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SR-17-01

Grizzly bear population in the Southern Lakes region 2012–2013:

Final report on population analysis

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Government of Yukon
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Contributors and Reviewers

A number of Fish and Wildlife and contract staff assisted with the experimental design, field logistics and data collection, including Ramona Maraj, Shelly Marshall, Nicole McCutchen, Peter Knamiller, Al Bear, Angela Milani, Lars Jessup, Carol Foster, Julia Ahlgren, Lloyd Freese, Matt Clarke, Tess McLeod, Ken Knutson, Aaron Koss-Young, Jane Harms, David Bakica, Dawn Barker, G. Sander, Bruce Hanbridge, Kyle Russell, Kelsey Tousignant, John Postma, Ken Reeder, Mike Martin, Delmar Washington, Raphael Roy-Jauvin, and Ken Anderson (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.

Murray Efford[1], 60 Helensburgh Road, Dunedin 9010, New Zealand. murray.efford@otago.ac.nz.
John Boulanger[2], Integrated Ecological Research, 924 Innes, Nelson, BC, V1L 5T2.
boulange@ecological.bc.ca.

Copies available from:
Government of Yukon
Fish and Wildlife Branch, V-5
Box 2703, Whitehorse, Yukon Y1A 2C6
Phone 867-667-5721
Email: environmentyukon@gov.yk.ca
Online: Yukon.ca and open.yukon.ca

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Abstract

We used spatially explicit capture–recapture methods to analyze DNA data on grizzly bears from hair snares in the Yukon Southern Lakes region in 2012 and 2013. The fitted detection model included sex differences, a learned response to lured sites, and a finite mixture to allow for otherwise unmodelled individual heterogeneity. We estimated a population of 95 bears (95% CI 76–118) with home ranges centred in the 7650 km^2 study area bounded approximately by Kusawa, Marsh and Tagish Lakes, Highway 1, and the BC border. A model without the finite mixture component gave a more conservative estimate (82 bears, 95% CI 69–97). The proportion of cubs and immature bears cannot be determined from the hair-snare data; lower detection rates of young bears may have been an important source of heterogeneity.

The sex ratio of the population was biased towards females (61%). There was no evidence for a change in population size between years. The density of grizzly bears was greater above the median elevation of 1250 m than at lower elevations (18.5 per 1000 km^2 compared to 6.2 per 1000 km^2), noting that elevations above 1600 m were sampled less intensively and human impacts are greater at lower elevation. The study area lies largely in two ecoregions: Yukon Southern Lakes (61%) and Yukon-Stikine Highlands (38%). No difference in average density was detected between these ecoregions.

The hair snare work was part of a larger Southern Lakes grizzly bear study that included tracking of collared bears. We summarised telemetry data from 2009–2014 for GPS-collared bears and incorporated telemetry in the capture–recapture estimates. This had negligible effect on population estimates because the hair-snare data were sufficient in themselves and few bears were collared at the time of hair-snare operation (8 in 2012 and 7 in 2013). Telemetry data shed light on long-distance movements in the hair snare data. Two collared bears that had been relocated in 2013 returned to near their point of capture; one of these, a female, was recorded at widely separated hair snares along the route, and appears to have been accompanied by an uncollared male detected at the same hair snares.

Contents

Introduction

We were contracted by the Government of Yukon Department of Environment to analyze data from the Southern Lakes grizzly bear study conducted by Yukon's Carnivore Biologist in 2012 and 2013. The purpose of the study was to develop bear population estimates for the region. The primary data came from hair snares operated in June and July of each year. These were supplemented by telemetry data from GPS-collared bears. Hair samples were individually identified from follicular DNA. The data were analysed by the method of spatially explicit capture–recapture for which one of us has written general software (Efford 2016). The software was extended to allow data from telemetry to be included in the analysis.

This report provides an account of the study and our analyses, drawing where necessary on text in the Yukon government request for proposals "Bear Population Estimation Analyses" July 2015.

Methods

Study area

The nominal study area[1] encompasses 7859 km^2 in the Southern Lakes Region of Yukon. Boundaries followed natural barriers to bear movement wherever possible (Fig 1). These were Kusawa Lake in the west, Marsh and Tagish Lakes in the east, the height of land between BC and Yukon to the south, and the Alaska Highway system in the north.

The study area is part of the Boreal Cordillera ecozone and made up primarily of the Yukon Southern Lakes and Yukon-Stikine Highlands ecoregions. The climate is cold and semiarid. Within major valleys the mean annual temperature is approximately –2.5°C with a summer mean of 10°C and a winter mean of –16.5°C. Lying within the rain shadow of the St. Elias Mountains, mean annual precipitation ranges 225–300 mm in the major valleys. Boreal forests are composed of open white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) intermixed with aspen (*Populus tremuloides*). South-facing slopes at low elevation are occupied by grassland communities. Subalpine elevations above 1200 m asl support open forest communities.

There are frequent recurring natural fires such that seral communities are most common. Mountain avens (*Dryas integrifolia*), dwarf shrubs, forbs, grasses, and lichens constitute the main vegetative cover in colder, more exposed alpine sections. Most of the terrain lies between 600–1500 m asl, but a few peaks are over 1800 m asl.

Land uses include hunting, trapping, and recreation. Some limited forestry and forage-based agricultural activities occur in warmer, lower valleys below 850 m asl elevation. Whitehorse, Carcross and Tagish are the major communities within the study area, but there are numerous country residential, cottages, and backcountry dwellings scattered throughout the landscape. The human population of the area is approximately 23,000. The settlements of Whitehorse and Carcross lay on the eastern edge of the study area.

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[1] This is based on the polygon shapefile provided. The area excluding lakes is about 7650 km^2.

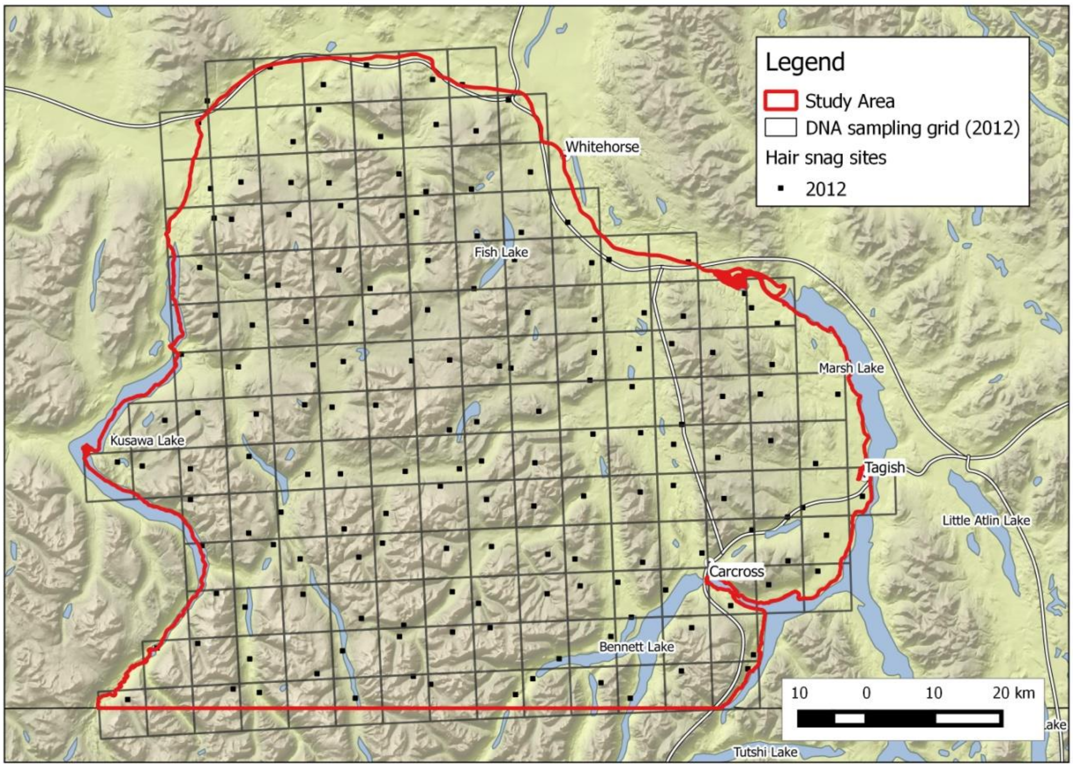

Fig. 1. The Southern Lakes grizzly bear study area 2012–2013 (solid red line) and sampling grid. Hair snare stations are shown for 2012 (n = 169). The southern boundary is the Yukon-BC border.

Field methods

Hair snares

A grid of 7-km x 7-km cells was overlaid on the study area and one lured hair-snare station was placed in each cell (Fig. 1). The selection of cells differed slightly between 2012 (169 cells) and 2013 (167 cells). Stations in adjoining cells were at least 1 km apart. Each station consisted of a single strand of double-strand barbwire, suspended in a triangular shape around trees or rebar poles. Wire height was set to and maintained at approximately 0.6 m in order to snag the hair of a bear whether it went under or over the wire. Liquid lures were chosen to attract bears to the site without providing a reward. A liquid lure consisting of animal liquid, fish fertilizer and canola oil was placed in the centre of the station and re-applied regularly. Stations were fixed within a year and moved between years (median distance 2.4 km). The data show a bias towards placement of sites at lower elevation within each grid square (Fig. 2).

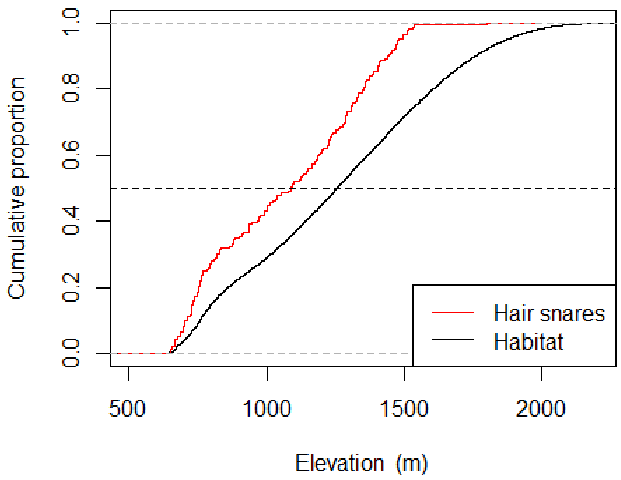

Fig. 2. Altitudinal distribution of hair snares in 2012 compared to the distribution of elevation within the study area ('Habitat'). Although 20% of the study area was above 1600 m, only one hair snare was placed above 1600 m in 2012 and three in 2013, presumably because of snow cover.

Work to establish hair snares began in early June when snow disappeared from the alpine regions of the study area. Stations were established over 7–13 June in 2012 and 13–19 June in 2013.

Hair snares were operated until the berry season ended, when bears had yet to finish shedding their summer coat (24 July to 6 August in 2012 and 17–19 July 2013). Each station was visited four times at roughly 10-day intervals, with a few exceptions noted below. Bear hair was identified and sampled at each site; a flame torch was run across the barbed wire removing excess hair and creating a clean site for the next sampling period. Approximately 80% of stations were visited by helicopter in 2012 and 72% in 2013.

Following a helicopter crash in July 2012 some samples were lost and not all stations could be visited that month. Accumulated hair was removed from some stations in August. For some stations it is unclear when hair was removed in July 2012.

GPS-collared bears

The larger Southern Lakes grizzly bear study included tracking of a total of 39 collared bears between 2009 and 2016 (18 females and 21 males). Only data from 2009-2014 were available at time of analysis as we were waiting to retrieve collars from the field (completed in fall 2016). A total of 37 bears were captured by various methods and received GPS collars over the period 2009–2014, and a further 2 bears received VHS collars. Eight bears were initially collared in 2009, and 2, 16, 4, 9, and 1 additional bear(s) were collared in 2010–2014 respectively. Collars were scheduled to drop off three years after deployment, but some bears were re-collared or killed within that time-frame. The last remaining collars were collected from the field in late summer 2016.

We chart the histories of collared bears in Appendix 1. Only 8 bears in 2012 and 7 bears in 2013 had active collars at the time of the population survey (dropping one in 2013 with only 3 fixes). GPS fixes were collected from the ARGOS satellite at a high frequency (8.1 ± 4.5 per day per bear, mean ± SD). We selected the first fix on each day to reduce redundancy. The resulting telemetry locations are plotted for each individual in Fig. 3.

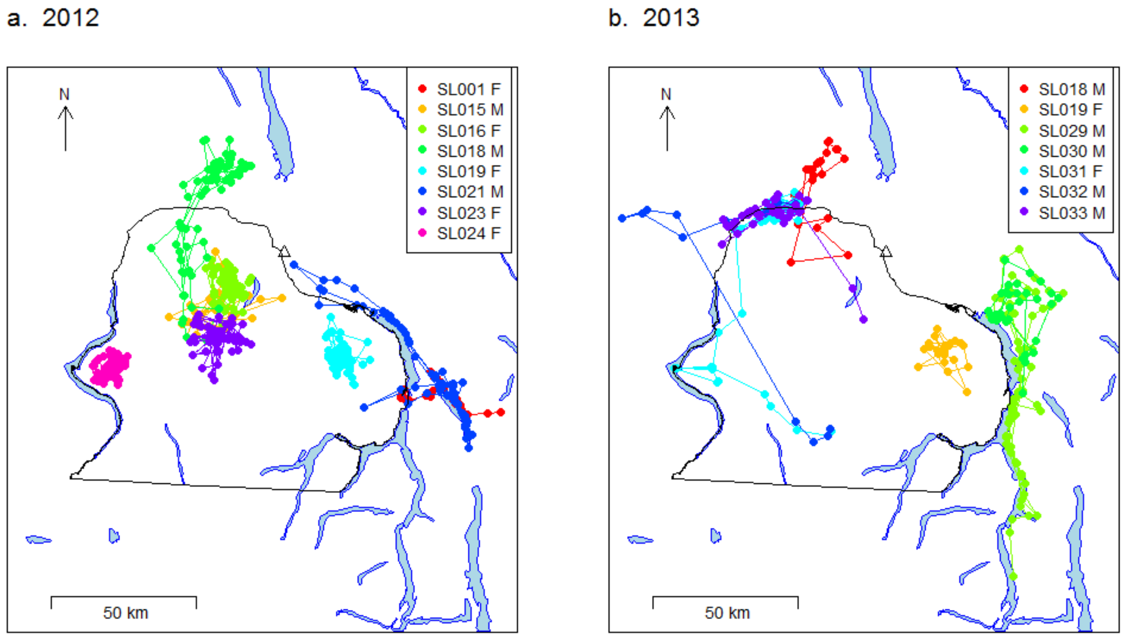

Fig. 3. Movements of individual grizzly bears with GPS collars (maximum 1 fix per day). Data from June–August. SL031, SL032 were relocated and returned to their initial location. See Appendix 2 for maps showing monthly shifts. Δ indicates location of Whitehorse.

Live–captured bears were also genotyped, allowing them to be recognised in the hair-snare dataset.

Laboratory methods

DNA analyses were performed by Wildlife Genetics International (Nelson, BC; projects G1243 and G1473). The hairs collected from a barb were treated as a single tissue sample during DNA analysis. Each sample was examined for roots under a dissecting microscope. Samples that had no roots or were obviously not a bear were discarded. DNA was extracted from the roots of up to ten hairs using QIAmp™ kits (Qiagen Inc., Ontario). A species test was performed on each sample by amplifying a section of the control region of mtDNA and comparing the results to a reference collection. All analysed grizzly bear samples were genotyped using eight microsatellite loci (one for sex determination) and assigned an individual identity. Error checking was performed on all samples (Paetkau 2003) and it is believed that the final dataset contained very few if any misidentifications.

Analysis methods

We used the Yukon Albers projection for all spatial analyses (datum NAD83; ESPG 3578).

Spatially explicit capture–recapture (SECR)

Spatially explicit capture–recapture (also called spatial capture–recapture) is a method for estimating the absolute density of a free-ranging animal population from samples of identified individuals detected at known points. A statistical model is fitted to the observations to remove potential bias when some individuals escape detection and the population lacks a natural boundary. The statistical model includes sub-models for the spatial distribution of animals (strictly, a spatial point process for their activity centres) and for the probability of detecting an animal at a point, given the distance from that point to its activity centre. The sub-models are an idealised representation of the actual distribution of animals and the actual detection process (Fig. 4).

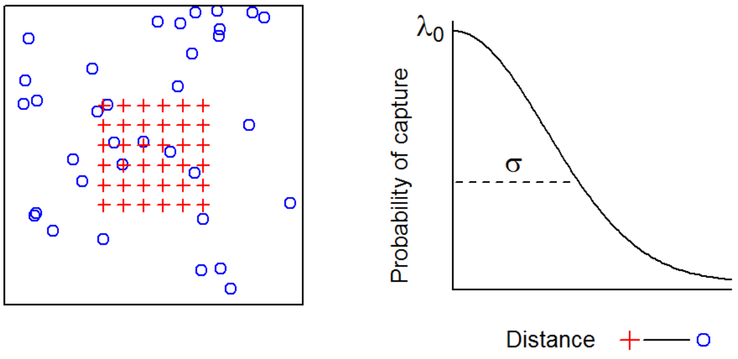

Fig. 4. Spatially explicit capture–recapture. The animal population is viewed as a scatter of animal activity centres in 2 dimensions (left, blue circle; parameter D density). The probability of detection at a fixed detector (red cross) is related to the distance between the activity centre and detector (right; parameters λ_0 intercept and σ spatial scale).

SECR models may be fitted by numerically maximising the likelihood (Borchers and Efford 2008, Efford et al. 2009) or by Markov chain Monte Carlo (MCMC) sampling in a Bayesian framework (Royle and Young 2008, Royle et al 2014). The maximum likelihood approach is used in the Windows application ‘Density’ and the R package ‘secr’, whereas the Bayesian approach may use software such as WinBUGS or JAGS or custom-written MCMC samplers. When uninformative priors are used in the Bayesian analysis it generally produces very similar estimates to the maximum likelihood method. The Bayesian method is preferred for variant models not available in standard software, which may be easily coded in BUGS or JAGS, but it is slower and less standardised. For that reason we rely here on maximum likelihood.

Application of SECR to data from Southern Lakes hair-snares

SECR is a flexible set of methods rather than a single method, and there are decisions to be made when applying it to a particular dataset. We consider these under three headings: the spatial configuration of the bear population, the choice of detection model, and models for spatial and temporal variation in bear density. Analyses were performed with version 2.10.4 of the R package ‘secr’ (Efford 2016). Annotated code is provided in Appendix 4.

1. Spatial configuration of bear population exposed to hair snares

The telemetry data show that bears sometimes crossed the nominal boundary of the study area. Thus some bears detected at hair snares may have been centred outside the nominal study area, and it is necessary to allow for these in the model. The mechanism for this in ‘secr’ is the ‘habitat mask’ that encompasses both the study area and any adjoining habitat from which resident bears may have accessed snares[2]. We used a 50-km buffer to define the habitat mask. The mask was represented as a large number of 2-km x 2-km cells for computational convenience. Cells centred in water were considered non-habitat and dropped from the mask.

The study was designed to take advantage of natural barriers. Telemetry data support the effectiveness of Kusawa, Marsh and Tagish lakes as barriers (movements of SL021, SL024, SL029, SL030 and SL031 appear to have been constrained)[3]. To allow for the constraint on travel imposed by the boundary lakes, we computed distances for the distance-detection model (Fig. 4) as non-Euclidean shortest 'dry-path' distances, avoiding any water crossing of more than 500 m (see Efford 2015a). This distance metric was also used to shrink the extent of the habitat mask: cells were discarded if all the dry-path distances from their centre to hair snares exceeded 50 km. The resulting habitat mask comprised 7233 2-km x 2-km cells (Fig. 5).

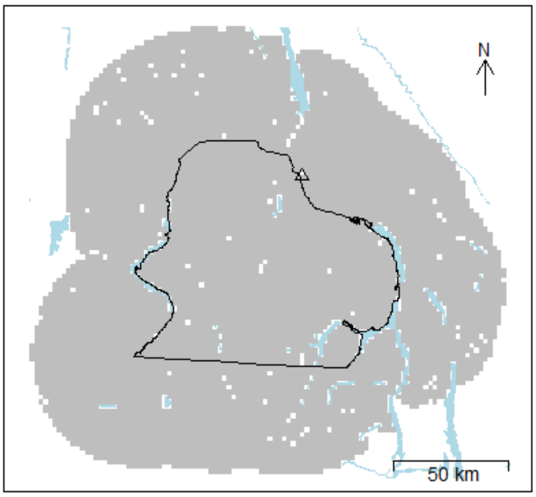

Fig. 5. Habitat mask for SECR model of grizzly bear detections in Southern Lakes study area (black outline).

2. Choice of detection model

We found it difficult to fit some models with the usual half-normal detection function, and asymptotic variance calculations failed for some parameters. The problem disappeared when we used the negative exponential detection function that is more robust to occasional long movements. Analyses reported here therefore used the negative exponential function

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[2] The habitat mask is closely related to the 'state space' as the term is used in Bayesian analyses e.g. Royle et al. (2014).

[3] SL001 and SL021 appear to have taken advantage of the road bridge at Tagish or the narrowed channel south of there.

for the hazard of detection[4] $\lambda(d) = \lambda_0 \exp(-d/\sigma)$. Note that the spatial scale parameter σ for the negative exponential cannot be compared directly to σ in the half-normal.

The SECR detection model is inevitably a simplification: the parameters of the spatial detection function (λ_0 and σ) are assumed by default to be constant over time and among animals. Variation not included in the model may cause bias in estimates and result in misleading confidence intervals. Conversely, variation may be controlled by including it in the model, although excessively complex models lose precision and are difficult to fit. It is usual therefore to fit a number of detection models and select the best model by some criterion, or to average estimates across models, weighting for the strength of the evidence for each model. The possible models form the 'model set'. The potential effects we controlled for are

- sex differences, particularly sex-specific home-range size
- learned response, particularly repeat visits to baited sites
- between-year differences

Sex differences in home-range size drive sex differences in both the detection parameters (λ_0, hazard of detection at home range center; σ, spatial scale) and we allowed for sex differences in all models.

Bears may learn from their first encounter with a baited site and visit it more (or less) frequently in future. We therefore allowed for a site-specific learned response.

We chose not to consider within-season temporal variation. Shifts in foraging behaviour are definitely important when sampling grizzly populations across seasons, but sampling for this study was done within a narrow window (June and July) when we expected relatively stable behaviour. There were also technical impediments: visits to collect hair samples were not fully synchronous across stations. A few data on visit dates were missing for 2012, when some sites may have been missed after the helicopter crash; we evaluate the possible impact of the missing data in Appendix 3 and conclude it is not critical.

3. Density comparisons

Our main models assumed the activity centres of bears were distributed uniformly at random within the masked area. We also considered models for the non-uniform spatial distribution of animals, and for year-to-year changes. Comparison of model fit is a formal way to assess the evidence for such effects. In the absence of a comprehensive vegetation map, we considered two proxies for habitat effects on bear density: elevation and ecoregions (Ecological Stratification Working Group 1995). Elevation data were obtained for each pixel in the habitat mask from the digital elevation model of Natural Resources Canada (https://www.nrcan.gc.ca/earth-sciences/geography/topographic-information/free-data-geogratis/11042). Ecoregion polygons were obtained from Agriculture and Agri-food Canada (http://sis.agr.gc.ca/cansis/nsdb/ecostrat/gis_data.html).

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[4] The instantaneous hazard of detection $\lambda(d)$ is related to $g(d)$, the probability of detection over one time interval (day), by $g(d) = 1 - \exp(-\lambda(d))$. We use the hazard form because it has a more direct relationship to the distribution of activity measured by telemetry.

We assessed a possible effect of elevation on grizzly bear density by contrasting lower and higher elevations (below and above the median elevation 1250 m). Data were not available from GeoGratis for 924 km^2 outside Canada (3% of the mask area); elevation for these pixels was set at random with equal probability above and below 1250 m. Models were also fitted using a flexible regression spline for the relationship between elevation and density (Efford 2015c).

The study area itself was split roughly equally between two ecoregions, but the habitat mask included other ecoregions not represented in the area directly sampled (Table 1). For analysis, minor ecoregions were merged with the adjoining dominant ecoregions: 174 and 175 with 177 (Yukon Southern Lakes), and 180 and 185 with 179 (Yukon-Stikine Highlands).

Table 1. Representation of ecoregions in the vicinity of the Southern Lakes grizzly bear study area. The habitat mask is the study area buffered by 50 km. Area excludes lakes and rivers and USA.

Ecoregion	Ecoregion name	Habitat mask		Study area	
		Area (km^2)	%	Area (km^2)	%
174	Ruby Ranges	2,125	7.0	0	0
175	Yukon Plateau-Central	148	0.5	0	0
177	Yukon Southern Lakes	15,759	51.8	4683	61.2
179	Yukon-Stikine Highlands	9,133	30.0	2911	38.1
180	Boreal Mountains and Plateaus	2,505	8.2	56	0.7
185	Northern Coastal Mountains	760	2.5	0	0

Models with different density in the two years and with an effect of elevation on density were compared to models with homogeneous density. These density comparisons used a detection model with sex differences in λ_0 and σ, a station-specific learned response in λ_0, and non-Euclidean dry-path distance calculations.

We used the small-sample form of Akaike's Information Criterion (AICc) to compare models; models with small AICc are preferred. Likelihood ratio tests were also used to compare nested pairs of models. Estimates are reported with 95% confidence intervals in parentheses. SECR models were fitted assuming a fixed number of individuals (N) in the area of the habitat mask, resulting in a binomial distribution for the number detected (*n*) rather than a Poisson distribution for *n*. The resulting confidence intervals are thus conditional on the particular realisation of the 2-D population process (Efford and Fewster 2013).

Joint analysis of telemetry and capture–recapture data

Information for estimating the parameter σ of the SECR model usually comes from the spatial pattern of detections of animals detected more than once (a large scatter implies large σ). If few animals are detected more than once then σ may be poorly estimated.

Telemetry data are a rich alternative source of information on σ, which is an argument for joint analysis of telemetry and hair-snare data when the latter are weak. Telemetry that is concurrent with SECR sampling also documents the locations of a sample of animals exposed to snares; their detection or non-detection at snares provides additional information on λ_0 and σ that may sometimes be useful.

There have been several studies that include telemetry data in a Bayesian SECR model (e.g., Sollmann et al. 2013 a,b; Whittington et al. in press), but none that does so using maximum likelihood. For this study we refined and extended code in the 'secr' package to include telemetry data. This will appear in the next public release of 'secr' (version 3.0). Initial documentation is provided online (Efford 2017).

We compared density estimates with and without concurrent telemetry in a pre-release version of the 'secr' package (3.0.0). For this comparison we used Euclidean distances, as the calculations required for non-Euclidean (dry-path) distances to all potential telemetry locations were too demanding. Daily telemetry data were available from June-August for 8 bears in 2012 and 8 bears in 2013. In 2013, one bear (SL028) had only 3 detections and two (SL031, SL032) were translocated and their subsequent movements were atypical (Appendix 2); we excluded these bears from the joint analysis, reducing the total to 5 for 2013.

Results

Data from hair snares

Overall, 75 and 65 individuals were detected in 2012 and 2013 respectively, with more females detected than males in both years (Table 2). Repeat detections of an individual within a sampling interval at the same site were ignored (i.e. hair snares were treated as 'binary proximity detectors' in the terminology of 'secr').

Table 2. Summary of grizzly bear detections at hair snares (Southern Lakes, Yukon) (discarding repeat detections of an individual at the same site in the same interval).

Statistic	**2012**			**2013**		
	Female	Male	Total	Female	Male	Total
Bears detected	40	35	75	38	27	65
Number of detections	99	89	188	63	66	129

A summary of tracks from repeated detections of individuals revealed widespread movements in both years (Fig. 6).

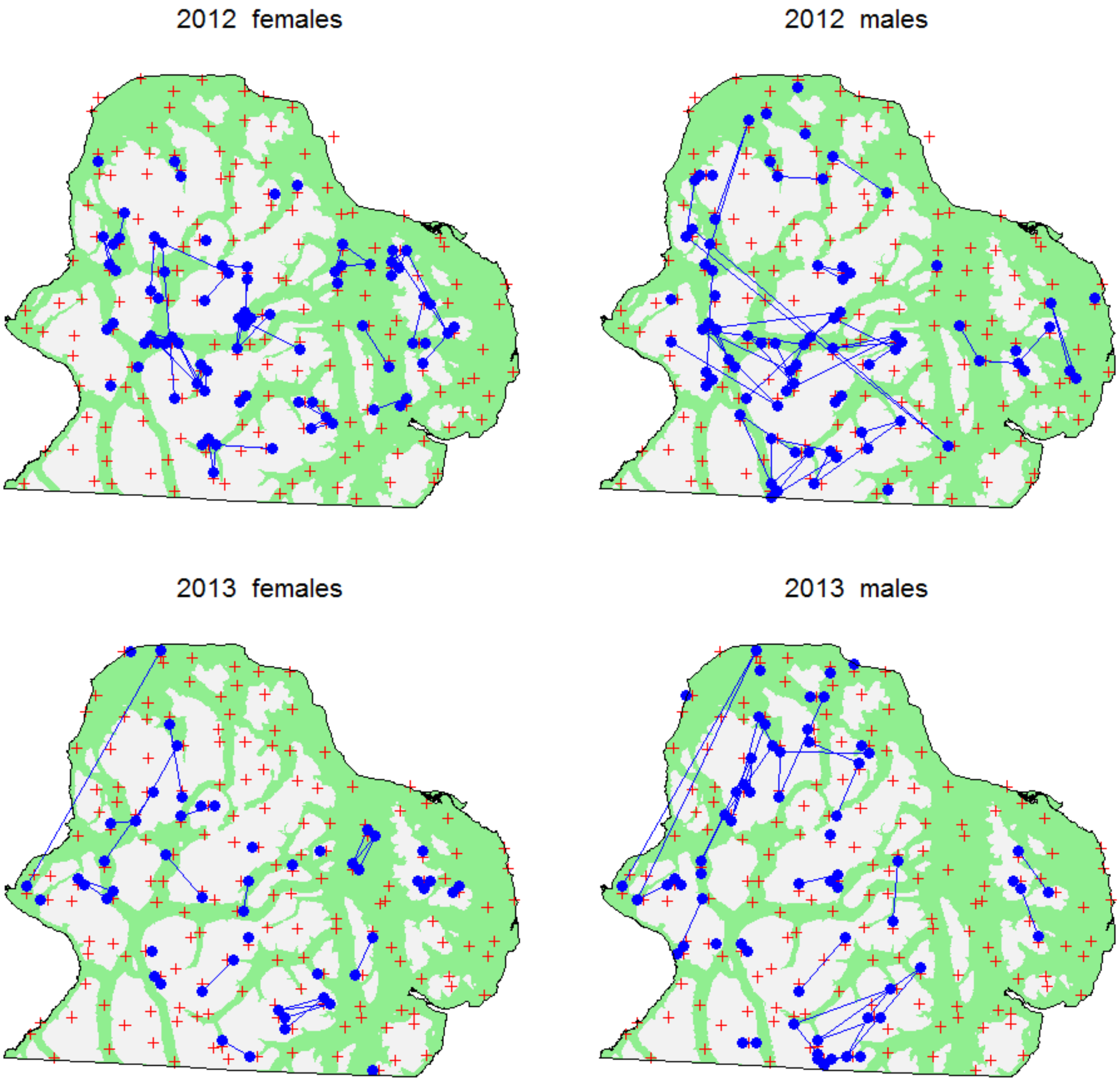

Fig. 6. Locations of hair snares (red crosses) and grizzly bear detections (blue dots) in Southern Lakes study area (black outline). Repeat detections of each bear are joined, but sequence is arbitrary for repeat detections within a sampling interval (hence double long movement of one male in 2013 may have been unidirectional). Land above 1250-m is shaded grey. Blue dots are displaced by 1.5 km from the snare site to reduce overlap.

Three animals (two males and a female) were recorded as moving more than 40 km (Fig. 7). For one animal (female SL031), telemetry corroborates a large movement in the third sampling interval in 2013: she was detected at hair snare 102 when about half way home (vicinity of hair snare 5) after being translocated (see Fig. 3 and the more detailed maps in Appendix 2). Male 6053 was also detected at stations 5 and 102 in that interval. As SL031 was mature and not translocated with cubs, it appears likely that she acquired a consort male who accompanied her on a homing movement. The remaining long movement by Male 7469 in 2012 is more problematic (it was detected at site 55 in samples collected on 28 June and 8 July, but also 75 km away at site 147 on 1 July between these dates). We had no other reason to reject the record, and retained it in the dataset.

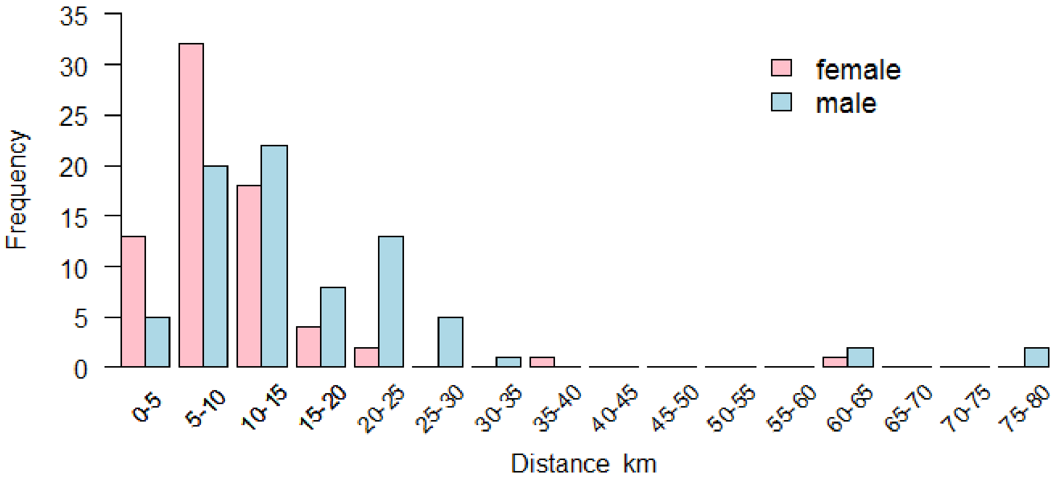

Fig. 7. Distribution of distances moved between detections (2012 and 2013 pooled)

Choice of detection model

We first consider models for the detection parameters with density held constant. We kept sex as a covariate in all models because sex had an indisputable effect on the scale of movement (Fig. 7).

Estimates from models with and without barriers are given in Table 3. The best model included a site-specific learned response and sex-specific detection parameters. Barriers to movement limit the contribution of peripheral populations to the sample of detected animals. Including barriers in the model tends to increase the estimate of density because the observed animals are 'attributed' to a smaller catchment area. We expect estimates from 'barrier' models to be more accurate as they more closely represent the field situation.

Table 3. SECR models with and without barriers to movement. SECR model parameters displayed are D (density), λ_0 (detection probability at home range center), and σ (scale of movement).   The model term 'bk' indicates a site-specific learned response. The number of parameters (np) in each model is also given. Estimates are given with 95% confidence intervals. ΔAICc refers to the difference in AICc between each model and the best model, for which ΔAICc=0.

Model	**np**	**ΔAICc**	**Bears per 1000 km^2**
a. Without barriers to movement			
D~1, λ_0~sex+year+bk, σ~sex+year	9	0	9.9 (8.3 – 11.9)
D~1, λ_0~sex + bk, σ~sex	7	0.9	9.8 (8.2 – 11.7)
D~1, λ_0~sex, σ~sex	6	66.7	8.9 (7.6 – 10.4)

D~1, λ_0~sex+year, σ~sex+year	8	66.8	8.9 (7.6 – 10.5)
b. With barriers to movement			
D~1, λ_0~sex+year+bk, σ~sex+year	9	0	10.7 (9.0 – 12.8)
D~1, λ_0~sex + bk, σ~sex	7	2.4	10.6 (8.9–12.6)
D~1, λ_0~sex+year, σ~sex+year	8	59.5	9.6 (8.2 – 11.3)
D~1, λ_0~sex, σ~sex	6	66.7	9.5 (8.1 – 11.1)

Density estimates

Elevation effect on density

Detections of grizzly bears were fairly evenly distributed across the study area (Fig. 8). Possible gaps might exist in the southwest and southeast, and along the northeastern edge, but these may have been chance effects.

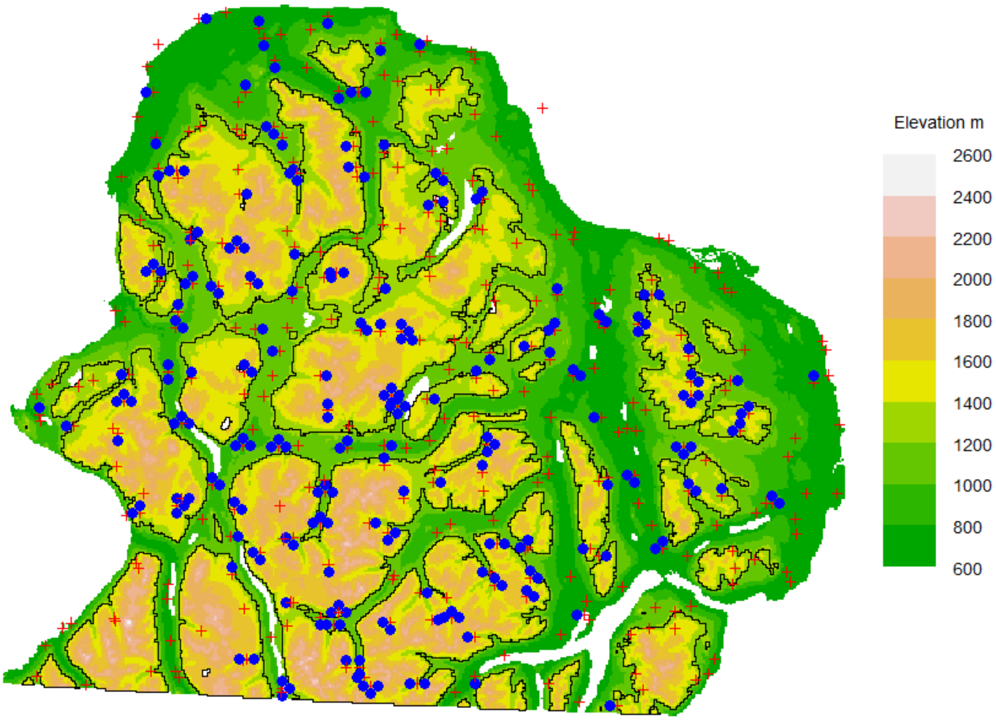

Fig. 8. Distribution of grizzly bear detections across Southern lakes study area. Pooled data from 2012 and 2013. Red crosses indicate the location of hair snares; detections (blue dots) are displaced slightly from the corresponding snare location for visual effect. Black line is 1250-m contour.

A model that assigned different densities to areas above and below 1250 m had substantially smaller AICc than the corresponding model with homogeneous density (Table 4) and a likelihood ratio test rejected the null hypothesis of constant density ($X^2 = 17.4$, 1 df, $P < 0.001$).

Table 4. Comparison of models for the effect of elevation on bear density. 'highground' is a binary indicator of elevation>1250 m. 's(elevation,k)' represents a regression spline of order k. np number of estimated parameters in each model, logLik maximised log likelihood, D bears per 1000 km^2. ΔAICc is the difference in small-sample-adjusted Akaike information criterion between each model and the best model.

Model	**np**	**logLik**	**ΔAICc**
D~s(elevation,3), λ_0~sex + bk, σ ~sex	9	–1758.1	0
D~s(elevation,5), λ_0~sex + bk, σ ~sex	11	–1757.9	4.2
D~highground, λ_0~sex + bk, σ ~sex	8	-1761.8	5.1
D~1, λ_0~sex + bk, σ ~sex	7	–1770.6	20.3

Regression spline models using elevation as a continuous predictor had smaller AICc again (Table 4), but interpretation is difficult; predicted density was highly uncertain relative to the central estimate at both low and high extremes of elevation (Fig. 9). We note that the estimated density applies to activity centres, and most home ranges centred at higher elevation include some ground at lower elevation. Apparent avoidance of lower elevations may be due to greater conflict with humans in extensive areas at lower elevation, including greater habitat modification

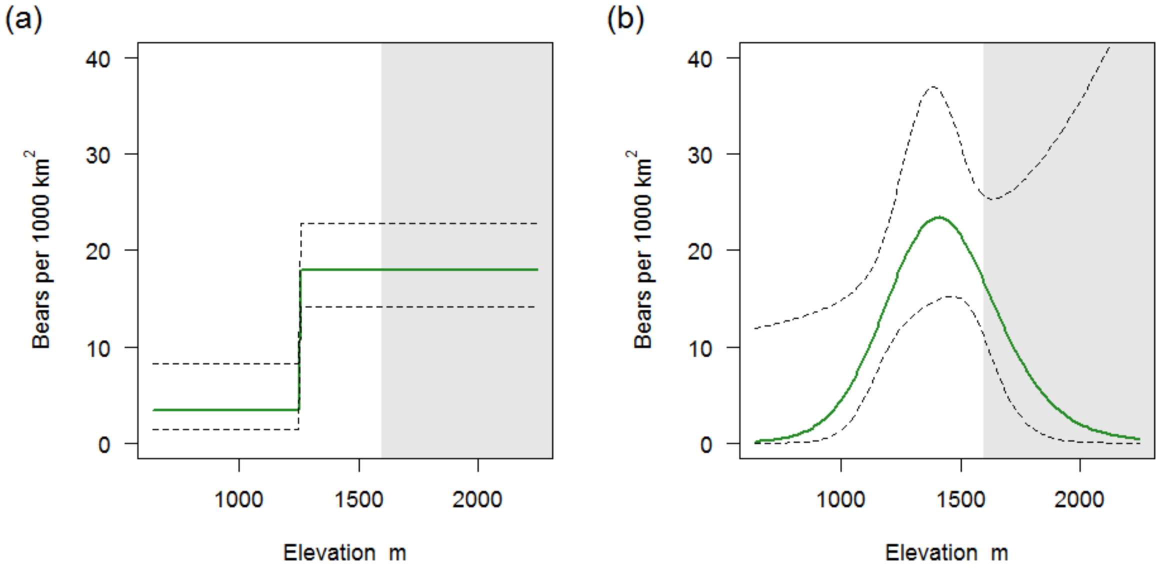

Fig. 9. Relationship between grizzly bear density and elevation under two models, (a) step function assigning different densities above and below median elevation (1250 m), and (b) regression spline with 3 degrees of freedom. Dashed lines are upper and lower 95% confidence limits. Shaded area indicates elevations undersampled by hair snares (cf Fig. 2).

Ecoregion as a predictor of density

There was no evidence for an overall difference in density between ecoregions and the model D~ecoregion was ranked lowest by AICc (Table 5). Including an additive effect of ecoregion in a binary elevation model (D~highground + ecoregion) gave a slight improvement in AICc. We did not consider this sufficiently important to stratify further analyses by ecoregion, although we later present estimates of population size with and without ecoregion as a covariate.

Table 5. Comparison of models for bear density. ‘highground’ is a binary indicator of elevation>1250 m; ‘ecoregion’ contrasts the Yukon Southern Lakes and Yukon-Stikine Highlands ecoregions. np number of estimated parameters in each model, logLik maximised log likelihood, D bears per 1000 km^2. ΔAICc is the difference in small-sample-adjusted Akaike information criterion between each model and the best model.

Model	np	logLik	ΔAICc

D~highground + ecoregion, λ_0~sex + bk, σ ~sex	9	–1759.1	0.0
D~highground * ecoregion, λ_0~sex + bk, σ ~sex	10	–1759.0	2.0
D~highground, λ_0~sex + bk, σ ~sex	8	-1761.8	3.2
D~1, λ_0~sex + bk, σ ~sex	7	–1770.6	18.4
D~ecoregion, λ_0~sex + bk, σ ~sex	8	–1770.5	20.4

Year-to-year variation in density

All models to this point have treated density as constant in 2012 and 2013. This is reasonable given the longevity of grizzly bears and the modest number of individuals in the dataset. We formally evaluated a year effect by fitting one further model with distinct densities in the two years, while retaining the major effects identified previously (sex, site-specific learned response, and elevation).

The model with different densities in the two years had larger AICc than the corresponding model with homogeneous density (ΔAICc = 1.2). A likelihood ratio test does not reject the null hypothesis of constant density (X^2 = 1.1, 1 df, P = 0.3).

Joint analysis of telemetry and hair-snare data

Telemetry data were used for 3 male and 5 female bears in 2012, and 4 male bears and 1 female bear in 2013. Two of the males in 2013 had telemetry ranges almost entirely outside the study area (SL029, SL030; Fig. 3). Of the GPS-collared bears, four were detected at hair snares in 2012 and two were detected in 2013 (Appendix 1). We used telemetry data from June to August, expecting that bears would occupy stable summer home ranges over this period. The number of fixes per bear ranged from 22 to 92.

Including data from GPS-collared bears (8 in 2012 and 5 in 2013) slightly increased the estimated density from a model with constant density across years (Table 6). The relative precision of density estimates did not improve – relative standard error (CV) increased from 9.1% to 9.4% and the length of the 95% confidence interval increased from 35.7% of the estimate to 36.8%.

Table 6. Comparison of density estimates with and without telemetry data. SECR model with negative-exponential detection function fitted to 2012–2013 data allowing for station-specific learned response on λ_0 (tabulated estimates refer to initial detection at a station). Estimates do not allow for barriers to movement.

Parameter	Sex	Hair snare only		Hair snare + telemetry	
		Estimate	95% CI	Estimate	95% CI
Density (per 1000 km^2)		9.82	8.22–11.73	10.1	8.41–12.13
Sex ratio	P(female)	0.641	0.550–0.722	0.666	0.578–0.743

Detection (λ_0)	female	0.183	0.124–0.272	0.25	0.183–0.341
	male	0.122	0.084–0.176	0.092	0.072–0.119
Scale (σ) km	female	3.72	3.16–4.38	3.06	2.79–3.36
	male	6.01	5.06–7.13	6.99	6.51–7.50

Unmodelled variation in detection parameters

For clarity we have so far avoided models with variation in detection parameters among individuals beyond that due to sex, year or previous detection. Individual heterogeneity is a persistent bugbear of capture–recapture estimation, with the potential to cause negative bias in estimates. Variation from unspecified causes may be handled with a ‘random effect’. In ‘secr’ one particular sort of random effect is allowed: probabilistic membership of discrete latent classes (also called ’finite mixtures’) (Pledger 2000; Efford 2015b).

In this section, we fit a 2-class finite mixture model to evaluate the possibility of additional unmodelled variation in λ_0 and σ. Previous models have estimated total density and sex ratio as parameters, using the ‘hcov’ formulation of ‘secr’. To address unmodelled heterogeneity it is necessary to switch parameterisations and separately estimate the density of each sex with the ‘group’ construct of secr. This allows each detection parameter to be modelled with distinct values for two latent classes that may be unrelated to sex; the proportion of animals in each latent class is a further parameter, unrelated to the sex ratio.

We assume site-specific learned response and allow unequal density in the two sexes (D~sex). Where the total density is required we sum the male and female density estimates. The sampling variance of this estimate is estimated as the sum of the squared group-specific SE (assuming independence), and asymmetric confidence intervals are derived from log-normal assumptions.

Table 7. Comparison of sex-specific models with and without additional heterogeneity (h2) in detection parameters using different criteria. np number of estimated parameters in each model, logLik maximised log likelihood, D bears per 1000 km^2. ΔAICc is the difference in small-sample-adjusted Akaike information criterion between each model and the best model.

Model	**np**	**logLik**	**ΔAICc**	**D**	**95% CI**
D~sex, λ_0~sex + bk + h2, σ ~sex + h2	10	–1763.3	0	12.0	9.5–15.1
D~sex, λ_0~sex + bk, σ ~sex	7	–1769.0	4.6	10.6	8.9–12.6
D~sex, λ_0~bk, σ ~1	5	–1777.7	17.7	10.4	8.9–12.2

Including a finite mixture to account for unmodelled heterogeneity results in a small but non-negligible reduction in AICc (Table 7). The sum of male and female density estimates from this model is about 13% greater than in the model without the finite mixture terms.

Final model

Based on the preceding sections, we selected a model for estimating the Southern Lakes grizzly bear population in which

- density depended on elevation (above vs below 1250 m) and sex,
- detection parameters (λ_0 and σ) differed between the sexes, between years, and between latent classes, and
- λ_0 depended on whether the bear in question had previously visited a station.

Distances were dry-path distances (i.e. lakes functioned as barriers) and a negative exponential shape was used for the detection function. Parameter estimates from the final model are shown in Table 8.

Table 8. Estimates of Yukon Southern Lakes grizzly bear population parameters 2012–2013 from a model with additive effects of sex and elevation on density, and additive effects of sex, year, experience and a 2-class finite mixture on detection parameters. Estimates of 'initial' λ_0 refer to the hazard of first detection of a bear at a particular hair snare; the hazard increases after initial detection ('redetection'). Detection parameter (λ_0, σ) estimates are the average over latent classes, weighted by mixing probability (not shown).

Parameter	Category	Event	Estimate	95% CI[5]
Density (bears/1000km^2)	female <=1250 m		3.81	1.81–8.01
	female > 1250 m		11.36	7.65–16.87
	male <= 1250 m		2.39	1.16–4.92
	male > 1250 m		7.14	4.94–10.31
Detection probability λ_0	female 2012	initial	0.155	0.083–0.289
		redetection	0.650	0.364–1.163
	female 2013	initial	0.090	0.034–0.236
		redetection	0.378	0.148–0.962
	male 2012	initial	0.120	0.064–0.227
		redetection	0.504	0.280–0.910
	male 2013	initial	0.070	0.027–0.182

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[5] Confidence intervals for estimates of λ_0 and σ do not allow for uncertainty in the mixing proportion.

		redetection	0.293	0.116–0.741
Scale of movement σ (km)[6]	female 2012		3.55	2.28–5.52
	female 2013		4.11	2.34–7.21
	male 2012		4.90	3.18–7.53
	male 2013		5.67	3.26–9.86

Population size

The estimated number of bears with home ranges centred in the nominal study area is the density multiplied by the area (~7650 km^2 excluding lakes), stratified by elevation. The overall density estimates from the final model (Table 8) correspond to a population of N = 95 individuals in the study area (Table 9). We estimate that 61% of the bears were females (about 58 individuals). Age cannot be determined from the hair DNA, and an unknown proportion of bears were cubs or sub-adults. Alternative models that included ecoregion as a predictor of density gave very similar estimates of total population (Table 9).

Table 9. Estimated numbers of grizzly bears centred in Southern Lakes study area 2012–2013. Final model with finite mixture h2, sex differences and site-specific learned response bk (λ_0~ sex + bk + h2 + year, sigma ~ sex + h2 + year). A model with ecoregion is also included for reference purposes.

Density model	Category	Estimate	95% CI[7]	Proportion females
D~sex + highground	Females	58.1	42.5–79.6	–
	Males	36.6	27.8–48.1	–
	Both sexes	94.8	76.0–118.1	61.3%
D~sex + highground + ecoregion	Females	56.9	41.6–77.8	
	Males	36.7	28.0–48.2	
	Both sexes	93.6	75.2–116.5	60.8%

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[6] This σ is the spatial scale parameter of a *negative-exponential* detection function. The corresponding values for the more usual *half-normal* detection function from a model without year effect are: females 7.04 (6.18–8.01) km, males 9.75 (8.56–11.09) km.

[7] Confidence intervals for estimates of λ_0 and σ do not allow for uncertainty in mixing proportion.

The inclusion of terms for finite mixture terms for unmodelled heterogeneity increased the estimate by 13 bears compared to models that did not included the mixture terms. The estimate of 82 bears from the models without the finite mixture terms represents a more conservative estimate of population size for the study area (Table 10).

Table 10. Estimated numbers of grizzly bears centred in Southern Lakes study area 2012–2013. Interim model without allowance for unmodelled heterogeneity, in detection, but allowing for site-specific learned response bk and sex differences (λ_0~sex + bk, σ ~sex).

Density model	Category	Estimate	95% CI	Proportion females
D~highground	Both sexes	81.9	69.0–97.1	61.9%
D~highground + ecoregion	Both sexes	81.9	69.3–96.8	

Discussion

Comments on study design

A 7-km x 7-km grid was used to ensure balanced sampling across the study area. Some discretion was allowed in the placement of hair snares within a grid cell, and the data show that sites above 1600 m were avoided, presumably because of snow cover that persisted into early summer. The density estimates relate to the entire land area within the study area boundary. The density estimates would be somewhat higher if non-habitat rocky barrens or snow were excluded, but the estimate of overall population size would be unchanged.

Hair snare stations were not moved during the sampling period in each year. Moving stations is often seen as desirable as it avoids the risk that detection rates will be distorted by experienced bears frequenting lured sites. We found strong evidence for a site-specific learned response, but we were able to allow for that in the model and do not believe that it biased the results.

Another argument for moving stations is that it increases the number of different locations sampled over the season, and thereby increases the chance that a bear with a small home range will be exposed to a snare at some time. The 7-km x 7-km sampling grid ensured a high density of hair snares (1 per 49 km^2). The estimated scale of detection implies an average female home range (95% activity area) on the order of 20 grid squares (942 km^2 or 935 km^2 depending on the detection model[8], data from Table 8). This suggests that even females with small home ranges were exposed to multiple fixed hair snares.

We conclude that the design served the intended purpose, and enough individuals were detected and re-detected for the density estimates to have reasonable precision (SE about 11% of the estimate). The DNA hair snares provided a spatially balanced sample across the Southern Lakes study area, which allows confidence in the overall density and population size estimates in that study area.

We also explored elevation and ecoregion as predictors of density within that region, and in the immediately adjacent habitat from which some bears were detected. Elevation was a strong predictor of density and ecoregion a weak predictor, after controlling for elevation. These conclusions are specific to the Southern Lakes study area, in which elevation is strongly correlated with unmeasured effects such as human influence. We advise against extrapolation of covariate effects beyond the study area, as no causal link has been established.

Joint analysis of hair-snare and telemetry data

Data from GPS collars were not directly useful for the population analysis. In part this reflects a general limitation of telemetry data: telemetry data are very informative about the extent of movement (parameter σ), but this parameter is usually well-estimated by the hair

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[8] A circle of radius 4.52σ encloses 95% of activity for a negative-exponential detection function, or radius 2.45σ for a half-normal detection function (see function ‘circular.r’ in secr).

snare data themselves, given a reasonable number of recaptures; telemetry data contribute little extra information about other parameters.

It is also problematic to use telemetry data from an ad hoc sample of individuals, particularly if these are problem bears and/or relocated. It is possible that telemetry undertaken specifically to complement hair snares would be more effective. However, the optimal deployment of GPS collars to complement SECR has not been researched. At a minimum, there should be a larger sample of active collars at the time of hair snaring.

Nevertheless, telemetry data provided a useful 'reality check' on bear behaviour as it related to key assumptions of the SECR model. Most collared bears occupied compact home ranges for which the idealised circular home-range implicit in SECR is a reasonable model. Two exceptions could be explained as a response to relocation. Movements of collared bears appeared to be constrained by the lakes, justifying the non-Euclidean distance model with lakes as barriers.

Uncertainties

We suggest three respects in which there remains some doubt about the estimates.

1. Age and reproductive status unknown

Age and reproductive status were unknown for snare-only bears. Cubs, yearlings and subadult bears tended to be sampled less often than adult bears in the study of Kendall et al. (2009). Age effects are a likely source of unmodelled heterogeneity in the present study.

2. Family groups

The tendency for sows to be accompanied by young, or for other transient associations, violates the assumption of SECR that individuals moved and were detected independently. As a result, the calculated confidence intervals may be slightly too short.

3. Unmodelled heterogeneity

Our final model used a finite-mixture to allow for otherwise unmodelled heterogeneity in detection parameters. This followed from our reliance on AICc for model selection. However, we are uneasy about this decision because it leads to a less transparent model and a step change in the estimates for a rather small reduction in AICc (ΔAICc = 4.6). There is disagreement among statisticians on the best way to address heterogeneity, and the choice of a 2-class finite mixture is itself somewhat arbitrary. The final model added 13 bears (16%) to the study-area population, when compared to models formulated without finite mixtures. Confidence intervals were also widened.

For management purposes we suggest it is wise to take a conservative approach and rely on the smaller estimate. If the larger estimate is used it is important to recognise its greater uncertainty.

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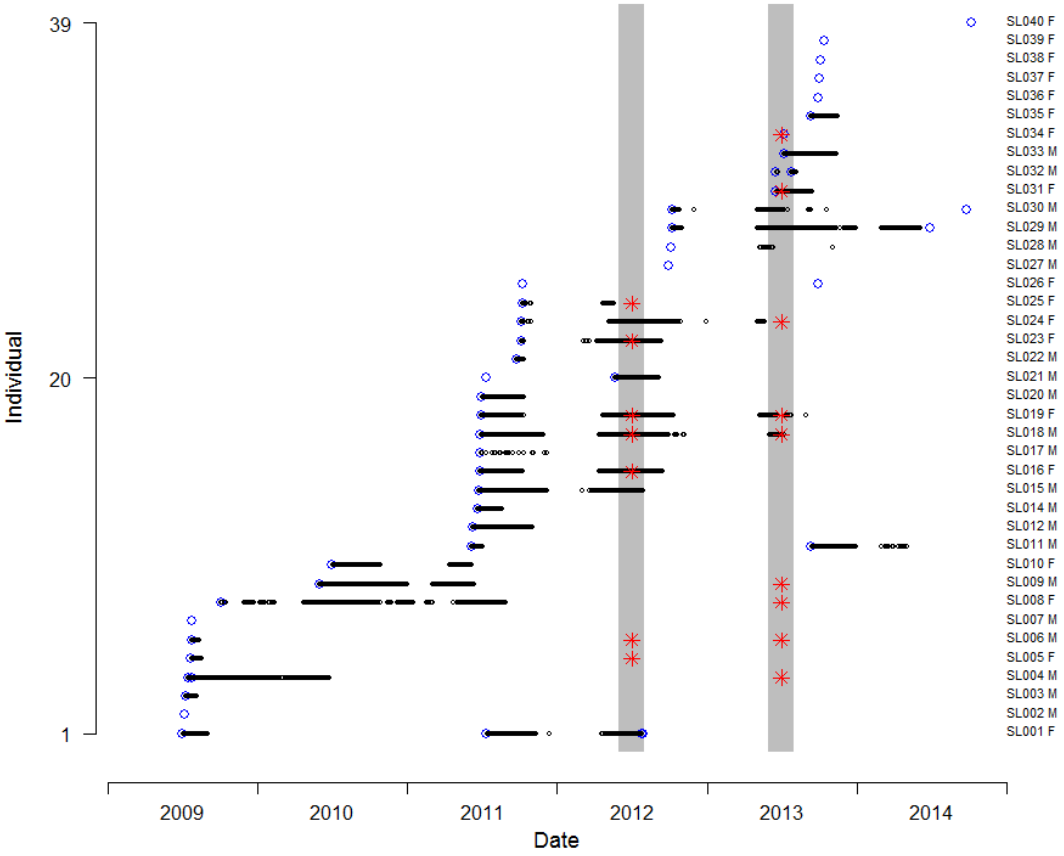
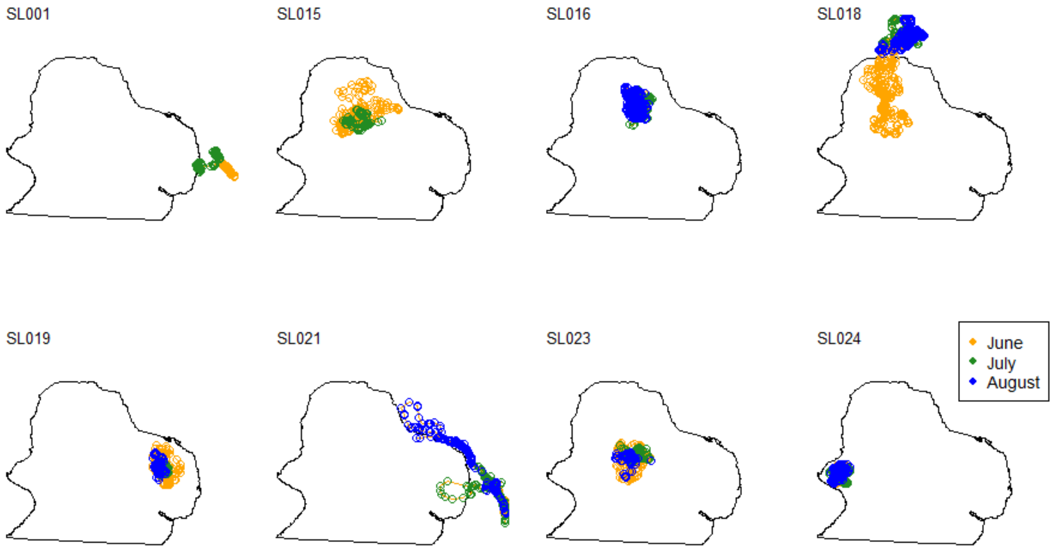
Appendix 1. Summary of GPS-collared grizzly bears 2009–2014



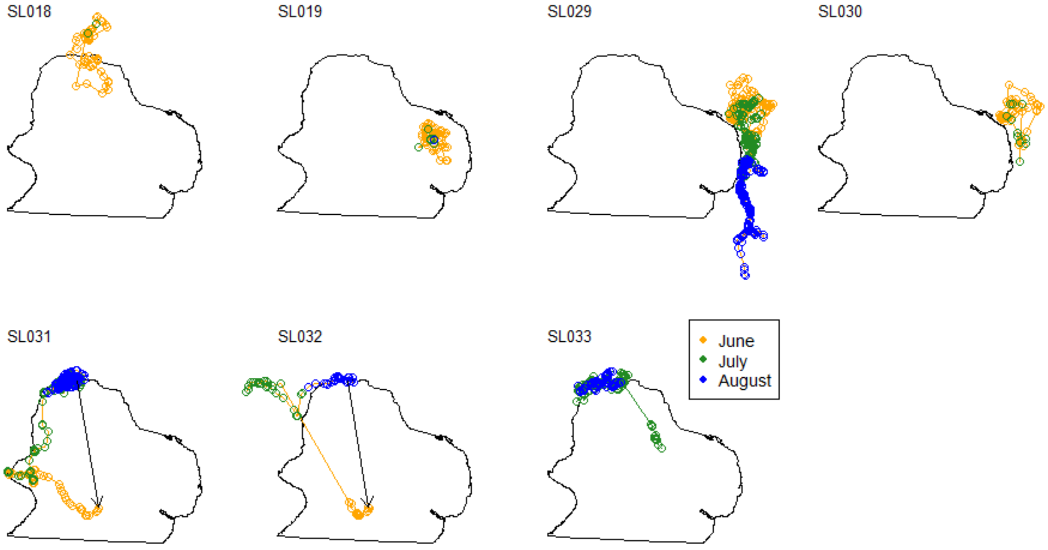
Appendix Fig. 1. Histories of GPS-collared grizzly bears in the Southern Lakes region, Yukon. Blue circles indicate dates of capture and collaring; small circles are telemetry dates. Grey bars indicate June and July in 2012 and 2013 when hair snares were operated. A red asterisk indicates that the bear was detected at least once at a hair snare in that season. SL013 does not appear in the GPS collar dataset, but a bear with this ID was recorded at hair snare 82 in 2012.

Appendix 2. Individual telemetry maps stratified by month

a. June–August 2012



b. June–August 2013



Note: SL031 and SL032 were recorded as relocated in June 2013 as shown by the black arrows. SL033 was captured at the same site by the same method soon after, but not recorded as relocated.

Appendix 3. Effect of lost visit data from July 2012

The helicopter crash on 10 July 2012, part way through the third set of visits to hair-snare stations, is believed to have resulted in the loss of some samples, and there remains some doubt about which stations were visited then. We obtained SECR estimates of density using two extreme interpretations of the data: either all stations were considered to have been active throughout the third and fourth sampling intervals in 2012, or stations were considered active only when there was positive evidence. ‘Positive evidence’ was equated with the recording of a visit date in the spreadsheet ‘SLGB_Snare and DNA data_Nov2016_JG_AM .xls’. Dates were generally recorded only when a sample of hair was retrieved from the station.

An SECR model was fitted as in the main text using dry-path distances and sex-specific detection parameters with a site-specific learned response, but using data only from 2012. Detector usage was coded in the ‘usage’ attribute of the ‘secr’ traps object. Usage was either ‘complete’ (all detectors on all occasions) or ‘incomplete’ (complete for the first two occasions and based on positive evidence for the last two).

The resulting estimates were very similar:

	Bears per 1000 km^2 (95% CI)
Complete usage	10.76 (8.59–13.47)
Incomplete usage	10.97 (8.74–13.75)

In view of the wide confidence intervals we can say that for practical purposes the estimates were unaffected by the interpretation of the missing data.