and along the Chilko in the fall which suggests that a "coastal" bear travelled over 100 km to the interior for salmon. Perhaps *coastal salmon availability* is also an important variable in determining the annual number of grizzly bears utilizing the Chilko River during the fall months. If this is true, the area of influence the Chilko salmon have on surrounding grizzly bear populations is more significant than previously thought.

Area of influence

The long distance movements to get to the river, the high movement rates from Tatlayoko to Chilko, and the high number of grizzly bears detected along the river during the salmon run are strong indicators of how unequivocally important the upper Chilko salmon are for grizzly bears in the West/ Central Chilcotin. In fact, the Chilko River salmon run influences an area that reaches over 41,000 square km (calculated by using the maximum detected movement distance as the radius of a circle around the upper Chilko River), which is an area over 4 times the size of Banff, Yoho and Kootenay National Parks combined (9,360 km^2) and over 4.5 times the size of Yellowstone National Park (8,983 km^2).

Conservation and management implications

Despite the small size of the sampling areas for this project, and the wide ranging habits of grizzly bears, the results from this research have provided valuable information for understanding grizzly bear ecology in the West/Central Chilcotin.

Grizzly bears are often used as a focal species for conservation planning because of their large area requirements, and their slow life-history traits - which make them sensitive to overkill (Nielson 2011). Maintenance of areas large enough to satisfy the needs and long term persistence of grizzly bears is thought to also promote umbrella effects to other species not directly affected by grizzlies simply because of the scale of landscapes needed to maintain viable bear populations. Such landscapes also need to have low human footprints, since grizzlies are vulnerable to population declines most often associated with human activity. Even within protected areas populations of grizzlies may not be secure where human activity is prevalent.

With its large expanses of wilderness, rich habitat zones, and small human population, the West/ Central Chilcotin is likely an area of fundamental importance for the future of grizzly bears.

Maintenance of valuable spring and fall habitats within the larger landscape of the West/ Central Chilcotin will go a long way towards maintaining current healthy grizzly bear populations in the region. Neilson (2011) found that "protection of grizzly bear source habitats does provide a reasonable umbrella effect or shortcut for protection of other important conservation features in grizzly bear range", and that source areas (or areas with high grizzly bear density and low mortality risk) are often irreplaceable on the landscape, making any loss of those areas a significant impact on the overall grizzly bear population.

The future of grizzly bears depends on the quality of their habitat, the number of people where they live, and also the *behavior of these people*. Re-opening the grizzly bear hunt in region, for example, may have significant impacts on how bears perceive humans and therefore negatively affect how they are able to utilize important habitats in proximity to humans. Increases in human activities such as bear viewing on the Chilko can also have negative impacts on bear behavior (BC Parks 2011). Habituation as a result of constant human presence often results in bear mortality. Proper management of human behavior towards grizzly bears in the region is essential and will require monitoring and management as human activity increases and changes over time.

Future research

The results from this research have provided valuable information for understanding grizzly bear ecology in the West/Central Chilcotin. While this study has begun to answer some important questions, such as estimating how many grizzly bears come to feed on the upper Chilko River salmon each year, it also creates more. For example:

- How big of an area is actually influenced by the availability of these salmon?
- Where are bears feeding in the fall if they are not travelling to access salmon?
- What proportion of the population, if any, migrates to the nearby coast for salmon? Conversely, what proportion of the coastal population of bears migrates to the interior for salmon? How does coastal salmon escapement influence bear movement to Chilko?
- The Tatlayoko and West Branch Valleys are acting as a spring “attractant” much in the way that the Chilko River attracts bears in the fall. Rich spring vegetation in the valley bottom draws bears from a larger area until green-up occurs at other elevations throughout the region. How far do bears travel to access this spring habitat?
- What are some of the important migration corridors used to access these high quality areas?
- Where are other important spring and summer habitats located throughout the region?
- Maintaining access to salmon for bears is of paramount importance. What are the trends and levels of human use and activity along the upper Chilko? What is an appropriate level of bear viewing activity and what are its impacts? What other sort of human management policies need to be established to protect the salmon resource for bears?

Grizzly bears in the West/Central Chilcotin appear to be healthy, abundant, and unique given that they have access to nutrient rich salmon in the fall months and that they live in a relatively undisturbed environment. As important habitats and critical food sources change with human pressures and global warming, we must ensure their long-term conservation. Further study is essential to continue monitoring the effects of changes to their environment and to increase our understanding of grizzly bear ecology in this region.

Acknowledgements

This project would not have been possible without valuable assistance from many people along the way. Many thanks go to the following people and organizations. Thank you to Wendy Vanasselt, Carol Orr, Dave Secord and the Wilburforce Foundation for generous project support and funding. Additional funding was also provided by the Canadian Wildlife Federation. Continued coordination and support came from Andrew Harcombe and staff from the Nature Conservancy of Canada in Victoria. Valuable support and advice came from Ric Careless and BC Spaces for Nature. Assistance in all aspects of data collection and project logistics came from Roderick de Leeuw and Fritz Mueller. Assistance with site selection and use of their private lands came from Alec Bracewell, Lars Satre, Walt and Carol Foster, Dave and Lori King, Mike and Audi King, and the Butler family. Peter Shaughnessy with NCC provided timely communications within the local community. Chief Marilyn Baptiste and Nancy McLean with the Xeni Gwet'in established research protocols and supported the scientific research on grizzly bears within Xeni Gwet'in territory. Chief Richard Harry and the Homalco (Xwemalhkwo) band supported research along the lower Homathko. Chuck and Sharon from Homathko Camp provided shelter, food and advice. White Saddle Air provided transportation to Bute Inlet and the Scar Creek area. Felix and Jasmin Schellenberg of the Chilcotin Abattoir provided the blood for the liquid lure and Pacific Bioproducts in Vancouver provided the fish. DNA analysis was conducted by Dr. David Paetkau and his Wildlife Genetics lab in Nelson. John Boulanger with Integrated Ecological Research conducted all statistical analyses and gave sound advice. Clayton Apps with the South Chilcotin and Southgate grizzly bear studies shared overlapping bear locations. And thanks to Steve Ogle, Fritz Mueller, Jr. and John Marriott for kindly providing photo contributions for reports and presentations. Last, but certainly not least, thank you to the grizzly bears of the West/Central Chilcotin.

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Appendices

Appendix 1: Mark-recapture analysis

Estimates of population size can be obtained using either mark-resight or capture-recapture methods. Genetic sampling capture-recapture methods are far more reliable for estimating grizzly bear populations than census or minimum count approaches. In its simplest form, a minimum of 2 capture "sessions" are conducted, and the proportion of individuals re-captured in the second session is used to estimate the number of unmarked individuals in the population. This proportion is called a capture probability and its application in the estimation of population size can be expressed as:

$$\hat{\mathbf{N}} = M / \hat{p}$$

Where M is the number of animals detected over sampling session, $\hat{p}$ is the proportion of those animals initially captured that were then recaptured (i.e. estimate of capture probability), and $\hat{\mathbf{N}}$ is the estimate of population size. Using traditional census methods, $\hat{p}$ is assumed to equal 1. That is, the model is based on the assumption that all animals are caught; however, different sampling approaches require different estimation models. In reality, capture probability $\hat{p}$ is rarely equal to 1, and there exists a variety of models that make differing assumptions on how $\hat{p}$ varies.

The Pradel (1996) model estimates apparent survival (ϕ), recapture rate (p), rate of additions (f), and population rate of change (λ) as a derived parameter.

- Apparent survival (ϕ) is the probability that a grizzly bear stays in the population between two sampling intervals. Apparent survival includes both mortality and emigration, since in both cases the grizzly bear would no longer be available for capture in subsequent sessions.
- Recapture rate (p) is the rate of recapture of marked grizzly bears in the population.
- Rate of addition (f) is the number of new individuals in the populations at time j + 1 per individual at time j. This includes both immigration and births between two sampling years.
- Apparent survival and rate of addition can be added to obtain an estimate of λ, the population rate of change ($\lambda = \phi + f$).
- The population rate of change (λ) also relates to population size by $N_{t+1} = \lambda N_t$ where N is the population size at times t and $t + 1$.
- Population trend will either be stable (λ=1), increasing (λ>1), or decreasing (λ<1) (Boulanger et al. 2004).

Proper sampling design is critical to obtaining reliable population estimates. The three main issues in the design of projects to estimate population size are as follows (Boulanger et al. 2007):

1. Meeting the assumption of geographic and demographic closure: If closed population estimation models are used, then it is assumed that the population is closed or “no animals leave, enter, die or are born during the sampling process.” Violation of closure can cause substantial biases in estimates from most mark-recapture models. If closure violation is occurring, mark-recapture population estimates will pertain to the “super-population” of bears in the sampling grid and surrounding area during the time that sampling was conducted. For estimation of density and comparison of different areas the average number of bears on the sampling grid is most applicable.

2. Sample size: Sample size is determined by the number of animals in the sampling area, the capture probability of the population, and the number of times the population is sampled. In general, higher population capture probabilities are needed for smaller population sizes to obtain adequate estimates. The primary effect of low sample size is reduced estimate precision. In addition, if sample size is low, then not enough data will be available to determine dominant capture probability variation in the data set leading to erroneous model selection.

3. Capture probability variation: Bears probably show unequal probabilities of capture which can lead to biased population estimates. Often it is possible to test data to determine the dominant type of capture probability variation, if the above issues are met. One of the most likely forms of capture probability variation in grizzly bear data sets, however, is heterogeneity variation due to females and cubs displaying reduced capture probabilities. Unfortunately, age cannot be determined from DNA therefore this is a non-identifiable form of variation. One way to confront heterogeneity is to use multiple methods to sample the population. For example, incorporate additional DNA ”captures” of grizzly bears obtained by collecting hair from un-baited bear rub trees concurrently with baited, grid-based, hair snag sampling (Boulanger et al. 2008).

The Pradel mark-recapture model is robust to heterogeneity of capture probabilities and violation of population closure. In addition, the Pradel model allows for the exploration of population demography and environment factors that influence demography through the use of covariates (Boulanger et al. 2004).

Appendix 2: Tatlayoko mark-recapture model selection

The following tables are summaries of mark-recapture model selection and demographic parameter estimates for grizzly bear spring population estimation in the Tatlayoko Valley.

Base detection probability models that considered a behavioural response to sampling were considered given that sites were fixed which could cause trap habituation or trap attraction. For the reduced data set a model with equal detection rates was most supported (Table 11, Model 1) whereas a behavioral response model was more supported for the full data set (Full, Model 1). This presumably could be due to lower power to detect behavioural response with the reduced data set. For rub trees, a sex specific detection model was most supported for the full data set (Model 1).

In terms of demographic trends, a model with constant trends for both additions and apparent survival was most supported for the reduced data set. For the full data set, a model with unique trends for the 2006 to 7 interval for both apparent survival and additions was used to account for the effect of study are size increase on demographic parameter estimates. A similar model with constant demographic trends for apparent survival and additions was also supported.

The full data set analysis was challenging due to multiple optimal convergence points when more complex base capture probability models. This could be due to the interaction of temporal variation in detection rates with change in study area size and trap alignment between 2006 and 2007. A more optimal way to deal with change in study area size would be the use of spatially explicit mark-recapture models as discussed later. For now, John suggests mainly using the trend estimates from the reduced analysis and the population estimates from the full data set analysis.

Table 11: Model selection for Tatlayoko Valley grid with full data set and reduced data set. The "67" denotes a unique parameter for the interval of 2006-7 for the full data set to account for the effect of study area increase on demographic parameters. . Akaike Information Criteria (AIC_c), the difference in AIC_c values between the *i*th model and the model with the lowest AIC_c value (ΔAIC_i), Akaike weights (w_i), number of parameters (*K*) and model deviance are presented.

No	Model	AICc	ΔAIC	wi	K	Deviance
	Reduced HS (same sites) and opportunistic					
1	Phi(.) f(.)Op(.) HS(p(sex))	690.47	0.00	0.50	5	680.07
2	Phi() f()Op(.) HS(p(sex) c(sex))	693.20	2.73	0.13	7	678.44
3	Phi(,sex) f(sex) Op(.) HS(p(sex))	693.37	2.90	0.12	7	678.61
4	Phi(T) f(T) Op(.) HS(p(sex))	693.89	3.42	0.09	7	679.13
5	Phi(sex) f()Op(.) HS(p(+sex) c(+sex))	695.39	4.92	0.04	8	678.41
6	Phi(sex) f(sex) Op(.) HS(p(sex+sessionXyr))	695.62	5.15	0.04	21	646.67
7	Phi(sex) fsex) Op(.) HS(p(sex) c(sex))	696.55	6.08	0.02	9	677.31
8	Phi(yr.) f(yr) Op(.) HS(p(sex))	696.59	6.12	0.02	9	677.35
9	Phi) f() Op(.) HS(p(sex) c(sex))	697.70	7.23	0.01	14	666.70
10	Phi(67,) f(67,) Op(.) HS(p(sex+yr) c(sex+yr))	697.89	7.42	0.01	15	664.44
11	Phi(67) f(year) Op(.) HS(p(+sex) c(sex))	698.92	8.45	0.01	10	677.40
	Full HS, opportunistic and rub trees					
1	Phi(67) f(67) RT(sex) Op(.) HS(p(sex) c(sex))	881.56	0.00	0.73	11	857.72
2	Phi(67+sex) f(67+sex) RT(sex) Op(.) HS(p(sex) c(sex))	883.90	2.34	0.23	13	855.32
3	Phi(67) f(67) RT(.) Op(.) HS(p(sex))	888.15	6.58	0.03	8	871.16
4	Phi(67,sex) f(67,sex) RT(.) Op(.) HS(p(sex))	891.64	10.08	0.00	10	870.11
5	Phi(67,) f(67,) RT(.) Op(.) HS(p(sex+yr) c(sex+yr))	891.88	10.31	0.00	16	855.93
6	Phi(67,sex) f(67,sex) RT(.) Op(.) HS(p(sex+yr) c(yr))	893.17	11.60	0.00	17	854.70
7	Phi(67,sex) f(67,sex) RT(.) Op(.) HS(p(sex) c(sex))	893.20	11.64	0.00	12	867.01
8	Phi(sex*yr) f(sex*yr) RT(.) Op(.) HS(p(sex) c(sex))	896.67	15.11	0.00	16	860.73
9	Phi(67,sex) f(67,sex) RT(.) Op(.) HS(p(sex+sessionXyr) c(sex))	901.75	20.19	0.00	26	838.79
10	Phi(67,sex) f(67,sex) RT(.) Op(.) HS(p(sex+sessionXyr) c(sex))	904.97	23.40	0.00	28	836.08
11	Phi(sex*yr) f(sex*yr) RT(sex*year) Opp(sex*year) HS(sex*yr*session)	944.69	63.12	0.00	53	782.01

Table 12: Demographic parameters from the Pradel model analysis of the Tatlayoko Valley grid. Full and reduced data set estimates are included

Parameter	sex	year	Estimate	SE	LCI	UCI
Reduced data set						
Phi	Male	2006-7	0.65	0.11	0.43	0.82
Phi	Male	2007-8	0.64	0.10	0.43	0.81
Phi	Male	2008-10	0.64	0.10	0.43	0.81
Phi	Female	2006-7	0.68	0.10	0.46	0.84
Phi	Female	2007-8	0.67	0.10	0.46	0.82
Phi	Female	2008-10	0.66	0.10	0.45	0.82
f	Male	2006-7	0.46	0.16	0.20	0.75
f	Male	2007-8	0.45	0.12	0.24	0.68
f	Male	2008-10	0.45	0.12	0.24	0.67
f	Female	2006-7	0.43	0.16	0.17	0.73
f	Female	2007-8	0.41	0.11	0.22	0.64
f	Female	2008-10	0.41	0.11	0.22	0.63
Lambda	Male	2006-7	1.09	0.12	0.85	1.34
Lambda	Male	2007-8	1.09	0.11	0.88	1.30
Lambda	Male	2008-10	1.09	0.10	0.89	1.30
Lambda	Female	2006-7	1.08	0.12	0.84	1.32
Lambda	Female	2007-8	1.08	0.10	0.88	1.28
Lambda	Female	2008-10	1.08	0.10	0.88	1.28
Full data set						
Phi	Male	2006-7	0.82	0.15	0.53	1.12
Phi	Male	2007-8	0.65	0.09	0.48	0.83
Phi	Male	2008-10	0.66	0.09	0.48	0.83
Phi	Female	2006-7	0.85	0.13	0.59	1.11
Phi	Female	2007-8	0.70	0.09	0.52	0.88
Phi	Female	2008-10	0.70	0.09	0.52	0.88
f	Male	2006-7	0.96	0.44	0.09	1.82
f	Male	2007-8	0.18	0.07	0.05	0.32
f	Male	2008-10	0.18	0.07	0.05	0.32
f	Female	2006-7	0.94	0.44	0.09	1.80
f	Female	2007-8	0.18	0.07	0.04	0.32
f	Female	2008-10	0.18	0.07	0.04	0.32
Lambda	Male	2006-7	1.78	0.44	0.92	2.64
Lambda	Male	2007-8	0.84	0.09	0.67	1.01
Lambda	Male	2008-10	0.84	0.09	0.67	1.01
Lambda	Female	2006-7	1.79	0.43	0.95	2.64
Lambda	Female	2007-8	0.88	0.09	0.71	1.05
Lambda	Female	2008-10	0.88	0.09	0.71	1.05

Appendix 3: Background on multi-strata model to estimate movement probabilities.

A robust design multi-strata model (Hestbeck et al. 1991, Brownie et al. 1993) was used to estimate movement of bears between the Tatlayoko and Chilko River DNA areas. The multi-strata robust design model, like the Pradel model robust design, uses closed models to estimate capture probabilities and population size for a closed sampling session. The Multi-strata portion of the model then estimates apparent survival and movement probabilities (termed transition probabilities as denoted by ψ) of bears from the Tatlayoko grid to the Chilko River and from the Chilko River to the Tatlayoko river grid for the interval between sampling sessions.

One issue was that sampling on the 2 grids occurred each spring (Tatlayoko) and fall (Chilko River) rather than at the same time which is the usual sampling design used for multi-strata analysis. To accommodate this issue data was entered as sequential samples (i.e. Tatlayoko spring 2006 as yearly session 1, Chilko 2006 as session 2, etc) but then fixed multi-strata capture probabilities to be 0 to inform the model that only one of the grids was sampled during each session. For example, capture probabilities were fixed to be 0 for the Chilko area for the first session in which only Tatlayoko was sampled. Certain ψ parameters were also fixed to be 0 to account for the fact that only directional movement could be measured between sessions. For example, only movement from Tatlayoko to Chilko could be estimated between session 1 (spring Tatlayoko) and session 2 (fall Chilko).

As with the Pradel robust design, sex and year-specific variation in movement rates was tested and the effect of temporal variation in salmon availability on movement to the Chilko River each fall was considered. Survival, capture probabilities, and population size were treated as nuisance parameters for this analysis given that they were already estimated for the Pradel model. The most supported capture probability models for Tatlayoko and Chilko as determined in the Pradel model analysis were used to model capture probabilities.


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