University of Alberta

Factors affecting the detectability and eastern distribution of grizzly bears in Alberta, Canada

by

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DEDICATION

In dedication to my parents Mark and Lori.

ABSTRACT

Effective and adaptive conservation of a species requires knowledge of trend in abundance and distribution. Monitoring species that are highly mobile, cryptic, and occurring at low densities is especially challenging. This research investigates the local factors affecting the detectability of grizzly bears (*Ursus arctos*) in west-central Alberta, as well as regional factors affecting their eastern distribution in the province. When surveyed using a permanent DNA hair trap design, grizzly bear detection is maximized when sites are placed in areas with abundant buffaloberry and clover cover and near pipelines, wellsites, cutblocks, and streams. To the east, grizzly bear range is limited by agricultural zones, human settlements, and the loss of secure wild land habitat. Such information can help guide the placement of monitoring sites in core and peripheral habitats, which may help lower the cost of long-term monitoring programs of grizzly bear populations and range edge.

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CHAPTER 1

GENERAL INTRODUCTION

Human actions underlie many species declines in North America. Terrestrial carnivores are particularly sensitive to habitat fragmentation, disturbance, and exploitation by humans (Weaver et al. 1996), which has led to mounting concern about their status and distribution (Gese 2001, Wilson and Delahay 2001, Treves and Karanth 2003, Barea-Azcón et al. 2007). As a result, it is becoming increasingly important in carnivore conservation and management (Kindberg et al. 2011) to monitor spatial and temporal trends in their distribution, abundance, and other biological and ecological measures (Yoccoz et al. 2001, Schwartz et al. 2007, Long 2008). Estimating these measures, however, is particularly challenging when dealing with rare or elusive species because of their low numbers and secretive and/or nocturnal behaviour. This is especially true of carnivores, which are often secretive, far-ranging, and exist at low densities in remote or densely vegetated areas (Gese 2001). Monitoring these species can therefore be both difficult and costly (e.g. Karanth et al. 2006, Golden et al. 2007, Balm et al. 2009, Proctor et al. 2011).

As a result, one of the biggest challenges to long-term monitoring programs of carnivores and other hard-to-detect species is to develop techniques and protocols that maximize the detection of the species while minimizing costs. It is highly unlikely that a species will always be detected when present at a site therefore failure to detect a species does not mean the species was not there

(MacKenzie et al. 2002). To avoid underestimates of occupancy and abundance, one must therefore account for detectability – the probability of detecting the species if present (MacKenzie et al. 2002). Habitat models can be biased by the imperfect detection of a species (Mackenzie and Royle 2005). Accounting for detectability in analytical methods and models continues to be one of the growing areas in biometric research (Thompson 2004). Detection probabilities are being incorporated into occupancy and abundance estimates for a wide range of taxa including plants (Chen et al. 2009, Emry et al. 2011), amphibians (Bailey et al. 2004, Seddon et al. 2011, Olson et al. 2012), reptiles (Christy et al. 2010, Durso et al. 2011), invertebrates (Pellet 2008, Hudgins et al. 2012, Ward, Stanley 2013), birds (Olson et al. 2005, Kissling et al. 2010, Latif et al. 2012, Malzof et al. 2013), bats (Meyer et al. 2011), and carnivores (Tyre et al. 2003, Hines et al. 2010, Jeffress et al. 2011, Schooley et al. 2012). The need to account for detectability has also been recently recognized for monitoring primates (Baker et al. 2011, Keane et al. 2012) and for marine conservation management (Katsanevakis et al. 2012, Monk 2013). For monitoring programs, one of the main challenges is the placement of data collection sites to maximize detection. MacKenzie and Bailey (2004) note that detection probabilities for many species will vary with local environmental conditions. As a result, understanding local factors that affect detection is necessary for improving survey designs and for directing survey efforts.

Understanding and maximizing detectability is one of the main challenges in the conservation of grizzly bears (*Ursus arctos*) in Alberta, which were listed as a threatened species in the province in June 2010. While single point population estimates in the province are known (Alberta Sustainable Resource Development and Alberta Conservation Association 2010), there are no monitoring programs in place to identify trends in population size or distribution, if or when recovery targets are reached (once targets are established), or the effectiveness of management actions. Knowledge and understanding of such trends will be crucial to directing recovery actions and evaluating the success of those efforts (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). As Boulanger et al. (2011) summarizes when using traditional methods of population monitoring, “In Alberta, the low densities and wide provincial distribution of grizzly bears, coupled with habitats that are often difficult to access, makes it both challenging and expensive to collect data to provide scientifically defensible population estimates”. Alberta requires cost-effective monitoring techniques to ensure recovery efforts are working successfully towards a goal of self-sustaining grizzly bear populations over the long term (Boulanger et al. 2011).

Noninvasive genetic sampling is ideally suited for monitoring rare or hard-to-capture species (Mills et al. 2000) because hair can be collected remotely without having to catch or disturb the animal (Taberlet et al. 1999). Traditional DNA hair sampling designs for estimating grizzly bears populations have moved hair-snag sites between sessions (Taberlet et al. 1999, Mowat and Strobeck 2000, Poole et al. 2001, Proctor et al. 2005, Boulanger et al. 2006, Kendall et al. 2008). Although this method is well accepted and precise, it is also effort intensive and costly, which makes it unsuitable for use in long-term population monitoring. An alternative that may lower costs and be better suited for monitoring grizzly bears is to use fixed sample plots in non-invasive DNA hair sampling designs (Boulanger et al. 2006). Because sites cannot be moved, the timing and location of these sites will be paramount for designing monitoring programs that maximize detectability while minimizing costs. Designing a cost-effective monitoring program using fixed sample plots will require knowledge of local factors affecting the detectability of grizzly bears, which remains uninvestigated.

In addition to population size, knowledge of a species distribution is fundamental to managing their conservation (Angert et al. 2011). Understanding why a species occurs in one area but not another can be integrated with land-use management decisions and conservation efforts to ensure their long-term persistence. It is also vital to planning networks of protected areas, wildlife corridors, and recovery zones, as well as predicting future range patters under varying landscape and environmental conditions. Climate change, habitat loss and fragmentation, over-exploitation, and other anthropogenic forces will undoubtedly influence species' geographic ranges – this may manifest as range contraction, expansion, or shifts (Brown et al. 1996). Due to the rapid rate of human-induced landscape change, conservation efforts also would benefit from long-term monitoring of species' geographic range (Opdam and Wascher 2004).

What limits species' geographic ranges remains a perplexing question in many research fields, including ecology, evolution, epidemiology, and physiology. Understanding where a species occurs and why it occurs where it does is complex; there are three main types of limiting factors that should be considered including: i) abiotic and biotic factors; ii) population dynamics; and iii) genetic mechanisms (Gaston 2003). Limiting factors to geographic ranges can also vary depending on the temporal and spatial scale of the analysis (Gaston 2009). A large body of research has focused on identifying the abiotic and biotic factors limiting species' ranges (Brown et al. 1996), especially at large spatial scales (e.g. Connell 1961, Gross, Price 2000, Holt, Keitt 2000, Case et al. 2005, Illera et al. 2006, Arntzen, Themudo 2008, McInnes et al. 2009, Bridle et al. 2010, Glor, Warren 2011, Gifford, Kozak 2012, Werner et al. 2013). Similarly, macroecological perspectives on species limits have investigated coarse-scale limiting factors (McInnes et al. 2009, Roy et al. 2009, Baselga et al. 2012). Larger scale investigations are also necessary for investigating genetic and evolutionary mechanisms behind geographic ranges (Price and Kirkpatrick 2009, Moeller et al. 2011, Stanton-Geddes et al. 2013). The role of population dynamics as limiting factors to species ranges has been investigated at the population scale (Keitt et al. 2001, Bahn et al. 2006, Melles et al. 2011), while community perspectives have been studied at larger scales (Case et al. 2005). The majority of species' ranges are studied using a single- or two-species approach, but multi-species approaches have also been attempted (Williams et al. 2002, Morin et al. 2007, Pigot et al. 2010). Nonetheless, we still lack a comprehensive understanding for any one species (Gaston 2009).

Grizzly bears are an example of a species whose range limits remain poorly understood. Although the range of the North American grizzly bear once spanned most of the continent (Schwartz et al. 2003), it has contracted substantially due to habitat loss and over-exploitation (Mattson and Merrill 2002; Ross 2002). Grizzly bears are threatened in the continental United States having lost 98% of their historical range (Servheen 1990). In Alberta, grizzly bear range is largely restricted to mountainous and forested habitats found in western portions of the province. Historically, roads, farming and ranching, settlements, and animal control measures have played a role in extirpating grizzly bears from other portions of Alberta (Nielsen et al. 2004, Mattson and Merrill 2002, Alberta Grizzly Bear Recovery Plan 2008). Further grizzly bear range contraction should be avoided if current populations are to be maintained or restored as part of the Alberta Grizzly Bear Recovery Plan. Additionally, if recovery efforts are successful, certain portions of the province could experience expanding grizzly bear range.

As a result, understanding the current distribution of grizzly bears in Alberta and the factors limiting this distribution is necessary for effective grizzly bear conservation and land-use management. Knowing what factors limit grizzly bear range could lend insight into areas susceptible to range contraction and/or areas suitable for range expansion therefore helping to prioritize conservation efforts. Monitoring grizzly bear populations along the range periphery would help to evaluate whether goals of the recovery plan are met and whether the long-term persistence of grizzly bears in Alberta is achieved. Additionally, identifying what factors limit grizzly bear range may also allow managers to predict how the distribution of grizzly bears might change following population increases, decreases, or changes in the environment (anthropogenic landscape change associated with resource extraction, etc.). Despite the importance to grizzly bear conservation and management, no formal study has been used to delineate range edge of grizzly bears in Alberta nor attempted to understand why it occurs where it does.

The overarching goal of this thesis is to support the development of trend monitoring techniques and aid in the conservation and management of grizzly bears in Alberta. It is hoped that the results of this study will help form the basis of long-term monitoring programs and targeted conservation efforts for the recovery and post-recovery management of grizzly bears. This thesis contains four chapters, including an introduction and conclusion, and is organized as two independent manuscripts formatted in accordance with author submission guidelines for the *Journal of Wildlife Management*.

In Chapter 2, I investigate issues of detectability concerning fixed DNA hair sampling methods. Specifically, I investigate how local environmental factors affect detectability of grizzly bears, understanding of which would allow managers to identify the best seasonal timing and spatial location for placement of fixed hair-snag sites. I also examine change in occupancy state between 2004 and 2011 as a way to explore change in occupancy patterns over time. In Chapter 3, I delineate the range of male and female grizzly bears in Alberta and use this to investigate limiting factors at the range edge. Knowledge of the factors limiting grizzly bear range in Alberta will aid the development of long-term monitoring protocol along the range periphery. Chapter 4 concludes with a general summary of my work and management implications.

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CHAPTER 2

IN THE TRAP: DETECTABILITY OF FIXED HAIR TRAP DNA METHODS IN GRIZZLY BEAR TREND MONITORING

1. INTRODUCTION

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

In arriving at such estimates, CMR approaches involve a number of technical challenges. A critical step when using detection-nondetection data in a noninvasive CMR study is to recognize that the failure to detect a species does not mean the species was not present (Kery 2002, MacKenzie et al. 2002, Tyre et al. 2003). As a result, the probability that a site is occupied by a species of interest will be underestimated if one simply divides the number of sites where the species was detected by the total number of sites surveyed (MacKenzie et al. 2002).

Instead, one must include the probability of detecting a species to get unbiased occupancy estimates (MacKenzie et al. 2002, Tyre et al. 2003, Stauffer et al. 2002, Wintle et al. 2004). A successful CMR survey also requires that researchers maximize the probability that a species of interest is detected while minimizing differences in individual detection rates (Long 2008); this is often referred to as the "big law of mark-recapture" (Lukacs and Burnham 2005). When monitoring species with small populations – such as endangered and threatened species – it is important that small changes in population trend can be detected, as even small changes could have significant impacts on the status of the population. The ability to do so requires adequate detection rates for the species of interest.

Maximizing detection rates is a challenge for many monitoring programs because detectability depends in part on population density, sampling approaches, and effort (Gu and Swihart 2004). Most monitoring programs, however, focus on rare species and operate under logistical and monetary constraints. Thus, it can be difficult to achieve the high probabilities of detection needed for low-density and wide-ranging species when trade-offs are required between sampling intensity and monitoring costs. Detectability also can be influenced by local landscape and habitat features, such as difficult terrain and dense cover (Nupp and Swihart 1996, Mancke and Gavin 2000, Odell and Knight 2001, MacKenzie 2006). As a result, low detectability can result from species that are cryptic, 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 (e.g. 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 explored the relationship between habitat covariates and detection.

One species that would benefit from such knowledge is the grizzly bear (*Ursus arctos*). Grizzly bears were listed as a threatened species in Alberta in 2010. To make educated and effective management and conservation decisions, a monitoring program needs to identify trends in population size and distribution, if or when recovery targets are reached (once established), and the effectiveness of various management activities. Noninvasive DNA hair trap sampling techniques have been used extensively to estimate population size of grizzly bears (e.g. Woods et al. 1999, Boulanger et al. 2002, 2005a, b; Poole et al. 2001; Kendall et al. 2008; Gervasi et al. 2010). For Alberta's foothills, it is likely that monitoring efforts will require some form of hair trap DNA method. 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). Sites are often moved according to random placement or in response to anticipated grizzly bear movements. This strategy is, however, effort-intensive and costly, which makes it unsuitable for use in long-term population monitoring.

Fixed (permanent) sample plots in hair trap survey designs may offer an alternative approach that lowers costs while retaining the ability to detect trends (i.e. sufficient detectability). Because the sites are not moved and because grizzly bears in Alberta are cryptic, wide-ranging, and occur at low densities, ensuring adequate detection rates is crucial for successful implementation. For example, grizzly bears are often sighted near the town of Robb, Alberta (Figure 2-1), but were rarely detected by hair traps in the area. 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 must be understood to optimize the timing and placement of fixed hair trap sites for maximum detectability. For example, one common assumption is that it is more effective to sample bears with hair traps in spring soon after bears emerge from their dens, as they are more likely to be wandering large distances in search of food and mates (S.E. Nielsen, University of Alberta, personal communication). Sampling may also 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) but they also might use roadside ditches, pipelines, and wellsites where there is a high risk of mortality (Nielsen et al. 2006, Roever et al. 2010, Sahlen 2010). Anthropogenic features and resource availability have been important for properly quantifying grizzly bear habitat quality (Nielsen et al. 2010); however, it is not clear how these factors influence grizzly bear behaviour near 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 I investigate local factors affecting the occupancy and detection of grizzly bears in west-central Alberta. Although occupancy is not useful for setting recovery targets and harvest quotas of grizzly bears, it is useful for better understanding detectability, which offers a way to stratify site placement. It is expected that grizzly bear detectability will vary considerably at different sites and seasons (time) due to the spatial and temporal variation of anthropogenic features and seasonal resource availability. I 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; and (2) anthropogenic features such as wellsites and forest cutblocks will positively affect detectability due to increased forage on disturbed sites (Martin 1983, Waller 1992). Due to the large time span (7 years) between grizzly bear DNA surveys in this area, I also examine change in occupancy between 2004 and 2011 by analysing the change in occupancy status of repeatedly sampled sites.

2. STUDY AREA

I delineated a 1,500-km^2 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 km^2 in size (Figure 2-1). The majority of the study area is located in core grizzly bear conservation areas where management objectives are to keep road densities below 0.6 km/km^2 (Nielsen et al. 2009). The remainder of the study area is located in secondary conservation areas where the management objective is to maintain road density below 1.2 km/km^2. The majority of the study area also overlaps a previous grizzly bear DNA inventory project conducted in 2004 (Boulanger et al. 2005a). Seven grizzly bear population units have been defined in Alberta (Alberta Sustainable Resource Development and Alberta Conservation Association 2010); this study area falls within the Yellowhead Population Unit.

Elevations in the foothills ranged from 936-m to 2772-m within the study area. Vegetation consisted of mixed forests of lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*) and tamarack (*Larix laricina*) associated with wet sites; and mixed aspen (*Populus tremuloides*), white spruce (*Picea glauca),* and open stands of lodgepole pine associated with drier sites. Open marshes and low gradient riparian areas are also common here where wetlands are mostly dominated by stunted black spruce and tamarack or shrub-graminoid communities. 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). Large carnivores in the study area include the American black bear (*Ursus americanus*), wolf (*Canus lupis*), and cougar (*Puma concolor*). A diverse range of ungulates are present including moose (*Alces alces*), elk (*Cervus canadensis*), white-tail deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and a population of big horn sheep (*Ovis canadensis*) (Munro et al. 2006). The American beaver (*Castor canadensis*) and other small mammal prey items are also found in the foothills.

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. Immediately adjacent to all but the northern portion of the study area are open pit coal mines. High resource extraction has resulted in changing land use patterns and landscape characteristics (Yamasaki et al. 2008) and a large increase in the number of roads in grizzly bear habitat (Alberta Forestry, Lands and Wildlife 1990). Widespread linear features provided access to the study area and included roads, pipelines, seismic lines, and ATV trails.

3. METHODS

Between June 1 and August 25 of 2011, I sampled grizzly bears using 60 fixed DNA hair traps located within a 1,500-km^2 study area in the Yellowhead Population Unit. Microsatellite analysis of hair samples allowed for the individual identification of bears. Using detection-nondetection data and a single-season model in program PRESENCE (Proteus Wildlife Research Consultants, Dunedin, New Zealand), I investigated local factors affecting the occupancy and detectability of grizzly bears at two spatial scales surrounding a sampling site – the patch (a 300 m radius) and the landscape (a 1690 m radius) scale. Factors hypothesized to affect occupancy or detectability included anthropogenic features, topographic features, landcover, and food variables; I also tested whether the detectability of grizzly bears varied over time or remained constant. Final models were model-averaged at each scale and illustrated as predictive maps of grizzly bear occupancy and detectability. I assessed the predictive ability of each model using area under the curve (AUC) and detection-nondetection data from the 2004 grizzly bear DNA survey. Lastly, I used a multiple-season model in program PRESENCE and common sites (repeat sampled DNA sites) to investigate changes in occupancy between 2004 and 2011.

3.1. DNA Sampling

I sampled grizzly bears using 60 fixed hair traps (2 per cell) surveyed over six 14-day sampling sessions (Figure 2-1). I selected 44 site locations based on historic DNA locations (Boulanger et al. 2006), whereas the remaining 16 site locations were selected using a GIS (Geographical Information System) program, expert opinion, and grizzly bear resource selection function models (Nielsen et al. 2002). 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. I 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 (5 work days per week) from June 1 to August 25 for a total of six survey sessions. At each visit, I collected the hair, stored it in paper envelopes, and dried the samples at room temperature. The scent lure was refreshed at each visit. Using molecular analyses (mtDNA) (Woods et al. 1999), hair samples were genotyped to 7-loci for individual identification and 18-loci for parentage analysis (Appendix A-1) at the Wildlife Genetics International lab in Nelson, BC.

I 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 (Nielsen et al. 2011) 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, I recorded the density of alpine sweet vetch (*Hedysarum alpinum*), buffaloberry (*Shepherdia canadensis*), cow parsnip (*Heracleum lanatum*), moose (*Alces alces*) pellets and ant piles within 1-m of either side of the transect (i.e. a 200-m^2 area). Along the same 100-m segment, I recorded the relative abundance (cover) of 28 prominent bear foods (Appendix A-2). 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.

3.2. Predictor Variables

Variables used to predict the probability of detection were divided into five broad themes: anthropogenic features, topographic and forest stand features, landcover, food, and time (Table 2-1). In addition to measuring the habitat variables at each site, I assembled a GIS (ArcMap 10; Economic and Social Research Institute, Redlands, CA) database at a 30-m pixel resolution for my study area from which additional spatial predictor variables were derived as raster layers. I summarized each predictor variable at two spatial scales using a moving window routine with a radius of 300 m and 1690 m. Previous studies have found the 300 m scale, or patch scale, to be an important predictor of bear occurrence

(Theberge 2002). 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). I used a 10-km buffer around the study area 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 wells; mining and forestry footprints; and distance to protected areas. I calculated distance 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, I coded each pixel as presence (1) or absence (0) for each variable and then calculated the proportion of mining and forestry within a 1690 m moving window. I 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.

I used five topographic variables and two forest stand features 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 (e.g. 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. I 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). I also used the DEM to derive terrain ruggedness (TRI) using an equation from Nielsen (2005). Crown closure was modeled in GIS from 0% to 100% (McDermid et al. 2005). I calculated distance to stream in GIS as the Euclidean distance in meters. My 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 (e.g. Nielsen et al. 2006, Mace et al. 1996, McLellan and Hovey 2001). I reclassified seven landcover types from McDermid et al. (2005) 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, I weighted estimates of cover using resource-specific diet weights (Munro et al. 2006, Nielsen et al. 2010). As a result, only bear foods with available diet weights were used (Appendix A-2). Nielsen et al. (2010) used percent digestible dry matter reported in Munro et al. (2006) to estimate ten by-monthly seasonal importance weights for each food item, starting in May and ending in September. Because I estimated cover class at a single point in time, I used a single importance weight for each food item calculated as that item's average importance weight from 07-June to 21-August. I grouped fruiting bear foods 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). I also modified two supplementary spatial (GIS) food variables to represent seasonal and total food availability (Nielsen et al. 2010) during my period of study. 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; however, I considered only the six bi-monthly seasons from 07-June to 21-August. I then estimated total food by summing the six bi-monthly food estimates. Site specific abundance estimates of alpine sweet vetch, buffaloberry, cow parsnip, moose pellets, and ant piles were log transformed, which is typical of count data in biology (McDonald 2009). Finally, time was modeled as a linear and quadratic variable to test whether detectability varies linearly over time or whether it peaks in 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 (>1700-m). For distance to protected areas, which is a large scale feature, I used a decay rate of 0.000142 so that distances remained relevant until they were greater than the average grizzly bear home range size (>21000-m) (Nielsen 2005, Stevens 2002). Original distance decay values ranged from 1 at the feature to 0 at very large distances; however, I then 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 (Nielsen et al. 2009). This allowed for easier interpretation of model coefficients (i.e. near distances are represented by negative coefficients and further distances by positive coefficients). Finally, I standardized each predictor variable using a z-score transformation; this is important for models using maximum likelihood methods and enables direct comparison of the predictor variable strength in model outputs.

3.3. Model Hypotheses and Univariate Analysis

Prior to modeling, I first outlined scale-specific *a-priori* hypotheses of factors affecting grizzly bear occupancy and detectability using five broad themes (Table 2-2) to minimize my candidate set of models (Burnham and Anderson 2002). Occupancy and detectability are modelled as two different responses, thus each has its own set of hypotheses. Because variables relating to terrain and topography have been used to successfully model grizzly bear occupancy in numerous other studies, topography was included in every occupancy hypothesis. Seasonal detectability models (linear or quadratic) were also included for every detectability hypothesis.

At the patch scale, I hypothesized that grizzly bear occupancy was affected by topographic and forest stand features, landcover, anthropogenic features, and food resources. I hypothesized that detectability of grizzly bears 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, I hypothesized that topographic features, landcover, and anthropogenic features would continue to influence grizzly bear occupancy; I did not test the effects of food resources on occupancy at the landscape scale, as I felt this site-specific variable was addressed most relevantly at the patch scale. For grizzly bear detectability at the landscape scale, I hypothesized that topographic features, anthropogenic features, and the interaction of anthropogenic features with food resources would be important predictors. Ciarniello et al. (2007) found that human use variables affected grizzly bear habitat selection at larger scales therefore I considered the landscape scale a more appropriate scale to investigate the effect of anthropogenic features and the interaction of anthropogenic features with broad food resources on detectability. Because site-specific estimates of bear foods could not be extrapolated from the patch to the landscape scale, I used two spatial food variables estimated from a GIS to test for interaction effects between anthropogenic features and food resources.

Due to the large number of predictor variables, I performed a univariate analysis to reduce the number of variables and minimize over parameterization (Burnham and Anderson 2002). The number of variables that could be included in the models was limited due to the study’s small sample – a result of logistical constraints (two week sessions) that meant only 60 sites could be sampled over the 1,500-km^2 study area. Although grizzly bear habitat models alone typically include between 6 and 24 variables (e.g. Nielsen et al. 2006, Apps et al. 2004, Mace et al. 1999), model complexity in this study was limited to a maximum of eight variables. I compared the AIC 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.

3.4. Single Season Models

Following univariate analysis, I used a single-species single-season model in Program PRESENCE to explore specific hypotheses of grizzly bear occupancy and detectability at two spatial scales. It is important to account for the probability of detecting a species when working with detection-nondetection data because the failure to detect a species does not mean that the species was not present (MacKenzie 2006). 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 has two sub-models – occupancy and detectability – that are modeled simultaneously. Although I was most interested in understanding factors affecting the detectability of grizzly bears using fixed hair traps, grizzly bear occupancy must also be modeled to accurately predict detectability (D.I.Mackenzie, Proteus Research & Consulting Ltd., personal communication). This, however, results in complex model procedure. For ease of communication, I present a simplified modeling procedure (see Appendix A for the detailed modeling procedure).

I used a modified two-phase modeling approach similar to that of Balas (2008) to estimate site occupancy and detectability at each scale. All models were ranked for support using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002). For the first phase of the analysis, I used an *a-priori* approach where I tested *a-priori* hypotheses of grizzly bear occupancy and detectability (Table 2-2) using only variables selected through univariate analysis (Table 2-1). Additionally, variables that were correlated ($|r|>0.7$) were not used in the same model. Because I was 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) (Steps 1 to 3). 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. I then selected the top ranked preliminary candidate model from each occupancy hypothesis and referred to these as candidate models (Step 4). The candidate models were re-ranked according to AIC and the top model selected as the final candidate model (Step 5).

For the second phase of the analysis, I used a *posteriori* approach where I added back in each previously removed variable from the univariate analysis to the final candidate model. Doing so allows one to identify possible confounding variables that would otherwise be missed (Hosmer and Lemeshow 2000). Variables were added back in one at a time to the occupancy sub-model while holding the detectability sub-model constant and vice versa creating preliminary *psi* models and preliminary *p* models (Steps 6 and 7). As in the *a-priori* approach, I 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 (Step 8). 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 (Step 9).

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, I model-averaged the final models and their associated beta coefficients at each scale using adjusted model weights. Model-averaged beta coefficients were then used in linear predictor and probability equations (Appendix A) from Mackenzie (2006) in a GIS to spatially estimate the probability of grizzly occupancy and detectability in west central Alberta. I 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.

Lastly, I assessed the predictive ability of the probability of occupancy (PSI) and the probability of detection given occupancy (PSI × P) maps using presence-absence data from the 2004 grizzly bear DNA hair trap survey. In doing so, occupancy and detectability are assumed to be constant among years despite changes being likely. I used the area under the curve (AUC) of the receiver operator characteristic curve (ROC) 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 are considered to have poor accuracy with AUC values of 0.6-0.7, 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).

3.5. Multi-season Models

I used a single-species multiple-season model in Program PRESENCE to explore change in occupancy between 2004 and 2011. Because the underlying population dynamics (extinction and colonization) were not of direct interest, I used the implicit multiple-season model in which underlying colonization and extinction dynamics are implied but are not explicitly counted for. In this way, the implicit model effectively combines several single season models and models patterns in occupancy each season, which is more appropriate for long gaps between sampling seasons (MacKenzie 2006). I used common sites – sites whose locations in 2004 and 2011 were within 500-m of each other – which reduced the total number of sites from 60 to 44. I then tested the hypothesis of no change in occupancy probability between years by comparing an equilibrium (null) occupancy model to one that included a year effect on the occupancy probability.

4. RESULTS

Grizzly bears were detected at 25 of the 60 sites (41.7%) (Figure 2-1; Appendix A-1) resulting in the identification of 21 unique grizzly bears – 12 females and 9 males. Three bears were recaptures from the 2004 DNA hair trap survey, and six bears were recaptures from other projects in the area, leaving 12 newly identified individuals. Following univariate analyses, I considered a total of 15 variables (Table 2-1) for *a-priori* (phase 1) analysis 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 2-3); detectability, however, was not found to vary over time. In the final candidate models at the patch scale, detectability hypotheses P_3 (food + topo) and P_5 (food) were selected most often (Appendix A-3). Final candidate models at the landscape scale consistently selected detectability hypothesis P_7 (food×anthro + topo) (Appendix A-3).

Following *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 wellsites ($\beta = -2.47 \pm 1.2$) (Table 2-4). In other words, grizzly bears are more likely to occur in higher elevation habitats containing buffaloberry and in areas near wellsites (Figure 2-2). Grizzly bear detectability at this scale was positively related to *Trifolium spp.* cover ($\beta = 0.50 \pm 0.17$) and negatively related to distance to stream ($\beta = -1.19 \pm 0.44$) (Table 2-4). 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 (Figure 2-2).

At the landscape scale, grizzly bear occupancy was negatively related to distance to protected areas (β = -2.17 ± 1.03), distance to pipelines (β = -1.21 ± 0.57), and the interaction of crown closure with CTI (β = -0.84 ± 0.58) (Table 2-4). The interaction of crown closure with CTI suggests that occupancy increases in open stands that are wet (Figure 2-3). Detectability of grizzly bears at the landscape scale was negatively related to distance to stream (β = -0.97 ± 0.42) and distance to wellsites (β = -0.28 ± 0.06) (Table 2-4). Detectability was also negatively related to the interaction of food resources with distance to (β = -0.30 ± 0.07) and density of (β = -0.72 ± 0.34) wellsites. In other words, grizzly bears are more likely to be detected near wellsites with low surrounding food availability and low wellsite density (Figure 2-3). Models from the *posteriori* analysis had lower AIC scores than *a-priori* models at both scales.

I 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 (Figure 2-4; Figure 2-5). Probability of grizzly bear detection was low (0.22 ± 0.19) at both scales. 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 survey sites. For the 2011 study area, the landscape scale model of detectability given occupancy had the highest AUC score (AUC=0.662) (Table 2-5), though all landscape models performed poorly in general, with AUC scores lower than 0.7. Model performance increased for the Yellowhead population unit for all but one model

(Table 2-5). 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 2-5). Overall, patch scale models had better predictive ability than landscape scale models according to AUC (Table 2-5).

Due to the poor performance of the landscape model for both the 2011 study area and the Yellowhead population unit, I created a multi-scale map (Figure 2-6) 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 (Table 2-6), which I used to predict probabilities of grizzly bear occupancy (PSI), detectability (P), and detectability given occupancy (PSI×P). The multi-scale model had poor performance initially when all variables were included in the model (Table 2-5); 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 quite high to the east. Although there is a negative relationship between detectability and wellsite density, its effect on detectability is weak (P = -0.72) in comparison to the effect distance to wellsite has on occupancy ($\beta = -2.47$). As a result, it does little to reduce the high probability of occupancy near wellsites at high densities. Given this, I removed the distance to wellsite variable, which significantly improved the performance of the multi-scale model for both occupancy and detectability given occupancy (Table 2-5). The multi-scale model with the highest AUC score

(AUC=0.757) resulted from estimates of occupancy for the Yellowhead population unit once wellsites were removed from the model (Table 2-5).

Change in grizzly bear occupancy between 2004 and 2011 was investigated using a multi-season model in program presence; however, because the 2004 DNA survey had only four sessions and because the majority of DNA sites in 2004 were moved between sessions (i.e. only sampled once), there was not enough data to explicitly model change in occupancy within the 2011 study area. As a result, I could not determine numerically whether grizzly bear occupancy increased, decreased, or remained the same over time. Instead, change in occupancy was approximated by assessing the change in occupancy pattern between 2004 and 2011. To do this, I recorded the occupancy status of common sites – DNA sites sampled in both 2004 and 2011 – within the 2011 study area (Figure 2-7). Dynamic sites are sites that had a change in occupancy status (0 to 1 or 1 to 0), whereas static sites are sites where occupancy status remained unchanged (0 to 0 or 1 to 1). Out of 44 common sites, 15 sites (34.1%) were classified as dynamic and 29 sites (65.9%) were classified as static (Table 2-6). Of the dynamic sites, 11 sites (25.0%) changed from 0 to 1 (unoccupied to occupied) and 4 sites (9.1%) changed from 1 to 0 (occupied to unoccupied) (Table 2-6). To model change in occupancy patterns, I compared an equilibrium (null) occupancy model to two dynamic occupancy models. For Model 1, I created a "state01" covariate where each site was labeled 0 or 1 where: 0= no change in occupancy status, 1= change in occupancy status (either from 0 to 1 or from 1 to 0). This allowed me to test whether the change in occupancy patterns between 2004 and

2011 was influenced by dynamic sites, but it did not allow me to distinguish which dynamic state (0-1 or 1-0) was influencing the change. For Model 2, I created a weighted change covariate "state012" where each site was labeled 0, 1 or 2 where: 0= no change in occupancy status, 1= change in occupancy status from 1 to 0, and 2= change in occupancy status from 0 to 1. By favouring the 0-1 dynamic state, I was able to test whether newly occupied sites in particular were influencing occupancy patterns over time. Model 1 had a ΔAIC of 5.31 when compared to the null model (Table 2-6), and a model weight of 12.7%. Model 2 held the majority of the model weight (86.4%) with a ΔAIC of 9.15 when compared to the null model (Table 2-6) suggesting that the dynamics observed were caused by changes in occupancy status from 0 to 1.

5. DISCUSSION

As hypothesized, the spatial variation of anthropogenic features and resource availability across the study area resulted in variations among sites of grizzly bear occurrence and detectability. Overall, grizzly bear detectability was low for each observed scale (0.22 ± 0.19). This is consistent, however, 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; therefore, 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 based on the results of this study will help to ensure that detection rates are at or above the 0.2 threshold.

5.1. Effects of Resource Availability

Resource availability was expected to influence grizzly bear detection rates at the patch scale. Buffaloberry (*Shepherdia canadensis*) in particular was found to have a strong, positive influence on grizzly bear occupancy ($\beta = 2.62$). This supports other research that has identified buffaloberry as a major food resource to grizzly bears in the foothills (Munro et al. 2006, Mace and Jonkel 1986, Hamer and Herrero 1987, Mattson et al. 1991, Alberta Sustainable Resource Development and Alberta Conservation Association 2010). In fact, LeFranc et al. (1987) concluded that buffaloberry is one of the dominant plant foods for grizzly bears across western North America. Buffaloberry is one of the most productive fruit species (McLellan and Hovey 1995), 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). This is important as bears will select productive landscapes (Hamer and Herrero 1987, Nielsen et al. 2004a, Robbins et al. 2004) that provide a balanced diet of foods high in protein and with foods high in energy (Rode and Robbins 2000, Rode et al. 2001, Felicetti et al. 2003) to meet their high nutritional demand during hyperphagic periods (Rode et al. 2006, Berland et al. 2008). As a result, certain food resources can be a good predictor of grizzly bear occurrence (Nielsen et al. 2010, Stelmock and Dean

1986), especially at finer scales (Ciarniello et al. 2007). 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 (Hamer 1996).

Another important food resource for grizzly bears – clover (*Trifolium spp.*) – was found to influence grizzly bear detectability but not occupancy. Like buffaloberry, clover is high in protein, fiber and gross energy (Frame and Newbould 1986, Pritchard and Robbins 1990) and it is highly palatable (Haeussler et al. 1999). As a result, clover is especially important to bears in the spring when other resources are scarce (Munro et al. 2006, Nielsen et al. 2004c). Unlike buffaloberry and other fleshy fruits, however, clover is not as limiting to grizzly populations (Mattson et al. 1991), which may explain why it was not found to influence 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 single-handedly influence habitat selection. On the other hand, clover's nectar-rich flowers have a strong, sweet odour that is known to powerfully attract bees and other pollinators (Bohart 1957). It is possible that this scent may also attract bears to an area due to their acute sense of smell, which might explain why clover near a hair trap site increases the likelihood of detecting a grizzly bear.

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, Nielsen et al. 2004c, Roberts and Zhu 2002). Grizzly bear occupancy was found to increase closer to wellsites (β = -2.47) at the patch scale and closer to pipelines (β = -1.21) at the landscape scale. Sahlen (2010) found that bears within a similar area selected for wellsites and hypothesized that this was likely due to the diversity and abundance of food resources present on these sites. Bears are also thought to occupy clear-cuts and roadsides for the same reason (Roever et al. 2010, Nielsen et al. 2004a). In addition to abundant food resources, pipelines are presumed to be important travel corridors for grizzly bears because they prefer to travel along linear features and other paths of least resistance (G.B. Stenhouse, Foothills Research Institute, personal communication). Similarly, Stewart (2011) found grizzly bears use pipelines in a similar pattern to roads. Travel corridors are used within a bear's home range to find critical resources (McLellan and Hovey 2001) and mates (Stenhouse et al. 2005). As a result, landscape conditions or features that facilitate movement, such as pipelines, can influence habitat use and occupancy of grizzly bears (McLellan and Hovey 2001). Distance to wellsite and distance to pipeline variables were correlated at each scale ($|r|>0.7$) and therefore not included in the same model; however, it is likely that wellsites and pipelines influence grizzly bear habitat selection at both scales due to important food resources found near these features.

5.2. Interaction of Food Resources and Anthropogenic Features

The interaction of anthropogenic features with food resources was investigated at the landscape scale. Sahlen (2010) presumed that the degree of wellsite use by grizzly bears would be higher when food availability in the surrounding matrix was poor. My results support this hypothesis, as the detectability of grizzly bears was found to increase closer to wellsites with low surrounding food resources. This suggests that grizzly bears are particularly attracted to the food resources on wellsites when alternative food sources are few; likewise, the scented lure of a hair trap in these areas could be especially attractive to nearby grizzly bears. The probability of detecting a grizzly bear was also found to increase in areas of low well density and low surrounding food resources. 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 (Gibeau et al. 2002, McLellan and Shackleton 1989). Eventually, higher wellsite densities might also cause enough habitat loss to outweigh the benefits of increased food resources. Sahlen (2010) also found that grizzly bears typically only use a few “favourite” wellsites 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. Because open pit mining occurs adjacent to rather than within the study area, an effect of mining on grizzly bear detectability was not found. Nonetheless, it is likely that open-pit mining has implications for grizzly bear occupancy and/or detectability given its effect on regional ungulate populations such as sheep and elk (MacCallum and Geist 1992, Bogdan 2013), two important prey species for grizzly bears. Recent research has shown bears use mined landscapes, especially for predation purposes (Bogdan 2013).

5.3. Effects of Topographic and Forest Stand Features

In addition to food and anthropogenic factors, topographic and forest stand features also influence grizzly bear occupancy and detectability. At the patch scale, grizzly bears are more likely to be detected in intermediate levels of crown closure. Grizzly bear food models developed by (Nielsen 2005) found that the maximum occurrence for seven common bear foods – including buffaloberry and clover – occurred at intermediate levels of crown closure. Timber extraction continues to be one of the main forest disturbances in this area, creating a range in forest age and crown closure levels (Nielsen et al. 2004a). As a result, forestry clear-cuts can provide areas of intermediate crown closure that support a diverse array of food resources. What is not clear, however, is why crown closure at the patch scale was found to affect grizzly bear detectability but not occupancy, given that previous habitat use studies have shown grizzly bears to select clear-cuts (Nielsen et al. 2004a). One hypothesis is that different levels of crown closure and foliage affect exposure levels and air movement through the forest stand (Rudnicki et al. 2003). This could have significant effects on the distribution of the scent lure – canopies that are too open may not provide adequate protection of the scent lure making it vulnerable to drying out under intense sunlight or washing away during periods of rain. On the other hand, canopies that are too dense may have limited wind movements through the stand leading to poor scent dispersal. Intermediate levels of crown closure, however, may create optimum conditions for scent dispersal by balancing air flow with proper protection of the scent lure.

At the landscape scale, grizzly bear occupancy was influenced by the interaction of crown closure and soil wetness (CTI). In other words, bears are more likely to select more open habitats that are wet. This is consistent with past research that has shown grizzly bears to select artificial openings such as clear-cuts (Nielsen et al. 2004*a, c*; Wielgus, Vernier 2003) and natural openings such as wet meadows and fens (Apps et al. 2004, Hamer and Herrero 1987, Herrero 1972, Blanchard 1980). Similarly, in a pilot study on the Appenine brown bear in central Italy, Gervasi et al. (2010) found that brown bear detectability was higher in ecotones. Nielsen et al. (2004c) also found the soil wetness index was an important predictor of grizzly bear foods and habitat quality.

Two variables that had a consistent effect across scales were mountainous habitat and distance to stream. Mountainous habitat was represented by elevation and distance to park variables, which were found to strongly influence grizzly bear occupancy at the patch and landscape scale, respectively. Mountainous areas represent more secure habitat for grizzly bears because they have lower human density and land-use levels while still providing a variety of food resources (Nielsen et al. 2006). Elevation and distance to protected areas have been used before to describe grizzly bear habitat selection (Nielson et al. 2002, Theberge 2002, Mace et al. 1996, McLellan and Hovey 2001, Apps et al. 2004). Past research has also shown that grizzly bears select streamside areas (Nielsen et al. 2002, Nielsen et al. 2009, Theberge 2002), primarily for travel. In this study, the detectability of grizzly bears was found to increase near streams at both scales, likely because a bear is more likely to intersect a hair trap site if it is placed along a commonly used travel path. Where streams are located in small valleys, wind movements through the valley may also affect the distribution of the scent lure and increase the likelihood of a bear detecting the hair trap.

5.4. Effects over Time

One unexpected result of this study was that grizzly bear detection rates did not vary over time (spring to summer period sampled). I expected that pulsing of seasonal foods, especially fruiting species, would compete with hair trap sites during hyperphagic periods causing a decrease in grizzly bear detections. No support was found, however, for this hypothesis. Rather, I found that at least one species, clover, actually increases the probability of detection at hair trap sites – but because clover is not a fruiting species, one could expect less competition between clover and the hair trap site. On the other hand, 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. Animal protein causes greater weight gain than do berries (Rode et al. 2001) and is therefore another valuable source of energy. 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, with the berry season running from August to October (Nielsen et al. 2004b). 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 my study area. It's possible that competition between hair trap sites and berry crops would be more apparent had sampling extended into September or October.

5.5. Model Performance

Model performance was assessed using detection-nondetection data from the 2004 grizzly bear DNA hair trap survey. Overall, patch scale models had the best predictive accuracy. A major difference between the patch and landscape scale models was the inclusion of two key grizzly bear food resources – buffaloberry and clover – in the patch scale model, which may be the reason for increased model performance. These results therefore stress the need for accurate spatial information on key bear foods and their importance in models of grizzly bear habitat, occupancy, and detectability (Nielsen et al. 2010).

The model with the second highest predictive ability resulted when single-scale models were combined into a multi-scale model. This could be expected, as numerous studies on a wide range of taxa have shown habitat selection to vary across scales (e.g. Orians and Wittenberger 1991, Lindenmayer et al. 1999, Steffan-Dewenter et al. 2002, Stoner and Joern 2004). Thus, results based on only one scale can be limited (Kotliar and Wiens 1990, Lord and Norton 1990, Guisan and Thuiller 2005). Several studies have demonstrated multi-scale habitat selection and movement of grizzly bears in particular (Ciarniello et al. 2007, Smulders 2009, Carra 2010). It's probable that both scales are required to adequately capture the effects of resource patches, anthropogenic features, and their interaction. In this study, the patch scale (300 m) effectively captured the influence of food items on grizzly bear occupancy and detectability whereas the landscape scale (1690 m) better captured the effects of broader habitat features and human use impacts. This is similar to the results of Ciarniello et al. (2007) who studied scale dependent grizzly bear habitat selection in British Columbia.

There is also a difference in sample size and area between the 2011 study area and the Yellowhead Population Unit, which may cause a difference in predictive performance between the two landscapes. For the 2011 study area, 117 sites over 1,500-km^2 were used to assess model performance versus 705 sites over 28,529-km^2 for the Yellowhead Population Unit. The larger area of the Yellowhead Population Unit allows for the full range of variation in habitat and human use variables to be represented, which may result in better predictive ability (Ciarniello et al. 2007).

5.6. Limitations and Future Research

Overall, model performance for the 2011 study area was poor. This was due in part to one limitation of this study: its small sample size. Because program PRESENCE models two different responses – occupancy and detection – it would be advantageous to include more variables. It is also thought that using intensive sampling regimes limits individual capture heterogeneity (Boulanger et al. 2004) and improves detection rates. This study – with 50 km^2 cells and six sampling sessions – is considered a robust study design (Boulanger et al. 2002). Nonetheless, a greater number of sites would improve our ability to model grizzly bear occupancy and detectability simultaneously.

Furthermore, it is probable that the factors affecting the detection of grizzly bears are complex. There are several factors that likely affect the success of hair trap sites that were not modeled in this study. Local weather conditions, for instance, would affect the quality and dispersal of the scent lure. Wind in particular would have a large effect on how the scent of the lure disperses through air, as would air temperature, vapour pressure, and relative humidity (Syrotuck 1972, Pearsall and Verbruggen 1982, Snovak 2004). Precipitation and other weather factors can also degrade a scent (Smith et al. 2005, Harrison 2006). Moreover, weather and environmental conditions have been found to influence a canine's ability to smell (Wasser et al. 2004); because a dog cannot sniff and pant simultaneously, higher temperatures can decrease scent detection due to excessive panting (Gazit and Terkel 2003). This may hold true for grizzly bears as they also lower their body temperature by panting. Dry conditions can also lead to a dry nose or dehydration, which further reduces the ability of an animal to detect a scent. Modeling weather variables, however, was beyond the scope of this project.

Biological factors (e.g. age, sex, reproductive status) and individual bear behaviours may also affect how strongly a grizzly bear is attracted to a hair trap site (Boulanger et al. 2004). Prey abundance or the productivity of last year's berry crop, for example, will affect hunger and competition and may motivate a bear to visit a hair trap site. On the other hand, over-cautious females with cubs or a male bear's preoccupation with the breeding season may result in a lack of interest in hair trap sites. Whether a bear has an association or familiarity with handling and/or capture could result in trap shyness or trap happiness; however, a separate analysis of the data by J. Boulanger (Integrated Ecological Research, unpublished data) did not find evidence of a behavioural response.

5.7. Changes in Occupancy (2004-2011)

A greater number of sites would also improve our ability to model changes in grizzly bear occupancy over time. Because only 44 sites were sampled in both 2004 and 2011 – and because many of the sites in 2004 were only sampled once – I had insufficient data to explicitly test whether occupancy differed between years. Instead, I explored changes in grizzly bear occupancy patterns by analyzing the change in occupancy state of each site. Twenty-five percent of the sites became occupied whereas only nine percent became unoccupied – at first glance, this suggests changing occupancy patterns between 2004 and 2011, with the majority of dynamic sites showing an increase in occupancy. I then tested this hypothesis in a modeling framework. There was little support for the equilibrium occupancy model, indicating that occupancy patterns between 2004 and 2011 were different. Model 2, a weighted change model favouring sites with a 0 to 1 occupancy state had a ΔAIC of 9.15 lower than the null model. As a rule of thumb, there is considerable evidence for the null model when $\Delta \text{AIC} < 2$, much less support when values are between 3 and 7, and essentially no support when

ΔAIC > 10 (Burnham and Anderson 2002). Thus, these results strongly suggest that grizzly bear occupancy patterns in the area have changed since 2004 and that this change has been influenced in particular by newly occupied sites. Although these results cannot directly discern whether occupancy has increased or not, or by how much, they indirectly support a hypothesis of increasing grizzly bear occupancy in this area.

5.8. Conclusion

Overall, this study demonstrates the importance of environment conditions and resources in the placement of fixed DNA hair traps and dismisses the need for careful timing of hair trap surveys. Sites should be placed near pipelines, wells, and streams in areas with high abundance of buffaloberry and clover but otherwise poor food availability to maximize the detectability of grizzly bears using fixed sample sites. Anthropogenic features, if properly managed at reasonable densities, can benefit grizzly bear populations and monitoring efforts in the province. Future studies should consider measuring prey abundance (e.g. ungulate pellet surveys) and extending a similar study into the hyperphagic berry season (September and October) to better test the influence of food resources on grizzly bear detection when using fixed hair trap sites. Additionally, future studies should explore how grizzly bear occupancy and detectability varies near the eastern range edge as monitoring in this area would be important for measuring range expansion and the success of recovery efforts. To the east, habitats change from mountain and foothill habitats to mixed-wood habitats with increased human densities and land use pressures. As a result, factors affecting habitat use and detection rates of grizzly bears in this area are likely very different from those identified in this study.

6. MANAGEMENT IMPLICATIONS

Maintenance of viable grizzly bear populations will remain a challenge wherever land use is extractive within grizzly bear habitat. This is already the case in Alberta’s foothills, and land use pressure and human populations in this area are only expected to increase (Nielsen et al. 2008). Careful management and conservation of grizzly bears will be critical to their persistence, which will require information gained from long-term monitoring programs. Non-invasive DNA hair trap methods that employ a fixed network of sample sites have proven to be a reliable strategy for sampling grizzly bears in this area. Optimal placement of hair trap sites will increase detection rates and also help, in part, to ensure the most cost-effective monitoring results. To maximize the detectability of grizzly bears using fixed sample sites, sites should be placed near pipelines, wellsites, cutblocks, and streams in areas with high abundance of buffaloberry and clover but otherwise poor food availability. As a result, oil and gas development in this area can benefit grizzly bear occupancy and detectability due to the high resource abundance found on these sites. Similarly, forestry practices can benefit grizzly bear habitat and detection rates by providing stand conditions that support a diversity of bear foods.

Unfortunately, pipelines, wellsites, and cutblocks have a high risk of mortality due to increased human-bear encounters (Nielsen et al. 2006). Because human caused mortality is the greatest source of mortality for grizzly bears (Nielsen et al. 2004b, Benn and Herrero 2002, Alberta Sustainable Resource Development and Alberta Conservation Association 2010), these areas can be attractive mortality sinks (Nielsen et al. 2006). Strict human access control, de-activation and re-vegetation of roads, and increased public education (Nielsen et al. 2004b, 2006; Sahlen 2010) could lower this risk. Habitat enhancements might also be used to improve grizzly bear habitat while also benefiting monitoring efforts. One example may be to establish supplemental food plots in suitable areas that are also within detection distance of a fixed DNA site. My results suggest that buffaloberry and clover would be ideal candidates for foothill habitats, while other research suggests alpine sweet-vetch (*Hedysarum alpinum*) may be preferred for alpine and sub-alpine habitats (Coogan et al. 2012).

Table 2-1. Summary of themes and associated variables hypothesized to influence grizzly bear occupancy or detectability at two scales (300 m and 1690 m) in west central Alberta, Canada. Variables selected for a-priori modeling following univariate analysis are denoted with subscripts; P = patch scale model (300 m), L = landscape scale model (1690 m). Time variables were tested regardless of univariate analysis results.

Theme	Variable Name	Abbreviation	Scale	Data Range
Anthropogenic Features				
Distance to (exponential transformation)	Road	rd_dec	300m; 1690m	0 to 1
	Trail	trl_dec	300m; 1690m	0 to 1
	Pipeline	pipe_dec	300m; 1690m	0 to 1
	Wellsites	well_dec	300m; 1690m	0 to 1
	Protected Area $_{P,L}$	park_dec	300m; 1690m	0 to 1
Density of (log transformation)	Road	rd_dns	1690m	0.3 to 1.1
	Trail	trl_dns	1690m	0 to 0.7
	Pipeline	pipe_dns	1690m	0 to 0.5
	Wellsites	well_dns	1690m	0 to 0.4
Proportion of	Forestry Cutblocks	cblock	1690m	0 to 100
	Mining	mine	1690m	0 to 100
Topographic Features, Forest Stand Features, & Risk	Compound Topographic Index (CTI) $_{L}$	CTI	300m; 1690m	6 to 14
	Terrain Ruggedness Index (TRI) $_{L}$	TRI	300m; 1690m	0 to 21
	Elevation (DEM) (m) $_{P,L}$	DEM	300m; 1690m	936 to 2772
	Distance to Stream (m) $_{P,L}$	stream	300m; 1690m	0 to 1
	Crown Closure (%) $_{L}$	CC	300m; 1690m	0 to 100
	Local Canopy Cover	cancov	300m	0 to 5
	Mortality Risk	risk	300m; 1690m	0 to 10
Landcover	Core	core	300m; 1690m	0 or 1
	Upland Tree	utree	300m; 1690m	0 or 1
	Wetland Tree $_{P,L}$	wtree	300m; 1690m	0 or 1
	Upland Herb	uherb	300m; 1690m	0 or 1
	Wetland Herb $_{L}$	wherb	300m; 1690m	0 or 1
	Shrub	shrub	300m; 1690m	0 or 1
	Water	water	300m; 1690m	0 or 1
	Barren	barren	300m; 1690m	0 or 1
	Forest Age (yr)	ForAge	300m; 1690m	0 to 160
Food				
Density of (log transformation)	*Hedysarum alpinum* $_{P}$	hedy_dns	300m	0 to 6.7
	Shepherdia canadensis $_{P}$	shecan_dns	300m	0 to 5.6
	Heracleum lanatum	herlan_dns	300m	0 to 5.5
Weighted Cover Class			300m	
Root	*Hedysarum alpinum* $_{P}$	hedy	300m	0 to 21
Herb / Forb	*Heracleum lanatum*	herlan	300m	0 to 12
	Equisetum spp.	equi	300m	0 to 4
	Trifolium spp. $_{P}$	trif	300m	0 to 6
	Taraxacum officinale	taroff	300m	0 to 2
Fruit	*Shepherdia canadensis*	shecan	300m	0 to 24
	Vaccinium spp.	vacc	300m	0 to 8
	Other Fruit $_{P}$	ofruit	300m	0 to 5
Other food metrics	Seasonal Food	sfood	300m; 1690m	0 to 100
	Total Food	tfood	300m; 1690m	0 to 600
Time	Linear $_{P,L}$	sess	300m; 1690m	0 to 6
	Quadratic $_{P,L}$	quad	300m; 1690m	0 to 36

Table 2-2. Scale-dependent a-priori model hypotheses based on combinations of themes (see Table 2-1 for details) 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 & 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**
300m	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		
1690m	PSI_1	Topo + Landcover + Anthro	P_1	Anthro + Anthro + Topo
	PSI_2	Topo + Landcover + Topo	P_2	Anthro + Anthro + Anthro
	PSI_3	Topo + Topo + Anthro	P_3	Anthro + Anthro + 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

Table 2-3. Summary of 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 relative to the top ranked model, and Akaike weights (w_i). Variables are described in Table 2-1.

Scale	Final Model Structure	AIC	ΔAIC	w_i
300m	psi(DEM + shecan_dns + well_dec), p(trif+ stream + CC + CC^2)	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
1690m	psi(CC*CTI + park + pipe_dec),p(tfood*well_dns + tfood*well_dec + stream)	232.81	0.00	0.35
	psi(CC*CTI + park + pipe_dec),p(tfood*well_dns + stream)	232.89	0.08	0.34
	psi(CC*CTI + park + pipe_dec),p(tfood*well_dns + stream + well_dec)	233.08	0.27	0.31
	psi(.),p(.)	253.58	20.77	0.00

Table 2-4. 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.

					90% CI	
Scale	**Parameter**	**Abbreviation**	**Estimate**	**SE**	**Upper**	**Lower**
300m	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 Intercept	P	-1.894	0.264	-1.461	-2.328
	Trifolium spp. Weighted 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 Closure^2	CC^2	-1.391	0.749	-0.162	-2.620
1690m	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
	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

Table 2-5. Area under the curve (AUC) scores for individual (300 m, 1690 m) 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.

			AUC by Study Area	
Scale	**Model**	**Description**	**2011**	**YH**
300m GIS	PSIxP		0.627	0.689
300m GIS	PSI		0.595	0.668
1.69km	PSIxP		0.662	0.618
1.69km	PSI		0.606	0.658
Multi-scale v1	PSIxP	All models	0.526	0.668
Multi-scale v1	PSI	All models	0.529	0.644
Multi-scale v2	PSIxP	All models without wells	0.548	0.682
Multi-scale v2	PSI	All models without wells	0.570	0.727
Multi-scale v3	PSIxP	GIS models without wells	0.524	0.623
Multi-scale v3	PSI	GIS models without wells	0.601	0.666

Table 2-6. 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 Averaged		**90% CI**	
Scale	**Parameter**	**Abbreviation**	**Estimate**	**SE**	**Upper**	**Lower**
	Occupancy Intercept	**PSI**	1.462	0.897	2.933	-0.009
300m	Elevation	DEM	2.753	1.205	4.729	0.776
300m	*Shepherdia canadensis* Density	shecan	2.621	1.095	4.417	0.825
	Distance to Wellsite	well	-2.470	1.200	-0.502	-4.439
	Distance to Park	park	-2.166	1.029	-0.478	-3.853
	Distance to Pipeline	pipe	-1.206	0.571	-0.270	-2.141
1690m	CC × CTI Interaction	CC×CTI	-0.843	0.528	0.023	-1.710
	Detectability Intercept	**P**	-1.862	0.279	-1.405	-2.320
300m	*Trifolium* spp. Weighted Cover Class	trif	0.500	0.167	0.773	0.226
300m	Crown Closure	CC	0.550	0.805	1.871	-0.771
300m	Crown Closure^2	CC^2	-1.391	0.749	-0.162	-2.620
	Distance to Stream	stream	-1.165	0.443	-0.437	-1.892
	Distance to Wellsite	well	-0.283	0.202	0.049	-0.614
1690m	Food × Well Density Interaction	tfood×well_dns	-0.715	0.338	-0.161	-1.270
1690m	Food × Distance to Wellsite Interaction	tfood×well_dec	-0.296	0.204	0.039	-0.631

Table 2-7. Change in grizzly bear occupancy status between 2004 and 2011 in west central Alberta, Canada. Number of sites in each occupancy state is recorded and compared to the total number of sites. Multi-season model results are shown below. Occupancy in year 2004 (psi) and detectability (p) were held constant while extinction (eps) was set to equal colonization (1-gam). Occupancy in year 2011 (gam) is modeled according to occupancy status. Static sites were coded as 0 and dynamic sites as 1 for the variable "status01"; for variable "status012", sites with an occupancy status of 1-0 were coded as 1 and sites with an occupancy status 0-1 were coded as 2 thus creating a weighted variable favouring 0-1 change in occupancy status.

State	Occupancy Status	Status Type	No. Sites	% of Sites
0 to 0	No detection in 2004; No detection in 2011	Static	25	56.8
0 to 1	No detection in 2004; Detection in 2011	Dynamic	6	13.6
1 to 1	Detection in 2004; Detection in 2011	Static	5	11.4
1 to 0	Detection in 2004; No detection in 2011	Dynamic	8	18.2
Model	**Multi-season Model Structure**	**AIC**	**ΔAIC**	**w_i**
2	psi(.),gam(state012),eps=1-gam,p(.)	268.61	0.00	0.8644
1	psi(.),gam(state01),eps=1-gam,p(.)	272.45	3.84	0.1267
Null	psi(.),gam(.),eps=1-gam,p(.)	277.76	9.15	0.0089

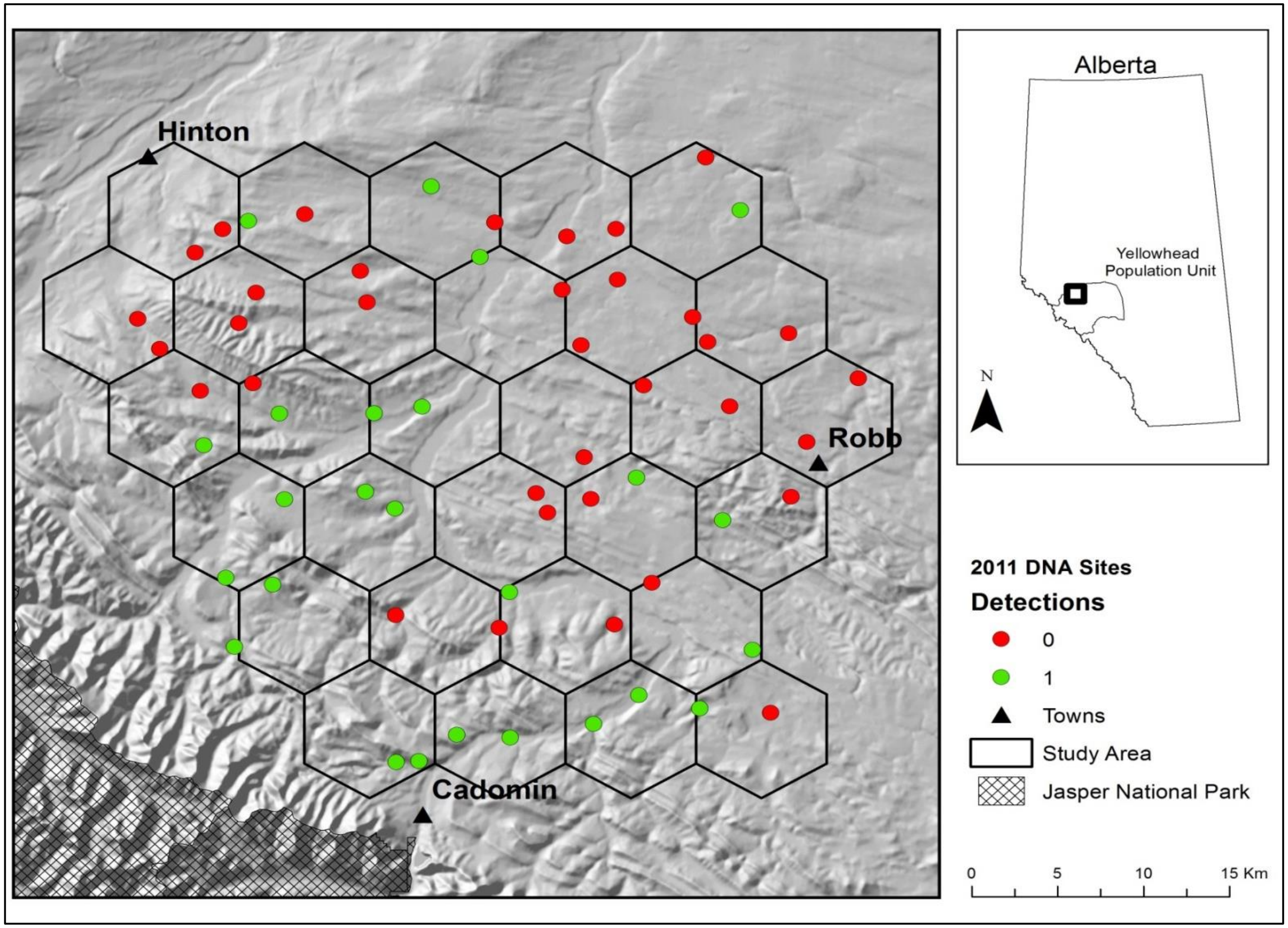

Figure 2-1. Study area comprised of 50 km2 hexagon cells, towns, and Jasper National Park eastern boundary. The location and detection-nondetection data of 60 DNA sites (two per cell) are shown. A value of zero indicates no detection; a value of one indicates confirmed grizzly bear detections.

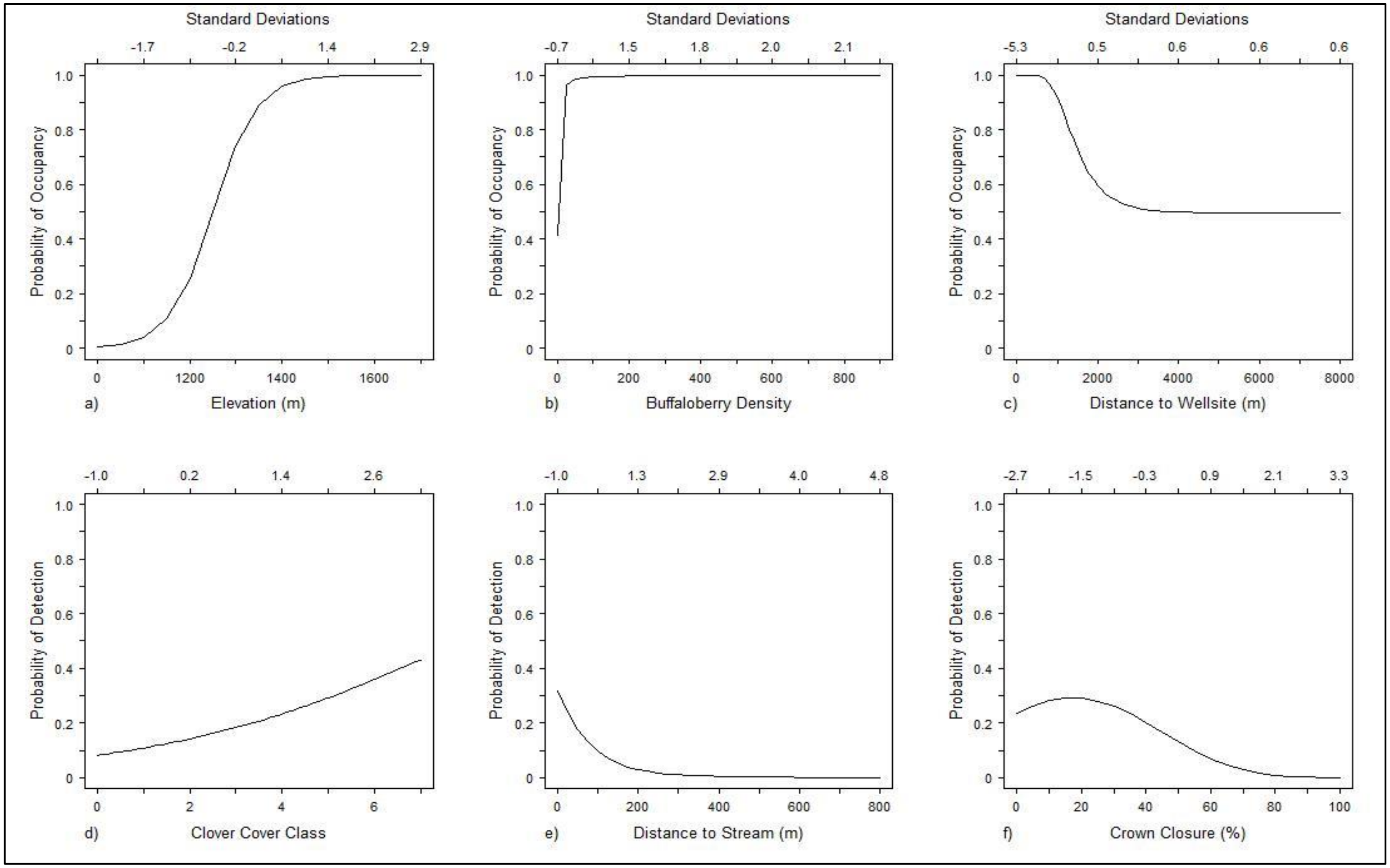

Figure 2-2. Predicted probability of occurrence or detection for selected anthropogenic, topographic, and food variables used to describe grizzly bear occupancy and detection at a 300 m (patch) scale. Each variable (a-f) is model across its natural range within the study area while remaining variables were held at their mean level (zero in this case as variables were standardized).

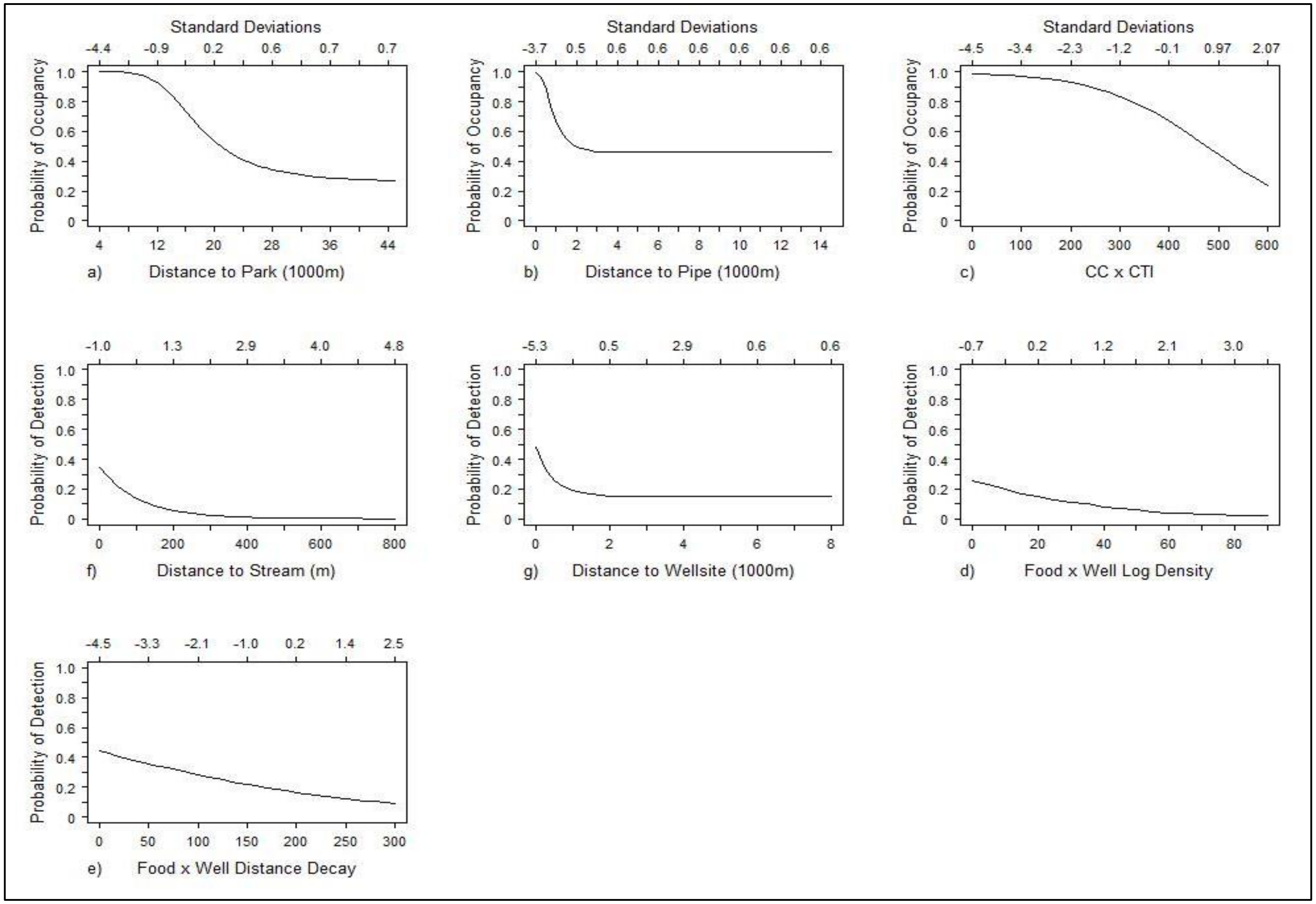

Figure 2-3. Predicted probability of occurrence or detection for selected anthropogenic, topographic, and food variables used to describe grizzly bear occupancy and detection at a 1690 m scale. Each variable (a-g) is model across its natural range within the study area while remaining variables were held at their mean level (zero in this case as variables were standardized).

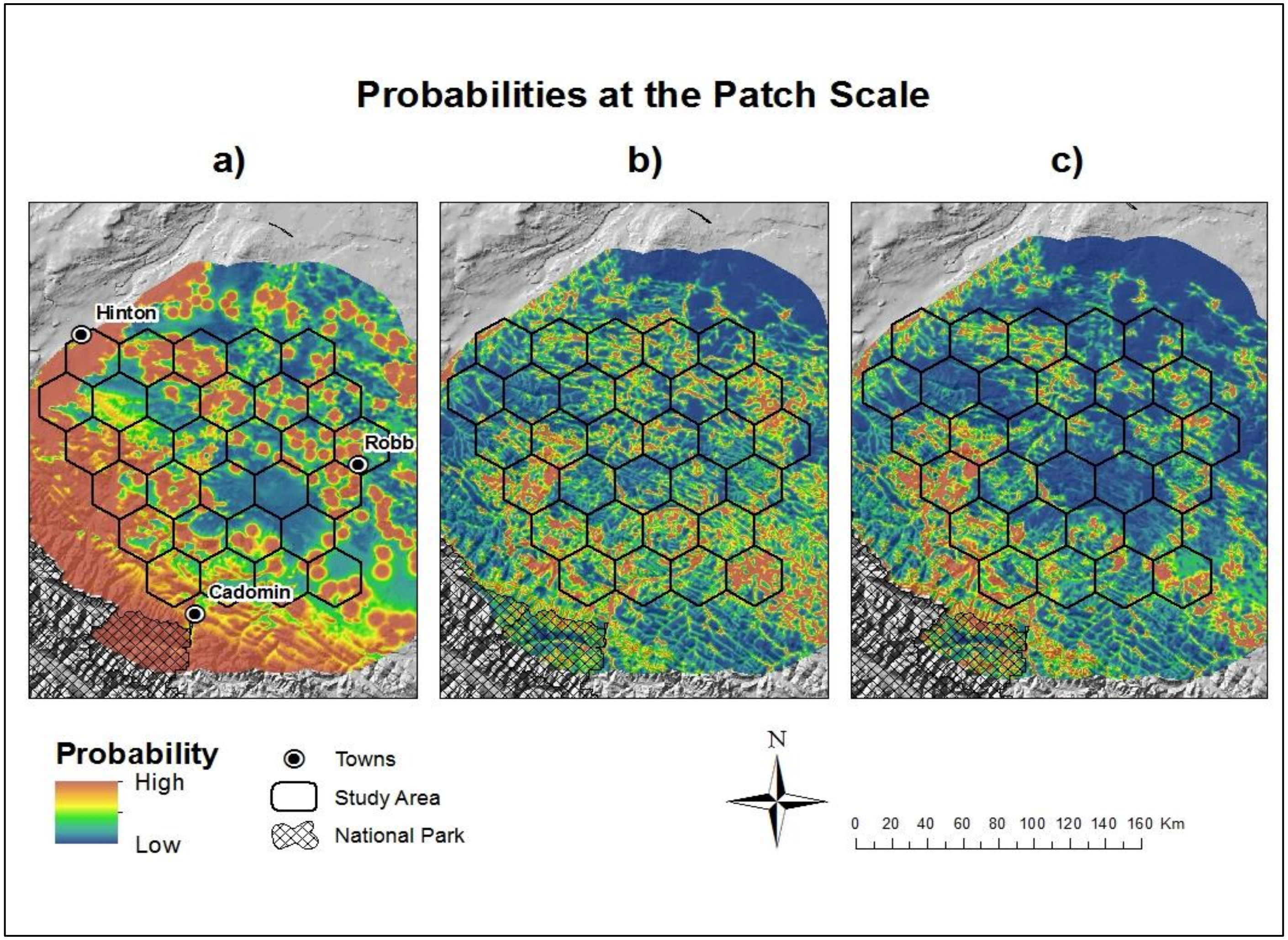

Figure 2-4. Probability of occupancy (a), detectability (b), and detectability given occupancy (c) of grizzly bears in west central Alberta, Canada at the patch scale (300 m). Probability ranges from 0 to 100%.

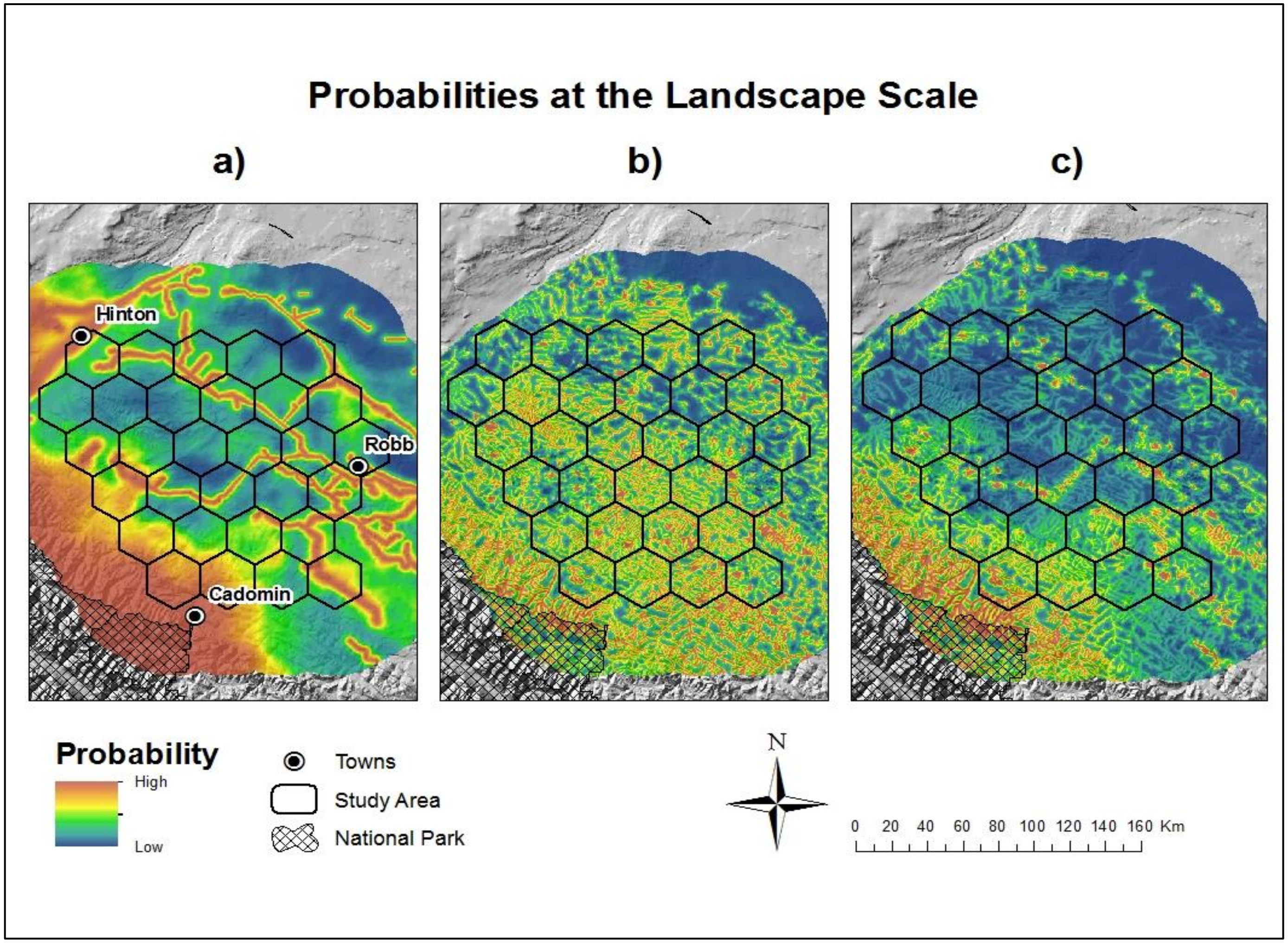

Figure 2-5. Probability of occupancy (a), detectability (b), and detectability given occupancy (c) of grizzly bears in west central Alberta, Canada at the landscape scale (1690 m). Probabilities range from 0 to 100%.

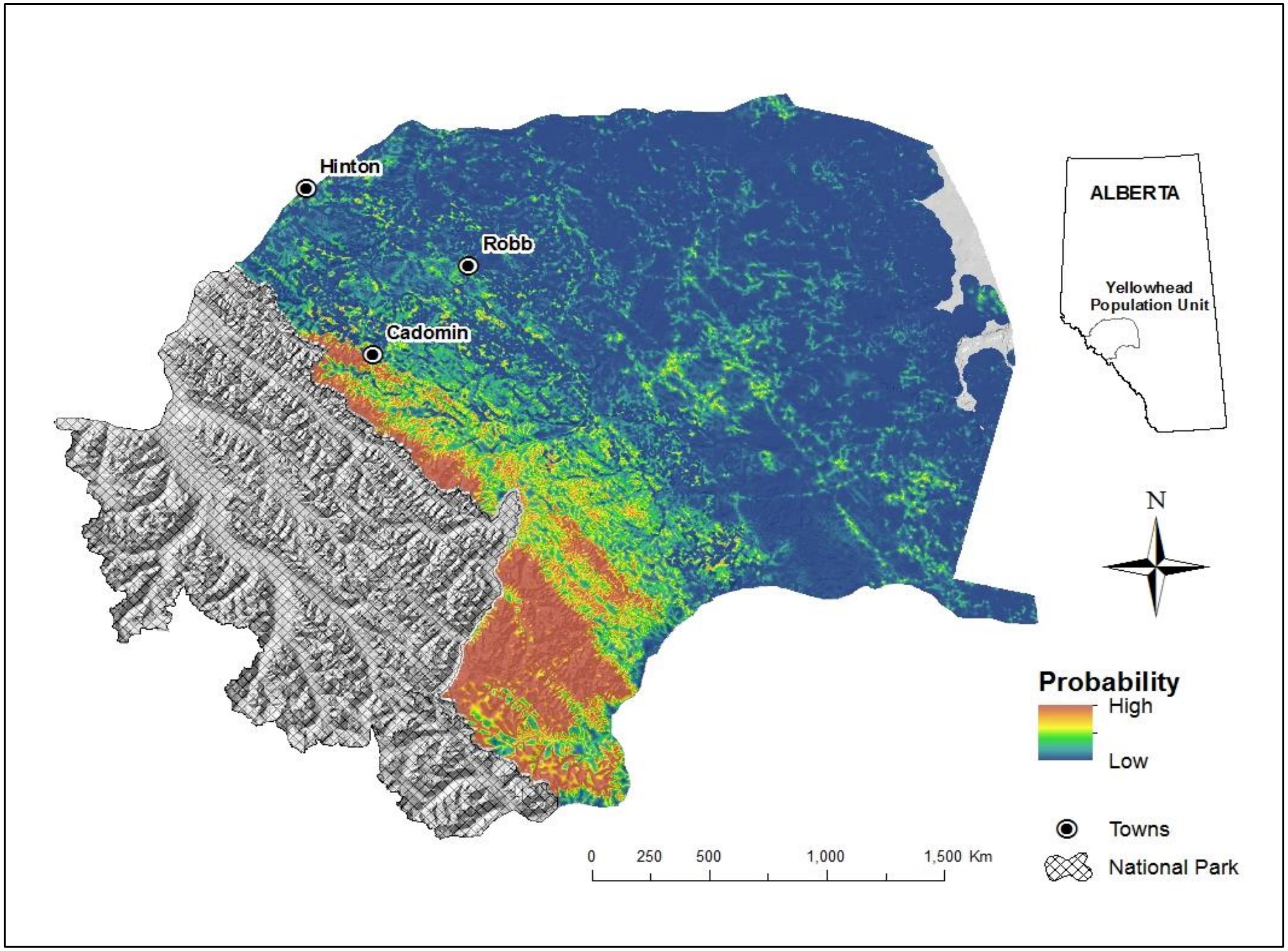

Figure 2-6. Predicted probability of detection given occupancy (PSI×P) for grizzly bears in the Yellowhead Population Unit using a multi-scale model that combined model results from patch (300 m) and landscape (1690 m) scale analyses.

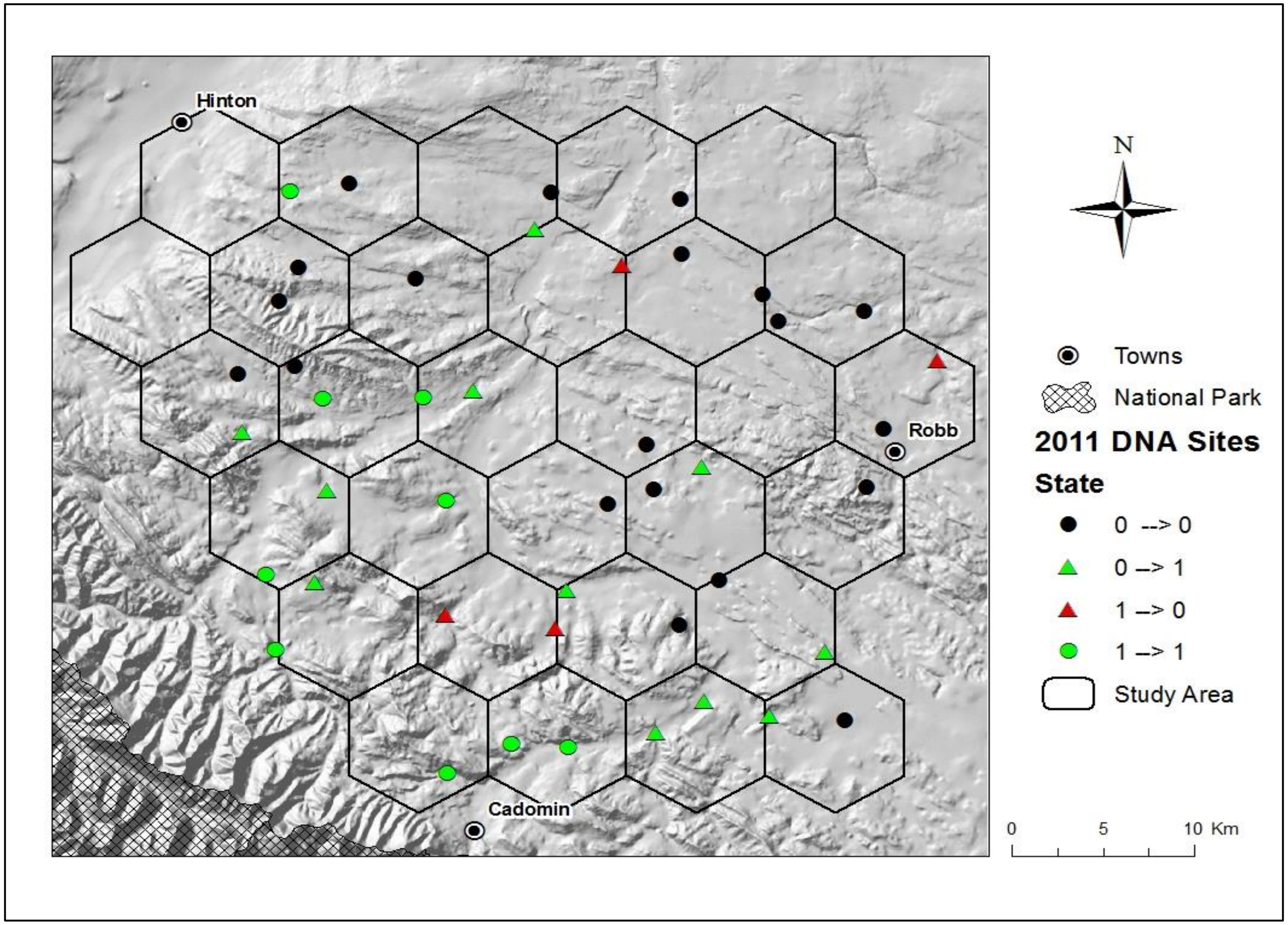

Figure 2-7. Occupancy state for 44 sites sampled in both 2004 and 2011 in west-central Alberta, Canada. Of the static sites, 20 sites remained unoccupied (0-0) and nine sites remained occupied (1-1); of the dynamic sites, four sites changed from occupied to unoccupied (1-0) whereas 11 sites changed from unoccupied to occupied (0-1).

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CHAPTER 3

LIVING AT THE EDGE: LIMITING FACTORS AT THE EASTERN BOUNDARY OF GRIZZLY BEAR RANGE IN ALBERTA

1. INTRODUCTION

Two basic yet fundamental questions in ecology are “Where does a species occur and why does it occur where it does?” (Krebs 1972). The answers to these questions, which continue to elude researchers, have important implications for the conservation and management of wildlife populations. The overall dynamics, resiliency and viability of a species are affected in part by its distribution (Wiegand et al. 2002). There is also a generally positive correlation between abundance and distribution (Brown 1984, Gaston and Blackburn 1996, Holt et al. 2002). In the case of recovery, a population that is increasing will either increase in density, expand in range (given suitable habitat), or both (Lawton 1993). The opposite will occur if the population is declining. The ability of a species to shift ranges therefore has important impacts on extinction risk and future community structure (Angert et al. 2011). Change in range edge – the limits of a species’ distribution – could also be used to evaluate if or when recovery has been achieved.

As a result, conservation and monitoring along the range periphery may hold great promise for conserving biological diversity, especially in the case of endangered and recovering species (Channell and Lomolino 2000). Indeed, Parmesan et al. (2005) argue that “future management plans will continue to rely heavily on basic research of species’ distributions”. Such research includes estimates of species distributions, an understanding of factors that influence distribution and range edge, and monitoring of spatiotemporal trends, all of which contribute to effective and adaptive conservation and management of a species (Apps and Bateman 2005). Understanding limiting factors at the range edge would allow for predictions about how the distribution of a species might change under different scenarios – i.e. following changes in the population or the environment. This would be of great value to wildlife managers as it enables targeted conservation and management efforts.

Gaining such an understanding, however, is challenging. It is the interaction of abiotic and biotic factors, population dynamics, and genetic mechanisms that determines the exact location of a range edge (Brown et al. 1996). To add to the complexity, the factors that limit geographic ranges can vary between species, along the range periphery of any given species, as well as between different spatial and temporal scales (Brown et al. 1996, Gaston 2003, Morin et al. 2007). Consequently, determining the location of and factors behind species ranges is extremely difficult. It is not surprising that we are still lacking an understanding of the ultimate causes of range edge for a majority of species (Gaston 2009); thus, science and conservation continues to be limited by our ability to quantitatively predict individualistic range shifts (Angert et al. 2011). In the face of rapid global change and significant environmental challenges, the need to resolve these knowledge gaps is becoming increasingly urgent.

The need to understand distributional limits is especially pressing for Alberta's grizzly bears (*Ursus arctos*). In North America, grizzly bears have suffered a dramatic reduction in distribution over the past century, largely as a result of habitat loss and fragmentation, over-exploitation, and human-bear conflict (Nielsen et al. 2004a). In Alberta, impacts of roads, farming and ranching, settlements, and animal control measures have caused grizzly bears to be extirpated from or transient in much of their historical range (Alberta Forestry, Lands and Wildlife 1990, Mattson and Merrill 2002, Nielsen et al. 2004a). Grizzly bears were designated a threatened species in Alberta in 2010, yet high rates of human-caused mortality continue to threaten their long-term persistence in the province (Nielsen et al. 2004a, 2006). This is especially true along the eastern range – an important and contentious interface between humans and bears in Alberta. As such, targeted conservation efforts along the range periphery are likely vital to the successful recovery of grizzly bears in the province. There is also potential for current and future population expansion in some areas of the province, especially if recovery efforts are successful. Scientifically and socially acceptable actions will vary dramatically depending on whether the population is expanding or contracting and where that change is occurring (i.e. risk of human-bear conflict). Thus, current and anticipated range dynamics have important implications for the conservation and management of grizzly bears. Little, however, is known about grizzly bear distribution, range dynamics, or factors affecting range edge in Alberta. This knowledge gap is of concern given the impact grizzly bear distribution has on population recovery and human-bear coexistence.

In 1999 and then again in 2004, boundaries of grizzly bear population units were estimated in Alberta (Alberta Forestry, Lands and Wildlife 1990, Alberta Grizzly Bear Recovery Plan 2008). Like most other range maps, the population units were, in the presence of limited empirical knowledge, estimated qualitatively based on expert knowledge and known or presumed occurrences (D. Hobson, Alberta Environment and Sustainable Resource Development, personal communication). Although this method is often used for defining range boundaries (Gaston 1991), Alberta's grizzly bear population units no longer include all the locations where bears have been recently recorded. Given recent increases in the quality and quantity of data (i.e. large electronic databases and standardized biological surveys) (Gaston 2003) as well as rapid rates of landscape change across the province, updated range maps of grizzly bears in Alberta are needed.

Once the current spatial distribution of grizzly bears in Alberta is known, the factors influencing this pattern can be determined and changes in distribution monitored. As in the case of many other species, grizzly bear range edge is both spatially and temporally dynamic (Brown et al. 1996, Gaston 2003) and is characterized by highly variable environmental conditions (Miller et al. 1997). As a result, grizzly bear populations may have varied responses to habitat and human factors (Apps et al. 2004). For the recovery of grizzly bears in Alberta, it is thus necessary to understand factors affecting the range edge to understand what conditions facilitate or prevent range expansion. A common first step in understanding the determinants of species ranges is correlating their distribution to biotic and abiotic factors (Hoffmann and Blows 1994, Parmesan et al. 2005). Numerous studies have attempted to do so (e.g. Connell 1961, Gross and Price 2000, Holt and Keitt 2000, Gaston 2003, Case et al. 2005, Illera et al. 2006, Arntzen and Themudo 2008, McInnes et al. 2009, Bridle et al. 2010, Glor and Warren 2011, Werner et al. 2013) but the unique ecological niche of each species cause numerous and diverse results that cannot be generalized (Brown et al. 1996). Consequently, each species may need to be studied individually (Hoffmann and Blows 1994). For grizzly bears in Alberta, this has not been done.

Such studies may rely on more than one method to investigate species distributional limits. The use of species distribution models (SDMs) is a traditional technique used extensively in ecology to make detailed predictions of species distributions (Elith and Leathwick 2009). SDMs use regression techniques and other algorithms to identify limiting factors by relating presence/absence or abundance of species to environmental predictor variables (Guisan and Thuiller 2005). In this way, environmental gradients are considered across all or a large portion of the species' range. A second method builds on the premise that species borders may also coincide with hard dispersal barriers and/or sharp changes in environmental gradients (Case et al. 2005). Overlapping boundaries can indicate the presence of underlying processes that either create or maintain boundaries (Holland et al. 1991, Fortin et al. 1996, Jacquez et al. 2000). As a result, edge detection techniques can be used to assess the spatial overlap of species boundaries with environmental boundaries; they thus offer a novel approach to investigating limiting factors. Edge detection techniques directly address the edge of range while SDM methods more broadly address species distributions. Considering both methods may result in a more comprehensive understanding of species distributional limits.

In this paper, I use multiple data sources to create an updated range map of male and female grizzly bears in Alberta. In doing so, I also investigate environmental and anthropogenic factors hypothesized to limit their eastern distribution. I anticipate that female grizzly bears will have a smaller geographic distribution than male grizzly bears. I also expect that range periphery will be affected most by anthropogenic rather than natural barriers. Although population processes, genetic mechanisms, and biotic interactions will also limit the distribution of a species, considering these factors is beyond the scope of this project. Based on the results of the study, I make recommendations for future monitoring and conservation of grizzly bears along the eastern range in Alberta.

2. STUDY AREA

I studied the range of grizzly bears across the province of Alberta, Canada (Figure 3-1). Grizzly bear population units were delineated in 2004 for management and conservation purposes (Figure 3-1). Data on known grizzly bear locations are most prolific for west-central and southern Alberta, while little information exists for northern portions of the province. West-central Alberta is dominated by mountainous and foothill environments. The Rocky Mountain region is influenced by a continental climate of cold winters and short cool summers, whereas the foothills region has generally warmer summer temperatures, higher annual precipitation, and a longer growing season (Natural Regions Committee 2006). Elevations in west-central Alberta range from 700 to 3,747 m and forests contain lodgepole pine (*Pinus contorta*), spruce (*Picea englemanii, P. glauca, P. mariana*), fir (*Abies lasiocarpa*), and trembling aspen (*Populus tremuloides*).

In south-western Alberta, there is a sharp interface between the mountains and the parkland and grassland regions, with limited foothill environments separating the two. The grassland natural region has the warmest and driest climate and longest growing season within the study areas whereas the parkland natural region has intermediate temperature, precipitation, and growing season values between the grasslands and foothills regions. Elevation ranges from 300 to 1,600 m and primary vegetation types include conifer forests, deciduous forests, shrub lands, and grasslands. Douglas fir (*Pseudotsuga menzeisii*), Englemann spruce, and lodgepole pine are common conifers while trembling aspen and cottonwood (*P. trichocarpa*) are the most common deciduous species.

Ungulate species common to Alberta include moose (*Alces alces*), elk (*Cervus canadensis*), white-tail deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Large carnivores in Alberta include the American black bear (*Ursus americanus*), wolf (*Canus lupis*), and cougar (*Puma concolor*) (Munro et al. 2006).

Energy exploration and development, mining, forestry, human settlements, and extensive recreation occur throughout the province. Road networks continue to expand due to high resource extraction activities and increasing human developments resulting in significant changes to landscape characteristics and land-use patterns (Alberta Forestry, Lands and Wildlife 1990). Cattle-ranching is the major land use in southwestern Alberta, occurring on both public and private land. Much of the area where human activities occur overlaps with grizzly bear habitat. Grizzly bears are also found in the three national parks along Alberta’s western border: Jasper National Park, Banff National Park, and Waterton National Park.

3. METHODS

I compiled grizzly bear location data from five different sources between 1999 and 2010 to determine grizzly bear range in Alberta and assess limiting factors at the range edge. From the location data, male and female grizzly bear range was defined using presence-absence grids with 20x20 km (400 km^2) grid cells. Once grizzly bear range was determined, I investigated limiting factors at the range edge for male and female grizzly bears using two methods. First, I explored limiting factors by assessing the spatial overlap of species boundaries and environmental boundaries using lattice-wombling in program BoundarySeer. Lattice-wombling is an edge detection technique that identifies boundaries as areas of high rates of change (Womble 1951, Fortin 1994). Second, I explored limiting factors to grizzly bear range with logistic regression using a traditional species distribution modeling (SDM) approach (Elith and Leathwick 2009). Lastly, I mapped areas of high rates of change in both grizzly bear range and limiting factors for the province of Alberta.

3.1. Grizzly Bear Range

I used five sources of grizzly bear point location data ranging from years 1999 to 2010 to determine male and female grizzly bear range in Alberta. These five sources include grizzly bear sightings, capture, mortality, telemetry and DNA point location data (Table 3-1). The spatial accuracy of the different data sources varied, especially for sighting data. For locations recorded in the Alberta Township System (ATS), I converted them to UTM using an online Government of Alberta ATS-to-UTM converter. I converted locations recorded in Wildlife Management Units (WMU) as the UTM of the center of the WMU.

Reproduction – or the presence of reproductive females – is often considered the definition of occupied range. For grizzly bears, the home range size and dispersal distance of male and female bears differ dramatically. Annual home ranges for females grizzly bears in Alberta range from approximately 150 km^2 to 2900 km^2 whereas males range from approximately 500 km^2 to 4750 km^2 (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). In a study of grizzly bears in both Canada and the US, Proctor et al. (2004) found that females dispersed an average of 14.3 km from their natal home range, whereas males dispersed an average of 41.9 km. As a result, I defined male and female grizzly bear range separately. I considered any female bear (regardless of age), yearling (regardless of gender), or cub of the year (COY) locations as female bear range; yearling and COY locations were included as their presence indicates that the area supported reproduction. Male bear range consisted of adult and sub-adult male bears and bears of unknown gender.

I created male and female grizzly bear range maps for the province of Alberta by spatially overlapping grizzly bear point locations from 1999 to 2010 to a province-wide grid of 20x20 km grid cells. A grid cell size of 20x20 km was chosen based on the average home range size of grizzly bears in Alberta. A grid cell with one or more grizzly bear locations or a grid cell that overlapped the national parks was considered presence whereas an empty grid cell was considered absence. To reduce the number of single, isolated presence cells, I used a majority resampling algorithm that replaces cells based on the majority of their neighbouring cells. This resulted in a more contiguous definition of grizzly bear range.

3.2. Predictor Variables

Once grizzly bear range in Alberta was determined, I used the range maps to explore limiting factors at the eastern range edge. At one time, grizzly bear range in North America spanned nearly the entire continent (Schwartz et al. 2003), a reflection of their habitat-generalist nature. Similarly, the omnivorous diet of grizzly bears means they consume a wide diversity of foods including grasses, forbs and their roots, berries, mammals, and insects (Munro et al. 2006). Habitat loss and degradation from increased anthropogenic footprints – such as agriculture, settlements, and resource-extractive industries – and human-caused mortality have caused dramatic reductions in grizzly bear range across North America and they continue to threaten the persistence of grizzly bears in Alberta (Mattson and Merrill 2002, Ross 2002 Nielsen et al. 2004a). For these reasons, I hypothesized that the factors limiting the eastern range edge of grizzly bears in Alberta are largely anthropogenic in nature. I considered a total of 17 predictor variables including four landcover variables, five human footprint variables, five anthrome (Ellis et al. 2010) variables, two human population variables, and a night-time light variable (Table 3-2). Anthromes describe global anthropogenic transformations of the terrestrial biosphere at a coarse scale (Ellis et al. 2010).

I obtained landcover data from the Alberta Biological Monitoring Institute and included conifer, grassland, agriculture, and development landcover types (Table 3-2). Landcover variables have been used in a number of models estimating grizzly bear habitat quality and occupancy (Mace et al. 1996, McLellan and Hovey 2001, Apps et al. 2004, Nielsen et al. 2006). Nielsen et al. (2009) found that agriculture in particular was an important predictor of regional occupancy of female grizzly bears. Human footprint data was also obtained from the Alberta Biological Monitoring Institute and included the footprints of urban, cultivation, industry, and hard linear features (Table 3-2). I created a fifth cumulative impacts footprint by combining urban, cultivation, and industry footprints. To my knowledge, broad estimates of human footprint (other than roads) have not been used in studies of grizzly bear occupancy and distribution, but it seems pertinent to include them given the effects of anthropogenic footprints on grizzly bear habitat quality (Apps et al. 2004, Mowat et al. 2005, Nielsen et al. 2010).

Similar to both landcover and human footprint variables are anthropogenic biomes – or anthromes. Anthromes were created by Ellis et al. (2010) as they characterized and mapped anthropogenic transformations of the terrestrial biosphere from years 1700 to 2000. Visual comparison of Alberta's anthromes and provincial grizzly bear population units suggested that anthromes could be an important predictor of range edge. Five major anthromes were used as predictor variables in this study, including settlement, cropland, rangeland, semi-natural areas and wild land anthromes.

Another simple but novel way of quantifying human impacts on the landscape is by mapping nighttime lights. The artificial night lighting that results from human occupation and alteration of the landscape – e.g. omnipresent settlements, industrial areas, and large-scale burning practices – is uniquely visible from space (Aubrecht et al. 2008). Thus, nighttime lights act as a surrogate for human impacts (Woolmer et al. 2008) and several studies have used nighttime lights to assess the ecological consequences of human stressors (e.g. Aubrecht et al. 2008, Jonas et al. 2013). Lastly, I included estimates of population density by census sub-divisions across Alberta to assess the impact of human population density on grizzly bear distribution.

Due to the different resolution between predictor variables and the large geographic size of the study area, landcover, human footprint and nighttime light variables were resampled to a binary raster of 5x5 km resolution. This resolution is small enough to detect variance but not so large that variability is reduced. Anthrome variables, which had an original raster resolution of 10x10 km, were not resampled nor were the population census data. Next, I summarized each predictor variable based on the same province-wide 20x20 km grid as the grizzly bear range maps. Proportion of landcover, human footprint, and anthrome variables were summarized for each grid cell, whereas an average value was calculated for population density and nighttime lights at each grid cell. To calculate proportion, I used Zonal Statistics to count the number of 5x5 km pixels of each predictor variable within every 20x20 km grid cell. Population data and nighttime light data was summarised using Zonal Statistics by calculating the mean value in each 20x20 km grid cell.

3.3. Edge Detection Methodology

Species distributional limits may coincide with hard barriers or thresholds along environmental gradients (Case et al. 2005). In other words, environmental gradients may experience sharp discontinuities along the edge of a species' range. As such, one approach to investigating limiting factors along the eastern range edge of grizzly bears in Alberta is to identify those predictor variables that experience a high degree of change in the same vicinity as changes in grizzly bear range. Program BoundarySeer is boundary analysis software that uses edge detection methods to identify boundaries as areas of high rates of change (TerraSeer Inc. 2001). For regularly sampled quantitative data, such as a grid, a lattice-wombling edge detection algorithm is used (Fortin and Drapeau 1995). The algorithm computes the first partial derivatives (i.e., rate of change) between adjacent units using a 2x2 unit search window with respect to spatial coordinates (Fortin and Drapeau 1995). This produces a map of rates of change, called boundary likelihood values; the boundary likelihood values that exceed a user-defined threshold become the boundary elements (BE's) that define the boundary. A threshold of 10%, for example, selects rates of change above the 10th percentile rank as boundaries. Depending on the objectives of the study, thresholds of 20% (Fortin and Dale 2005, Polakowska et al. 2012), 15% (St-Louis et al. 2004, Hall and Maruca 2001), and 10% (Barbujani et al. 1989, Fortin 1994, Fortin and Drapeau 1995) have been used. Boundaries are defined as the average of the rates of change of all variables at a given location for multivariate data sets (Fortin and Drapeau 1995).

To explore limiting factors at the range edge using BoundarySeer, I first had to delineate the boundaries of grizzly bear range and of the 17 potential limiting factors. To determine the appropriate threshold value for selecting BE's, I performed a preliminary sensitivity analysis using a range of thresholds (20%, 15%, 10%, and 5%). A threshold of 20% resulted in many, scattered BE's indicating the detection of noise (St-Louis et al. 2004). On the other hand, thresholds of 10% and 5% resulted in too few BE's to form cohesive boundaries. As a result, I chose an intermediate threshold value of 15% to define boundaries, which has also been used in other studies of ecological boundaries (Hall and Maruca 2001, St-Louis et al. 2004). Two exceptions to this were the rangeland

and settlement anthromes, which required a threshold value of 7% due to limited data.

One issue with using an arbitrary threshold value for selecting BE’s is that a certain number of boundaries will always be found for a given threshold regardless of whether the boundaries are statistically unusual (Jacquez et al. 2000). Thus, one should perform boundary statistics, which assesses the contiguity of boundaries to determine whether the boundary differs significantly from those found in a random pattern (Fortin and Drapeau 1995). Cohesive boundaries should be characterized by few BE’s that are long in length, whereas fragmented boundaries have many, short BE’s (Fortin and Dale 2005). As such, cohesive boundaries are expected to have fewer BE’s (N_S), fewer single, scattered BE’s (N_1), higher BE length (L_{MAX} and L_{MEAN}) and diameter (D_{MAX} and D_{MEAN}), and lower branchiness (D/L - mean diameter-to-length ratio) than might be expected if boundaries were to occur by chance. However, I assessed the significance of boundaries using four properties: N_1, N_S, L_{MAX} and L_{MEAN}. Monte Carlo procedures are used to compare the boundary statistics to a randomized reference distribution. I performed univariate boundary statistics on all 17 predictor variables using restricted distance decay Monte Carlo randomization and 9999 permutations. A restricted randomization procedure was chosen as it can provide more realistic randomizations than complete spatial randomness (Fortin and Dale 2005). Equation 3.1 was used to calculate the distance decay constant, where g is a probability, b is the decay constant, and p is distance.

$$g = \frac{1}{1+bp} \qquad \textbf{3.1}$$

I calculated a distance decay constant of 0.00007 based on a probability of 0.5 and a distance of 14,300 m – the average dispersal of a female grizzly bear (Proctor et al. 2004). Because I was only interested in detecting cohesive boundaries, I used a one-tailed test ($p < 0.01$) to assess the significance of the boundary statistics (Fortin 1994).

Once boundaries are defined and assessed for significance, it is possible to assess the spatial association between boundaries. To determine which predictor variables were limiting factors of grizzly bear range, I assessed whether grizzly bear range boundaries overlapped significantly with the boundaries of predictor variables. I used three overlap statistics to determine whether grizzly bear range edge and predictor variable boundaries coincide more than might be expected by chance: i) the directional association of grizzly bear range edge with a predictor variable (O_G); ii) the simultaneous association of grizzly bear range edge and a predictor variable (O_{GH}); and iii) the direct overlap of grizzly bear range edge with a predictor variable (O_S). Statistics O_G and O_{GH} are the mean distance between a grizzly bear range boundary and a predictor variable boundary whereas O_S is the number of BE’s that occur in both sets of boundaries. Consequently, one would expect values of O_G and O_{GH} to be low and values of O_S to be high where there is overlap between boundaries. However, I assessed the significance of spatial overlap between grizzly bear range edge and a variable boundary using two properties: O_G and O_S. The overlap of each variable was assessed individually as BoundarySeer currently lacks true multivariate techniques where the contribution of each variable can be quantified (Jacquez et al. 2000). Similar to the boundary statistics, I tested the significance of overlap statistics using a restricted randomization procedure with a decay constant of 0.00007, 9999 permutations, and a one-tailed test ($p < 0.01$). Because I am interested in whether grizzly bear range edge is a response to high rates of change in predictor variables, I only randomized the grizzly bear range boundaries. Predictor variables that had significant boundaries and significant overlap with grizzly bear range boundaries were considered limiting to eastern range edge of grizzly bears in Alberta. I ranked the importance of each limiting factor based on the amount of direct overlap (O_S) of its boundary with the grizzly bear range boundary. Predictor variables were assessed separately for male and female grizzly bear range.

Lastly, I produced a map showing areas of high rates of change in male and female grizzly bear range and their respective limiting factors. To do so, I created two multivariate data sets: one comprised of female bear range and its limiting factors, the other comprised of male bear range and its limiting factors. I then delineated boundaries for each multivariate data set using threshold values of 15% and 10%. Recall that for multivariate data sets, BoundarySeer simply averages the rates of change across all variables; thus, the contribution of a single variable to the boundary cannot be quantified.

3.4. Species Distribution Modeling (SDM)

While edge detection methods are a novel approach for exploring limiting factors at the range edge (Fortin et al. 1996), species distribution models (SDMs) are a traditional approach with a long history of use in ecological research of species' range (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and Leathwick 2009). SDMs use linear regression and various other methods to attempt to understand why a species occurs in one area but not another. I used the same male and female grizzly bear range maps and the same 17 predictor variables to explore limiting factors using SDM methods. Because grizzly bear range is defined as either 0 or 1, I modelled grizzly bear occupancy as a function of predictor variables in a univariate analysis using a logistic linear regression model. I used a cut-off p-value of 0.05 to assess the significance of each variable and I ranked their importance using Akaike's Information Criterion (AIC) (Burnham, Anderson 2002). Modeling was carried out in program R 2.15.0 (R Core Development Team 2012).

4. RESULTS

4.1. Grizzly Bear Range

I determined male and female grizzly bear range in Alberta by spatially overlapping grizzly bear point locations (presences) from 1999 to 2010 to a province-wide grid of 20x20 km grid cells (Figure 3-2). Occupied grizzly bear range is described by females, yearlings, and COY whereas potential grizzly bear range is described by male bears. Female bear range is more restricted than male bear range and does not extend as far eastward (Figure 3-2). Female grizzly bear range is also within or westward of population unit delineations (Figure 3-2).

Male bear range extends eastward of current population units in many areas, especially southern Alberta and the Yellowhead population unit (Figure 3-2). Because grizzly bear location data for northern Alberta is limited, it is likely that this map does not accurately estimate grizzly bear range north of Grande Prairie.

4.2. Edge Detection Methods

Next, I explored the factors limiting the eastern range edge of grizzly bears in Alberta using the male and female range maps and two methods: edge detection method and a species distribution modeling approach. Using edge detection methods in program BoundarySeer, boundaries of grizzly bear range and boundaries of 17 predictor variables were delineated using a lattice-wombling algorithm and a threshold value of 15% or 7%. I then assessed the significance of each variable boundary using the following four properties: N_S, N_1, L_{MEAN}, and L_{MAX}. Nine predictor variables had significantly contiguous boundaries, meaning that boundaries were longer and had fewer sub-boundaries and singletons (one BE) than expected by chance (Table 3-3). Seven predictor variables had more singleton boundaries than were expected by chance (Table 3-3); this result is not surprising for the settlement anthrome and urban human footprint predictor variables given that human settlements are scattered across the landscape. The cumulative impact human footprint variable (OptA) had shorter maximum boundary length than is expected by chance and the semi-natural anthrome had shorter boundaries, more singletons, and more subboundaries than expected from random pattern (Table 3-3).

To determine which predictor variables were limiting to grizzly bear range in Alberta, I assessed the spatial overlap between grizzly bear range boundaries and the boundaries of each predictor variable using two properties: O_G and O_S. Although female bear range overlaps significantly with semi-natural anthrome, I did not consider semi-natural anthrome as a limiting factor because it failed to have a significant boundary in three of four properties (Table 3-3). Male and female range boundaries were found to overlap with five of seventeen variable boundaries: agriculture landcover, cropland and wild anthromes, and urban and cultivation human footprints (Table 3-4). However, the importance of each limiting factor – assessed by O_S – differed slightly between male and female bear range (Table 3-6). The limiting factors of male bear range had clear rankings, whereas several factors had tied rankings for female bear range. The top three limiting factors for male bear range are cropland anthrome, cultivation human footprint, and urban human footprint (Table 3-6). For female bear range, cropland anthrome and cultivation human footprint tied for first, agricultural landcover and urban footprint tied for second, and wild land anthrome ranked third (Table 3-6). Urban footprint was found to be more limiting than agricultural landcover for male bear range but was tied with agricultural landcover for female bear range (Table 3-6).

4.3. Species Distribution Modeling (SDM) Methods

For the second approach to exploring limiting factors at the eastern range edge of grizzly bears in Alberta, I used a traditional species distribution modeling approach. I modelled grizzly bear occupancy as a function of predictor variables using a logistic regression model in a univariate analysis. Eleven variables were found to be significant predictors of male bear range whereas and twelve variables were found to be significant predictors of female bear range (Table 3-6). When ranked by AIC, the top five predictors of male bear range are cropland anthrome, semi-natural anthrome, conifer landcover, agriculture landcover, and cultivation footprint (Table 3-7); the top five predictors for female range are agricultural landcover, anthrome cropland, and cultivation human footprint, industry footprint, and the cumulative impact of industry, urban, and cultivation footprints (Table 3-7). Semi-natural anthrome and conifer landcover positively influence male bear distribution while cropland, agriculture, and cultivation have negative impacts (Table 3-6). Cropland, agriculture, and cultivation also negatively impact female grizzly bear distribution, as do industry and cumulative impact footprints (Table 3-6).

Overall, the SDM approach identified more limiting factors than edge detection methods. BoundarySeer identified five limiting factors for both male bear and female bear range whereas SDM methods identified eleven and twelve limiting factors, respectively. For male bears, cropland anthrome was identified as the first-ranked limiting factor and agricultural landcover as the fourth-ranked limiting factor by both edge detection and SDM methods (Table 3-7). The top three limiting factors for female bear range – agricultural landcover, cropland anthrome, and cultivation human footprint – were identified by both methods but ranked differently (Table 3-7).

4.4. Areas of High Rates of Change

Lastly, I produced a map showing areas of high rates of change in bear range and the limiting factors identified by edge detection techniques. Thus, the boundaries largely correspond to high rates of change in grizzly bear range, wild land habitat, agricultural areas, and urban areas. The maps produced for male bear range (Figure 3-3) and female bear range (Figure 3-4) are similar given that the limiting factors are the same. Strong north-south boundaries are evident in central and southern Alberta while strong east-west boundaries are found near Grande Prairie (Figure 3-3). In most cases, male bear range extends beyond the boundaries of its limiting factors (Figure 3-3), whereas female bear range typically does not (Figure 3-4). However, both male bear and female bear range extend beyond the boundaries of limiting factors in areas south of Lethbridge (Figure 3-4). Interestingly, there also areas that neither support grizzly bears nor are characterized by drastic changes in the limiting factors identified in this study, such as areas east of Hinton and areas north-west of Red Deer.

5. DISCUSSION

An important step in addressing grizzly bear conservation issues in Alberta, such as recovery objectives and long-term monitoring programs, is to understand the spatial distribution of the population (Apps and Bateman 2005). A basic understanding of the distribution of grizzly bears across an area such as Alberta allows one to understand the factors influencing this pattern (Apps and Bateman 2005). In simple terms, a species range is a geographic expression of its demographic response to a world constantly changing in time and space (Holt et al. 2005). Thus, the determinants of range limits can be discussed in terms of how they influence demographic parameters of birth, death, immigration and emigration (Gaston 2009). As previously discussed, I created range maps for male and female grizzly bears in Alberta and used them to explore factors hypothesized to limit the eastern range edge. The results demonstrate that grizzly bears in eastern Alberta are predominately limited by high proportions of agricultural zones and human settlements. Using this information, I mapped areas of rapid change in grizzly bear range and limiting factors as a means to prioritize conservation and monitoring along the range periphery.

5.1. Female Grizzly Bear Range and Limiting Factors

As expected, female grizzly bear range is more restricted than male bear range in Alberta (Figure 3-2). Results from a large-scale study of grizzly bear movement and population fragmentation by Proctor et al. (2012) suggest that females naturally move less than males, especially near disturbances such as human settlements. Female grizzly bears also have smaller home ranges and shorter dispersal distances than males (McLellan and Hovey 2001, Proctor et al. 2004). To establish a home range, juvenile male grizzly bears disperse farther over a longer period of time than do females (McLellan and Hovey 2001). Adult male grizzly bears may also wander large distances in search of food (McLoughlin et al. 1999), but may not contribute to reproduction in these areas. Gaston (2009) argues that dispersal limits the geographic range of most, if not all, species but that the extent of this limitation varies. Thus, the restricted range of female grizzly bears is partly explained by their limited dispersal relative to male bears. Because male bears are not necessarily surviving to reproduce near the range margin, occupied grizzly bear range is best described by the presence of reproductive females, despite grizzly bear occurrences outside of this range (Alberta Grizzly Bear Recovery Plan 2008).

Factors limiting female grizzly bear range identified by edge detection methods include cropland anthrome, cultivation footprint, and agricultural landcover, as well as urban footprints and wild anthrome (Table 3-5). The fact that three separate agricultural variables were selected, and that they showed the most overlap with bear range boundaries (Table 3-7), suggests that agriculture has a significant impact on grizzly bear range. Similarly, in a study in southwestern Alberta, Northrup et al. (2012) found that that habitat highly selected by grizzly bears overlapped with human development, especially on private land. Although bears are known to occur in the agricultural zone (Alberta Sustainable Resource Development and Alberta Conservation Association 2010), there is a low chance of survival due to human-bear conflict and human-caused mortality (Johnson et al. 2004, Wilson et al. 2005, Northrup 2010). Bears are easily attracted to poorly secured grain storage bins and calving grounds, and they are known to scavenge on dead livestock (Wilson et al. 2005, Wilson et al. 2006, Northrup 2010), which can lead to relocation or death of bears in defense of persons and property. Relocating bears can cause serious injury to the animal (Cattet et al. 2008) and also increases the risk of repeat conflict or death (Blanchard and Knight 1995, Linnell et al. 1997).

For grizzly bears, agricultural areas can be considered ecological traps (Northrup et al. 2012) – i.e. areas where habitat quality is favorable but the risk of mortality is high (Dwernych and Boag 1972, Nielsen et al. 2006). Nielsen et al. (2009) have previously found agriculture to have a negative impact on the regional occupancy of grizzly bears. If bears enter the agricultural zone, the high risk of mortality reduces the likelihood that bears will survive or reproduce. Inadequate levels of successful reproduction are a common cause of range limits (Gaston 2009). If local deaths exceed local births, then immigration into agricultural zones simply maintains a sink population and prevents range expansion (Lawton 1993, Holt et al. 2005, Gaston 2009).

Similarly, bears face a high risk of human-caused mortality near human settlements, as human tolerance of grizzly bears is generally very low. Northrup et al. (2012) found that human-bear conflict in southern Alberta was more likely to occur in areas with houses and increased human populations. Likewise, Proctor et al. (2012) suggest that settlements have been and continue to be a primary cause of population fragmentation in grizzly bears; they also found that female grizzly bear movement rates declined drastically when settlements increased to greater than 20 percent of the study area (Proctor et al. 2012). In this way, human settlements can influence grizzly bear dispersal and mortality – two important drivers of species range (Gaston 2009).

The proportion of agricultural zones and density of human settlements increases as one moves east across Alberta. Consequently, grizzly bears are largely confined to forested, mountainous, and otherwise “wild land” habitats that are found primarily in western Alberta (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). Out of five limiting factors identified by edge detection techniques, urban footprint ranked second (tied with agricultural landcover) and wild land anthrome ranked third (Table 3-7) for female bear range. The interface where “wild” habitats end and human settlements and agricultural zones begin is therefore a major limitation to the eastern range of female grizzly bears in Alberta.

In addition to identifying other variables, SDM methods identified the same limiting factors for female bear range as edge detection techniques (Table 3-6). The three agricultural variables were ranked highest once again (Table 3-7), reaffirming their strong, negative impact on female grizzly bear distribution. Industry footprint and a cumulative anthropogenic footprint were also found to have negative impacts on female grizzly bear distribution and ranked fourth and fifth, respectively (Table 3-7). Industry footprint includes well sites, mine sites, and other rural industrial sites. At local scales, grizzly bears are known to use well sites and mine sites because they can support an abundance of bear foods (Sahlen 2010, Bogdan 2012). At regional scales, however, the number and density of industrial features can contribute to landscape fragmentation and/or habitat loss (Schneider et al. 2003). Fragmentation and habitat loss can result in range limits if habitat patches cannot be colonized, even if the quality of the patches remains suitable (Holt and Keitt 2000). Additionally, the risk of mortality and of human-bear conflict increases near industrial features, such as natural gas facilities (Northrup et al. 2012). Like agricultural areas, habitats characterized by high industrial and cumulative footprints likely act as ecological traps for grizzly bears, which may prevent bears from expanding beyond these areas.

5.2. Male Grizzly Bear Range and Limiting Factors

When edge detection techniques were used, male grizzly bear range was found to have the same limiting factors as female bear range (Table 3-5). However, urban footprint ranked higher than agricultural landcover for male bears (Table 3-7). As previously discussed, the fact that male grizzly bear range extends beyond female bear range is partly explained by the difference in dispersal abilities and home range size. It is also possible that male and female bears have different tolerances or thresholds for disturbance. Difference in behaviour between male and female bears has been documented near well sites (Sahlen 2010), roads (Gibeau et al. 2002, Proctor et al. 2012), and human settlements (Gibeau et al. 2002, Proctor et al. 2012). If male bears are more tolerant of agricultural areas than female bears, they may disperse further east until limited by a greater increase of human settlements.

For male bears, the results identified by SDM methods differed in part from those identified by edge detection techniques. Cropland anthrome, agricultural landcover, and cultivation footprint remain in the top five limiting factors, similar to edge detection techniques. However, semi-natural anthrome and conifer landcover are also rank in the top five. In contrast to agricultural-related variables, semi-natural anthrome and conifer landcover positively influenced male grizzly bear distribution (Table 3-6). This result is expected given that grizzly bears are largely confined to the forested and mountainous habitats of western Alberta. Semi-natural areas likely provide a balance of natural and disturbed areas (Ellis et al. 2010), which creates a diversity of habitat types. A heterogeneous landscape is beneficial to grizzly bears as it provides an abundance and diversity of important food resources (Nielsen et al. 2004b).

Conifer landcover is often associated with the sub-alpine, montane and foothill natural subregions that occur in western Alberta (Natural Regions Committee 2006). Nielsen et al. (2009) found grizzly bear occupancy was positively influenced by alpine, sub-alpine, montane, upper foothill, and lower foothill subregions, but negatively influenced by central mixedwood, foothills fescue, and foothills parkland sub-regions. Coniferous and semi-natural habitats are likely of higher quality and security; thus bears are present and have high survival (Nielsen et al. 2006). Higher survival then leads to greater reproductive success and higher abundances of bears in semi-natural and coniferous habitats. As one moves east across the province, semi-natural anthromes and coniferous habitats are lost to areas dominated by agriculture and human settlements where habitat security, survival, and reproductive success are much lower. The loss of secure, high-quality habitat thereby contributes to the eastern range limits of grizzly bears in Alberta. Long-term monitoring along the range periphery is needed to ensure their persistence in these areas (Proctor et al. 2012) and to better understand grizzly bear demographics at their range edge.

5.3. Areas of High Rates of Change

One challenge to future monitoring along the eastern range edge will involve the placement of monitoring sites. Because grizzly bear research has typically occurred in core grizzly bear habitat, less is known about grizzly bear movement and behaviour along the range periphery. One way to guide the placement of monitoring sites is determining where limiting factors and bear range change dramatically. Areas that experience high rates of change can be the most important areas for monitoring as their locations reflect underlying ecological processes at work (Jacquez et al. 2000). I created a map showing the geographic location of rapid changes in grizzly bear range and the limiting factors identified by edge detection methods. The boundaries reflect the interface between wild land habitat, agricultural zones, human settlements, and bear range. Clear boundaries exist in southern Alberta where mountainous and forested habitats (i.e. “wild land”) are immediately adjacent to agriculture (Figure 3-3, Figure 3-4). For female grizzly bears, these boundaries extend almost continuously as far north as Red Deer (Figure 3-4). The same effect is seen near Grande Prairie where coniferous forests transition sharply into agricultural zones (Figure 3-3, Figure 3-4). Male bear range often extends beyond the boundaries of its limiting factors (Figure 3-3) whereas female bear range typically does not (Figure 3-4), which may further suggest different disturbance tolerances for male and female grizzly bears. Both male and female bear range extend beyond the boundaries of limiting factors in southern Alberta (Figure 3-4), and male bear range extends well beyond the population unit boundary (Figure 3-3). Further research is needed to understand why this is the case, but it is possible that grizzly bear populations are increasing in these areas. Grizzly bears in southern Alberta are also well connected to more than 900 bears in southern BC and northern US (Proctor et al. 2012), which may support increased immigration.

Monitoring along these areas of high rates of change would be an important first step in further investigations of grizzly bear range, range dynamics, and peripheral population estimates. In addition, it is also important to note where (a) grizzly bear range does extend to the boundaries of limiting factors, and (b) neither grizzly bear range nor drastic changes in limiting factors exist. In both cases, it is unclear what is limiting grizzly bear range in these areas. Limiting factors, if present, do not occur at drastic proportions, therefore it’s likely that other factors are influencing grizzly bear range. As a result, these areas are equally important for monitoring to better understand the limits to grizzly bear range in Alberta.

In addition, knowing the locations where grizzly bear range and limiting factors change abruptly lends insight into where human-bear conflict might occur. Understanding and predicting where conflicts occur is fundamental first step to conflict reduction (Treves and Karanth 2003), which is acknowledged as a critical step in the recovery of grizzly bear populations in Alberta (Alberta Grizzly Bear Recovery Plan 2008). In southern Alberta, both male and female bear range extend beyond the boundaries of limiting factors (Figure 3-4), which may increase human-bear conflicts. Northrup et al. (2012) also mapped the probability of human-bear conflict for southwestern Alberta, but not the remainder of the province. Thus, this study helps to identify potential conflict areas at a broad scale for both female and male bears in Alberta.

5.4. Other Limiting Factors

For reasons previously discussed, I have restricted my study of range determinants to anthropogenic-related factors. Other factors, however, may be limiting the eastern range of grizzly bears in Alberta that were not investigated here. Landscape connectivity, for example, has been found to impact grizzly bear demographics (Proctor et al. 2012). Poor landscape connectivity coupled with short dispersal distances can increase the risk of extinction along range limits by draining individuals from core habitat (Holt 1985). Consequently, connectivity may be an important barrier to bear range, especially in central and eastern portions of the province where landscapes become more fragmented. Proctor et al. (2012) have expressed the need to secure habitat that facilitates safe, long-term connectivity between subpopulations.

Genetic mechanisms also influence the distribution of species (Case and Taper 2000, Bridle and Vines 2007, Kawecki 2008). In Alberta, Proctor et al. (2012) found limited gene flow in bears occurring in Swan Hills and weak genetic fractures across most of Alberta’s major east-west highways. Fragmented populations could lead to range contraction if the number of dispersing individuals is insufficient (Wilson et al. 2002, Nielsen et al. 2008). On the other hand, sufficient gene flow from central Alberta populations and from across the Continental Divide (Proctor et al. 2012) could ‘swamp’ adaptation to marginal conditions (Hoffmann and Blows 1994, Kirkpatrick and Barton 1997, Lenormand 2002). Whether gene flow primarily restricts or enhances range limits remains poorly understood (Butlin et al. 2003).

The interaction between range limits and behaviour also has been poorly studied (Gaston 2009). For mobile species, the adequacy or inadequacy of certain behaviours can influence their withdrawal from areas when conditions become unfavorable (Ontiveros and Pleguezuelos 2003, Gaston 2009). Knowledge of grizzly bear habitat selection along the range periphery could provide valuable insight to eastern range limits. Conversely, climate is one of the most widely studied range limits (Gaston 2003). Though climate is often significantly associated with distribution boundaries (Parmesan et al. 2005, Sexton et al. 2009), it is not expected to have major consequences for grizzly bear range given their habitat-generalist nature. Finally, the low density and slow reproductive rate of grizzly bears in Alberta means that grizzly bears along the range periphery could be in risk of Allee effects – where populations below a threshold density are unable to maintain a positive growth rate (Sexton et al. 2009). For example, many females may remain unmated due to low encounter rates caused by low population densities (Sexton et al. 2009).

5.5. Limitations and Future Research

In my analysis of abiotic and biotic range determinants of grizzly bears in Alberta, I found it useful to use both edge detection and species distribution modeling methods. Edge detection methods identify locations where sharp boundaries in grizzly bear range and environmental variables coincide. As a result, one can specifically investigate factors limiting marginal populations at the range edge. In contrast, SDM methods attempt to predict species distributions by relating the presence or absence of a species to environmental predictors (Elith and Leathwick 2009). In this way, SDM methods consider central and marginal populations, which may explain why more limiting factors were identified using this method. While edge detection techniques allow one to investigate whether the location of a bear boundary is associated with the location of a variable boundary (Fortin et al. 1996), regression methods can model more complex ecological relationships (Elith and Leathwick 2009). Using both approaches in a complementary framework can advance our knowledge of grizzly bear distribution and range edge. Managers and conservationists will benefit from a more comprehensive understanding of grizzly bear range and range edge, especially in the case of conservation planning and forecasting.

One limitation of edge detection techniques was that I could not use multivariate statistics to explore limiting factors. Environmental and ecological data co-occur on the landscape and many have complex relationships between them. Consequently, the effect and importance of each variable should be assessed relative to all other variables. To determine the rate of change for multivariate data sets, BoundarySeer simply averages the rates of change across all variables, therefore the contribution of a single variable to the boundary cannot be quantified (Jacquez et al. 2000). SDM methods have the advantage of being able to perform multivariate statistics; however, I used a univariate approach in my SDM analysis to more easily compare results between the two approaches. Although I have attempted to rank the limiting factors identified by edge detection techniques based on the amount of direct overlap between bear range boundaries and the boundaries of limiting factors, multivariate statistics are required to truly understand the relationship between factors.

On the other hand, consensus as to what factors are most important to a species range is rarely reached. The number and importance of limiting factors can vary at different spatial scales, between different parts of the range, and at different times (Porter et al. 2002, Gaston 2003, Morin et al. 2007). I believe the spatial scale of our study was appropriate given the large extent of our study area and the fact that grizzly bears are a highly mobile species with large home ranges. Furthermore, the study of species ranges needs to be investigated at a scale relevant to land use planning – i.e. the regional or landscape scale (Opdam and Wascher 2004, McInnes et al. 2009). The proper temporal scale over which to analyze species’ ranges remains largely unanswered (Holt et al. 2005). Due to data limitations, it was necessary to investigate the range limits of grizzly bears in Alberta as a “snapshot” in time from 1999 to 2010. Lastly, the grizzly bear range maps created in this study was based on known and presumed occurrences of bears. Grizzly bear locations reported as sightings, though probable, are generally unconfirmed. Despite the unknown accuracy of sighting data, it was necessary to use it to get more complete description of potential range in eastern Alberta. Occupied bear range is described by female bear locations and is therefore a conservative estimate of range.

Nonetheless, much of the data informing male range or potential range needs to be verified with future monitoring along the eastern range periphery. Systematic monitoring would be advantageous as sighting, mortality, and capture data may be spatially biased near roads and/or near areas with higher numbers of people. Significant knowledge gaps remain where both grizzly bear range and drastic changes in limiting factors are absent. It is unclear what limits grizzly bear range in these areas therefore further research is needed. In northern Alberta, which currently has low anthropogenic footprint and a relatively “wild” habitat, grizzly bear distribution has not been widely investigated. If this were rectified prior to further landscape modifications, northern Alberta may provide a unique opportunity to study the effects of landscape change on grizzly bear distribution. Lastly, the ability to incorporate time into analyses of range maps and/or distribution models is currently limited but necessary to study the range dynamics of grizzly bears and other species (Holt and Keitt 2005). Due to the rapid pace of landscape change and the number of potential limiting factors that could not be investigated here, future research should continue to study the range limits and range dynamics of grizzly bears in Alberta.

5.6. Conclusion

Overall, this research indicates that the eastern range of grizzly bears in Alberta is limited primarily by agricultural zones and urban areas. The range edge of female bears in Alberta typically occurs at the interface between wild land habitat and agricultural zones. Male bear range appears to extend into agricultural zones until limited by an increasing proportion of human settlements, but future monitoring is needed to determine the accuracy of these observations. The placement of future monitoring sites can be aided by knowledge of where grizzly bear range and its limiting factors change rapidly. Because these areas are susceptible to human-bear conflict, management may also target these areas for proactive conflict management. Conversely, further research and/or monitoring is required in areas where neither grizzly bear range nor dramatic changes in limiting factors are found as it is unclear in this case what is limiting grizzly bear range. Grizzly bears can exist in human-dominated landscapes provided that human-caused mortality and bear relocations are minimized. Consequently, special efforts are needed in areas surrounded by agricultural zones and human settlements where habitat conditions are good but the risk of mortality is high, yet manageable.

6. MANAGEMENT IMPLICATIONS

This research helps to understand the spatial distribution of grizzly bears in Alberta as well as the factors influencing this pattern. The next step to addressing grizzly bear conservation issues is integrating knowledge of bear range and limiting factors within local and regional planning (Apps, Bateman 2005). Many of the same ecological characteristics that make grizzly bears susceptible to anthropogenic population fragmentation also influence the limits to their eastern distribution – that is their sensitivity to anthropogenic mortality, short dispersal, male-biased dispersal, slow reproductive rate, and low population density.

Agricultural zones and human settlements were identified as the primary factors limiting the eastern range edge of grizzly bears in Alberta. The mortality risk to bears, rather than habitat loss, likely prevents bears from occurring permanently in these areas. As a result, agricultural areas may be an ecological trap for grizzly bears (Northrup et al. 2012). Proctor et al. (2012) expressed concern that a possible west-east source-sink dynamic is already operating in Alberta as shown by the rapid decline in grizzly bear abundance from west to east across the province. Nielsen et al. (2006) have also suggested a west-east source-sink dynamic in Alberta, identifying source habitat in alpine and protected areas and attractive sink habitat in the foothills and to the east. Conflict reduction has been acknowledged as a critical step in the recovery of grizzly bear populations in Alberta (Alberta Grizzly Bear Recovery Plan 2008).

In particular, managers must reduce the risk of mortality and the probability of population sinks along the eastern periphery. Proper grain storage, feed storage, and disposal of dead livestock are paramount in reducing conflict with grizzly bears in agricultural areas. Similarly, urban areas should adopt BearSmart community best practices, which include managing bear attractants such as garbage, landfills, pet food, bird feeders, green spaces, and gardens (Government of Alberta 2011). A consistent protocol for dealing with conflict is needed to minimize unnecessary bear deaths or bear relocations (Nielsen et al. 2009). Changing human attitudes towards bears is also pivotal to successful human-bear coexistence (Nielsen et al. 2009).

Because grizzly bears in Alberta are bounded by agriculture and human settlements to the east, long-term monitoring is needed to ensure the persistence of grizzly bears along the eastern periphery (Proctor et al. 2012). The impact of limiting factors on levels of immigration, births, deaths, and/or emigration will vary spatially and temporally at range limits; therefore, abundances at range limits also are expected to vary (Gaston 2009). This has important implications for management as the risk of local population extinctions along range margins is exacerbated by small population sizes (Thomas et al. 1994, Mehlman 1997, Williams et al. 2003, McClenachan and Cooper 2008). On the other hand, grizzly bear range may expand if provincial recovery efforts are successful, and range expansion could be one way to evaluate recovery success. Furthermore, monitoring along the eastern range periphery may also help to confirm the validity of sighting data – a wealth of information that currently has limited use because of the uncertainty associated with these records.

The location of monitoring sites should concentrate in areas where dramatic changes in grizzly bear range and limiting factors coincide. These are areas of highly dynamic habitat that are most likely to have ecological consequences (Jacquez et al. 2000), such as direct impacts to grizzly bear range.

As a result, monitoring in areas with rapid change in limiting factors and grizzly bear range may be particularly fruitful. If hair-snag genetic surveying at permanent sites is to be used for monitoring, understanding local factors influencing the detection of grizzly bears as identified in Chapter 2 may guide the placement of sites at a finer scale. However, these factors may vary considerably between core and peripheral habitats.

Table 3-1. Grizzly bear location point data from 1999 to 2010 used to create grizzly bear and female grizzly bear range maps in Alberta, Canada. Data from Alberta Fish and Wildlife has been abbreviated to F&W and data from Foothills Research Institute has been abbreviated to FRI.

		No. Points		
Data Type	**Source**	**Female**	**Male / Unkown**	**Total**
Capture	F&W	160	229	389
DNA	FRI	1,868	1,499	3,367
Telemetry	FRI	188,835	126,492	315,327
Mortality	F&W	122	180	302
Sighting	F&W	0	3,806	3,806

Table 3-2. Summary of environmental and anthropogenic variables hypothesized to limit grizzly bear range in Alberta, Canada. Variables selected as limiting factors following univariate overlap analysis are denoted by (*).

Source	Group	Variable	Variable Code	Type	Unit	Scale	Re-Scale	Type	Data Range
ABMI	**Landcover**	**Conifer**	LC_con	Vector	m	1 ha	5 km	Proportion	0 to 1
		Agriculture*	LC_ag	Vector	m	1 ha	5 km	Proportion	0 to 1
		Grassland	LC_grass	Vector	m	1 ha	5 km	Proportion	0 to 1
		Development	LC_devel	Vector	m	1 ha	5 km	Proportion	0 to 1
ABMI	**Human Footprint**	**Urban***	HF_urb	Vector	m	3 x 6 km	5 km	Proportion	0 to 1
		Cultivation*	HF_cult	Vector	m	3 x 6 km	5 km	Proportion	0 to 1
		Industry	HF_ind	Vector	m	3 x 6 km	5 km	Proportion	0 to 1
		Urban+Cultivation+Industry	HF_opta	Vector	m	3 x 6 km	5 km	Proportion	0 to 1
		Hard Linear Features	HF_HLF	Vector	m	3 x 6 km	5 km	Proportion	0 to 1
Ellis et al. 2010	**Anthrome**	**Cropland***	A_crop	Raster		10 km		Proportion	0 to 1
		Rangeland	A_rnge	Raster		10 km		Proportion	0 to 1
		Wild*	A_wild	Raster		10 km		Proportion	0 to 1
		Semi-natural	A_semi	Raster		10 km		Proportion	0 to 1
		Settlement	A_sett	Raster		10 km		Proportion	0 to 1
Canada Census	**Population Density**	**Population Density 2011**	Popden11	Vector	m	Census sub-divisions		Average	0 to 4617
		Population Density 2006	Popden06	Vector	m	Census sub-divisions		Average	0 to 4698
NOAA-NDGC	**Night-time Lights**	**Night-time Lights**	Lights	Raster		2.7 km	5 km	Average	0 to 63

Table 3-3. Boundary statistics for boundaries delineated from environmental and anthropogenic variables. Boundary elements were delineated at the 15% threshold with the exception of two variables (rangeland and settlements). NS is the number of sub-boundaries (boundaries with >1 BE); N1 is the number of singletons (1 BE); LMAX is the maximum boundary length; LMEAN is the mean boundary length; DMAX is the maximum boundary diameter; DMEAN is the mean boundary diameter; D/L is the mean diameter to length ratio (branchiness). Statistical significance is based on 9999 permutations.

			Boundary Statistics						
Group	**Covariate**	**Threshold**	**N_s**	**N_1**	**L_{MEAN}**	**L_{MAX}**	**D_{MEAN}**	**D_{MAX}**	**D/L**
Landcover	**Conifer**	15	112• (-9.89)†	56• (-7.06)	2.2 • (15.66)	14• (6.58)	2.2 • (15.66)	14• (7.58)	1 (0.50)
	Agriculture	15	92• (-10.64)	32• (-8.29)	2.7• (19.14)	13** (4.50)	2.6• (19.15)	11** (4.42)	1 (-1.21)
	Grassland	15	89• (-5.49)	34** (-2.45)	2.9• (7.77)	29• (8.79)	2.6• (5.34)	16** (4.66)	1• (-7.18)
	Development	15	112• (-7.57)	53• (-5.45)	2.2• (10.81)	13** (4.62)	2.1• (9.99)	11** (4.20)	1• (-7.02)
Anthrome	**Cropland**	15	55• (-23.06)	17• (-13.84)	4.5• (83.49)	38• (39.29)	4.0• (69.56)	30• (30.02)	1• (0.00)
	Rangeland	7	23• (-3.92)	3 (1.55)	5.1• (4.97)	17** (4.39)	4.4• (9.04)	16• (7.94)	0.9 (4.52)
	Wild	15	97• (-16.8)	39• (-11.97)	2.6• (34.79)	11• (8.70)	2.5• (34.24)	11• (8.70)	1• (0.00)
	Semi-natural	15	96 (0.64)	41 (1.82)	2.7 (-0.11)	16* (2.68)	2.6 (0.53)	12* (2.87)	1 (2.86)
	Settlement	7	18• (-6.17)	1 (0.15)	6.4• (9.44)	15* (3.02)	4.8• (10.49)	10* (2.98)	0.8 (-0.71)
Human Footprint	**Urban**	15	81* (-2.03)	24 (0.65)	3.1* (2.24)	28• (8.20)	2.8 (1.58)	22• (8.20)	1 (-0.61)
	Cultivation	15	91• (-10.76)	35• (-7.95)	2.7• (19.44)	13** (4.47)	2.7• (19.88)	13** (6.00)	1 (0.16)
	Industry	15	78• (-6.38)	29** (-2.58)	3.2• (9.53)	29• (9.99)	2.9• (7.92)	20• (8.06)	1* (-2.78)
	OptA	15	113• (-7.64)	55• (-5.61)	2.2• (11.08)	8 (1.56)	2.2• (11.29)	8 (1.96)	1 (0.59)
	HLF	15	104• (-6.81)	51• (-4.21)	2.4• (9.69)	30• (14.52)	2.2• (7.87)	20• (10.33)	1• (-7.68)
Population Density	**Popden 2011**	15	79** (-5.64)	21 (0.31)	3.1** (3.07)	16* (3.07)	2.9* (2.13)	11 (1.82)	1• (-4.24)
	Popden 2006	15	83* (-2.05)	22 (0.38)	3.0* (2.25)	16* (3.22)	2.8 (1.45)	11 (1.92)	1** (-3.67)
Night-time Lights	**Lights**	15	82** (-2.44)	29 (-1.05)	3.1** (2.87)	17* (3.17)	2.9** (3.25)	15* (4.91)	1 (0.92)

† Values in parentheses are standardized z-scores indicating the strength and direction of the difference between observed values and expected values. To be significant, N_S, N_1, and D/L should be in the lower 1% tail and L_{MAX}, L_{MEAN}, D_{MAX}, and D_{MEAN} should be in the upper 1% tail of the randomized reference distribution. Statistical significance of values isindicated at $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (●).

Table 3-4. Spatial boundary overlap statistics for environmental and anthropogenic variables and male grizzly bear range. OG is the directional association of bear boundaries to predictor variable boundaries; OGH is the simultaneous association of bear and predictor variable boundaries; OS is the direct spatial overlap of boundary elements in the two sets of boundaries. Statistical significance is based on 9999 permutations.

			Male Bear Spatial Boundary Overlap Statistics		
Group	**Covariate**	**Threshold**	**O_G**	**O_{GH}**	**O_S**
Landcover	**Conifer**	15	44707.64** (-2.78)†	91954.27 (16.67)	28.00 (-1.52)
	Agriculture	15	21546.80● (-7.99)	42238.29 (-0.11)	54.00* (1.604)
	Grassland	15	98543.11 (4.133)	114210.01 (15.61)	18.00 (-2.59)
	Development	15	53564.17* (-1.73)	92861.21 (12.61)	21.00 (-2.44)
Anthrome	**Cropland**	15	20070.03● (-9.39)	31671.90● (-3.70)	78.00● (5.065)
	Rangeland	7	107126.94** (-2.74)	143735.85 (8.673)	9.00 (-0.74)
	Wild	15	27471.52● (-5.93)	73248.29 (8.967)	49.00* (1.516)
	Semi-natural	15	30998.13● (-5.15)	77290.41 (11.36)	36.00 (-1.29)
	Settlement	7	66987.61● (-4.57)	69203.66* (-1.39)	16.00 (-0.63)
Human Footprint	**Urban**	15	21005.22● (-6.37)	44531.63 (3.554)	55.00* (1.771)
	Cultivation	15	25791.05● (-7.07)	54095.30 (2.509)	56.00** (2.63)
	Industry	15	55699.56 (-0.85)	98696.40 (15.60)	18.00 (-3.06)
	OptA	15	62115.56 (-0.59)	108079.15 (15.63)	10.00 (-4.48)
	HLF	15	33030.95** (-2.75)	59608.96 (10.58)	26.00 (-2.50)
Population Density	**Popden 2011**	15	37385.14● (-3.04)	61058.96 (8.085)	36.00 (-1.09)
	Popden 2006	15	31719.78** (-2.04)	57716.13 (7.802)	36.00 (0.167)
Night-time Lights	**Lights**	15	35084.90● (-3.18)	66816.40 (11.05)	32.00 (-1.21)

† Values in parentheses are standardized z-scores indicating the strength and direction of the difference between observed values and expected values. To be significant, O_G and O_{GH} should be in the lower 1% tail and O_S should be in the upper 1% tail of the randomized reference distribution. Statistical significance of values is indicated at $p < 0.1$ (*), $p < 0.01$ (**), and $p < 0.001$ (●).

Table 3-5. Spatial boundary overlap statistics for environmental and anthropogenic variables and female grizzly bear range. OG is the directional association of bear boundaries to predictor variable boundaries; OGH is the simultaneous association of bear and predictor variable boundaries; OS is the direct spatial overlap of boundary elements in the two sets of boundaries. Statistical significance is based on 9999 permutations.

			Female Bear Spatial Boundary Overlap Statistics		
Group	**Covariate**	**Threshold**	**O_G**	**O_{GH}**	**O_S**
Landcover	**Conifer**	15	63888.134 (1.761)†	137124.06 (10.41)	15.00 (-0.17)
	Agriculture	15	22772.23● (-5.35)	71566.35 (2.468)	31.00* (1.193)
	Grassland	15	56590.51* (-1.78)	17644.71 (6.542)	8.00 (-0.56)
	Development	15	35800.44● (-2.89)	115087.50 (4.462)	17.00 (0.097)
Anthrome	**Cropland**	15	22062.81● (-5.79)	59473.22 (1.107)	34.00* (1.462)
	Rangeland	7	129622.24* (-1.85)	191439.18 (4.908)	6.00 (0.456)
	Wild	15	23817.33● (-3.78)	102499.76 (5.154)	27.00* (0.885)
	Semi-natural	15	22165.15● (-3.67)	95144.07 (4.794)	32.00* (0.806)
	Settlement	7	57682.71● (-3.33)	91000.84 (2.59)	9.00 (0.111)
Human Footprint	**Urban**	15	21775.99● (-3.79)	70530.84 (3.498)	31.00* (1.156)
	Cultivation	15	20407.32● (-4.97)	68894.94 (2.496)	34.00** (1.441)
	Industry	15	45525.42* (-1.76)	119151.13 (4.601)	23.00 (0.537)
	OptA	15	43930.69** (-2.28)	126885.39 (4.823)	20.00 (0.065)
	HLF	15	18720.30● (-4.23)	77480.49 (3.203	25.00 (0.57)
Population Density	**Popden 2011**	15	33104.16* (-1.49)	87279.52 (8.114)	20.00 (-0.21)
	Popden 2006	15	29278.29** (-1.99)	84161.69 (7.735)	20.00 (-0.21)
Night-time Lights	**Lights**	15	2010.43** (-2.73)	85264.67 (23.06)	28.00 (-8.99)

† Values in parentheses are standardized z-scores indicating the strength and direction of the difference between observed values and expected values. To be significant, O_G and O_{LB} should be in the lower 1% tail and O_S should be in the upper 1% tail of the randomized reference distribution. Statistical significance of value is indicated at $p < 0.1$ (*), $p < 0.01$ (**), and $p < 0.001$ (●).

Table 3-6. Coefficient, p value and Akaike's Information Criterion (AIC) of environmental and anthropogenic variables hypothesized to limit grizzly bear range in Alberta following univariate logistic regression analysis (SDM approach).

		Male Bear Range			Female Bear Range		
Group	**Covariate**	**Coefficient**	**p value**	**AIC**	**Coefficient**	**p value**	**AIC**
Landcover	**Conifer**	1.358	4.99E-11 ***	1978.4	1.192	7.33E-06 ***	1430.3
	Agriculture	-0.899	4.57E-12 ***	1978.5	-1.628	8.58E-16 ***	1369.5
	Grassland	1.131	4.83E-07 ***	2000.9	1.000	0.000545 ***	1440.6
	Development	0.609	5.74E-06 ***	2008.9	-0.072	0.653	1454.4
Anthrome	**Cropland**	-1.096	6.63E-16 ***	1957.5	-1.599	3.61E-15 ***	1373.7
	Rangeland	-3.396	0.136	2027.1	-9.211	0.0942	1449.0
	Wild	0.759	3.11E-09 ***	1993.5	1.260	1.49E-12 ***	1397.2
	Semi-natural	2.905	9.48E-16 ***	1961.5	1.876	7.61E-07 ***	1432.6
	Settlement	-3.288	0.162	2027.3	-14.663	0.0997	1447.1
Human Footprint	**Urban**	-0.711	1.81E-07 ***	2001.7	-1.266	3.81E-11 ***	1404.2
	Cultivation	-0.829	1.39E-10 ***	1986.3	-1.568	2.12E-15 ***	1374.3
	Industry	-0.429	0.00158 **	2020.3	-1.406	< 2E-16 ***	1379.9
	OptA	-0.252	0.0713	2026.9	-1.305	6.37E-16 ***	1391.6
	HLF	0.168	0.201	2028.5	-0.356	0.0314 *	1450.0
Population Density	**Popden 2011**	0.000	0.661	2029.9	0.000	0.936	1454.6
	Popden 2006	0.000	0.677	2030.0	0.000	0.998	1454.6
Night-time Lights	**Lights**	-0.039	0.00132 **	2017.7	-0.108	2.53E-06 ***	1421.7

Significance codes: 0.0001 (***); 0.001 (**); 0.05 (*)

Table 3-7. Importance of individual limiting factors to the eastern range edge of grizzly bears in Alberta, Canada. Limiting factors identified by edge detection methods were ranked based on the direct overlap of grizzly bear range edge with the predictor variable boundary (OS). Limiting factors resulting from the SDM method were ranked based on Akaike's Information Criterion (AIC).

Range	BoundarySeer	O_S	Rank
Male	A Cropland	78	1
	HF Cultivation	56	2
	HF Urban	55	3
	LC Agriculture	54	4
	A Wild	49	5
Female	A Cropland	34	1
	HF Cultivation	34	1
	LC Agriculture	31	2
	HF Urban	31	2
	A Wild	27	3
Range	**SDM**	**AIC**	**Rank**
Male	A Cropland	1957.5	1
	A Semi-natural	1961.5	2
	LC Conifer	1978.4	3
	LC Agriculture	1978.5	4
	HF Cultivation	1986.3	5
	LC Grassland	2000.9	6
	HF Urban	2001.7	7
	LC Development	2008.9	8
	Nigh-time Lights	2017.7	9
	HF Industry	2020.3	10
	A Rangeland	2027.1	11
Female	LC Agriculture	1369.5	1
	A Cropland	1373.7	2
	HF Cultivation	1374.3	3
	HF Industry	1379.9	4
	HF OptA	1391.6	5
	A Wild	1397.2	6
	HF Urban	1404.2	7
	Nigh-time Lights	1421.7	8
	LC Conifer	1430.3	9
	A Semi-natural	1432.6	10
	LC Grassland	1440.6	11
	HF HLF	1450.0	12

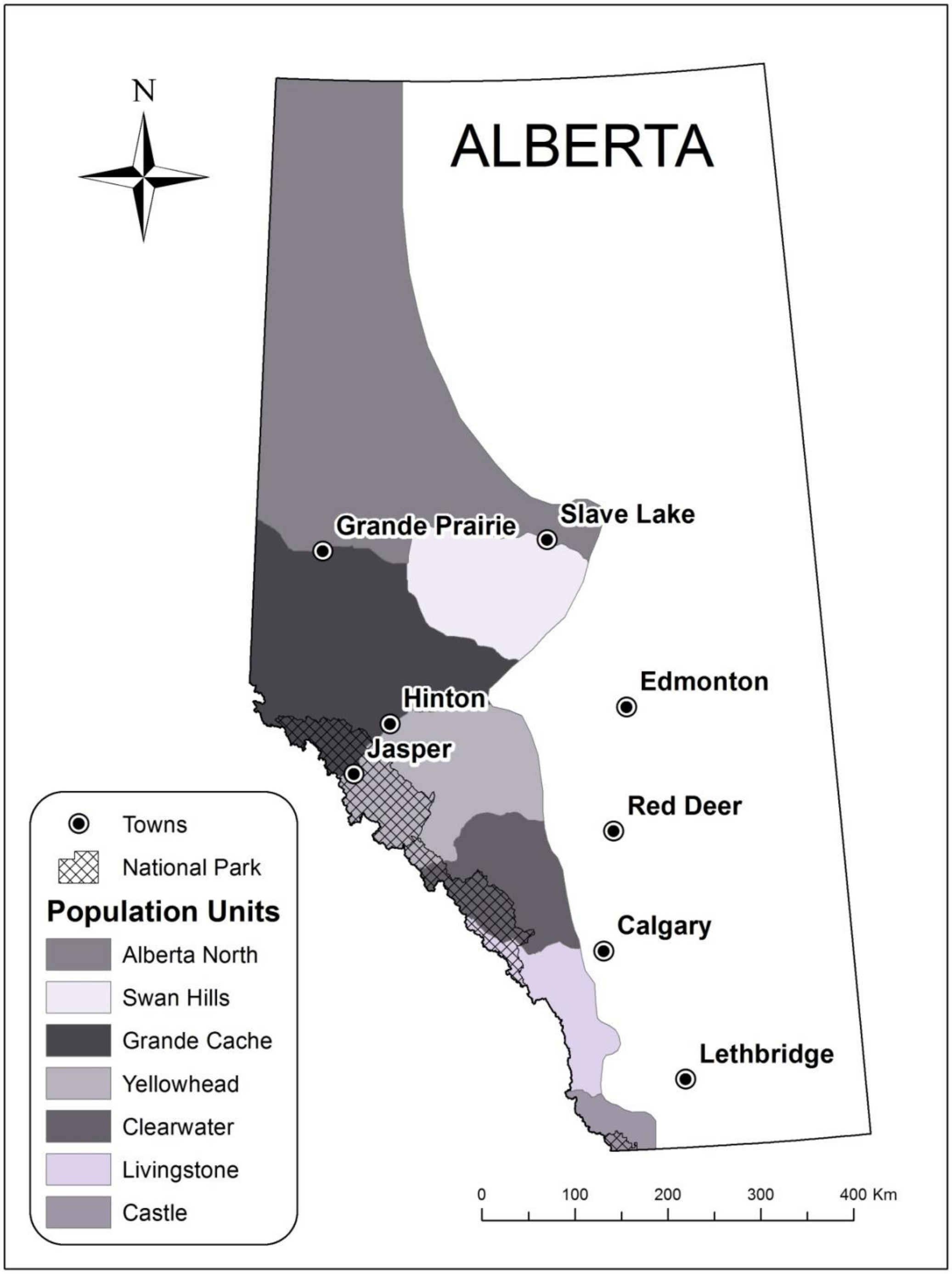

Figure 3-1. Geographic location of the province of Alberta and its major urban settlements, national parks, and the seven provincial grizzly bear population units.

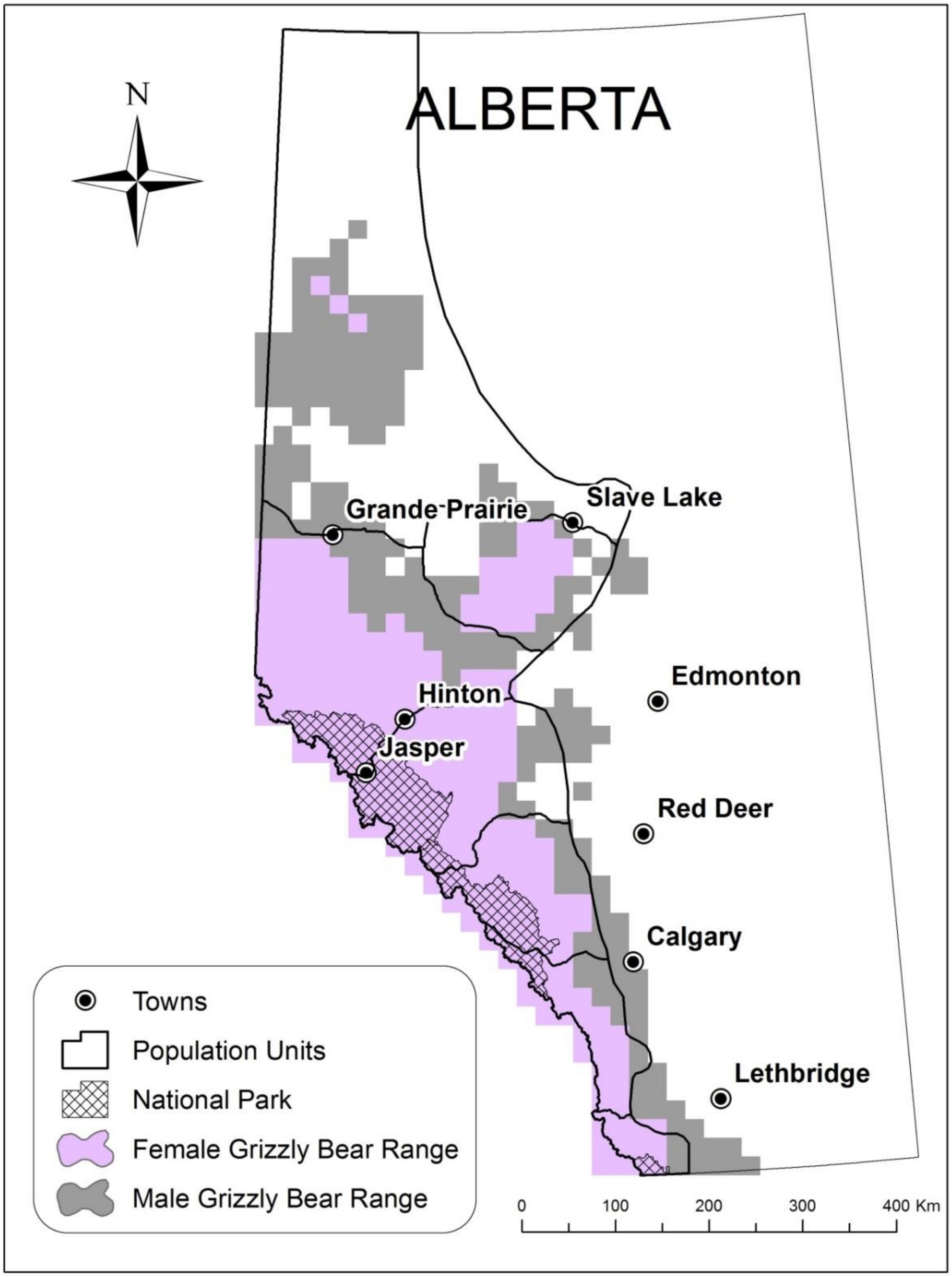

Figure 3-2. Grizzly bear and female grizzly bear range in Alberta, Canada determined from point locations of sightings, capture, mortality, telemetry and DNA data sources from years 1999 to 2010. The point locations were then used to determine the presence-absence of 20x20 km grid cells spanning the entire province.

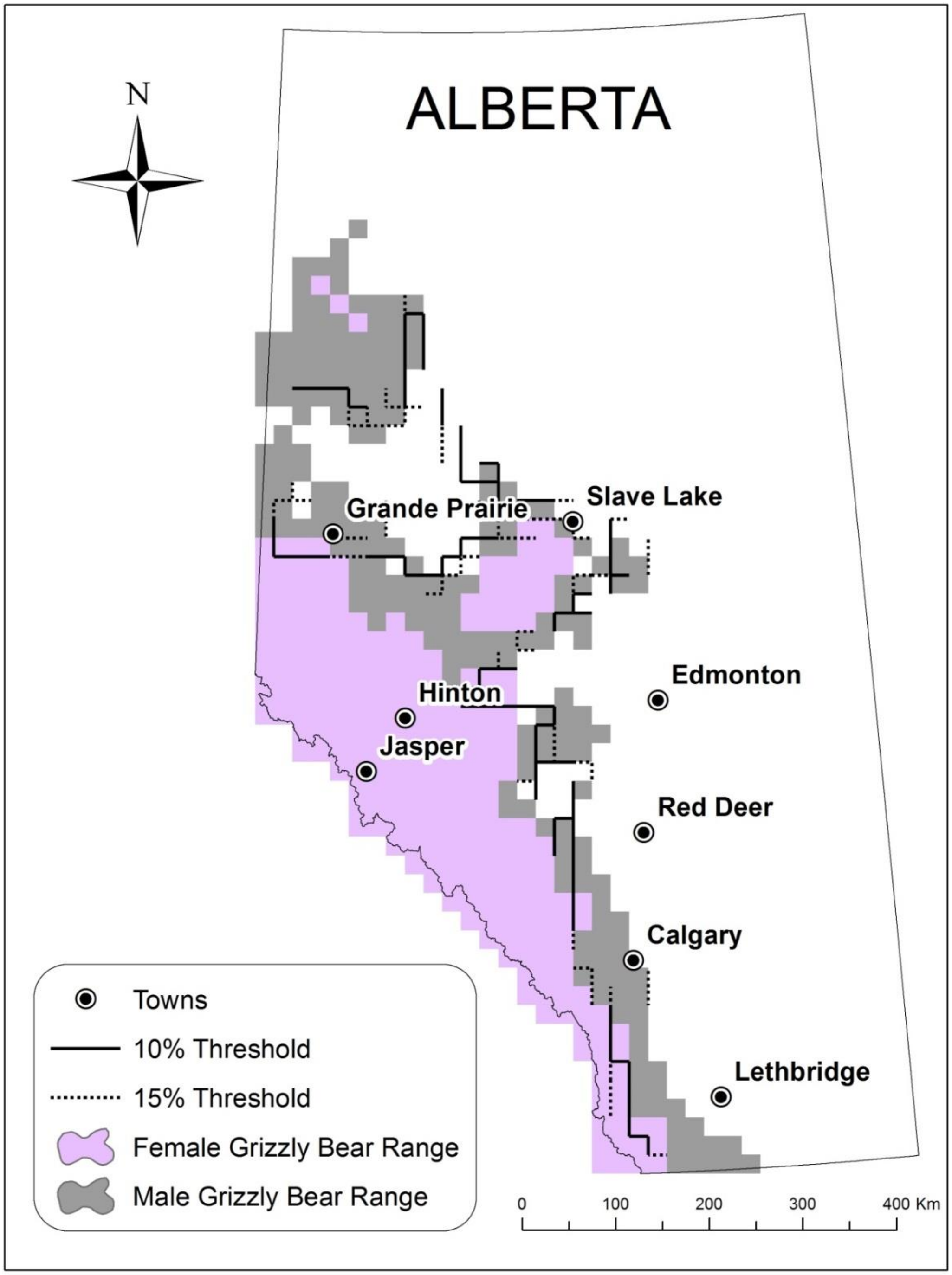

Figure 3-3. Boundaries based on male grizzly bear range from 1999 to 2010 and four limiting factors: agriculture landcover, cropland anthrome, wild anthrome, urban footprint, and cultivation footprint. A solid line indicates boundaries delineated at a 15% threshold whereas a dotted line indicates boundaries delineated at a 10% threshold.

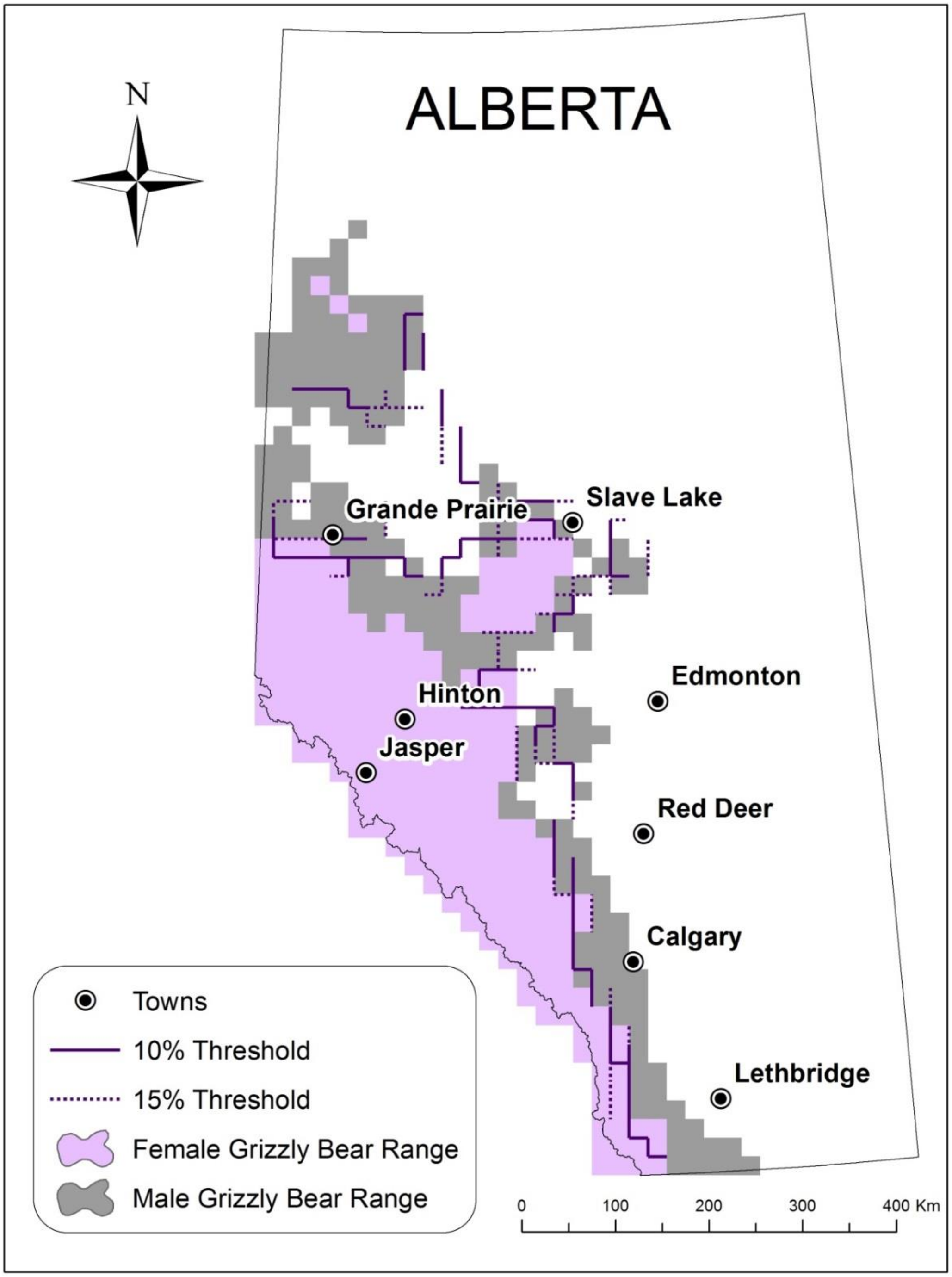

Figure 3-4. Boundaries based on female grizzly bear range from 1999 to 2010 and four limiting factors: agriculture landcover, cropland anthrome, wild anthrome, urban footprint, and cultivation footprint. A solid line indicates boundaries delineated at a 15% threshold whereas a dotted line indicates boundaries delineated at a 10% threshold.

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CHAPTER 4

GENERAL DISCUSSION AND CONCLUSIONS

Grizzly bear conservation and recovery in Alberta is a formidable task given their sensitivity to anthropogenic stressors and the escalating amount and variety of land-use in grizzly bear habitat. Long-term and cost-effective monitoring of grizzly bear abundance and distribution is needed to ensure the persistence of grizzly bears in Alberta – especially along eastern portions of their range. The purpose of this research was to address several challenges to establishing a long-term grizzly bear monitoring program. In Chapter 2, I explored local factors affecting the detectability of grizzly bears when they are surveyed using a permanent network of DNA hair traps. My results demonstrate that (1) a permanent network of DNA hair traps can be used to reliably monitor grizzly bears in Alberta's foothills, and (2) the probability of detecting a grizzly bear increases when sites are placed near pipelines, wellsites, cutblocks, and streams in areas with high abundance of buffaloberry and clover but otherwise poor food availability. A comparison of site occupancy between 2004 and 2011 also suggests that grizzly bear occupancy in the study area is increasing, which stresses the importance of future population monitoring. In Chapter 3, I explored factors limiting the eastern distribution of grizzly bears in Alberta and mapped where these factors and grizzly bear range change rapidly across the landscape. My results show that eastern grizzly bear range is primarily limited by agricultural areas, human settlements, and the subsequent loss of forested, wild land habitat.

One of the biggest challenges of wildlife monitoring is knowing where to place sites to maximize the detection of a species. This knowledge is critical for permanent hair trap sites as they are not moved once established. The results of Chapter 2 help to identify where, at a local scale, to place permanent hair trap sites in forested, foothill habitats. Such habitats are found within core grizzly bear range where grizzly bears are already known to occur (Nielsen et al. 2009). As a result, managers can use this information to identify optimal site placement, which helps, in part, to ensure the most cost-effective monitoring results. On other hand, grizzly bear occupancy is poorly understood along their eastern range making monitoring of peripheral populations difficult as there is little information to guide the placement of sites. In Chapter 3, I identified where grizzly bear range and its limiting factors experience rapid change across the landscape. Where this occurs reflects underlying processes that may create or maintain boundaries (Holland et al. 1991, Fortin et al. 1996, Jacquez et al. 2000) and thus affect grizzly bear survival and abundance. The map also highlights areas of uncertainty where neither grizzly bear range nor dramatic changes in limiting factors are found. Consequently, managers can use this information to identify where, at a regional scale, to place sites along the eastern range edge. This is an important first-step to monitoring grizzly bear distribution and peripheral populations despite the regional scale of the analysis.

Another challenge to grizzly bear conservation in Alberta is reducing human-bear conflict and human-caused mortality. Grizzly bear detectability can increase near pipelines, wellsites, and cutblocks (Chapter 2) because of important bear food growing on these sites. Because these anthropogenic features are easily accessible by humans, the risk of human-bear conflict increases and that can lead to bear mortality. Without careful management, pipelines, wellsites, and cutblocks could become ecological traps – habitat that has an abundance of food but also high rates of mortality (Dwernych and Boag 1972). Previous research has also identified roads, forest harvesting, and agricultural areas as ecological traps (Nielsen et al. 2006, Nielsen et al. 2008, Roever et al. 2008, Northrup et al. 2012), the latter which is a limiting factor to eastern grizzly bear range (Chapter 3). General habitat preferences and individual habitat selection are important for predicting the level of risk ecological traps pose to grizzly bears (Lima and Zollner 1996, Delibes et al. 2001). The ecological characteristics of a species – such as reproductive rate – also play a key role (Wiegand et al. 1998, Delibes et al. 2001). Grizzly bears in Alberta have a low reproductive potential because of a late age of first reproduction, small litter sizes, and a long interval between litters (Nagy et al. 1989, Garshelis et al. 2005, Schwartz et al. 2006). A low reproductive rate makes grizzly bear populations especially sensitive to changes in mortality rate, which elevates the risk of ecological traps. Consequently, I, and many others, continue to stress the need for consistent and dedicated efforts to reduce human-bear conflict and human-caused mortality of grizzly bears.

This thesis has filled important knowledge gaps regarding factors affecting grizzly bear detectability (Chapter 2) and distribution (Chapter 3). This information can be used to guide the development of long-term monitoring of grizzly bear abundance and distribution. However, research on local factors affecting grizzly bear detection (Chapter 2) occurred in foothill habitat within a relatively small area of west-central Alberta. I suspect that different local factors may influence grizzly bear detection in other habitats, such as along the eastern range periphery. Although I identify important areas for monitoring along the eastern range periphery at a regional scale, this information should be used as a guide for finer-scale research. Future research on habitat selection along the eastern range margins would improve our knowledge of optimal site location, of limiting factors at the range edge (Gaston 2009), and of the risk posed by attractive sinks (Lima and Zollner 1996, Delibes et al. 2001). To gain a more comprehensive understanding of the factors limiting grizzly bear range, future research must also improve multivariate techniques in edge detection modeling. The relative importance of each factor to the range boundary is necessary for accurate predictions of future range shifts – a major benefit to wildlife managers and land-use planners (Channell and Lomolino 2000, Parmesan et al. 2005). At present, edge detection techniques cannot determine the relative importance of each limiting factor to the range boundary (Jacquez et al. 2000) therefore our ability to predict shifts in grizzly bear range remains limited.

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APPENDIX A MODELING PROCEDURE

Phase 1: A-priori Approach

Step 1: Beginning with the first occupancy hypothesis (PSI$_1$), select the top ranked variable in each theme of the occupancy sub-model. With these variables selected, hold the occupancy sub-model constant and model each hypothesis of detectability (P_1 … P_n). Vary only the variables in the last theme of the detectability sub-model while holding the other themes constant using the top ranked variable.

Step 2: Return to the occupancy sub-model, select the next top ranked variable in the last theme, and repeat step 2 until all the variables in the last theme have been modeled.

Step 3: Repeat steps 1 and 2 for the remaining occupancy hypotheses (PSI$_1$ … PSI$_n$). Refer to these models as **preliminary candidate models** and rank them according to AIC.

Step 4: Select the top ranked preliminary candidate model from each occupancy hypothesis and rank them according to AIC. Refer to these as **candidate models.**

Step 5. Select the top ranked candidate model and refer to this model as the **final candidate model.**

*This is the top model using the *a-priori* approach.*

Phase 2: Posteriori Approach

Step 6. Select the final candidate model from the *a-priori* approach. While holding the detectability sub-model constant, add back in each previously removed variable from the univariate analysis one at a time to the occupancy sub-model. Refer to these models as **preliminary *psi* models** and rank them according to AIC.

Step 7. Select the final candidate model from the *a-priori* approach. While holding the occupancy sub-model constant, add back in each previously removed variable from the univariate analysis one at a time to the detectability sub-model. Refer to these models as **preliminary *p* models** and rank them according to AIC.

Step 8. Select the top ranked preliminary psi model. Hold the occupancy sub-model constant and model with it every preliminary p model with a ΔAIC < 2 compared to the top model. Refer to these as **preliminary final models** and rank them according to AIC.

Step 9. Select the top preliminary final models that have a ΔAIC < 2 compared to the top model for a maximum of three models. Refer to these as the **final models.** *These are the final models using a combined *a-priori* and *posteriori* approach.*

EQUATIONS

To illustrate a predictive map of grizzly bear occupancy and detectability in a GIS, I modeled occurrence and detectability using the following linear predictor equation

$$\mathrm{LP} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i$$

where LP refers to the linear predictor, χ refers to variable, β_{is} the model coefficient, and β_0 is intercept term. I then used the linear predictor in the following equation to determine the probability of occupancy and probability of detection

$$\mathrm{Pr} = (\exp(\mathrm{LP})) / (1 + \exp(\mathrm{LP}))$$

where Pr refers to the probability of occurrence and LP refers to the linear predictor. A map of the probability of occupancy (PSI), the probability of detection (P), and the probability of detection given occupancy (PSI × P) were created for each scale.

Table A-1. Individual identification, sex, parentage, and time and location of grizzly bears in west central Alberta as determined by molecular analysis.

Bear ID	Sex	Parentage	Site(s)	Session(s)	2004 DNA Survey Detections	Detected since 2004
G202	M	-	TS29	4		x
G119	F	(M)G100; (F)G053	89, 119	4		
G118	F	(M)G037; (F)G017	50, 31, 29, 53, 67, 54	2,4,5,6,7		x
G115	M	(M)G016; (F)8080a	89, 102, 119, 102, 88, 52, TS37	2,3,5	x	x
G113	F	(M)G100; (F)G055	102, 119, 89	4,6		x
G100	F	(M)G023	93	2		x
G037	F	(F)G017	88	3	x	x
G007	F	-	99	6		x
95-1a-2	M	-	95, 74, 91, 94, 59, 58	2,4,5		
93-6e-3	F	(M)G023(F)G017	93	3		
93-5d-3	M	(F)G068	93, 18, 99	3,5,6,7		
93-2b-2	M	(M)G100; (F)G017	93, 102	2,3		
93-1a-2	F	(M)G100; (F)G017	93	2		
8080a	M	-	93	5		x
70-2b-4	F	-	70	4		
67-2a-7	F	(M)G037; (F)G017	67	7		
53-7c-6	M	(F)G017	53	6		
34-1a-3	M	-	34, 9	3,4		
119-2a-6	M	(M)010; (F)G001	119	6		
11632Tc	F	-	3	6	x	
107-1a-7	F	(F)G017	107	7		

Table A-2. Prominent bear foods sampled in west central Alberta, Canada. Species with available diet weights from Nielsen et al. (2010) are marked by an asterisk (*).

Food Group	Scientific Name	Common Name
Roots	*Hedysarum alpinum* *	Alpine Sweetvetch
Fruit	*Amelanchier* spp*	Saskatoon
	Aralia nudicaulis *	Sarsaparilla
	Arctostaphylos uva-ursi *	Bearberry
	Fragaria spp.*	Strawberry
	Lonicera spp.	Honeysuckle
	Prunus spp.	Chokecherry
	Ribes spp.	Gooseberry
	Ribes spp.*	Currents
	Rubus spp.*	Raspberry
	Rubus idaeaus *	Wild Red Raspberry
	Rubus parviflorus	Thimbleberry
	Shepherdia canadensis *	Buffaloberry
	Vaccinium cespitosum *	Dwarf blueberry
	Vaccinium membranaceum *	Huckleberry
	Vaccinium myrtilloides *	Velvetleafed bluberry
	Vaccinium scoparium *	Grouseberry
	Vaccinium vitis-idaea *	Bog Cranberry
	Viburnum spp.*	Cranberry
Forbs / Shrubs	*Heracleum lanatum* *	Cow parsnip
	Lathyrus ochroleucus *	Peavine
	Rosa spp.	Rose
	Salix spp.	Willow
	Taraxacum officinale *	Dandelion
	Trifolium spp.*	Clover
	Equisetum spp.*	Horsetail
Protein	*Alces alces* *	Moose
	Formicidae spp*	Ants

Table A-3. Model structure, Akaike Information Criterion (AIC), change in AIC relative to the top ranked model (ΔAIC), and Akaike weights (w_i) of candidate models used to predict grizzly bear occupancy and detectability at two scales in west central Alberta, Canada. The top models (in bold) were selected as the confidence set of models and used for model averaging of parameters. See Table 2-1 for variable descriptions and Table 2-2 for a-priori model hypotheses descriptions.

Scale	Phase	Model	Model Structure	AIC	ΔAIC	w_i
300m	A-priori	$PSI_6 + P_3$	psi(DEM+shecan_dns), p(trif+stream)	234.64	0.00	0.4346
		$PSI_1 + P_3$	psi(DEM+wtree+shecan_dns), p(trif+stream)	236.56	1.92	0.1664
		$PSI_4 + P_5$	psi(DEM+stream+shecan_dns), p(trif)	237.77	3.13	0.0909
		$PSI_9 + P_5$	psi(DEM+stream), p(trif)	237.83	3.19	0.0882
		$PSI_8 + P_3$	psi(DEM+wtree), p(trif+stream)	237.93	3.29	0.0839
		$PSI_7 + P_5$	psi(stream+park), p(trif)	238.06	3.42	0.0786
		$PSI_3 + P_5$	psi(DEM+wtree+stream), p(trif)	239.83	5.19	0.0324
		$PSI_2 + P_4$	psi(stream+wtree+park), p(trif+hedy)	240.36	5.72	0.0249
		Null	psi(.),p(.)	253.58	18.94	0.0000
300m	Posteriori		**psi(DEM+shecan_dns+well_dec), p(trif+stream+CC+CC^2)**	**227.00**	**0.00**	**0.4334**
			psi(DEM+shecan_dns+well_dec), p(trif+stream+CC)	**228.61**	**1.61**	**0.1938**
			psi(DEM+shecan_dns+well_dec), p(trif+stream)	229.15	2.15	0.1479
			psi(DEM+shecan_dns+well_dec), p(trif+stream+cancov+cancov^2)	229.83	2.83	0.1053
			psi(DEM+shecan_dns+well_dec), p(trif+stream+cancov)	230.12	3.12	0.0911
			psi(DEM+shecan_dns), p(trif+stream+CC+CC^2)	233.24	6.24	0.0191
		$PSI_6 + P_3$	psi(DEM+shecan_dns), p(trif+stream)	234.64	7.64	0.0095
		Null	psi(.),p(.)	253.58	26.58	0.0000
1690m	A-priori	$PSI_4 + P_7$	psi(CC*CTI+park),p(tfood*well_dns+stream)	237.88	0.00	0.3203
		$PSI_1 + P_7$	psi(CC*CTI+wherb+park),p(tfood*well_dns+stream)	238.95	1.07	0.1876
		$PSI_3 + P_7$	psi(CC*CTI+CTI+park),p(tfood*well_dns+stream)	239.31	1.43	0.1567
		$PSI_6 + P_7$	psi(CC*CTI+CTI),p(tfood*well_dns+stream)	239.77	1.89	0.1245
		$PSI_5 + P_7$	psi(CC*CTI+wherb),p(tfood*well_dns+stream)	239.85	1.97	0.1196
		$PSI_2 + P_7$	psi(DEM+wherb+CC+CC^2),p(tfood*well_dns+stream)	240.39	2.51	0.0913
		Null	psi(.),p(.)	253.58	15.70	0.0001
1690m	Posteriori		**psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+tfood*well_dec)**	**232.81**	**0.00**	**0.1386**
			psi(CC*CTI+park_dec+pipe_dec_dec),p(tfood*well_dns+stream)	**232.89**	**0.08**	**0.1331**
			psi(CC*CTI+park_dec+pipe_dec+CC+CTI),p(tfood*well_dns+stream+tfood*well_dec)	**233.04**	**0.23**	**0.1235**
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+well_dec)	233.08	0.27	0.1211
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+tfood*rd_dns)	233.99	1.18	0.0768
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+trl_dns)	234.03	1.22	0.0753
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+tfood*trl_dns)	234.21	1.40	0.0688
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+rd_dns)	234.36	1.55	0.0638
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+sfood+well_dec)	234.47	1.66	0.0604
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+sfood)	234.53	1.72	0.0586
			psi(CC*CTI+park_dec+pipe_dec),p(tfood*well_dns+stream+quad)	234.60	1.79	0.0566
			psi(CC*CTI+park_dec),p(tfood*well_dns+stream+tfood*well_dec)	237.64	4.83	0.0124
		$PSI_4 + P_7$	psi(CC*CTI+park_dec),p(tfood*well_dns+stream)	237.88	5.07	0.0110
		Null	psi(.),p(.)	253.58	20.77	0.0000