In the trap: detectability of fixed hair trap DNA methods in grizzly bear population monitoring

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A significant challenge to monitoring wildlife that are secretive, wide ranging, and at low densities is the need to achieve adequate detection rates. Knowledge of spatial patterns in occupancy and the spatial and/or temporal patterns in detectability allows for stratification of traps and improved detection rates. This study investigated how local variation in habitats affected the detectability of grizzly bears in west–central Alberta when monitored with a fixed DNA hair snag design. Bear hair samples were collected in 2011 at 60 sites across 1500 km² over six sessions, each 14 days in length, between June and August. Microsatellite analysis of hair samples revealed grizzly bear detections at 25 of 60 sites and 21 individual bears. We investigated occupancy and detectability of grizzly bears at the patch and landscape scales using detection histories and program PRESENCE. At the patch scale, grizzly bear detection was highest when sites were placed near streams with clover and in intermediate levels of forest crown closure. At the landscape scale, probability of detection increased near streams and oil and gas wellsites, especially when food resources and wellsite density in the surrounding area was low. Our results highlight the importance of considering local food resources and habitat conditions during placement of fixed DNA hair snag sites. Detectability was not found to vary over time, suggesting that sampling in west–central Alberta can occur at any time between June and August.

Capture–mark–recapture methods (CMR) are the most frequently employed approach for estimating wildlife population size (Nichols 1992, Pradel 1996, Long 2008). CMR methods have been effectively adapted for noninvasive survey techniques (Taberlet and Luikart 1999, Mills et al. 2000, Waits and Paetkau 2005, Lukacs and Burnham 2005), such as the use of track stations, scat surveys and hair traps. Such approaches are ideally suited for monitoring measures of occupancy, distribution, and population size of rare and hard-to-detect species because they do not require the animals be caught (Taberlet et al. 1999).

CMR approaches have, however, a number of technical challenges. For detection-nondetection data the failure to detect a species does not mean the species was not present (Kery 2002, MacKenzie et al. 2002, Tyre et al. 2003). One must instead include the probability of detecting a species to estimate unbiased occupancy rates (MacKenzie et al. 2002, Stauffer et al. 2002, Tyre et al. 2003, Wintle et al. 2004). A successful CMR survey also requires that researchers maximize the probability that a species is detected while minimizing differences in individual detection rates (Long 2008). Maximizing detection rates at reasonable costs is a challenge for many monitoring programs because detectability depends in part on population density, sampling approaches, and effort (Gu and Swihart 2004). Detectability can also be influenced by local landscape and habitat features, such as steep terrain and dense cover (Nupp and Swihart 1996, Mancke and

Gavin 2000, Odell and Knight 2001, MacKenzie 2006). As a result, low detectability rates can result from species that exist at small population sizes or at low densities, and/or that occur in habitats that interfere with their detection. Although numerous studies have used detection-nondetection data to examine the relationship between habitat characteristics and occupancy (Connell 1961, Hinsley et al. 1995, Brown et al. 1996, Buckland et al. 1996, Odom et al. 2001, Scott et al. 2002), few studies have specifically explored the relationship between habitat covariates and detection. Those that have explored this relationship have focused on amphibians (Bailey et al. 2004a, b), birds (Conway et al. 2004, Alldredge et al. 2007, Nadeau et al. 2008, Conway and Gibbs 2011), small mammals (O'Connell et al. 2006), ungulates (Krishna et al. 2008), and plants (Chen et al. 2009).

A large carnivore species that would benefit from such knowledge is the grizzly bear *Ursus arctos*, which was listed as a threatened species in Alberta in 2010. Reliable and precise estimates of grizzly bear populations have resulted from traditional hair trap survey designs that move sites between sampling sessions (Taberlet et al. 1999, Mowat and Strobeck 2000, Poole et al. 2001, Proctor et al. 2004, Kendall et al. 2008, Boulanger et al. 2006), often by random placement or in response to anticipated grizzly bear movements or habitat use. This strategy is, however, effort-intensive and thus costly making its use in long-term population monitoring implausible. Fixed (permanent) sample plots in hair trap

survey designs may offer an alternative that lowers costs while retaining the ability to detect population trends (i.e. sufficient detectability). Fixed hair traps have already had success in wildlife management as a modified method for surveying problematic brown bears at specific survey locations (Kopatz et al. 2013). In Alberta, grizzly bears are secretive, wide-ranging, and occur at low densities, making them difficult to detect. Because the sampling sites are not moved, ensuring adequate detection rates and understanding temporal effects is crucial for successful implementation in long-term monitoring programs. A thorough understanding of detectability is therefore needed to make informed decisions on when and where to place sampling sites to guarantee cost-effective monitoring protocol for grizzly bears in Alberta.

In particular, local factors affecting the success of grizzly bear hair trap sites need to be understood to optimize the timing and placement of fixed hair trap sites that maximize detectability. For example, sampling may be less effective during late summer because bears may alter their movement patterns in search of berries ripening during this time, which could result in reduced detectability (Poole et al. 2001). Similarly, bears are known to alter their movements to avoid encounters with humans (Gibeau et al. 2002, Nellemann et al. 2007), but they also may use roadside ditches, pipelines, and oil and gas wellsites where there is a high risk of mortality (Nielsen et al. 2006, Graham et al. 2010, Roever et al. 2010, McKay et al. 2014). Anthropogenic features and food resource availability have been important for quantifying grizzly bear habitat quality (Nielsen et al. 2010); however, it is not clear how these factors influence grizzly bear behaviour near hair trap locations. Despite its importance for effective monitoring protocol, the detectability of fixed DNA hair trap sampling methods for grizzly bears has not been addressed.

In this paper, we investigate local factors affecting the occupancy and detection of grizzly bears in west–central Alberta. Although occupancy alone is not useful for setting population recovery targets and harvest quotas of grizzly bears, it is useful for better understanding detectability, which offers a way to stratify site placement. We hypothesize that 1) hair trap sites will compete with the pulsing of seasonal foods, such as fruit, and thus detectability will decrease during hyperphagic periods in late summer; and 2) anthropogenic features such as oil and gas wellsites and forest cutblocks will positively affect detectability due to increased forage associated with these disturbed sites (Martin 1983, Waller 1992, Nielsen et al. 2004b).

Material and methods

Study area

We delineated a 1500 km² study area in the eastern foothills of the Canadian Rocky Mountains of west–central Alberta (53°15′N, 117°30′W) using a systematic grid design composed of 30 separate hexagon-shaped sampling cells each 50 km² in size (Fig. 1). The majority of the study area overlaps a previous grizzly bear DNA inventory conducted in 2004 (Boulanger et al. 2005). In total seven grizzly bear population units have been defined in Alberta based on genetic information (Proctor et al. 2011) with this study
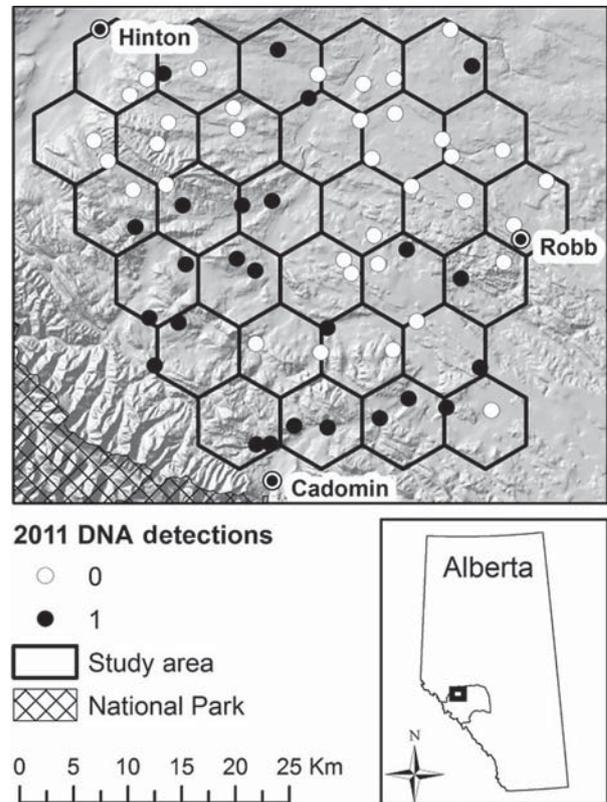

Figure 1. Study area in west–central Alberta comprised of 50 km² hexagon cells, towns, and Jasper National Park eastern boundary. The location and detection-nondetection data of 60 fixed DNA sites (two per cell) are shown. A value of zero indicates no detection; a value of one indicates a confirmed grizzly bear detection.

occurring within the Yellowhead Grizzly Bear Population Unit. Proctor et al. (2011) found these population units had weak genetic fragmentation, largely due to major east–west highways in the province and limited gene flow across the Continental Divide, but there are no long-standing (several generations) isolated populations.

Elevations in the study area ranged from 936 m to 2772 m representing foothills to the east of the Canadian Rocky Mountains. Vegetation consisted of mixed forests of lodgepole pine *Pinus contorta*, black spruce *Picea mariana* and tamarack *Larix laricina* associated with wet sites; mixed aspen *Populus tremuloides*, white spruce *Picea glauca*, and open stands of lodgepole pine were associated with drier sites. Important bear foods in the area include alpine sweet vetch *Hedysarum alpinum,* buffaloberry *Shepherdia canadensis*, cow parsnip *Heracleum lanatum* and various blueberry species *Vaccinum* spp. (Munro et al. 2006).

Human activities in the study area include oil and gas exploration and development, mining, forestry, human settlements, and extensive recreation including the use of ATVs. Widespread linear features provided access to the study area and included roads, pipelines, seismic lines and ATV trails.

DNA sampling and analysis

Grizzly bears were sampled using 60 fixed hair traps (two per cell) surveyed over six 14-day sampling sessions resulting

in 360 total observations (Fig. 1). We selected 44 site locations based on previous DNA hair snag locations from 2004 (Boulanger et al. 2006), whereas the remaining 16 site locations were selected using a Geographical Information System (GIS) program, expert opinion, and grizzly bear resource selection function models (Nielsen et al. 2002, 2009). Following methods outlined by Woods et al. (1999) and Mowat and Strobeck (2000), hair traps consisted of approximately 30 m length of 4-prong barbed wire encircling 4–6 trees at a height of 50 cm. We poured 2.5 l of scent lure – a 2:0.5 mixture of aged cattle blood and canola oil – on forest debris piled in the center of the corral at least 2 m from the wire. Sites were visited on a 14-day sample rotation (five work days per week) from 1 June 2011 to 25 August 2011 for a total of six survey sessions. At each visit, hair samples were collected and stored in paper envelopes and dried at room temperature. The scent lure was refreshed at each visit.

Using molecular analyses (mtDNA) (Woods et al. 1999), hair samples were genotyped to seven loci (G10J, G1A, G10B, G1D, G10H, G10M and G10P) (Paetkau et al. 1995) for individual identification at the Wildlife Genetics International lab in Nelson, BC. DNA was extracted using QIAGEN DNeasy Tissue kits following standard protocols (Paetkau 2003). For species identification, we used one nuclear microsatellite marker G10J at which alleles with an odd number are diagnostic of black bears. When this allele is present, species was confirmed with an independent test of species identity using six microsatellite markers other than G10J. All seven microsatellite markers plus a ZFX/ZFY gender marker were used to identify individuals and sex of samples that passed the G10J pre-screen (Paetkau et al. 1998). In the first phase of the analysis, samples that failed to produce high-confidence (3-digit) genotypes for ≥ 5 markers were removed; following this procedure, most samples produce complete data for all markers or are culled. Second, samples that were missing data for one or two markers were attempted again using 5 µl of DNA per reaction instead of 3 µl in the initial reaction. Finally, error checking involved selective reanalysis of similar genotypes (all 1MM-, 2MM- and 3MM-pairs of genotypes) to detect and eliminate genotypes created through genotyping error (Paetkau 2003). An independent assessment by Kendall et al. (2009) has shown this protocol is capable of reducing genotyping error rates to a trivial level.

Predictor variables

Variables used to predict the probability of detection were divided into five themes: anthropogenic features, topographic and forest stand features, landcover, food, and time (Supplementary material Appendix 1 Table A1). We recorded site-specific habitat variables at each site, including habitat type, dominant species and canopy cover. Vegetation surveys were conducted in August using 500-m line transects to identify the abundance of key bear foods. Nodes were generated at 100-m intervals along each transect, resulting in five segments per transect. Along each 100-m segment, the density of alpine sweet vetch *Hedysarum alpinum*, buffaloberry *Shepherdia canadensis*, cow parsnip *Heracleum lanatum*), moose *Alces alces* pellets and ant piles were recorded within 1-m of either side of the transect (i.e. a 200-m² plot). Along the

same 100-m segment, the relative abundance (cover) of 28 prominent bear foods was also recorded. Cover was estimated using a 0 to 4 ordinal scale ranging from 0 to 100% cover (0 = absent, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%). This was repeated for each segment along the 500-m transect.

In addition to measuring the habitat variables at each site, we assembled a GIS (ArcMap 10; Economic and Social Research Institute, Redlands, CA) database at a 30-m pixel resolution for our study area from which additional spatial predictor variables were derived as raster layers. Each predictor variable was summarized at a patch and landscape scale using a moving window with a radius of 300 m and 1690 m respectively. Previous studies have found the 300 m scale, or patch scale, to be an important predictor of bear occurrence (Theberge 2002, Nielsen et al. 2013). The 1690-m scale represents a larger landscape scale and is the estimated encounter distance of bears to hair trap sites (Boulanger et al. 2004). A 10-km buffer around the study area was used to eliminate any edge effects on sites near the outer study area limits.

Anthropogenic features hypothesized to affect grizzly bear occupancy and detectability included distance to and density of roads, trails (reclaimed roads), pipelines and oil and gas wellsites; mining and forestry footprints; and distance to protected areas. Distance was calculated as the Euclidean distance in meters and density as the number of features or length of features within a 1690 m radius. Density variables were log transformed to improve normality. To estimate mining and forestry footprints, each pixel was coded as presence (1) or absence (0) for each variable and then calculated the proportion of mining and forestry within a 1690 m moving window. We did not calculate the density or footprints of anthropogenic features at the patch scale because most features were further than 300 m from a hair trap site.

Five topographic variables and two forest stand features were used to assess the effect of terrain-influenced conditions on occupancy and detectability of grizzly bears. This included elevation, terrain ruggedness, soil wetness, distance to streams, GIS modeled crown closure, and site measured canopy cover. These are common variables used to predict grizzly bear habitat use (Mace et al. 1996, McLellan and Hovey 2001, Naves et al. 2003, Apps et al. 2004, Nielsen et al. 2006). Furthermore, topography can affect a dog's ability to detect odour far from its source (Wasser et al. 2004). If this is also true for grizzly bears, topographic features might also affect the ability of bears to detect a hair trap site. We used a 30-m digital elevation model (DEM) and script from Rho (2002) to calculate the compound topographic index (CTI), which is an index of soil wetness (Moore et al. 1993, Gessler et al. 1995). We also used the DEM to derive terrain ruggedness (TRI) using an equation from Nielsen (2005). Forest crown closure was modeled in GIS from 0% to 100% (McDermid et al. 2005). Distance to stream was calculated in GIS as the Euclidean distance in meters. Our final topographic variable was a model of mortality risk created by Nielsen et al. (2009) with values ranging from low (0) to high risk (10).

Like topography, landcover is another important predictor of grizzly bear occupancy (Mace et al. 1996, McLellan and Hovey 2001, Nielsen et al. 2006). Seven landcover types from McDermid et al. (2005) were reclassified as

either presence (1) or absence (0) and used a raster layer from Nielsen et al. (2009) representing core (1) and secondary (0) grizzly bear conservation areas on a watershed basis. Satellite imagery layers prepared by Hilker et al. (2011) were used to determine the year of forest stand origin and therefore forest age.

For food variables, we weighted estimates of cover using resource-specific diet weights (Nielsen et al. 2010). As a result, only bear foods with available diet weights were used. Nielsen et al. (2010) used percent digestible dry matter reported in Munro et al. (2006) to estimate 10 by-monthly seasonal importance weights for each food item, starting in May and ending in September. Because cover class was estimated at a single point in time, we used a single importance weight for each food item calculated as that item's average importance weight from 7 June to 21 August. Fruiting bear foods were grouped into either 'vaccinium' (all *Vaccinium* species) or 'other fruit' (all remaining fruiting bear foods) variables to reduce the total number of food variables. Buffaloberry was left as a single variable due to its importance for grizzly bears in the foothills (Munro et al. 2006). We also modified two supplementary spatial (GIS) food variables to represent seasonal and total food availability (Nielsen et al. 2010). Seasonal food availability for 10 bi-monthly seasons was calculated by Nielsen et al. (2010) as the product of a resource's abundance and its seasonal importance weight, summed over all food resources. We used only the six bi-monthly seasons from 7 June to 21 August and summed the six bi-monthly food estimates to estimate total food. Site specific abundance estimates of alpine sweet vetch, buffaloberry, cow parsnip, moose (indexed by pellet group counts), and presence of ants were log transformed. Finally, time was modeled as a linear and quadratic to test whether

detectability varied linearly over time or whether it peaked mid-season.

Distance variables were transformed using an exponential decay of the form e^{-ad} where d was the distance in meters to the feature and a was the decay rate (Nielsen et al. 2009). The decay rate was set to 0.0018 for all distance variables, with the exception of distance to protected area. This causes the effects of local features on occupancy and detectability to decline rapidly beyond a few hundred meters and become irrelevant at large distances (e.g. >1700 m). For distance to protected areas, which is a large scale feature, a decay rate of 0.000142 was used so that distances remained relevant until they were greater than the average grizzly bear home range size ($>21\,000$ m) (Stevens 2002, Nielsen 2005). Original distance decay values ranged from 1 at the feature to 0 at very large distances; however, we subtracted the distance decay variable from a value of 1 so that values ranged from 0 at the feature to 1 at very large distances for easier interpretation of model coefficients with near distances being negative and further distances positive (Nielsen et al. 2009). Finally, each predictor variable was standardized using a z-score transformation to enable direct comparison of the predictor variable strength in model outputs.

Model hypotheses and univariate analysis

We first outlined scale-specific a priori hypotheses of factors affecting grizzly bear occupancy and detectability using five themes (Table 1) to minimize our candidate set of models (Burnham and Anderson 2002). Thus competing hypotheses are described where each theme can contain multiple variables. Occupancy and detectability were modelled as two different responses, thus each had its own set of

Table 1. Scale-dependent a priori model hypotheses based on themes (details in Supplementary material Appendix 1 Table A1) used to investigate grizzly bear occupancy and detectability at two scales in west–central Alberta, Canada. Two factors, 'Anthropogenic features' and 'Topographic features, stand features and risk', have been abbreviated to Anthro and Topo, respectively. Time variables were tested in all detectability models and are therefore not listed.

		Model hypotheses		
Scale	Sub-model no.	Occupancy	Sub-model no.	Detectability
300 m	PSI_1	Topo + Landcover + Food	P_1	Food + Food + Topo
	PSI_2	Topo + Landcover + Anthro	P_2	Food + Food + Food
	PSI_3	Topo + Landcover + Topo	P_3	Food + Topo
	PSI_4	Topo + Topo + Food	P_4	Food + Food
	PSI_5	Topo + Topo + Anthro	P_5	Food
	PSI_6	Topo + Food	P_6	Topo
	PSI_7	Topo + Anthro		
	PSI_8	Topo + Landcover		
	PSI_9	Topo + Topo		
1690 m	PSI_1	Topo + Landcover + Anthro	P_1	Anthro + Anthro + Topo
	PSI_2	Topo + Landcover + Topo	P_2	Anthro + Anthro + Anthro Anthro + Anthro +
	PSI_3	Topo + Topo + Anthro	P_3	Food × Anthro
	PSI_4	Topo + Anthro	P_4	Anthro + Topo
	PSI_5	Topo + Landcover	P_5	Anthro + Anthro
	PSI_6	Topo + Topo	P_6	Anthro + Food × Anthro
			P_7	Food × Anthro + Topo
			P_8	Anthro
			P_9	Topo
			P_{10}	Food × Anthro

hypotheses. Seasonal detectability models (linear or quadratic) were included for every detectability hypothesis.

At the patch scale, we hypothesized that occupancy was affected by topographic and forest stand features, landcover, anthropogenic features, and food resources. We hypothesized that detectability at the patch scale would be affected by topography as well as local food resources – i.e. food may attract a bear toward a hair trap site or food may preoccupy the animal away from the hair trap site. At the landscape scale, the effects of food resources on occupancy were not tested as we felt this site-specific variable was addressed most relevantly at the patch scale. For detectability at the landscape scale, we hypothesized that topographic features, anthropogenic features, and the interaction of anthropogenic features with food resources would be important predictors of occupancy. Ciarniello et al. (2007) found that human use variables affected grizzly bear habitat selection at larger scales. We therefore considered the landscape scale to be more appropriate for investigating the effects of anthropogenic features and the interaction of anthropogenic features with food resources on detectability. Because site-specific estimates of bear foods could not be extrapolated from the patch to the landscape scale, two spatial food variables were estimated from a GIS to test for interaction effects between anthropogenic features and food resources.

Due to the large number of predictor variables, we performed a univariate analysis to reduce the number of variables and minimize over parameterization (Burnham and Anderson 2002). We compared the Akaike information criterion (AIC) (Burnham and Anderson 2002) score of each predictor variable to that of a null model for both occupancy and detectability sub-models. Variables that had an AIC score lower than the null model were kept while variables that had an AIC score higher than the null model were rejected.

Single season models

Following univariate analysis, we used a single-species single-season model in program PRESENCE to explore specific hypotheses of grizzly bear occupancy and detectability at two spatial scales. Program PRESENCE uses a maximum likelihood approach to calculate occupancy (MacKenzie 2006) while accounting for sites where the species was likely present but not detected. In this way, each model in program PRESENCE had two sub-models – occupancy and detectability – that are modeled simultaneously. A modified two-phase modeling approach similar to that of Balas (2008) was used to estimate site occupancy and detectability at each scale. All models were ranked for support using AIC.

For the first phase of analysis, we used an a priori approach where we tested a priori hypotheses of grizzly bear occupancy and detectability (Table 1). Each hypothesis contains one or more themes and each theme contains one or more variables that were selected through univariate analysis (Supplementary material Appendix 1 Table A1). For the analysis, each variable within a theme was individually included in the model, while holding the other themes constant, until all the variables within a theme were tested. Variables that were correlated ($|r|$ > 0.7) were not used in the same model. Because we were most interested in factors affecting detectability rather than occupancy, each occupancy hypothesis (sub-models PSI_1 to PSI_n) was modeled with every detectability hypothesis (sub-models P_1 to P_n). This created several preliminary candidate models for each occupancy hypothesis and allowed for the greatest amount of flexibility in modeling detection while still accounting for occupancy. The top ranked preliminary candidate model was selected from each occupancy hypothesis and referred to as candidate models. Candidate models were re-ranked according to AIC and the top model selected as the final candidate model.

For the second phase of analysis, we used an a posteriori approach where we added back in each previously removed variable from the univariate analysis to the final candidate model. Doing so allowed us to identify possible confounding variables that would otherwise be missed (Hosmer and Lemeshow 2000). Variables were added back to the occupancy sub-model one at a time while holding the detectability sub-model constant and vice versa creating preliminary PSI and P models. As in the a priori approach, we then modeled the top preliminary PSI model with every preliminary P model that had a ΔAIC < 2 compared to the top model and referred to these as the preliminary final models. The preliminary final models were ranked, and a maximum of three models with a ΔAIC < 2 between them were chosen as the final models of grizzly bear occupancy and detectability.

Ecological models are often most beneficial to wildlife managers as predictive maps, which can assist decision-making and conservation-planning efforts. To illustrate a predictive map of grizzly bear occupancy and detectability in a GIS, the final models and their associated beta coefficients were model averaged at each scale using adjusted model weights. Model-averaged beta coefficients were then used in linear predictor and probability equations from MacKenzie (2006) in a GIS to spatially estimate the probability of grizzly occupancy and detectability in west–central Alberta. We created a map of the probability of occupancy (PSI), the probability of detection (P), and the probability of detection given occupancy (PSI × P) at each scale. We also created a multi-scale map for the Yellowhead Population Unit to determine whether the predictive performance could be improved by combining variables from both scales. New model-averaged parameter estimates were calculated using the final models from each scale, which we used to predict probabilities of grizzly bear occupancy (PSI), detectability (P), and detectability given occupancy (PSI × P).

Lastly, we assessed the predictive ability of the probability of occupancy (PSI) and the probability of detection given occupancy (PSI × P) maps using detection–nondetection data from the 2004 grizzly bear DNA hair trap survey. In doing so, occupancy and detectability were assumed to be constant among years despite possible changes. Area under the curve (AUC) of the receiver operator characteristic curve (ROC) was used to measure model accuracy. AUC is a threshold-independent evaluation of model performance (Manel et al. 2001) that measures the ability of the model to differentiate between sites where a species is considered present versus where it is considered absent. Models were considered to have poor accuracy with AUC values of 0.5–0.7, fair accuracy with values of 0.7–0.8, good accuracy with values of 0.8–0.9, and excellent accuracy with values > 0.9 (Swets 1988).

Results

In total, we collected over 600 hair samples and analysed 371 hair samples for DNA. Of these 371 samples, 158 (43%) samples were not extracted because their appearance was inconsistent with that of grizzly bear hair when viewed under a dissecting microscope. Another 20 (5%) samples lacked suitable material for extraction. Of the 193 (52%) remaining hair samples, 75 (20%) were black bear and 92 (25%) were given an individual grizzly bear identity. Samples with ≥ 3 guard root hairs had a success rate of 94% with the pre-screen marker G10J; the overall success rate for multilocus genotyping was 88%. Based on the observed mismatch distribution, most similar genotypes in our dataset were two pairs that matched at six of the eight markers used to identify individuals. Given that matches at all markers are expected to be less common than matches at all-but-one marker (Paetkau 2003), and given that we observed no matches at all-but-one marker, it is almost certain that the selected marker system produced a unique genotype for each individual that we sampled.

Grizzly bears were detected at 25 of the 60 sites (41.7%) (Fig. 1) resulting in the identification of 21 unique grizzly bears – 12 females and 9 males. Following univariate analyses, a total of 15 variables (Supplementary material Appendix 1 Table A1) were considered for a priori (phase 1) analyses of grizzly bear occurrence and detectability. As expected, grizzly bear occurrence and detectability was found to vary across sites due to spatial variation of anthropogenic features and food resource patches (Table 2). Contrary to our prediction, detectability was not found to vary over time.

Following a posteriori (phase 2) analysis, grizzly bear occupancy at the patch scale was positively related to elevation ($\beta = 2.75 \pm 1.21$) and buffaloberry density ($\beta = 2.62 \pm 2.09$) and negatively related to distance to oil and gas wellsites ($\beta = -2.47 \pm 1.2$) (Table 3). In other words, grizzly bears were more likely to occur in higher elevation habitats containing buffaloberry and in areas near oil and gas wellsites. Grizzly bear detectability at this scale was positively related to clover *Trifolium* spp. cover ($\beta = 0.50 \pm 0.17$) and negatively related to distance to stream ($\beta = -1.19 \pm 0.44$) (Table 3). A quadratic response of grizzly bear detectability

and crown closure was found (CC: $\beta = 0.55 \pm 0.81$, CC^2: $\beta = -1.39 \pm 0.75$) indicating that intermediate levels of crown closure had the highest probability of detection.

At the landscape scale, grizzly bear occupancy was negatively related to distance to protected areas ($\beta = -2.17 \pm 1.03$), distance to pipelines ($\beta = -1.21 \pm 0.57$), and the interaction of crown closure with terrain wetness (CTI $\beta = -0.84 \pm 0.58$) (Table 3). The interaction of crown closure with wetness suggests that occupancy increases in open stands that are wet. Detectability of grizzly bears at the landscape scale was negatively related to distance to stream ($\beta = -0.97 \pm 0.42$) and distance to oil and gas wellsites ($\beta = -0.28 \pm 0.06$) (Table 3). Detectability was also negatively related to the interaction of food resources with distance to ($\beta = -0.30 \pm 0.07$) and density of ($\beta = -0.72 \pm 0.34$) oil and gas wellsites. In other words, grizzly bears were more likely to be detected near oil and gas wellsites with low surrounding food availability and low wellsite density.

We applied each model in a GIS to estimate predicted probabilities of grizzly bear occupancy (PSI), detectability (P), and detectability given occupancy (PSI × P) for the 2011 study area (Fig. 2, 3). Probability of grizzly bear detection was low (0.22 ± 0.19) at both scales. For the multi-scale model, new model-averaged parameter estimates (Table 4) were calculated using the final models from each scale, which we used to predict probabilities of grizzly bear occupancy (PSI), detectability (P), and detectability given occupancy (PSI × P). Model performance was assessed for the 2011 study area and the wider Yellowhead Population Unit using the area under the curve (AUC) of the receiver operator characteristic (ROC) and detection–nondetection data from the 2004 grizzly bear DNA hair snag survey. For the 2011 study area, the landscape scale model of detectability given occupancy had the highest AUC score (AUC = 0.662) (Table 5), although all landscape models predicted poorly, with AUC scores lower than 0.7. Model performance increased for the Yellowhead population unit for all but one model (Table 5). The highest AUC scores resulted from patch (300 m) scale models of detectability given occupancy (AUC = 0.768) and occupancy (AUC = 0.705) for the Yellowhead population unit (Table 5). Overall, patch models had better predictive ability than landscape models (Table 5).

Table 2. Final model structure use to predict the probability of grizzly bear occurrence and detection at two scales in west–central Alberta, Canada. Each scale reports Akaike's information criterion (AIC), change in AIC (ΔAIC) relative to the top ranked model and Akaike weights (w$_i$). Variables are described in the Supplementary material Appendix 1 Table A1.

Scale	Final model structure	AIC	ΔAIC	w$_i$
300 m	psi(DEM + shecan_dns + well_dec), p(trif + stream + CC + CC²)	227.00	0.00	0.69
	psi(DEM + shecan_dns + well_dec), p(trif + stream + CC)	228.61	1.61	0.31
	psi(.), p(.)†	253.58	26.58	0.00
1690 m	psi(CC× CTI + park_dec + pipe_dec), p(tfood× well_dns + tfood× well_dec + stream)	232.81	0.00	0.35
	psi(CC× CTI + park_dec + pipe_dec), p(tfood× well_dns + stream)	232.89	0.08	0.34
	psi(CC× CTI + park_dec + pipe_dec), p(tfood× well_dns + stream + well_dec)	233.08	0.27	0.31
	psi(.), p(.)	253.58	20.77	0.00

† The null model is indicated as psi(.), p(.)

Table 3. Model-averaged parameter estimates, standard errors (SE), and 90% confidence intervals (CI) for the final models used to model the probability of grizzly bear occurrence and detection at two scales in west–central Alberta, Canada. Coefficients are standardized to indicate the strength between factors and therefore do not directly relate to the unit of measure of the variables.

Scale	Model	Parameter	Variable	Estimate	SE	90% CI Upper	90% CI Lower
300 m	Occupancy	Occupancy intercept	PSI	1.554	0.880	2.997	0.112
		Elevation	DEM	2.753	1.205	4.729	0.776
		Shepherdia canadensis density	shecan_dns	2.621	2.085	4.417	0.825
		Distance to wellsite	well_dec	–2.470	1.200	–0.502	–4.439
	Detectability	Detectability intercept	P	–1.894	0.264	–1.461	–2.328
		Trifolium spp. cover class	trif	0.500	0.167	0.773	0.226
		Distance to stream	stream_dec	–1.186	0.441	–0.462	–1.909
		Crown closure	CC	0.550	0.805	1.871	–0.771
		Crown closure²	CC²	–1.391	0.749	–0.162	–2.620
1690 m	Occupancy	Occupancy intercept	PSI	0.597	0.528	1.464	–0.269
		Distance to park	park_dec	–2.166	1.029	–0.478	–3.853
		Distance to pipeline	pipe_dec	–1.206	0.571	–0.270	–2.141
		CC × CTI interaction	CC×CTI	–0.843	0.579	0.106	–1.793
	Detectability	Detection intercept	P	–1.562	0.265	–1.128	–1.997
		Distance to stream	stream_dec	–0.968	0.415	–0.288	–1.649
		Distance to wellsite	well_dec	–0.283	0.062	–0.181	–0.385
		Food × Well density interaction	tfood×well_dns	–0.715	0.338	–0.161	–1.270
		Food × Distance to wellsite interaction	tfood×well_dec	–0.296	0.072	–0.178	–0.414

The multi-scale model (Table 4, Fig. 4) had poor performance when all variables were included in the model (Table 5). This was likely because the distance to wellsite variable used to estimate occupancy within the 2011 study area (where wellsite density is low) extrapolates poorly to the Yellowhead Population Unit where wellsite density is high in the east. Predictive performance of the multi-scale model for both occupancy and detectability given occupancy improved once distance to wellsite was removed (Table 5). The multi-scale model with the highest AUC score (AUC = 0.757) resulted from estimates of occupancy for the Yellowhead population unit after oil and gas wellsites were removed from the model (Table 5).

Discussion

As hypothesized, the spatial variation of anthropogenic features and resource availability resulted in variation among sites of grizzly bear occurrence and detectability. Overall, predicted grizzly bear detectability was low for each observed scale (0.22 ± 0.19). This is consistent with detection rates of other grizzly bear mark recapture studies (Boulanger et al. 2002). Difficult terrain and poor access in this region make optimal site placement a challenge and thus higher detection rates are rarely achieved. Capture probabilities (i.e. detection rates) > 0.2 are, however, considered reasonable and provide adequate statistical power to estimate population size and detect trends (Mowat et al. 2002). Consequently, DNA hair trap sampling methods that use a network of fixed sample sites can be used for long-term grizzly bear monitoring programs in west–central Alberta. Strategic placement of sites will help to ensure that detection rates are at or above the 0.2 threshold.

Resource availability was expected to influence grizzly bear detection rates at the patch scale. Buffaloberry in particular was found to have a strong, positive influence on grizzly bear occupancy. Buffaloberry is one of the most productive fruit
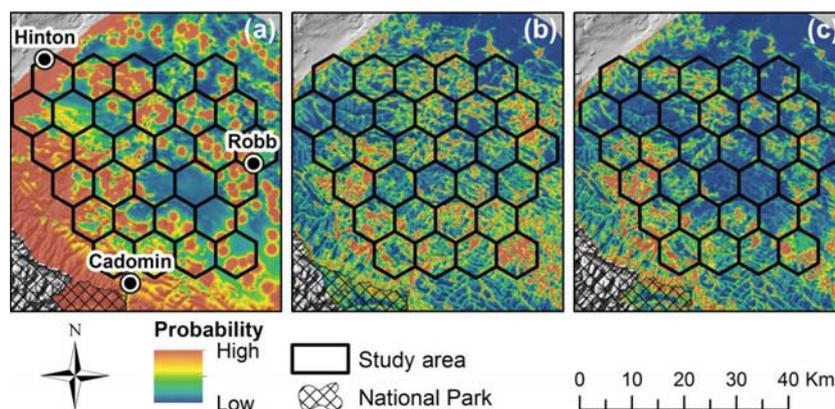

Figure 2. Probability of occupancy (a), detectability (b), and detectability given occupancy (c) of grizzly bears in west–central Alberta, Canada at the patch scale (300 m). Probabilities range from 0 to 100%.
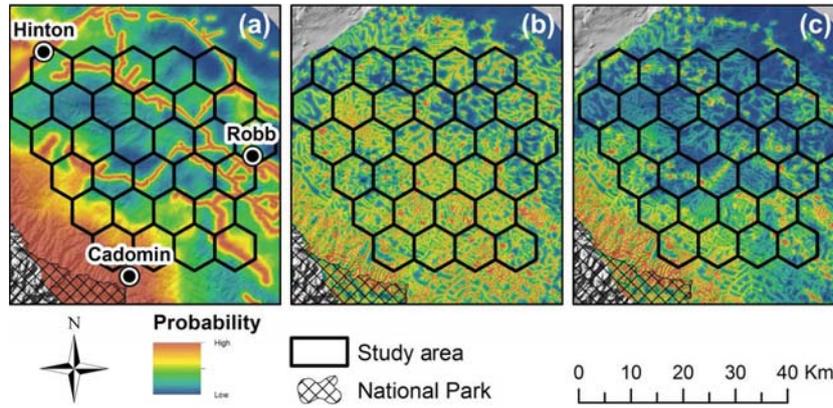
Figure 3. Probability of occupancy (a), detectability (b), and detectability given occupancy (c) of grizzly bears in west–central Alberta, Canada at the landscape scale (1690 m). Probabilities range from 0 to 100%.

species (McLellan and Hovey 1995, Nielsen et al. 2004b), and its fruit is high in soluble carbohydrates (Hamer and Herrero 1987), apparent digestive energy (McLellan and Hovey 1995), and protein (Coogan et al. 2012). The results of this study confirm the assumption that bears in the foothills will select habitats based on the presence and density of buffaloberry shrubs during June, July and August (Hamer 1996). Clover *Trifolium* spp. influenced grizzly bear detectability, but not occupancy. Rode et al. (2001) found that clover was used extensively by grizzly bears where it was abundant and associated with other food resources, which suggests that clover does not solely influence habitat selection (i.e. occupancy). Rather, clover and other species such as pea vine, dandelions, and alfalfa are often associated with disturbed areas that include ditches, clear-cuts, reclaimed mine sites, pipelines and oil and gas wellsites (Haeussler et al. 1999, Roberts and Zhu 2002, Nielsen et al. 2004b).

The interaction of anthropogenic features with food resources was investigated at the landscape scale. Grizzly bear occupancy was found to increase closer to oil and gas wellsites at the patch scale and closer to pipelines at the landscape scale. McKay et al. (2014) presumed that the degree of wellsite use by grizzly bears would be higher when food availability in the surrounding matrix was poor. Our results support this hypothesis, as the detectability of grizzly bears was found to increase closer to oil and gas wellsites with low surrounding food resources. Probability of detecting a grizzly bear also increased in areas of low oil and gas wellsite density. Grizzly bears may avoid wellsites at higher wellsite densities due to increased traffic volume and higher likelihood of encounters with humans, especially if there is reduced cover, which is often the case (McLellan and Shackleton 1989, Gibeau et al. 2002). McKay et al. (2014) also found that grizzly bears will repeatedly visit certain wellsites over others within their home range therefore hair traps placed in areas of higher wellsite densities would not necessarily increase the probability of a grizzly bear encountering a trap.

One unexpected result of this study was that grizzly bear detection rates did not vary over time (spring to summer period sampled). We expected that pulsing of seasonal foods, especially fruiting species, would compete with hair trap sites during hyperphagic periods causing a decrease in grizzly bear

Table 4. Model-averaged parameter estimates, standard errors (SE), and 90% confidence intervals (CI) for the multi-scale model used to model the probability of grizzly bear occurrence in west–central Alberta, Canada. Coefficients are standardized to indicate the strength between factors and therefore do not directly relate to the unit of measure of the variables.

Model	Parameter	Variable	Scale	Estimate	SE	90% CI Upper	90% CI Lower
Occupancy	Occupancy intercept	PSI		1.462	0.897	2.933	−0.009
	Elevation	DEM	300 m	2.753	1.205	4.729	0.776
	Shepherdia canadensis density	shecan_dns	300 m	2.621	1.095	4.417	0.825
	Distance to wellsite	well_dec		−2.470	1.200	−0.502	−4.439
	Distance to park	park_dec		−2.166	1.029	−0.478	−3.853
	Distance to pipeline	pipe_dec		−1.206	0.571	−0.270	−2.141
	CC × CTI interaction	CC×CTI	1690 m	−0.843	0.528	0.023	−1.710
Detectability	Detectability intercept	P		−1.862	0.279	−1.405	−2.320
	Trifolium spp. cover class	trif	300 m	0.500	0.167	0.773	0.226
	Crown closure	CC	300 m	0.550	0.805	1.871	−0.771
	Crown closure^2	CC^2	300 m	−1.391	0.749	−0.162	−2.620
	Distance to stream	stream_dec		−1.165	0.443	−0.437	−1.892
	Distance to wellsite	well_dec		−0.283	0.202	0.049	−0.614
	Food × Well density interaction	tfood×well_dns	1690 m	−0.715	0.338	−0.161	−1.270
	Food × Distance to wellsite interaction	tfood×well_dec	1690 m	−0.296	0.204	0.039	−0.631

Table 5. Area under the curve (AUC) scores for individual and multi scale models used to predict grizzly bear occurrence and detectability in west–central Alberta, Canada. At each scale, the predictive ability of occupancy models (PSI) and detectability given occupancy (PSI × P) models were assessed. Predictive ability was assessed across two areas: the 2011 study area and the larger Yellowhead Population Unit.

Scale	Model	Description	AUC by study area	
			2011	YH
300 m	PSI × P		0.543	0.768
300 m	PSI		0.529	0.705
1690 m	PSI × P		0.662	0.618
1690 m	PSI		0.606	0.658
Multi-scale	PSI × P	all variables	0.507	0.672
Multi-scale	PSI	all variables	0.567	0.699
Multi-scale	PSI × P	without wellsite variable	0.472	0.677
Multi-scale	PSI	without wellsite variable	0.654	0.757

detections. No support was found for this hypothesis. One possibility is that the blood lure at a hair trap site (suggesting the presence of carrion) may be as attractive to bears as fruit during hyperphagia when bears must accumulate considerable mass before the denning period. Male bears in particular rely more on animal protein than do females to sustain their larger size (Jacoby et al. 1999, Hobson et al. 2000). As a result, grizzly bears may not discriminate between fruit and animal protein, effectively eliminating any competition of the hair trap site with berry crops.

It is also possible that sampling did not extend far enough into the hyperphagic period to adequately address this question. Grizzly bears do not enter the den until November (Graham and Stenhouse 2014), with the berry season running from August to October (Nielsen et al. 2004a).
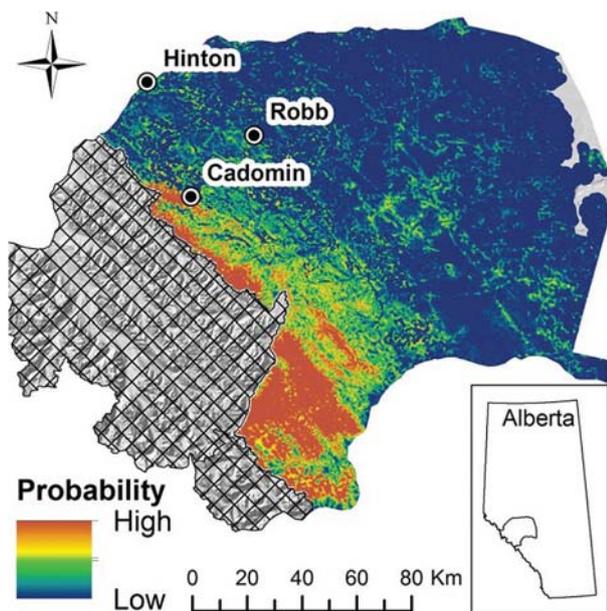

Figure 4. Predicted probability of detection given occupancy (PSI × P) for grizzly bears in the Yellowhead Population Unit using a multi-scale model that combined model results from the patch (300 m) and the landscape (1690 m) scale analyses.

Sampling for this study would have only overlapped with the first month of the berry season, which may be insufficient if berries are slow to emerge or ripen. Due to a wetter than normal summer, berry production appeared to be later than normal within our study area. It is possible that competition between hair trap sites and berry crops would be more apparent had sampling extended into September or October. An extended sampling season would therefore be more valuable, potentially, than completing a second season of sampling. Most of the variables identified in our results are unlikely to vary significantly year to year, such as elevation, canopy cover, and streams. Likewise, pipelines and wellsites are prominent features on the landscape and regeneration of these features is slow. As a result, it's unlikely that the factors affecting grizzly bear detection identified in this study would themselves change, although the strength of some factors could fluctuate as a result annual variation in local habitat conditions.

Model performance was assessed using detection–nondetection data from the 2004 grizzly bear DNA hair trap survey. Model predictive performance for the 2011 study area was generally poor. The number of variables included in the models was limited due to the study's small sample size – a result of logistical constraints (two week sessions) resulting in 60 sites sampled over a 1500-km² study area, but repeatedly sampled across six sessions. Although grizzly bear habitat models alone typically include between 6 and 24 variables (Mace et al. 1999, Apps et al. 2004, Nielsen et al. 2006), model complexity in this study was limited to a maximum of eight variables. Small numbers of site level observations of spatial variables can lead to an increase in type II errors where one fails to detect significance when present. Hierarchical model building and the testing of every variable within a theme reduced the risk of excluding a significant variable while over parameterization was reduced by limiting variables within a theme from the univariate analysis and the use of AIC to penalize for over-fitting. Because the number of observations was the number of sites × the number of sessions (60 sites × 6 session = 360 observations), over-fitting was not a concern. This study – with 50 km² cells and six sampling sessions – is considered a robust study design (Boulanger et al. 2002) with an adequate number of observations for modeling variation in detection probabilities. Nonetheless, a greater number of sites would improve our ability to consider complex models of both occupancy and detectability simultaneously.

There are several factors that likely affect the success of hair trap sites that were not included in this study. Wind, air temperature, relative humidity, precipitation and other local weather conditions could affect how the scent of the lure disperses through air or even degrade a scent (Syrotuck 1972, Pearsall and Verbruggen 1982, Snovak 2004, Smith et al. 2005, Harrison 2006). Biological factors (e.g. age, sex, reproductive status, health) and individual bear behaviours may also affect how a grizzly bear is attracted to a hair trap site (Boulanger et al. 2004). We minimized the risk of sex-based heterogeneity by using a cell size that is relatively small compared to the average home range size of a female grizzly bear with cubs (Boulanger et al. 2004). Because sites are not moved, fixed sites are thought to increase risk of behavioural bias due to habituation to a site (Boulanger et al. 2006). In

a comparison of fixed and moved sites, however, Boulanger et al. (2006) did not find a difference in capture frequencies between the two methods. Similarly, a separate analysis of our data by J. Boulanger (Integrated Ecological Research, unpubl. data) did not find evidence of a behavioural response due to previous handling and/or capture.

Overall, the same sources of heterogeneity exist in moved and fixed designs and no one source of heterogeneity is amplified for fixed sites. Consequently, the fixed design is capable of robust and precise estimates of abundance given an adequate cell size and number of sampling sessions. When the cell size is the same, projects using fixed sites are significantly less expensive than projects that move sites between sessions (Boulanger et al. 2006), making it an appealing option for long term monitoring. By demonstrating the importance of environmental conditions and resources for grizzly bear detection, this study can help to guide optimal placement of fixed hair trap sites. Optimal placement of fixed hair trap sites will increase detection rates and help, in part, to ensure the most cost-effective monitoring results.

Nonetheless, grizzly bears will remain logistically challenging to monitor. Remote cameras could be used to better understand the proportion of bears that encounter a fixed site but do not leave hair, which could better inform detection probabilities of DNA hair traps. To further reduce costs of monitoring, future studies should investigate the detection probabilities of other DNA sampling methods such as scat and hair collected from rub trees (alone and in combination). A better understanding of search effort and optimal study design for long term trend monitoring using a multi DNA source approach is also needed. Lastly, given that grizzly bears are a recovering species in Alberta, a better understanding of how grizzly bear occupancy and detectability varies near the eastern range edge would aid monitoring in this area, which is important for measuring range expansion and the success of recovery efforts.

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Supplementary material (available online as Appendix wlb-00033at <www.wildlifebiology.org/readers/appendix>). Appendix 1.