

**Quantifying spatial-temporal change in habitat occupancy patterns of grizzly bears (*Ursus arctos*) in the context of industrial activities in western Alberta**

by

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B.Sc. Natural Resource Sciences, Thompson Rivers University, 2016

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF  
MASTER OF SCIENCE

in

THE COLLEGE OF GRADUATE STUDIES

(Earth and Environmental Sciences)

THE UNIVERSITY OF BRITISH COLUMBIA

(Okanagan)

July 2021

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Quantifying spatial-temporal change in habitat occupancy patterns of grizzly bears (*Ursus arctos*) in the context of industrial activities in western Alberta

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## Abstract

Landscape change is a primary driver of global species decline, requiring effective approaches for monitoring wildlife populations. Occupancy modelling, which estimates the probability of a species being present on a landscape, has become a popular method for monitoring wildlife populations and habitat quality. Among large mammal species in North America, grizzly bears (*Ursus arctos*) are particularly vulnerable to and threatened by anthropogenic pressures.

Using hair-snag data collected in 2004 and 2014 from a threatened grizzly bear population in Alberta, Canada, this research developed single-season occupancy models to understand how anthropogenic disturbance and landscape conditions influence occupancy patterns of male and female grizzly bears over a decade. I then quantified spatial patterns of grizzly bear occupancy and density using measures of spatial autocorrelation to assess relationships between occupancy and density and landscape processes related to anthropogenic disturbance and topography. By examining the spatial relationships between predicted grizzly bear occupancy-abundance estimates over a decade, I was able to provide a better understanding how observed patterns are influenced by disturbance and identify important habitat.

Occupancy models showed the average occupancy probability decreased slightly (0.35 to 0.34), despite observed increases in grizzly bear population (36.0 to 71.3 individuals) over a decade. However, spatial patterns of occupancy showed previously unoccupied cells in eastern portions of the study area were colonized from 2004 to 2014. Male occupancy was negatively related to anthropogenic disturbance, including cutblocks and all disturbance, compared to females. Anthropogenic disturbance had an increased influence over time, highlighting the need to consider cumulative effects in occupancy monitoring. Spatial patterns of occupancy and density estimates were similar, with clusters of high occupancy and density occurring where terrain is complex and human access is limited. These areas may act as important source

habitat for the population with dispersers occupying potential sink habitats where disturbance and mortality are higher. The occupancy modelling framework and results provide a better understanding of the impacts of anthropogenic disturbance on grizzly bear occupancy and population persistence for regulatory bodies, wildlife managers, and industry, which will contribute to the conservation of grizzly bears and other large carnivores.

### **Lay Summary**

Habitat occupancy, representing the presence or absence of a species on a landscape, is increasingly used to monitor wildlife populations and understand human impacts on threatened species. This study developed occupancy estimates to assess changes in a threatened grizzly bear population in Alberta, Canada from 2004 to 2014. Spatial patterns of habitat occupancy and abundance were compared to identify important areas of grizzly bear habitat. Results showed grizzly bear occupancy decreased slightly, despite the population nearly doubling in size. However, grizzly bears appear to be expanding into previously unoccupied habitat. Spatial patterns indicate that areas of high occupancy and abundance occur in areas with complex terrain that limits human access. This study highlights the need for on-going monitoring of grizzly bears and the conservation of habitat where human influence is limited to support population recovery.

## **Preface**

This study was conducted by Mackenzie Kate Irwin under the supervision of Dr. Mathieu Bourbonnais at the University of British Columbia Okanagan. All data was collected and provided by the fRI Research Grizzly Bear program. The literature review, data analysis, writing, and figures were completed by Mackenzie Kate Irwin and supervised by Dr. Mathieu Bourbonnais. Mr. Gordon Stenhouse and Dr. Lael Parrott reviewed this study for clarity and content. All advice provided by the Supervisory Committee and all literature are correctly cited. The study area maps in this thesis were generated using ESRI ArcGIS® software. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used under license. Copyright © 2019 ESRI. All statistical analyses and additional figures were generated using the open-source R language for statistical computing, version 3.6.2. Copyright © 2019 The R Foundation for Statistical Computing.

A version of Chapters 2 and 3 will be submitted for peer-reviewed publication. This research used data collected from live animals, and therefore required ethics approval. The UBC Animal Care Committee (A19-0073) granted approval on June 21, 2019.

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## Acknowledgements

I would first like to acknowledge and thank Weyerhaeuser and the Forest Resource Association of Alberta for their funding of this project. Without their contribution, this research would not have been possible. Next, I would like to thank my supervisor, Dr. Mathieu Bourbonnais for the endless guidance, feedback and encouragement. Thank you for being patient with me, I could not have asked for a better mentor on this project. This research could not have happened without Dr. Gordon Stenhouse, who not only encouraged me to pursue graduate school, but also provided me with the opportunity. I have greatly benefitted from his continued support and expertise throughout the entire process. I extend my deepest appreciation for all the shared wisdom. I would also like to thank my committee member Dr. Lael Parrott for her part in providing feedback and editing this thesis.

I would like to express my gratitude to the team at fRI Research for ongoing support, inspiration, or encouragement at various points throughout this process. Specifically, thank you to Dan Wismer, Karen Graham, Anja Sorensen, Isobel Phoebus, Tracy McKay, and Laura Finnegan. Also, thank you to the fantastic administrative staff of the Earth, Environmental Science, and Geography Department who are always incredibly helpful and friendly, especially Janet Heisler. To my fellow EOSEL lab mates, primarily Mackenzie Clarke, Natalie Cowell, Tina Deenik, and Lithy Morley, I am so grateful for the time we had on campus together although far too brief thanks to COVID-19. I look forward to being reunited one day.

On a personal note, I would like to thank my friends and family, particularly the Jessicas for being ideal life companions, and my partner, Riley Wall, for always being there to balance me out and comfort me. Finally, I would like to express my unwavering gratitude towards my amazing parents, Robin and Kirk Irwin. I am so fortunate to have such *outstanding* supporters who work tirelessly to help their children live happy, comfortable lives.

Thank you all. I am so incredibly lucky to have such a strong support network, and accredit all that I accomplish to all of you.

## **Dedication**

I dedicate my thesis to the memory of Sid and Joan Fensome, the best stand-in, non-biological grandparents anyone could ask for. They were a benevolent pillar in my childhood, and I believe helped to foster my interest in flora and fauna.

# Chapter 1

## Introduction

### 1.1 Overview and rationale

Land-use change is the single most important driver of global biodiversity loss (Sala et al., 2000). With rising human populations there are increased demands for natural resources resulting in encroachment of humans in once remote wildlife habitat (Ceballos & Ehrlich, 2002). Anthropogenic disturbance includes two general types of disturbance: the presence of humans and the footprint of infrastructure (Nickel et al., 2020), and each can have direct and indirect impacts on wildlife (Sawyer et al., 2006). Resource extraction activities alter the function and structure of forested ecosystems (Ledig, 1992; Reed et al., 1996; Trombulak & Frissell, 2000; Saunders et al., 2002), and reduce and fragment available habitat (Baldwin et al., 2004; Jędrzejewski et al., 2004; McDonald & St. Clair, 2004; Vistnes et al., 2004; Hansen et al., 2005; Fischer & Lindenmayer, 2007). Altered and fragmented habitat can act as barriers animal to movement (Kamler et al., 2003; Fahrig, 2007; Tucker et al., 2018), which in turn can further influence ecosystem processes by impacting seed dispersal, predator-prey interactions, and disease dynamics (Bauer & Hoyer, 2014). Linear features created by resource extraction activities, such as roads and pipelines contribute to fragmentation and can increase predation rates on prey species (Bergerud et al., 1984; Rich et al., 1999; James & Stuart-Smith, 2000; Marchand & Litvaitis, 2004). These man-made barriers can also result in decreased genetic connectivity between sub-populations (Proctor et al., 2012).

Direct loss of habitat is a result of alteration of the landscape for resource extraction and infrastructure, while indirect habitat loss often occurs as a result of avoidance behaviour (McLellan & Shackleton, 1988; Cameron et al., 1992; Mace et al., 1996; Stevens & Boness, 2003). Anthropogenic disturbance can elicit avoidance behaviour, or anti-predator response, in various wildlife species and can resemble the effects of predation risk due to behavioural trade-

offs that occur between security and other activities such as mating or foraging (Frid & Dill 2002). In certain scenarios, behavioural responses can have negative physiological or social implications (Bradshaw et al., 1997; Dyke et al., 1986; Skogland & Grøvan, 1988), especially by interfering with breeding and rearing activities, resulting in reduced fecundity and recruitment (White & Thurow, 1985; Goodrich & Berger, 1994; Linnell et al., 2000; Müllner et al., 2004). Avoiding and responding to disturbance can create additional stress, reducing individual fitness, reproductive function, and population productivity (MacArthur et al., 1979; Kerley et al., 2002; Wingfield & Sapolsky, 2003; Constantine et al., 2004). In response to anthropogenic disturbance, various species change their diel activity, becoming nocturnal (Gaynor et al., 2018). Noise alone from industrial activities has been shown to have major effects on behaviour (Schaub et al., 2008; Siemers & Schaub, 2011; Shannon et al., 2016). Perceived risk surrounding human presence can also have an impact (Gaynor et al., 2018); however, it can be difficult to determine if behavioural responses result from perceived risk of humans or disturbance events such as noise or rapidly approaching objects (Frid & Dill, 2002; Stankowich, 2008). Regardless of the mechanism causing behavioural changes, fear responses to human presence can exceed the fear of natural predators for prey species (Ciuti et al., 2012; Clinchy et al. 2016), and impact the way that predator species use the landscape (Dyke et al., 1986; Smith et al., 2017; Suraci et al., 2019).

Resource extraction activities, such as forestry, mineral mining and oil and gas development, depend on extensive networks of roads (McLellan & Shackleton, 1988). Human access into wildlife habitat can directly impact wildlife populations through increased mortality, resulting from legal hunting, poaching, vehicle collisions, or destruction of problem animals due to human-wildlife conflict (Wilkie et al., 2000; Johnson et al., 2004; Coffin, 2007; Roever et al., 2008; Hill et al., 2019). Mortality can be particularly high in areas of industrial expansion, such as oil and gas development and mining, where violations of wildlife laws (e.g., poaching) are more likely to occur compared to agricultural and recreational areas (Berger & Daneke, 1988).

Additionally, roads and other resource extraction activities can be associated with improved food resource availability (Rea, 2003; Roever et al., 2008a; Hill et al., 2021), which coupled with increased mortality risk causes an ecological trap, where selection for road-like habitat results in reduced fitness (Dwernychuk & Boag, 1972; Lamb et al., 2017).

As demand for natural resources continues to increase (Huang et al., 2010), monitoring wildlife populations to assess influences of anthropogenic disturbance and prioritize conservation efforts is of critical importance (Soule & Kohm, 1989). Estimates of state variables, parameters used to quantify the status of wildlife populations and communities (MacKenzie et al., 2017), are important tools to help inform conservation and management decisions (Kendall, 2001). A natural approach for monitoring initiatives and other investigations of animal population dynamics is to obtain empirical estimates of abundance (i.e., the amount of individuals in a population; Pollock et al., 1990). The most common method for estimating abundance ( $N$ ) is the use of mark-recapture models (Pollock et al., 1990; Nichols, 1992; Pradel, 1996). This process involves capturing an initial sample of the population ( $n_1$ ), marking each individual, and releasing them all back into the population. A second sample is caught some time later ( $n_2$ ), and the number of marked individuals in the second sample is recorded ( $m_2$ ). The proportion of marked individuals in the second sample is assumed to be equal to the proportion of marked individuals in the population ( $m_2/n_2=n_1/N$ ), allowing population size to be estimated ( $N=n_1n_2/m_2$ ; Nichols, 1992). Variations of mark-recapture methods, in conjunction with DNA-sampling techniques, are particularly useful for elusive, wide-ranging species as a non-invasive approach for monitoring (Taberlet et al., 1999; Mills et al., 2000; Long & Zielinski, 2008). However, reliable estimates of abundance from mark-recapture models require the probability of detecting a specific individual (Yoccoz et al., 2001; Williams et al., 2002; Schmidt, 2003). Detection often requires markings to distinguish individuals (MacKenzie & Nichols, 2004), resulting in high costs and extensive effort (Lancia et al., 1994; Pollock et al., 2002; MacKenzie et al., 2002).



Despite the importance of monitoring wildlife species and their habitat, the costs and effort required to thoroughly assess habitat quality and monitor populations is commonly unfeasible (Johnson, 2005; MacKenzie et al., 2017). Consequently, proper assessments of habitat quality and its impact on wildlife cannot be obtained (Johnson, 2005), and, in regards to rare and elusive species, developing estimates of abundance is often impossible or have considerable uncertainty (MacKenzie et al. 2005). Recently, habitat occupancy, defined as the presence or absence of a species on a landscape, has become a popular metric for assessing wildlife populations as a cost and effort efficient alternative to abundance estimates (MacKenzie et al. 2003; Bailey et al., 2014; MacKenzie et al., 2017).

## 1.2 Occupancy modelling

Recognizing the difficulty in obtaining estimates and monitoring changes in absolute abundance of wildlife species, and seeing the value in occupancy for large-scale monitoring and investigations of metapopulation dynamics, MacKenzie et al (2002) proposed the use of occupancy as a proxy to abundance. For example, identifying the number of landscape units in a given area where a species is present allows the *proportion of area occupied* to be quantified. However, this naïve approach underestimates occupancy (MacKenzie et al., 2017) and the effect of extrinsic and intrinsic variables on occupancy (MacKenzie et al., 2003; Tyre et al., 2003). In order to accurately estimate state variables, it is critical to incorporate detectability and spatial variation (Lancia et al., 1994; Thompson et al., 1998; MacKenzie et al., 2002; Williams et al., 2002). The approach of MacKenzie et al. (2002) parallels that of a closed-population mark-recapture model, with additions to the statistical framework to allow for more flexibility and to reduce potential biases. In closed-population models, information obtained from individuals encountered at least once is used to estimate the number of individuals that were not encountered (Otis et al., 1978; Williams et al., 2002). In the occupancy model proposed by MacKenzie et al. (2002), sites are analogous to individuals, with the total number of sites ( $N$  in a

mark-recapture framework) known. The focus with this approach is to estimate the fraction of the sites that are occupied, using a set of detection histories for each site (MacKenzie et al., 2002), which determines *occupancy probability* for the area (MacKenzie et al., 2017).

MacKenzie et al (2002) emphasized that although species detection signifies presence at a study site, non-detection does not necessarily signify absence. In order to reduce negative bias, or false negatives, they highlighted the importance of multiple site visits to formulate detection probabilities needed for reliable inferences on occupancy (MacKenzie et al., 2002). Including detection histories for each site composed of detections (1) and non-detections (0) from multiple sampling session, allows parameters for detectability ( $p$ ) and occupancy ( $\psi$ ) to be incorporated in the standard mark-recapture framework. Other modelling approaches for detection-only data have been developed (Elith et al., 2006; Phillips et al., 2006; Elith & Leathwick, 2009; Dorazio, 2012; Royle et al., 2012). However, it is argued that some of the key assumptions of such models, being that an area is sampled randomly and that covariates which influence detection do not also influence distribution, are seldom met (Dorazio, 2012; Phillips et al., 2009; Royle et al., 2012; Yackulic et al., 2013). Additionally, methods have been developed for detection/non-detection data from a single sampling session (Moreno & Lele, 2010; Lele et al., 2012); however, including data from multiple sampling sessions provides more accurate inference on detection and occupancy (MacKenzie et al., 2017).

The MacKenzie et al. (2002) model to estimate occupancy probability for a given area assumes that: 1) occupancy is constant and does not change during a season (i.e., amongst sessions), 2) occupancy probabilities are equal amongst sites, 3) there is no unmodeled heterogeneity in detection probabilities, 4) survey outcomes are independent from each other, and 5) given occupancy, species are not falsely detected or misidentified (i.e., a false positive). Consequently, the MacKenzie et al. (2002) model assumes a closed system and is only reasonable if applied to a single year (MacKenzie et al., 2003). Mackenzie et al. (2003) relaxed the model assumptions to permit monitoring of populations over time, using parameters to

account for the probability of unoccupied sites becoming colonized ( $\gamma$ ) and the probability of occupied sites becoming locally extinct ( $\Phi$ ) between seasons. Although occupancy had previously been used to estimate local extinction and colonization probabilities, those parameters had not previously been included in occupancy probability estimates (MacKenzie et al., 2002). This extension allowed for “open” systems where changes in occupancy status between sampling periods can be accounted for in the model (Royle & Link, 2006) assuming a closed system within sampling seasons (MacKenzie et al., 2003).

Mackenzie et al (2002) explained how to account for missing detection data resulting from logistical issues in the field using model likelihood measurements. They also provided insight on appropriate numbers of sampling sessions and sites sampled, and how to model occupancy probabilities as a function of site-specific variables. These contributions relaxed the assumptions of previous methods and provided a flexible framework for incorporating covariates to examine the influence of habitat characteristics on species presence (MacKenzie et al., 2003). Developments of the original model have further relaxed the model assumptions allowing false-absences (MacKenzie et al., 2006 & 2009), false-positives (Miller et al., 2013), or species misidentification (Miller et al., 2011). Additionally, methods have been developed to allow for heterogeneous detection probabilities (MacKenzie et al., 2006; Royle, 2006), to address lack of independence of surveys at a sampling unit (Nichols et al., 2008; Hines et al., 2010; Guillera-Arroita, 2011), and to deal with closure assumption violations (Rota et al., 2009; Kendall et al., 2013). For wide range species, meeting the assumption of closure throughout a sampling season can be difficult. However, if movement of the species in and out of the sampling unit during the survey season is random, the occupancy estimate can be expected to be unbiased, although the occupancy parameter is better interpreted as the probability that sites are used during a season as opposed to permanent residency (Mackenzie & Royle, 2005; Latif et al., 2016). Extensions of the original occupancy model have been used to model community dynamics with multiple species (Dorazio & Royle, 2005; Kéry & Royle, 2009), multiple

occupancy states (Royle, 2004; Royle & Link, 2005; Nichols et al., 2007; Mackenzie et al., 2009), and multiple spatial or temporal scales (Nichols et al., 2008; Kendall, 2009; McClintock et al., 2010; Mordecai et al., 2011; Pavlacky et al., 2012), allowing researchers to address complex ecological questions.

Occupancy modelling allows for a single inferential framework that includes survey data, ecological processes, and observation processes (Karanth et al., 2011), providing a flexible approach for understanding the status of biological systems (Bailey et al., 2014). As a result, occupancy modelling has been widely used for assessing species-habitat relationships and population dynamics (Bailey et al., 2014), and various approaches can be taken for quantifying factors that influence range dynamics and species distributions due to the flexibility of the definition of occupancy (MacKenzie et al., 2017). The development of occupancy modelling since the seminal work of Mackenzie et al (2002 and 2003) has allowed researchers to study disease and parasite prevalence (Adams et al., 2010; Elmore et al., 2014), life history stages (Bailey et al., 2008) and breeding success (Fisher et al., 2014; MacKenzie, et al., 2012; Martin et al., 2009) in wildlife species.

Occupancy modelling is a useful tool for assessing the influence of anthropogenic disturbance on wildlife species. It has been used to quantify the influence of fragmentation on avian species (Bolger et al., 1991; Boulinier et al., 2001; Hames et al., 2001; Ferraz et al., 2007; Zipkin et al., 2009; Collier et al., 2012), responses of various mammal species to disturbance (such as roads, forest harvesting, and mining; Pillay et al., 2011; Das et al., 2014; Fuller et al., 2016; Lkhagvasuren et al., 2016; Rivera et al., 2020), and investigate responses in predator prey dynamics to anthropogenic disturbance (Burr et al., 2017; Thomas et al., 2019). By simultaneously modelling dynamic relationships between habitat and occupancy, researchers can identify the effect of vegetation succession, environmental variability, or human activity influence on species occupancy over time (Mackenzie et al., 2011). Consequently, occupancy modelling can quantify the persistence of species on a landscape over consecutive seasons

(MacKenzie et al., 2017). However, occupancy modelling is seldom applied to quantify population trends over large spatial and temporal scales (Ellis et al., 2014; Steenweg et al., 2016) and wildlife detection data spanning long periods of time are rare (MacKenzie et al., 2017).

Occupancy is considered a useful state variable in wildlife studies (MacKenzie et al., 2017), and a key metric for assessing wildlife habitat. Hall et al (1997) defined habitat as “the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism”. Inferences on occupancy change can also provide insight on factors influencing changes in the range of a species, as geographic range includes the area of occupancy (MacKenzie et al., 2017). Understanding the distribution of species is critical for species monitoring and conservation efforts (Purvis et al., 2000). Occupancy may be parameter of interest in certain studies (e.g., range size, metapopulation dynamics, geographic distribution), but it also may be used as a proxy for abundance (MacKenzie & Nichols, 2004). However, occupancy may only be suitable as a metric representing population status in the underlying assumption of a linear relationship between abundance and occupancy is met (Stanley & Royle, 2005). Due to overlapping home ranges in many species, this relationship may not be straight forward (Efford & Dawson, 2012; Noon et al., 2012). As a result, the use occupancy modelling to replace or act as a proxy for abundance monitoring to address long-term conservation and wildlife management questions represents an opportunity for further research.

### **1.3 The occupancy/abundance relationship**

Occupancy has been used in broad-scale monitoring of various species by including detection/non-detection data (Stauffer et al., 1995; Zielinski & Stauffer, 1996; Carroll et al., 1999; MacKenzie et al., 2003, 2004 & 2005; Martínez-Solano et al., 2003; Zonneveld et al., 2003; Weber et al., 2004; Fellers et al., 2005; Weir & Mossman, 2005). Often, occupancy is

used as an alternative metric to abundance (MacKenzie et al., 2017). The rationale for applying occupancy in place of abundance for population monitoring is at appropriate scales occupancy and abundance should be positively correlated (MacKenzie & Nichols, 2004). The occupancy-abundance (OA) relationship is a fundamental pattern in ecology (Gaston et al., 2000; Zuckerberg et al., 2009; Passy, 2012), which may result from density-dependent habitat selection (Rosenzweig, 1991). The OA relationship is particularly evident in territorial species, where occupancy is closely related to the number of individuals (or pairs) when the size of sampling units is equivalent to the estimated size of their territory (Azuma et al., 1990; MacKenzie & Nichols, 2004; MacKenzie et al., 2003). There are many examples of positive OA relationships in ecology (Hanski, 1982; Gaston et al., 2000; Blackburn & Gaston, 2004). However, these two state variables address different facets of population dynamics (MacKenzie & Nichols, 2004), and a relationship is not always evident (Fuller et al., 1995; Chamberlain & Fuller, 2001; Blackburn et al., 2006; Reif et al., 2006; Symonds & Johnson, 2006; Van Turnhout et al., 2007; Webb et al., 2007).

Although the proportion of a landscape occupied by a species and the number of individuals on a landscape are often related, changes in abundance may not be reflected in changes in occupancy (MacKenzie & Nichols, 2004). Despite being common, the OA relationship is highly variable amongst species (Zuckerberg, Porter, & Corwin, 2009). Generally, higher quality habitats are associated with higher densities of animals (Fretwell & Lucas, 1969; Garshelis, 2000; Bock & Jones, 2004). In areas with high food availability, range sizes may decrease with increases in population density as a result of intruder pressure, or interspecific competition (Wolff, 1993), and many species have overlapping home ranges amongst conspecifics (Steenweg et al., 2018). Therefore, if the landscape supports sufficient resources, occupancy may not increase despite increases in abundance. Positive OA relationships have been simulated with random distribution and overlapping ranges; however, the relationship can change depending on spatial and temporal scales (Steenweg et al., 2018). As a result, an

understanding of the relationship between occupancy and abundance for a species of interest is necessary to determine whether occupancy can be used as an effective surrogate for monitoring population trends.

#### **1.4 Grizzly bears and landscape change**

Among large mammal species in North America, grizzly bears (*Ursus arctos*) have a complicated relationship with anthropogenic disturbance and mortality risk (Boulanger et al., 2018), and are particularly vulnerable to anthropogenic pressures due to low reproductive potential (Weaver et al., 1996). Grizzly bears have been extirpated throughout North America, with the largest remaining populations found primarily in Canada and Alaska, where humans are sparser compared to the contiguous United States (Mattson & Merrill, 2002). As of 1990, grizzly bears were extirpated from 24 % of their former range, and 63 % of the remaining habitat was considered to be either threatened or vulnerable in Canada (Banci, 1991). In the province of Alberta, Canada, grizzly bears are currently listed as “threatened” under the provincial Wildlife Act (Kansas & Festa-Bianchet, 2010). Historically, the limiting factors for grizzly bear populations were habitat loss due to conversion of natural lands for agriculture and unrestricted hunting, including initiatives for predator control. Today, the primary factor contributing to population reductions are anthropogenic activities and pressures, which includes resource extraction, road expansion, habitat modification, and habitat loss (Kansas & Festa-Bianchet, 2016), which have resulted in historically low numbers of grizzly bears on the landscape (McLellan et al., 1999).

A multiple-use and integrated management approach was used to shape land use throughout grizzly bear habitat in Alberta, which includes but is not limited to extraction of mineral resources (including coal, oil and natural gas), timber development, and recreation (Alberta Government, 1977). The resulting mosaic of land use types and land cover can increase habitat value for grizzly bears, who prefer a heterogeneous landscape consisting of forest and non-forest habitat (Herrero, 1972). Unlike coastal grizzly bears which are highly

dependent on salmon as a primary food source (Mowat & Heard, 2006), grizzly bears in Alberta depend on foraging (including roots and berries) availability, which is influenced by anthropogenic activities and landscape dynamics (Nielsen et al., 2004). Throughout Alberta, wildfire suppression has resulted in a lack of natural forest openings, which encourage early seral vegetation (Baron & Aguero, 2003). Clearings from forestry practices now act as a surrogate to wildfire by reducing canopy cover and influencing the availability of key grizzly bear foods (Nielsen et al., 2004; Stewart et al., 2012). Recently disturbed areas, including cutblocks, roads, and oil and gas infrastructure, tend to be associated with nutrient rich foods. Specifically, cutblocks provide various bear foods such as grasses, forbs, berries, and ants (Nielsen et al., 2004b; Stewart et al., 2012; Denny et al., 2018). Grizzly bears have been shown to select for pipelines and oil and gas well sites (Laberee et al., 2014; Sorensen et al., 2021), compared to forested areas, as these anthropogenic disturbance features can have higher occurrence of clover, dandelion, horsetail (*Equisetum sp.*), and sedges (*Carex sp.*) (Mckay et al., 2014; MacDonald et al., 2020). Edge habitats created by resource extraction activities are known to increase the availability of berries, herbaceous forage, and ungulates (Nielsen et al., 2004 & 2017; Munro et al., 2006; Roever et al., 2008a; Stewart et al., 2012; Bourbonnais, 2018). Additionally, reclaimed mine sites present an opportunity for grazing on herbaceous material (Cristescu et al., 2016).

While linear features associated with resource extraction such as roads, seismic lines, and pipelines provide food resources and can facilitate movement of grizzly bears (Roever et al., 2010; Finnegan et al., 2018; MacDonald et al., 2020), they also provide human access into grizzly bear habitat (Berland et al., 2008; Linke et al., 2005), often resulting in increased human-caused mortality (McLellan et al., 1999; Nielsen et al., 2004; Schwartz et al., 2010; Boulanger et al., 2014). Additionally, roads influence stress (Bourbonnais et al., 2013), body condition and survival in grizzly bears (Boulanger et al., 2013; Bourbonnais et al., 2014), and fragment populations (Proctor et al., 2012). Edges associated with anthropogenic features can be



considered an attractive sink, where high bear occurrence is coupled with high mortality risk (Nielsen, Herrero, et al., 2004; Nielsen et al., 2006). Such conditions can be considered an ecological trap, where selection for specific habitat results in reduced fitness (Dwernychuk & Boag, 1972; Lamb et al., 2017). Apex predators, such as grizzly bears, can be especially vulnerable to ecological traps as they lack natural predators (Ripple et al., 2014), and population recovery in areas of high human-caused mortality is made more difficult due to low reproductive rates (McLellan, 1989; Miller, 1990; Garshelis et al., 2005). Grizzly bears are also indirectly affected by anthropogenic disturbance through avoidance and changes in behaviour resulting from human presence (Alberta Sustainable Resource Development, 2008; Bourbonnais, 2018). As a result, understanding how human access, road densities, and anthropogenic activities influence grizzly bear population persistence is critical for informing conservation and management (Wilkinson et al., 2008).

As resource extraction activities continue and human access into grizzly bear habitat increases (Berland et al., 2008; Linke et al., 2005), there is a need for comprehensive approaches to monitor grizzly bear populations and habitat to quantify anthropogenic influence (Stenhouse et al. 2015). While the relationship between anthropogenic disturbance and grizzly bear mortality is well understood (Benn & Herrero, 2001; Nielsen et al., 2004; Roever et al., 2008), it is unclear how anthropogenic disturbance and habitat change influence spatial patterns of occupancy over time. A better understanding of the spatial-temporal relationships between grizzly bears and anthropogenic landscape disturbance has the potential to influence the conservation of this iconic species in Canada through informed resource management practices.

## 1.5 Knowledge gaps and research goals

With increasing human populations, access, and recreation in remote areas, maintaining viable grizzly bear populations in Canada is challenging (McLellan, 1998). Facilitating human-grizzly bear co-existence in Alberta requires information to guide wildlife and landscape management (Franklin et al., 2001). Regular monitoring of grizzly bear populations is recommended as part of the Alberta Grizzly Bear Recovery Plan to inform ongoing land management and recovery efforts of grizzly bears (Alberta Grizzly Bear Recovery Team 2008). Grizzly bear populations are commonly monitored using a non-invasive adaptation of mark-recapture methods that focuses on obtaining hair samples, allowing researchers to estimate population size and acquire genetic information (Woods et al., 1999; Mowat & Strobeck, 2000; Boulanger et al., 2001 & 2005; Stenhouse et al., 2015). Non-invasive approaches are well suited for obtaining information from elusive and hard to catch species such as grizzly bears (Taberlet et al., 1999; Mills et al., 2000); however, require intensive efforts (Lancia et al., 1994; Pollock et al., 2002), and are very expensive (Steenweg et al., 2016a). With an increasing need to monitor wildlife populations, and limited economic resources to do so, there is a need for effective, low-cost monitoring approaches (Johnson, 2005; MacKenzie et al., 2017).

Occupancy modelling has been employed to investigate trends in Alberta grizzly bear populations (Fisher et al., 2014; Steenweg et al., 2016b; Ladle et al., 2018). However, these studies were focused on protected areas, where resource extraction and human activities are limited in comparison to the majority of grizzly bear habitat in Alberta. This study examines the Yellowhead population (BMA 3), one of seven grizzly bear management areas (BMAs) in Alberta, using hair snag data from 2004 and 2014. The study area is important habitat for grizzly bears in Alberta. The majority of the study area is designated as either *core habitat* or *secondary habitat*. Core habitat is where habitat value is high and mortality risk is low, which is equally important habitat compared to the adjacent Jasper National Park (Nielsen et al., 2009). Secondary habitat is where habitat value is still good, but higher road densities provide more

human access (Nielsen et al., 2009). An active source-sink dynamic is present in BMA 3 (Boulanger et al., 2018), where local recruitment exceeds replacement in productive core areas (i.e., source), providing secondary areas with dispersers (Pulliam, 1988).

The objectives of Chapter 2 are to 1) quantify the change in grizzly bear habitat occupancy from 2004 to 2014 as a function of anthropogenic disturbance and habitat characteristics; and 2) identify differences in occupancy patterns between male and female grizzly bears. Chapter 2 presents competing occupancy models, to determine if grizzly bear occupancy in BMA 3 is better explained by disturbance or by habitat features. By analyzing occupancy over time as a function of landscape change and resource availability, there is potential to predict occupancy of grizzly bears outside of BMA 3 where disturbance patterns and habitat dynamics are comparable. The results provide a better understanding of the impacts of anthropogenic landscape disturbance on grizzly bear occupancy and persistence, and valuable insight to regulatory bodies, wildlife managers, and industry, which will contribute to the conservation and management of grizzly bears.

Grizzly bears are considered a keystone species in North America, having an important impact on the health of ecosystems (Carroll et al., 2001). Additionally, the conservation of grizzly bears and their habitat can positively influence the longevity of other species. Grizzly bears can be considered an “umbrella species” as their relatively large home ranges include numerous other species who may benefit from conservation initiatives. As a result, long-term persistence of grizzly bears, as well as other large predators, can serve as an indicator of the impact of land-use practices on wildlife populations over time (Wilkinson et al, 2008).

Quantifying change in habitat occupancy of grizzly bears over time will help identify factors that are impacting or limiting occupancy in Alberta, which is important for the conservation of the species, as limited geographic range combined with a declining population is linked with high extinction risk (Purvis et al., 2000).

It is critically important to consider spatial structures of ecological processes, spatial heterogeneity and functioning of ecosystems in conservation and management (Legendre, 1993). The objectives of Chapter 3 are to 1) identify and compare spatial patterns of grizzly bear occupancy and density using measures of spatial autocorrelation, and 2) quantify relationships between observed spatial patterns of occupancy and density and landscape processes (e.g., disturbance and topography). By examining the spatial relationships between predicted grizzly bear occupancy-abundance estimates over a decade, there is an opportunity to better understand how observed patterns are influenced by anthropogenic disturbance. Local indicators of spatial association (LISA) statistics are frequently used to quantify spatial patterns of continuous variables (Anselin, 1995; Getis & Ord, 1996; Kowe et al., 2019) by classifying values into spatial clusters and outliers using significance testing (Anselin, 1995). By identifying spatial “hot spots” of grizzly bear occupancy and density over time, we can identify important areas for grizzly bear habitat. While occupancy-abundance relationship for grizzly bears in Alberta are highly dependent on habitat quality (Nielsen et al., 2010), it is unknown how these variables interact spatially. A better understanding of the OA relationship for grizzly bears in Alberta in areas of resource extraction will inform management on the feasibility of occupancy modelling as a monitoring approach.

Finally, in Chapter 4, concluding remarks are presented, which summarize the theoretical and applied outcomes of this study and how this research contributes to grizzly bear management. Chapter 4 also presents future opportunities for the application of occupancy modelling for monitoring wildlife species. Overall, this study also seeks to assess the utility of occupancy modelling to address long-term landscape change and its impact on wildlife species. Combined, this research and its results will advance monitoring approaches of grizzly bears in Alberta, as well as provide insight on monitoring wide-ranging apex predators across the globe.

## Chapter 2

### Occupancy analyses of the BMA 3 grizzly bear population in 2004 and 2014

#### 2.1 Synopsis

Habitat occupancy, defined as the presence or absence of a species on a landscape or the proportion of an area occupied (MacKenzie et al., 2002), has become a popular metric used by researchers and wildlife managers as a cost-effective alternative to abundance inventories (MacKenzie et al., 2017). By simultaneously modelling dynamic relationships between habitat and occupancy, researchers can identify the effects of habitat dynamics, environmental variability, and landscape disturbance and human activity on species occupancy (Mackenzie et al., 2011). Consequently, occupancy modelling can help quantify factors influencing the persistence of species on a landscape over time (MacKenzie et al., 2017). However, occupancy modelling is seldom applied to quantify population trends over large spatial and temporal scales (Ellis et al., 2014; Steenweg et al., 2016) and datasets detailing animal detections over long time periods are rare (MacKenzie et al., 2017). As a result, the use of occupancy modelling to address long-term conservation and wildlife management questions represents an opportunity for further research.

Using a repeated population inventory data set from a threatened grizzly bear (*Ursus arctos*) population in Alberta, Canada, this research explores the application of occupancy modelling to describe long-term changes in grizzly bear persistence resulting from anthropogenic disturbance and habitat change. Grizzly bears are ideally suited for investigating the influence of landscape disturbance on wildlife habitat occupancy and persistence as they are exposed to multiple anthropogenic pressures in Alberta (Berland et al., 2008). Since the 1990s, Alberta has experienced an increase in resource extraction activities, including forestry, mining, and oil and gas exploration (Alberta Forestry, Lands and Wildlife 1990), which require extensive all-weather road networks (Graham et al., 2010). Previous research has shown a link

between landscape disturbance related to resource extraction activities and increased grizzly bear habitat use during foraging seasons (Nielsen et al., 2004a; Berland et al., 2008; Roever et al., 2008b; Laberee et al., 2014; McKay et al., 2014). However, selection of disturbance features can vary depending on disturbance type and age (Nielsen et al., 2002a), level of human activity, and sex (Laberee et al., 2014).

Anthropogenic landscape disturbance influences availability of key foods important for grizzly bears (Nielsen et al., 2004a), as recently disturbed areas (including cutblocks, roads, and oil and gas well-sites) tend to be associated with nutrient rich grasses and forbs (Nielsen et al., 2004b), ungulates (Nielsen et al., 2017) and fruit (Denny et al., 2018). However, associations between anthropogenic disturbance and resource availability can result in ecological traps, which occur when human-caused grizzly bear mortality increases in areas with abundant food resources (Lamb et al., 2017; Nielsen et al., 2006). Grizzly bear mortalities have been shown to be linked to anthropogenic activities and infrastructure by increasing the risk of human-bear conflict (Benn & Herrero, 2001; Nielsen et al., 2004; Roever et al., 2008b), and by facilitating access into grizzly bear habitat (Nielsen et al., 2004a). Although occupancy modelling is not concerned with mortality, its application to examine range dynamics and persistence over time in relation to anthropogenic disturbance can help identify industrial pressures that negatively influence their presence on a landscape.

Occupancy is a useful state variable in wildlife studies (MacKenzie, 2006; Manley et al., 2006; Martin et al., 2009; MacKenzie et al., 2017), and a key metric for assessing wildlife habitat. The 2008-2013 Alberta recovery plan for grizzly bears identifies sustained and persistent occupancy (specifically for breeding females) as a measure of conservation success (Alberta Sustainable Resource Development, 2008). In order to support grizzly bear conservation in Alberta, it is critical to understand factors influencing occupancy and population persistence in areas with anthropogenic landscape disturbance. Broadly, the goal of this chapter is to quantify the influence of anthropogenic landscape change on long-term spatial patterns of

grizzly bear occupancy and population persistence. Specifically, the objectives of this study are to 1) quantify the change in grizzly bear habitat occupancy from 2004 to 2014 as a function of anthropogenic disturbance and habitat characteristics; and 2) identify differences in occupancy patterns between male and female grizzly bears. In order to achieve these goals, candidate occupancy models were developed for all grizzly bears, as well as males and females separately, using an information theoretic framework (Burnham & Anderson, 2002) to investigate the influence of anthropogenic disturbance and habitat characteristics on grizzly bear occupancy in 2004 and 2014. The outcomes of this research will contribute to the understanding of how anthropogenic landscape disturbance influences grizzly bear persistence over time and help inform conservation and management of the species. The modelling approach also highlights the application of occupancy modelling over long time periods in support of wildlife conservation and management.

## **2.2 Methods**

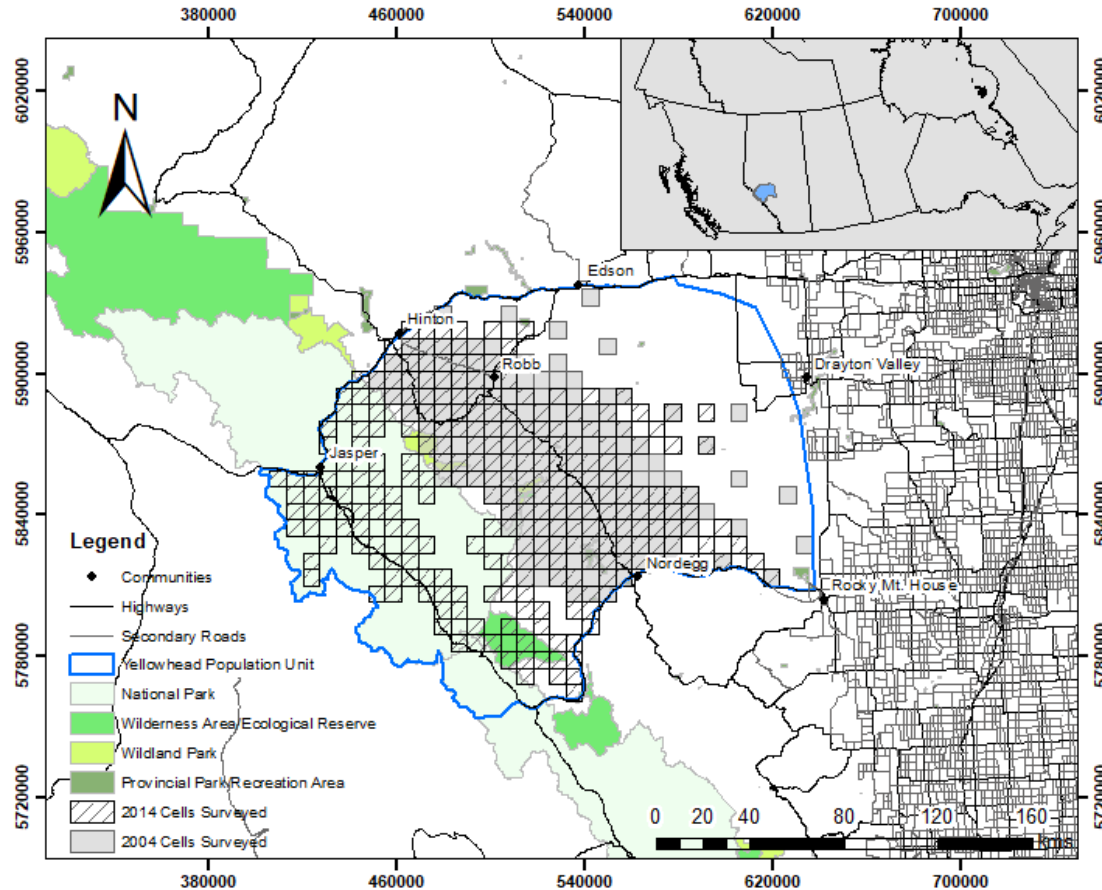
### **2.2.1 Study area**

The study was carried out in the Yellowhead grizzly bear management area (BMA 3) in Alberta, Canada (Figure 1). The 28,529 km<sup>2</sup> area contains approximately 30% of all available grizzly bear habitat in the province (Franklin et al., 2001). It consists of provincial lands that are designated as either core or secondary conservation zones for grizzly bears (Stenhouse et al., 2015). The study area is within the eastern foothills of the Rocky Mountains, bordered by Highway 16 to the north and Highway 11 to the south. The elevation ranges between 772 to 3030 m and includes alpine, subalpine, and upper/lower foothills sub-regions. A variety of land cover classes are found in the foothills including deciduous, mixed, and conifer forests, early seral forests resulting from fire and forest harvest, open and treed-bogs, and small herbaceous meadows (Franklin et al., 2001). The study area is home to other large predators, including

black bears (*Ursus americanus*), cougars (*Puma concolor*), and wolves (*Canis lupus*). Several ungulate prey species are also found here including white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), elk (*Cervus canadensis*), and bighorn sheep (*Ovis canadensis*) (Munro et al., 2006). Important forage species that occur in the study area include various blueberry species (*Vaccinium* spp.), buffaloberry (*Shepherdia canadensis*), alpine sweet vetch (*Hedysarum alpinum*), and cow parsnip (*Heracleum lanatum*) (Stenhouse et al., 2015).

There are multiple resource extraction activities throughout BMA 3. The area has experienced increasing industrial activity over the past century, including coal mining and extensive forest harvesting, as well as more recent expansions in oil and gas exploration (Linke et al., 2013). These anthropogenic activities are supported by a large network of linear features including roads and seismic lines, which provide human access to grizzly bear habitat (Nielsen et al., 2006). Additionally, recreational activities are common in the area including hiking, hunting, trapping, mountain biking, and the use of all-terrain vehicles (Graham & Stenhouse, 2014). Several provincial and federal parks found within the study area exclude resource extraction activities.





**Figure 1:** Study area in west-central Alberta, showing the BMA 3 grizzly bear population unit, hair snag cells surveyed in 2004 and 2014, parks and protected areas, and nearby communities. Only cells that were surveyed in both 2004 and 2014 were used for this analysis.

## 2.2.2 Field methods

Presence/absence data can be obtained using non-invasive approaches, including hair snags, which are useful for monitoring wide-ranging, elusive species, such as grizzly bears (Steenweg et al., 2016a). This study utilizes genetic hair snag data collected in 2004 and 2014, and landscape condition data generated for those years. Hair samples were collected by fRI Research throughout BMA 3 to assess grizzly bear population abundance in the spring to early summer over multiple two-week sessions using scent-lured hair snag sites. In 2004, hair snag

set-up occurred between May 25 and June 1 and in 2014 set-up took place between May 27 and June 4. Sites were selected based on GPS collar location, aerial photographs, remote sensing-based habitat mapping, resource selection function models (RSF), and in the case of 2014, expert opinion and past bait site locations where possible.

Hair snag sites consisted of approximately 50 m of barbed wire, strung around trees at a height of 50 cm. In the center of each corral, a bait pile was constructed using branches with moss on top for scent lure absorption. The lure (a mixture of 2 L of rancid cattle blood and 0.5 L of canola oil) was poured on top of the bait pile and protected from rain using conifer branches. Hair snag sites were built large enough to ensure that bears would have to fully enter in order to investigate the bait pile. Sites were visited every two weeks to collect hair samples and refresh the scent lure (Stenhouse et al., 2015). The same grid system (49 km<sup>2</sup> cells) was used in 2004 (180 cells) and 2014 (197 cells) in order to allow for direct comparison of results (Figure 1). However, the grid system was expanded in 2014 to include Jasper National Park and the Whitegoat Wilderness Area (Stenhouse et al., 2015). In order to compare occupancy changes between years, only the grid cells surveyed in both 2004 and 2014 were used for this analysis (148 cells). All hair data used in this study were collected using non-invasive methods approved by the UBC animal care committee (#A19-0073).

### **2.2.3 Data**

When the target species is not observed during a sampling session, it indicates the species is truly absent or the species is present but not detected. Using repeat surveys, a detection probability is estimated which is needed to account for imperfect detection in occupancy modelling (MacKenzie et al., 2002). The presence of at least one viable grizzly bear hair sample during a sampling session was considered a detection (1), whereas no viable hair sample resulted in a non-detection (0). Hair samples were categorized into three groups: all grizzly bear, grizzly bear male, and grizzly bear female (Table 1). Studies on other large

mammals have shown that specifying sex increases the model's ability to explain habitat occupancy (Conde et al., 2010), and identifying differing sex-specific responses can help monitor breeding success, which has value for conservation (Fisher et al., 2014). Species confirmation and sex specification was done using genotyping analysis at Wildlife Genetics International in Nelson, British Columbia (Stenhouse et al., 2015). Black bear hair samples were identified and removed through a preliminary visual examination followed by a pre-screen, which used a specific genetic marker to distinguish between species (Paetkau, 2003). Where sufficient genetic material was available, samples were analyzed to sex (Stenhouse et al., 2015). Samples which lacked sufficient genetic information to be analyzed to sex but were confirmed to be grizzly bear were included in the detection count for the "all" sex category. The "all" category, although a combination of male and female detections, is not simply the count of male and female detections. During a single sampling session, both males or females may be detected, which translates to a binary detection regardless of frequency.

**Table 1:** Total detections from the 2004 and 2014 grizzly bear population inventory studies in BMA 3 for 148 sites sampled over four sessions. The presence of at least one viable hair sample during a sampling session was considered as a detection.

	<b>2004</b>	<b>2014</b>
<b>All</b>	45	75
<b>Males</b>	28	56
<b>Females</b>	25	35

The probability of occupancy can be modeled as a function of landscape covariates to account for heterogeneity in occupancy probabilities across a landscape, or to infer to the relationship between the parameter and the covariates (MacKenzie et al., 2002; Tyre et al., 2003; Nichols et al., 2008). In order to examine the influence of anthropogenic disturbance and

habitat conditions on grizzly bear occupancy over time, disturbance and habitat variables provided by fRI Research for BMA 3 in 2004 and 2014 were used as model covariates (Table 2). Anthropogenic disturbance variables, generated using the Alberta Biodiversity Monitoring Institute (ABMI) Human Footprint Inventory and the Alberta Application Dispositions (DIDS), include pipeline and well sites, all cutblocks, old cutblocks (15 years and older), intermediate cutblocks (6 to 14 years old), new cutblocks (5 years old or less), mines (open pit and coal), and roads. A single covariate with percent area of all cutblocks, pipelines, well sites, and open pit coalmines combined was used to represent the total footprint for all anthropogenic disturbances. This covariate was used in a univariate model as a parsimonious candidate and to represent all anthropogenic disturbance in models considering both disturbance and habitat characteristics. Disturbance variables were measured in percent area per 49 km<sup>2</sup> cell, with the exception of roads, which was measured using density (meters per hectare).

Habitat variables include mean terrain ruggedness index (TRI), mean crown closure, Shannon index, proportion of land cover class, and measures of forest habitat configuration including edge density, aggregation index, division index, and fractal dimension index (Table 2). TRI (Riley, 1999), was derived using data from the Canadian Digital Elevation Model (CDEM) from Natural Resources Canada. Crown closure was derived by extracting tree cover in 2000 (Hansen et al., 2013) using the Google Earth engine and updated with the ABMI Human Footprint Inventory. Mean crown closure values in areas with wildfire burns and cutblocks were predicted based on time since disturbance. Land cover data representing tree, herb, shrub, wetland, and upland habitat with a 30 m resolution were used to calculate proportion of each land cover class for each grid cell. Land cover data were originally developed by McDermid et al. (2005) and then updated by fRI Research using ABMI Human Footprint Inventory vector features by type and age. The land cover classes were used to calculate the Shannon index as a measure of landscape heterogeneity, which has been shown to positively influence grizzly bear habitat selection (Denny et al., 2018a).

The R package *landscapemetrics* (version 1.4.3) was used to calculate the aggregation index, division index, edge density, and fractal dimension index for the tree land cover class to characterize configuration of tree cover. Specifically, aggregation index, a measure of clumpiness of a specific class (He et al., 2000), was used to represent continuity of tree cover. This was used as a proxy for forest fragmentation, as a reduction in connectivity is thought to contribute to increased mortality and lower reproduction for large mammalian carnivores (Carroll et al., 2001). Tree edge density represents microhabitats between treed and open areas, which are often favoured by grizzly bears due to increased food resources (Nielsen et al., 2008). Tree fractal dimension was used as a measure of patch complexity (Hesselbarth et al., 2019) and tree division index was used as a measure of landscape fragmentation as an alternative to aggregation index.

All covariates were centered by subtracting the mean and scaled by dividing by the standard deviation to standardize the range of data, allowing parameter effects in models to be directly comparable (Schielezeth, 2010). Where appropriate, covariates were log transformed for normality. A small constant (0.0001) was added to all covariate values to allow log transformations when covariates included zeros.

**Table 2:** Landscape covariates characterizing anthropogenic disturbance and habitat conditions employed in the habitat occupancy analysis.

Code	Covariate	Unit	Category
PI_Ws_P	Pipelines and well sites	% area	Disturbance
Bloc_P	Cutblock (all ages)	% area	Disturbance
O_Bloc_P	Old cutblock density (>15 years)	% area	Disturbance
I_Bloc_P	Intermediate cutblock density (6-14 years)	% area	Disturbance
N_Bloc_P	New cutblocks (<5 years)	% area	Disturbance
Road_D	Road density	km/km <sup>2</sup>	Disturbance
Mines_P	All open pit and coal mines	% area	Disturbance
Dist_P	All anthropogenic disturbance footprint	% area	Disturbance
TRI_MEAN	Mean terrain ruggedness index	Relative values	Habitat
CC_MEAN	Mean crown closure	%	Habitat
shannon	Shannon index (heterogeneity)	Relative values	Habitat
P_tree	Proportion tree cover	%	Habitat
P_herb	Proportion herb cover	%	Habitat
P_shr	Proportion shrub cover	%	Habitat
P_wet	Proportion wetland cover	%	Habitat
P_up	Proportion of upland habitat	%	Habitat
T.ed	Tree edge density	m/ha	Habitat
T.ai	Tree aggregation index	Relative values	Habitat
T.fr_cv	Tree fractal dimension index	Relative values	Habitat
T.div	Tree division index	Relative values	Habitat

#### 2.2.4 Analysis

We developed candidate model sets to test hypotheses on how anthropogenic disturbance and habitat characteristics influence grizzly bear occupancy over time. A Pearson

correlation coefficient was used to test collinearity ( $> 0.7$ ) of variables included in the models. Pipelines and well-site percent area were combined to represent cumulative percent area of oil and gas activities to avoid collinearity. Candidate models were developed to ensure that collinear variables were not included in the same model. The first model candidate set only considers the influence of anthropogenic disturbance to test the hypothesis that grizzly bear occupancy is primarily a function of anthropogenic landscape change and activities. The second model candidate set considers combinations of landscape composition and configuration, proxies for grizzly bear resource availability, and terrain ruggedness to test the hypothesis that grizzly bear occupancy is primarily a function of habitat characteristics. The third model candidate set includes combinations of both disturbance and habitat covariates. Each of the candidate models was limited to five covariates and demonstrated constant detection probabilities ( $p$ ) with occupancy ( $\Psi$ ) varying dependent on disturbance or habitat characteristics (Table 3).

**Table 3:** Candidate occupancy model sets for each sex-year category for BMA 3. Model candidate sets, including a null model, reflect competing hypotheses related to anthropogenic disturbance driven occupancy dynamics, habitat driven occupancy dynamics, or a combination of anthropogenic disturbance and habitat.

Candidate set	Hypothesis	Model*
0	Null	$p(\sim 1)\Psi(\sim 1)$
1	Disturbance	$p(\sim 1)\Psi(\sim \text{PI\_Ws\_P} + \text{Bloc\_P} + \text{Road\_D})$
1	Disturbance	$p(\sim 1)\Psi(\sim \text{PI\_Ws\_P} + \text{Bloc\_P} + \text{Road\_D} + \text{Mines\_P})$
1	Disturbance	$p(\sim 1)\Psi(\sim \text{PI\_Ws\_P} + \text{Road\_D})$
1	Disturbance	$p(\sim 1)\Psi(\sim \text{Bloc\_P} + \text{Mines\_P})$
1	Disturbance	$p(\sim 1)\Psi(\sim \text{O\_Bloc\_P} + \text{I\_Bloc\_P} + \text{N\_Bloc\_P})$
1	Disturbance	$p(\sim 1)\Psi(\sim \text{Dist\_P})$
2	Habitat	$p(\sim 1)\Psi(\sim \text{TRI\_MEAN} + \text{T.ai} + \text{T.fr\_cv})$
2	Habitat	$p(\sim 1)\Psi(\sim \text{TRI\_MEAN} + \text{T.ed} + \text{shannon})$
2	Habitat	$p(\sim 1)\Psi(\sim \text{TRI\_MEAN} + \text{P\_tree} + \text{P\_herb} + \text{P\_shr})$
2	Habitat	$p(\sim 1)\Psi(\sim \text{P\_wet} + \text{T.div} + \text{P\_up})$
2	Habitat	$p(\sim 1)\Psi(\sim \text{P\_wet} + \text{T.ed} + \text{T.fr\_cv})$
2	Habitat	$p(\sim 1)\Psi(\sim \text{P\_wet} + \text{CC\_MEAN} + \text{P\_shr})$
3	Disturbance + Habitat	$p(\sim 1)\Psi(\sim \text{TRI\_MEAN} + \text{T.ai} + \text{T.fr\_cv} + \text{Dist\_P})$
3	Disturbance + Habitat	$p(\sim 1)\Psi(\sim \text{TRI\_MEAN} + \text{T.ed} + \text{shannon} + \text{Dist\_P})$
3	Disturbance + Habitat	$p(\sim 1)\Psi(\sim \text{TRI\_MEAN} + \text{P\_tree} + \text{P\_herb} + \text{P\_shr} + \text{Dist\_P})$
3	Disturbance + Habitat	$p(\sim 1)\Psi(\sim \text{P\_wet} + \text{T.div} + \text{P\_up} + \text{Dist\_P})$
3	Disturbance + Habitat	$p(\sim 1)\Psi(\sim \text{P\_wet} + \text{T.ed} + \text{T.fr\_cv} + \text{Dist\_P})$
3	Disturbance + Habitat	$p(\sim 1)\Psi(\sim \text{P\_wet} + \text{CC\_MEAN} + \text{P\_shr} + \text{Dist\_P})$

\*The covariate codes represent: PI\_Ws\_P is percent area of pipelines and well sites; Bloc\_P is percent area of all aged cutblocks; Road\_D is road density; Mines\_P is percent area of mines; O\_Bloc\_P is percent area of old cutblocks (>15 years); I\_Bloc\_P is percent area of intermediate cutblocks (6-15 years); N\_Bloc\_P is percent area of new cutblocks (<5 years); Dist\_P is percent area of all anthropogenic



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disturbance footprint; TRI\_MEAN is mean terrain ruggedness index; T.ai is aggregation index of tree cover; T.fr\_cv is fractal dimension index of tree cover; T.ed is tree edge density; shannon is Shannon index; P\_tree is proportion of tree cover; P\_herb is proportion of herb cover; P\_shr is proportion of shrub cover; P\_wet is proportion of wetland cover; T.div is division index of tree cover; P\_up is proportion of upland habitat; and CC\_MEAN is mean crown closure.

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Single season occupancy models were developed for all grizzly bear detections as well as males and females separately for each year (2004 and 2014) in the statistical software R (R Development Core Team, 2011), using the package *RMark* (version 2.2.7; Laake, 2013, MacKenzie et al., 2002). A null model, which assumes constant occupancy probabilities and uniform detection probabilities across sites, was included in the candidate set. The same candidate model sets were used for each sex/year combination and Akaike information criterion scores corrected for small sample sizes (AICc) were used to evaluate model support (Burnham & Anderson, 2002). The model with the lowest AICc score for each category was compared to top models from other categories to determine which hypothesis best explained observed patterns of grizzly bear habitat occupancy. The model with the lowest AICc value for each sex/year combination was used to predict habitat occupancy for each 49 km<sup>2</sup> grid cell in BMA 3 for all grizzly bears, males and females for both 2004 and 2014. When multiple models had a delta-AICc below two, model averaging was used to predict occupancy probabilities (Anderson, 2008). Finally, to compare which hypothesis was most supported for each year-sex combination, AICc model weights in each candidate set were combined. AICc weights can be viewed as the weight of evidence for a specific model compared to all the other models in the set (Burnham & Anderson, 2002; MacKenzie et al., 2017). When multiple models are included in a candidate set for the same hypothesis (i.e., multiple make-ups of the same hypothesis), model weights can be summed to determine the overall level of support for each hypothesis (Burnham & Anderson, 2004). Using this approach, all Disturbance model weights were combined, all

Habitat model weights were combined, and all Disturbance + Habitat model weights were combined to determine which hypothesis best explained grizzly bear occupancy in BMA 3.

In order to test whether changes in mean occupancy per grid cell for each sex category were significant from 2004 to 2014, the Wilcoxon signed-rank test was employed using the *stats* package in R (version 3.6.2). As an alternative to the paired Students t-test, this approach is a non-parametric statistical test for comparing sample means from non normal distributions (J. H. McDonald, 2014). Further, the variance of the predicted occupancy estimates were tested using the Levene's test (1960) in the *lawstat* package (version 3.2).

## **2.3 Results**

Detection probabilities obtained in this study were adequate ( $>0.2$ ) for precise occupancy model estimates (Mackenzie & Royle, 2005). Model selection statistics show evidence that grizzly bear occupancy probability was influenced by a combination of habitat and disturbance variables in both 2004 and 2014. By combining AICc model weights to assess the overall support for each hypothesis (Burnham & Anderson, 2004), it was determined that there is substantial support for the Disturbance + Habitat hypothesis (Table 5). In most year-sex categories (male 2004, female 2004, all bears 2014, and male 2014) the Disturbance + Habitat hypothesis had the most overall support (combined AIC weights of 0.50, 0.52, 0.41, and 0.47, respectively), whereas the Habitat hypothesis had the most support for all bears in 2004 and female bears in 2014 (0.53 and 0.65, respectively). However, there was a similar level of support for the Habitat and the Disturbance + Habitat hypotheses for female bears in 2004 (0.48 and 0.52), and all bears in 2004 (0.53 and 0.47) and 2014 (0.39 and 0.41). There was also comparable support for the Disturbance hypothesis and the Disturbance + Habitat hypothesis for male bears in 2014 (0.46 and 0.47). For all sex categories, the weight of Disturbance only models was greater in 2014 than in 2004.

**Table 4:** Summary of model selection statistics for the top competing occupancy models for all, male and female grizzly bears (*Ursus arctos*) in BMA 3 in Alberta from n = 148 hair snag sites in 2004 and 2014.

Npar is the number of parameters estimated by the model (including Psi, p, covariates, and the intercept), AICc is Akaike information criterion scores corrected for small sample sizes,  $\Delta AICc$  is the difference in AICc values relative to the model with the lowest AICc, W is the AIC model weight, Real Psi is the real (as oppose to beta) estimate for occupancy probability, and MA estimate is the model averaged estimate.

Category	Model	Npar	AICc	$\Delta AICc$	W	Deviance	Real Psi	MA estimate
All 2004	p(~1)Psi(~IP_wet + T.div + P_up1)	5	273.28	0	0.49	262.86	0.35	
All 2004	p(~1)Psi(~IP_wet + T.div + P_up1 + IDist_P)	6	273.87	0.59	0.37	261.28	0.34	<b>0.35</b>

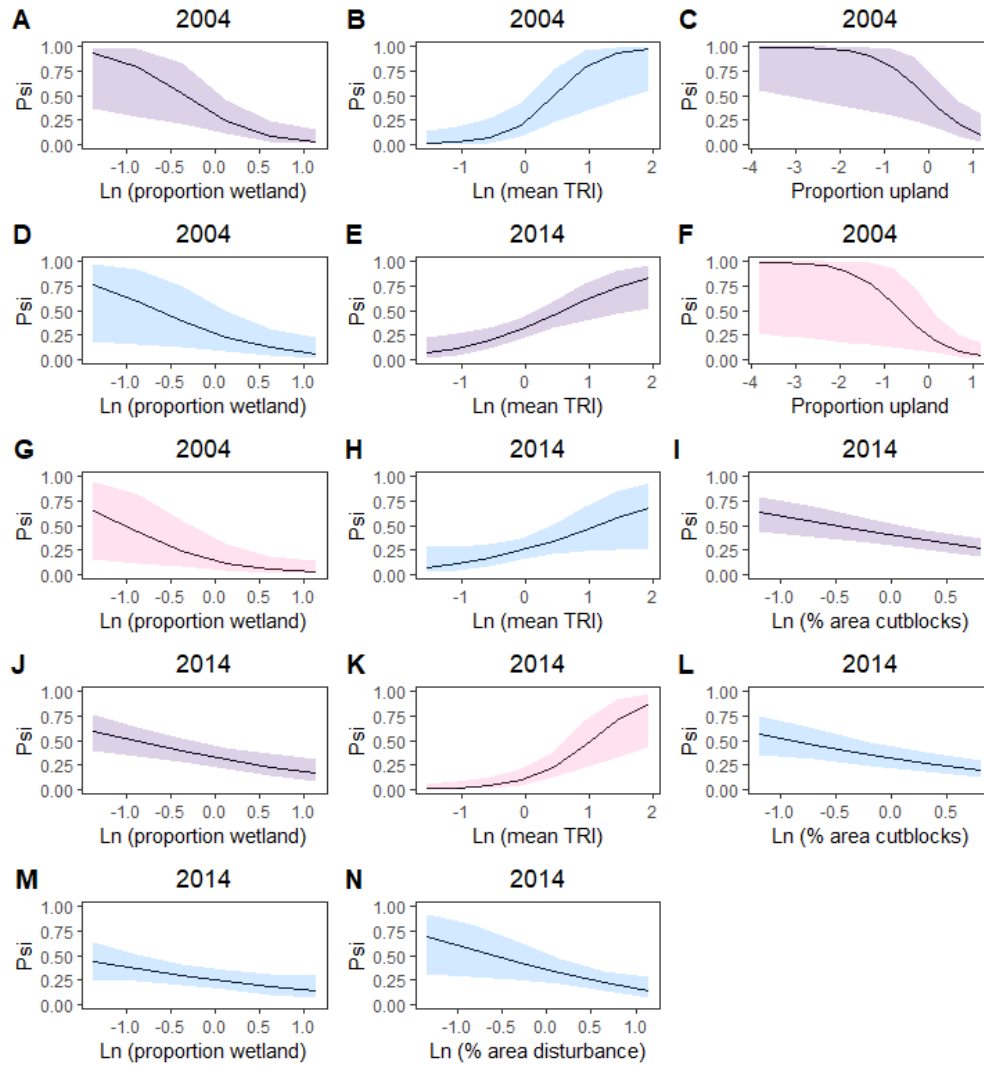
Category	Model	Npar	AICc	$\Delta$ AICc	W	Deviance	Real Psi	MA estimate
All 2014	p(~1)Psi(~IP_wet1 + CC_MEAN1 + IP_shr1 + IDist_P1)	6	397.11	0	0.15	384.52	0.34	
All 2014	p(~1)Psi(~IP_wet1 + CC_MEAN1 + IP_shr1)	5	397.27	0.16	0.13	386.85	0.34	
All 2014	p(~1)Psi(~IBloc_P1 + IMines_P1)	4	397.79	0.68	0.10	389.51	0.34	
All 2014	p(~1)Psi(~IP_wet1 + T.ed1 + T.fr_cv1 + IDist_P1)	6	398.26	1.15	0.08	385.67	0.34	
All 2014	p(~1)Psi(~IP_wet1 + T.div1 + P_up1 + IDist_P1)	6	398.31	1.19	0.08	385.71	0.35	<b>0.34</b>
All 2014	p(~1)Psi(~ITRI_MEAN1 + T.ed1 + shannon1 + IDist_P1)	6	398.43	1.32	0.07	385.84	0.34	
All 2014	p(~1)Psi(~IP_wet1 + T.div1 + P_up1)	5	398.49	1.38	0.07	388.07	0.34	
All 2014	p(~1)Psi(~ITRI_MEAN1 + T.ed1 + shannon1)	5	398.70	1.59	0.07	388.28	0.34	
All 2014	p(~1)Psi(~IP_wet1 + T.ed1 + T.fr_cv1)	5	398.92	1.80	0.06	388.49	0.34	

Category	Model	Npar	AICc	$\Delta$ AICc	W	Deviance	Real Psi	MA estimate
Male	p(~1)Psi(~IP_wet1 +	6	204.51	0	0.46	191.91	0.47	
2004	T.ed1 + T.fr_cv1 +							<b>0.37</b>
	IDist_P1)							
Male	p(~1)Psi(~IBloc_P1 +	4	324.54	0	0.27	316.26	0.26	
2014	IMines_P1)							
Male	p(~1)Psi(~ITRI_MEAN1	6	324.99	0.45	0.21	312.40	0.27	
2014	+ T.ed1 + shannon1 +							<b>0.27</b>
	IDist_P1)							
Male	p(~1)Psi(~IP_wet1 +	6	326.03	1.49	0.13	313.43	0.26	
2014	T.ed1 + T.fr_cv1 +							
	IDist_P1)							
Female	p(~1)Psi(~IP_wet1 +	5	179.55	0	0.43	169.13	0.16	
2004	T.div1 + P_up1)							
Female	p(~1)Psi(~IP_wet1 +	6	180.56	1.01	0.26	167.97	0.17	<b>0.17</b>
2004	T.div1 + P_up1 +							
	IDist_P1)							
Female	p(~1)Psi(~ITRI_MEAN1	6	218.36	0	0.44	205.77	<b>0.12</b>	
2014	+ P_tree1 + P_herb1 +							
	IP_shr1)							

**Table 5:** Combined model weights for each competing hypothesis. The highest values for each category are bolded.

	2004			2014		
Hypothesis	All	Male	Female	All	Male	Female
Disturbance	0.00	0.02	0.00	0.20	0.46	0.10
Habitat	<b>0.53</b>	0.49	0.48	0.39	0.07	<b>0.65</b>
Disturbance + Habitat	0.47	<b>0.50</b>	<b>0.52</b>	<b>0.41</b>	<b>0.47</b>	0.25

Among the occupancy models with the greatest support for all grizzly bears, males and females in 2004 and 2014, five covariates significantly influenced habitat occupancy: proportion of wetland habitat (P\_wet), proportion of upland habitat (P\_up), mean terrain ruggedness index (TRI\_MEAN), percent area of cutblocks of all ages (Bloc\_P), and percent area of all anthropogenic disturbance (Dist\_P). As proportion of wetland habitat increased, habitat occupancy decreased for all year-sex combinations except female grizzly bears in 2014 (Figure 2A, 2D, 2G, 2J, and 2M). As proportion of upland habitat increased, habitat occupancy for all grizzly bears and female grizzlies in 2004 decreased (Figure 2C and 2F). Percent area of all anthropogenic disturbance footprint demonstrated a negative relationship with grizzly bear occupancy in 2014 but not in 2004 (Figure 2N). Percent area of cutblocks of all ages also had a negative relationship with occupancy in 2014 for all grizzlies and male grizzlies (Figure 2I and 2L); whereas percent area of all anthropogenic disturbance footprint negatively influenced only males in 2014 (Figure 2K). For male grizzly bears in 2004 and all sex categories in 2014, habitat occupancy increased as mean TRI increased (Figure 2B, 2E 2H, and 2K).

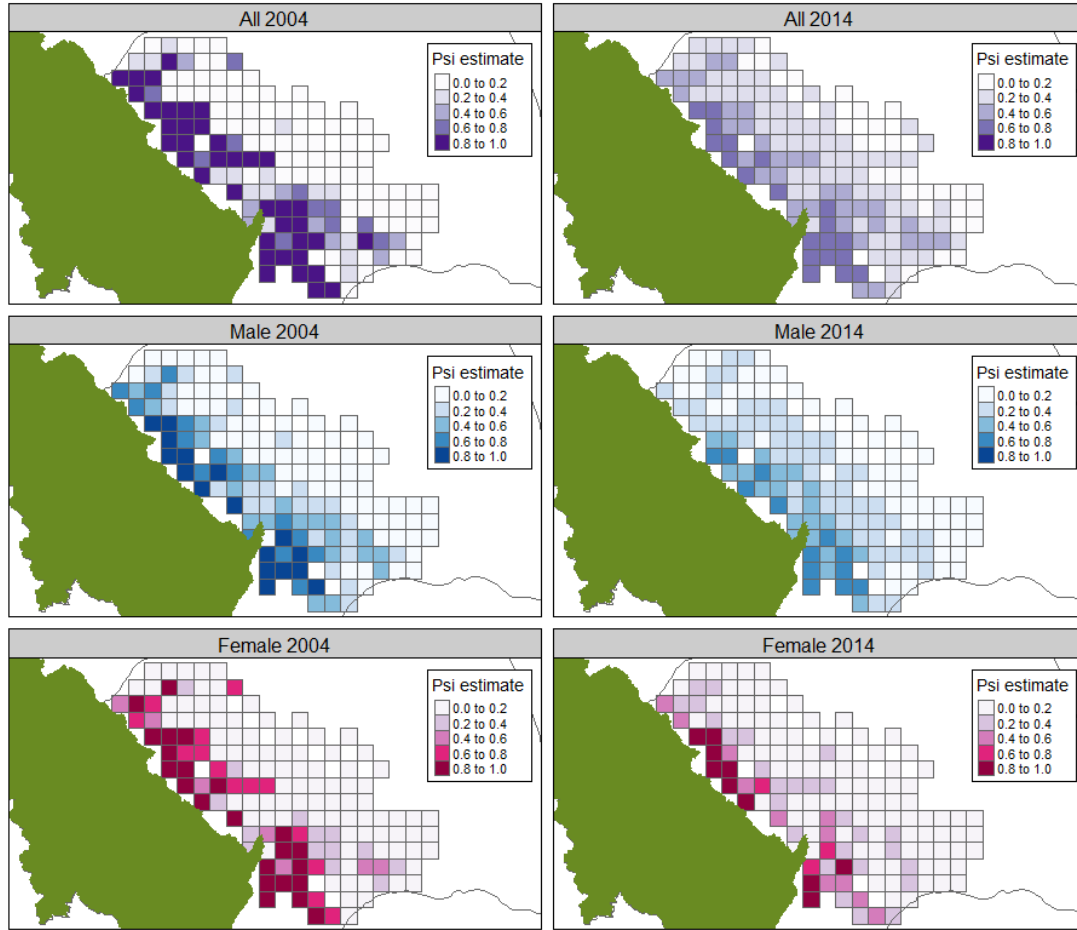


**Figure 2:** Covariates that significantly influenced grizzly bear occupancy in BMA 3 in 2004 and 2014.

Covariates that influenced all bears are in purple, those that influenced males are in blue and females are in pink. The plots represent: all grizzly bear 2004 occupancy (Psi) and proportion of wetland habitat (A); male grizzly 2004 Psi and mean terrain ruggedness index (TRI) (B); all grizzly 2004 Psi and proportion of upland habitat (C); male grizzly 2004 Psi and proportional of wetland habitat (D); all grizzly 2014 Psi and mean TRI (E); female grizzly 2004 Psi and proportion of upland habitat (F) female 2004 Psi and proportion of wetland habitat (G); male grizzly 2014 Psi and mean TRI (H); all grizzly 2014 Psi and percent area of all cutblocks (I); all grizzly 2014 Psi and proportion of wetland habitat (J); female 2014 Psi and mean TRI (K); male 2014 Psi and percent area of all cutblocks (L); male 2014 Psi and proportion of wetland habitat (M); and male 2014 Psi and percent area of all anthropogenic disturbance footprint (N).

Of the 148 cells that were included in the study, 36 had detections in 2004 and 44 in 2014 for all grizzly bears, yielding proportions of units occupied of 0.24 and 0.30 respectively. Males were detected at least once at 24 sites in 2004 and 34 sites in 2014, yielding proportions of units occupied of 0.16 and 0.23 respectively, and females were detected at 20 sites in 2004 and 23 sites in 2014, yielding proportions of units occupied of 0.14 and 0.16 respectively. These values, unlike occupancy probabilities, assume no heterogeneity in detection or occupancy estimates amongst cells and therefore does not consider the influence of covariates on occupancy (MacKenzie et al., 2017). Based on model outputs, the occupancy probability based on real Psi for all grizzly bears in 2004 was 0.36 in 2004 and 0.34 in 2014. Male occupancy decreased from 0.28 in 2004 to 0.27 in 2014. Female occupancy also decreased from 0.17 in 2004 to 0.12 in 2014 (Table 4). Based on year/sex predictions from the models with the greatest support, all sex categories demonstrated similar occupancy patterns with concentrated patterns of high probability of occupancy in the western part of the study area in 2004 (Figure 3). In 2014, occupancy probability patterns are increasingly diffuse reflecting the observed lower occupancy estimates, with less occupancy in the western areas and increased occupancy in the eastern areas (Figure 3).

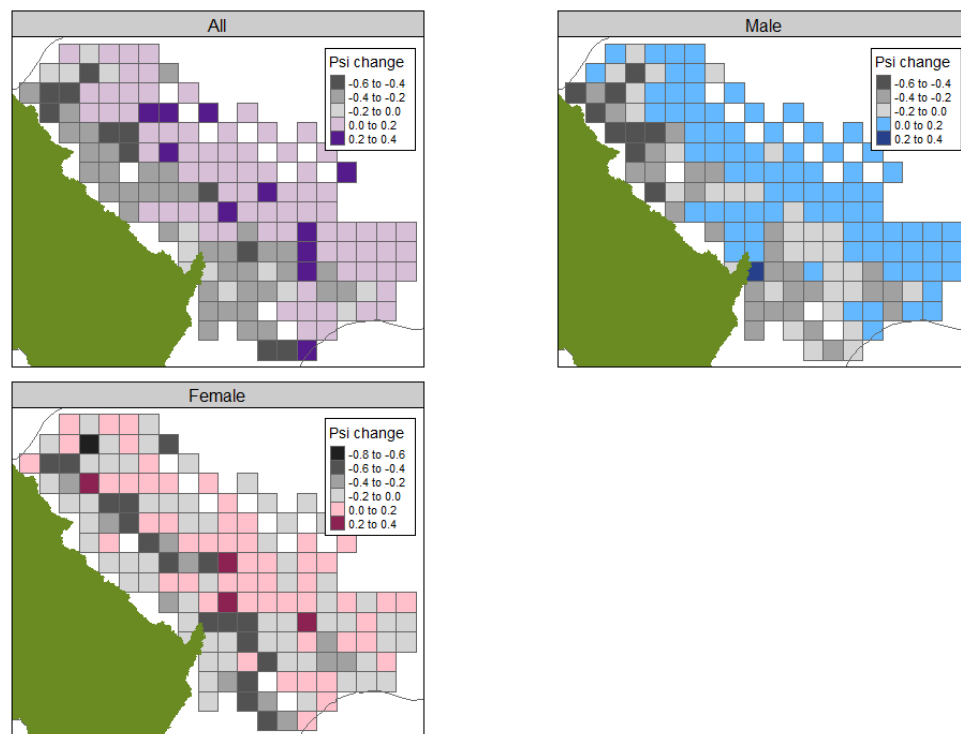




**Figure 3:** Predicted grizzly bear habitat occupancy for BMA 3 in 2004 (0.35) and 2014 (0.34) for all grizzly bears shown in purple. Males are shown in blue for 2004 (0.37) and 2014 (0.27), and female are shown in pink for 2004 (0.17) and 2014 (0.12). Predictions were generated using top competing models (i.e., lowest AICc), or where a top model was not obvious, model averaged estimates were used.

Increases in occupancy from 2004 to 2014 for all sex categories were most evident in the eastern portion of the study area and decreases were most evident along the border of Jasper National Park (Figure 4). For male grizzlies, substantial occupancy decreases were observed in the northwestern portion of the study area (- 0.4-0.6), with one cell of occupancy increase directly adjacent to Jasper National Park (+ 0.2-0.4), and smaller increases throughout the eastern half of the study area (+ 0.0-0.2). For female grizzlies, noticeable decreases in occupancy were observed along the eastern slopes (- 0.4-0.6) with one cell of considerable

occupancy decline (- 0.6-0.8). There were a few scattered cells with modest increases in occupancy (+ 0.2-0.4), with smaller increases observed throughout the study area (+ 0.0-0.2). However, increases in female occupancy were more dispersed compared to the observed changes for males. Results of the Wilcoxon test indicated that the changes in mean grizzly bear occupancy probabilities from 2004 to 2014 were significant for all grizzlies ( $W=9262$ ,  $p=0.02$ ), but not for males ( $W=10287$ ,  $p=0.37$ ) or females ( $W=11423$ ,  $p=0.52$ ). Results of the Levene test indicate that variances were statistically different for all grizzly bear occupancy ( $F=51.632$ ,  $p<0.05$ ), male occupancy ( $F=37.493$ ,  $p<0.05$ ), and female occupancy ( $F=9.3925$ ,  $p<0.05$ ) between 2004 and 2014. For all sex categories, variances were higher in 2004 than in 2014.



**Figure 4:** Predicted grizzly bear habitat occupancy probability changes in BMA 3 from 2004 to 2014 per each cell. All grizzly bear occupancy changes are shown in purple, males are shown in blue, and females are shown in pink. Positive changes are displayed in colour and negative changes are displayed in grey. Jasper National Park is shown in green.

## 2.4 Discussion

The goal of this study was to quantify changes in grizzly bear occupancy in BMA 3 from 2004 to 2014 and to determine the influence of anthropogenic landscape disturbance and habitat features on occupancy patterns for all bears, males, and females. By comparing multiple competing candidate model sets, we set out to determine whether disturbance, habitat or a combination of both best characterized grizzly bear occupancy in the area. Our results indicate that all bear occupancy probability decreased slightly between 2004 and 2014, and according to the Wilcoxon test, mean occupancy probabilities per grid cell were significantly different. When male and female occupancy were modeled separately, both decreased from 2004 to 2014, however mean occupancy probabilities per grid cell were not significantly different according to the Wilcoxon test. For all sex categories, variances were found to be statistically higher in 2004 than in 2014. The difference in variance could be a result of increased sampling consistency in 2014; however, it is beyond the scope of this study to verify this. Alternatively, the differences in variances could be a function of changes in landscape conditions from 2004 to 2014, which will be explored in the subsequent chapter.

From a conservation and management standpoint, decreased occupancy in the reproductive element of the population requires further investigation as the Alberta Grizzly Bear Recovery Plan (2008-2013) explicitly considers occupancy as the presence of females with cubs. Since female grizzly bears do not mate annually, an adequate female population is essential to alleviate extirpation risk in fragmented populations (Proctor et al., 2012). However, population estimates for the BMA 3 grizzly bear population suggest that the number of females increased from 2004 to 2014 so it is not likely that the population is in decline (Stenhouse et al., 2015). There were comparable detections of males (28) and females (25) in 2004, but in 2014 males were detected considerably more than females (56 and 35 respectively). The lower occupancy probability of females in 2014 is reflective of the lower detection rate, which could be a result of lower movement rates. Male grizzly bears have larger home ranges than females and

tend to move longer distances than females especially during mating season, likely because they are in search of reproductive females (Blanchard & Knight, 1991; Dahle & Swenson, 2003; Krofel et al., 2010; Graham & Stenhouse, 2014). Additionally, female dispersal has been shown to be far shorter and more gradual compared to males (McLellan & Hovey, 2001; Proctor et al., 2004). If female movements in the study area are limited, they may have a reduced likelihood of encountering a hair snag site and being detected.

Despite the lower overall occupancy probability in 2014 compared to 2004, the spatial pattern of occupancy change observed indicates that grizzly bear occupancy is becoming more widely distributed in BMA 3. For all sex categories, occupancy probability decreased in the western portion of the study area, directly adjacent to Jasper National Park, and increased in the eastern portion of the study area. Throughout North America, the size and distribution of grizzly bear populations have been dramatically reduced as they have been extirpated from much of their historic range (Nielsen, 1975; Servheen, 1990). When considering the conservation of sensitive species, it is important to consider geographic range, as the loss of range in conjunction with a declining population increases the risk of extirpation or extinction (Purvis et al., 2000). Here, spatial patterns in occupancy indicate that despite increasing anthropogenic pressure in BMA 3, and the resulting increase in mortality risk (Nielsen et al., 2004), grizzly bear range could be increasing. We observed new occupancy in eastern grid cells over a decade (i.e., an increase in proportion of area occupied, where previously unoccupied cells became colonized) despite the overall decrease in occupancy probability, suggesting the population may be expanding into new habitats. Considering the study area occurs along the easternmost edge of current grizzly bear range in Canada, increases in the geographic extent of occupancy, in conjunction with increases in population size observed from 2004 to 2014 (Stenhouse et al. 2015), could indicate a positive trend for the threatened grizzly bear population in Alberta.

A possible explanation for the expanding occupancy patterns observed in this study is individuals are dispersing into new habitat because of increased density. Stenhouse et al. (2015) estimated an increase in grizzly bear population size from 36.0 in 2004 to 71.3 in 2014. With more bears on the landscape, individuals, particularly juvenile bears, may seek out new habitat in the eastern portion of the study area that was previously unoccupied (McLellan & Hovey, 2001). Whether or not the anthropogenic disturbance occurring in BMA 3 is creating suitable habitat in the east that will allow grizzly bears to persist over time is unknown. We recommend further research to determine if grizzly bear occupancy has persisted in the eastern portion of the study area since 2014. Ultimately, grizzly bear occupancy appears to have changed from 2004 to 2014; however, the change does not reflect changes in population abundance (Stenhouse et al., 2015). The spatial patterns of occupancy and density will be explored in the subsequent chapter to examine where the changes have occurred.

Habitat variables were influential for all year-sex categories. Our results indicate that habitat occupancy in BMA 3 was influenced primarily by mean terrain ruggedness index (TRI) and proportion of wetland cover in both 2004 and 2014. Mean TRI exhibited a positive influence on grizzly bear occupancy for all year-sex categories except all grizzly bears and females in 2004. Boulanger et al., (2018) found that TRI positively influenced grizzly bear detection in BMA 3 as valleys associated with greater terrain ruggedness can increase detection of individuals, which is likely due to fact that valley bottoms tend to be utilized for both wildlife and humans as movement corridors in rugged areas (Noss et al., 1996). Further, TRI reflects terrain complexity (Nellemann & Fry, 1995), and influences the placement of roads and human activity in grizzly bear habitat (Roever et al., 2008). Within west-central Alberta, roads generally occur at low to intermediate TRI (Roever et al., 2008). Roads can provide attractive forage for grizzly bears (Roever et al., 2008), but are correlated with human–caused mortality (Nielsen et al., 2004). Over time, the influence of TRI may be increasing as it provides a refuge from risks associated

with roads and human activity. It is important to note, however, that roads density did not influence occupancy in this study.

Proportion of wetland cover showed a negative influence on grizzly bear occupancy for all year-sex categories except female 2004. This is consistent with grizzly bears in the central Arctic of Canada which displayed preference for habitats other than wetlands (McLoughlin et al., 2002). Additionally, grizzly bear habitat selection in Alberta has been found to be inversely related with wetland habitats such as bogs, which tend to lack high quality foods (Nielsen et al., 2004; Nielsen et al., 2006) and are challenging to travel through (Roever et al., 2008). Stewart et al. (2013) found that selection of wetland edges was variable for female grizzly bears in Alberta and suggested that use of this habitat type may relate to other factors such as ungulate presence. Proportion of upland habitat also negatively influenced occupancy for two year-sex categories (all 2004 and female 2004), which may be related to food availability. McLoughlin et al (2002) found that grizzly bears' habitat selection in the Canadian arctic corresponded with both spatial and temporal food availability, and although upland habitats may have higher fruit production compared to clearcuts (Nielsen et al., 2004b), upland berries are generally unavailable during the spring hair sampling time period.

Our results revealed a negative relationship between grizzly bear occupancy (all 2014 and male 2014) and cutblocks regardless of age. Previous studies have shown logged areas may serve as a surrogate for natural openings and therefore provide opportunities for forage (Nielsen et al. 2004 & 2006). However, due to regeneration over time these features become less attractive (Kearney et al., 2019). A negative relationship was also observed between total anthropogenic footprint (including pipelines, well sites, cutblocks and mines) and male occupancy in 2014. For two year-sex categories (all 2014 and male 2014) mines (open pit coal) were a covariate in a top competing model, although they did not significantly influence occupancy. It is likely that occupancy responses of grizzly bears to mines varies depending on

the level of activity (i.e., active or reclaimed), the available food resources in the area, and differs depending on sex-age class (Cristescu et al., 2016).

We found male grizzly bear occupancy was influenced more by anthropogenic disturbance compared to females. Prior studies have noted varying behavioural responses of grizzly bears to anthropogenic disturbance by sex-age class in Alberta. Specifically, male grizzly bears have been shown to avoid anthropogenic disturbance, including roads and mines, compared to females (e.g., Stewart et al., 2013; Cristescu et al., 2016). It was also found that yearlings and females with cubs used habitats in close proximity to roads (McLellan & Shackleton, 1988), and road-like habitat has been associated with female selection but not with male selection (Roever et al., 2008b). Use of roads also varies temporally, as females tend to cross roads in the daytime while males tend to cross at night (Graham et al. 2010). A possible explanation for the differing behaviours between males and females might be due to adaptive behaviour of female grizzly bears with cubs who seek refuge from potential infanticide from conspecific males by using habitat close to anthropogenic activity (Libal et al., 2011; Steyaert et al., 2013; Elfström et al., 2014).

We found the influence of anthropogenic disturbance on grizzly bear occupancy increased between 2004 and 2014 in BMA 3. In 2004, there were no significant disturbance covariates for any sex category, but in 2014, total anthropogenic footprint and all cutblocks influenced occupancy. The disturbance model had more support in 2014 compared to 2004 for all sex categories, and disturbance covariates that influenced occupancy were only evident in 2014. West-central Alberta has seen dramatic land use changes related to resource extraction activities creating younger and more fragmented forested landscapes (Schneider et al., 2003). Forest practices have resulted in an increasing number of small, dispersed cutblocks since the early 2000's (White et al., 2011), which combined with increasing oil and gas exploration has resulted in the expansion of the road network throughout grizzly bear habitat. While road densities represent the primary factor influencing grizzly bear demographics in Alberta

(Boulanger et al., 2014), our results demonstrate that the cumulative effects of increasing anthropogenic footprint can influence spatial-temporal patterns of grizzly bear occupancy.

Changes in land use patterns are likely to negatively influence grizzly bear occupancy as demonstrated by the negative relationship of occupancy to cutblocks and all disturbance. However, it was difficult to identify the influence of specific resource sectors based on the spatial scale of data collection as the 49 km<sup>2</sup> grid cells used for hair capture in this study were relatively heterogeneous in terms of habitat or land cover type. The scale of the grid cell system was utilized in order to obtain a broad coverage of the landscape for a population inventory (Stenhouse et al. 2015, Boulanger 2005), not to test the influence of specific landscape variables. Although covariates representing proportions of habitat and landscape characteristics can be used to explore occupancy dynamics, MacKenzie et al. (2017) advises that sampling units should be defined at a scale where covariate values are reasonably homogeneous within the unit as multiple habitat or disturbance types may mask the influence of specific variables. The cumulative nature of anthropogenic disturbance within the grid cells creates complex interactions among disturbance types, landscape patterns and resource availability. As a result, the spatial scale of the hair sampling may be masking finer scale habitat characteristics that influence grizzly bear occupancy.

Increasing disturbance over a decade has negatively influenced grizzly bear occupancy despite the potential for increased food availability resulting from anthropogenically driven landscape heterogeneity (Denny et al., 2018). These results highlight the importance of considering the impact of resource extraction on grizzly bears over time, as there are likely cumulative impacts of disturbance and human activities on habitat and grizzly bear behaviour. Individual factors may not appear meaningful, however the cumulative effects may exert a significant influence on occupancy (Johnson et al., 2005; Theobald et al., 1997). Occupancy modelling has become a common approach for identifying negative influences of anthropogenic disturbances on wildlife species. Specifically, fragmentation resulting from anthropogenic activity



has been shown to negatively impact the occupancy of avian species (Bolger et al., 1991; Boulmier et al., 2001; Hames et al., 2001; Ferraz et al., 2007; Zipkin et al., 2009; Collier et al., 2012). Anthropogenic disturbance has been shown to elicit negative occupancy responses for several mammalian species (e.g., roads, forest harvest and mining) (Das et al., 2014; Pillay et al., 2011; Fuller et al., 2016; Lkhagvasuren et al., 2016; Rivera et al., 2020), and alter predator prey dynamics (Burr et al., 2017; Thomas et al., 2019). These studies, along with the results of this research, highlight the complexity of wildlife behaviour, habitat use, and distribution in relation to anthropogenic disturbance. Not only is the relationship multifaceted, as our results have shown, can change over time.

The cumulative effects of resource development not only alters the structure of the forested landscape, it also influences ecological integrity (Nitschke, 2008). Confounding effects, such as avoidance behaviours, changes in population dynamics, and altered habitat use and occupancy, can ensue, particularly in heterogeneous habitat with various anthropogenic pressures (Erb et al., 2012). Developing accurate predictions and appropriate management initiatives requires an understanding of both individual and cumulative effects of anthropogenic development on wildlife. If habitat change is not quantified over time, impacts to wildlife habitat selection from resource development may be misrepresented (Houle et al., 2010). It is possible that in areas with concentrated anthropogenic disturbance, occupancy is discouraged over time. For example, grizzly bear habitat use was found to decrease in areas with road densities over 6 km/km<sup>2</sup> (Mace et al., 1996). However, habitat relative to specific disturbances may still be selected influencing survival and source-sink dynamics in the population (Nielsen et al., 2006; Lamb et al., 2017). Further research is required to identify occupancy patterns related to thresholds of anthropogenic disturbance. Occupancy modelling could be applied to identify these thresholds by considering varying densities of disturbance features.

Habitat characteristics, including wetlands and terrain ruggedness, in combination with anthropogenic footprint influence grizzly bear occupancy in BMA 3. Overall, grizzly bear

occupancy decreased in BMA 3 from 2004 to 2014, with female occupancy decreasing substantially. Although the overall occupancy estimate decreased, the spatial variation in occupancy suggests that there is potential for grizzly bear range to expand in Alberta as the portion of cells occupied increased. This study provides new insight into the distribution of the BMA 3 grizzly bear population and shows that an increase in abundance may not correspond with an increase in habitat occupancy. Although this research specifically examined grizzly bears in west-central Alberta, grizzly bears are exposed to resource extraction activities throughout their existing range and our findings may provide insight to responses of bears in other regions.

This study highlights the need to monitor both wildlife populations and their habitat over time, as the influence of anthropogenic activity and disturbance may not be immediately apparent. With shifting environmental conditions associated with climate change and increasing demands for natural resources associated with an increasing human population, the need to monitor species distributions for conservation initiatives is essential. Occupancy modelling is a valuable tool for exploring range dynamics and understanding how populations respond to landscape change and habitat characteristics over time. However, if concerns regarding abundance or density are a management priority, occupancy alone is not sufficient to assess population dynamics. As anthropogenic landscape change continues to accelerate, occupancy modelling will continue to develop as a critical tool for monitoring change in wildlife populations and range-dynamics.

## Chapter 3

### Exploring spatial patterns of grizzly bear occupancy and density over a decade in BMA 3

#### 3.1 Synopsis

As the impacts of anthropogenic pressures on wildlife populations increase, effective approaches to monitor biodiversity are required (Sala et al., 2000). Populations are commonly monitored by observing changes in abundance; however, developing estimates of abundance and density are time consuming and expensive (Lancia et al., 1994; MacKenzie et al., 2002; Pollock et al., 2002). Since the expansion of the mark-recapture framework to incorporate parameters for detectability and occupancy probability by MacKenzie et al. (2002), habitat occupancy (the presence/absence of a species on a landscape) has widely been used as a cost-effective alternative to abundance estimates to study wildlife populations (Bailey et al., 2014; MacKenzie et al., 2017). Utilizing detection/non-detection data, occupancy modelling is a flexible framework that can incorporate existing data sets (MacKenzie et al., 2017).

Detection/non-detection data has been used to monitor various species, including endangered insects (e.g., the Mahoenui giant weta [*Deinacrida mahoenui*; Mackenzie et al., 2004, 2005] and the Quino checkerspot butterfly [*Euphydryas editha quino*; Zonneveld et al., 2003]), amphibians (Martínez-Solano et al., 2003; Fellers et al., 2005; Weir & Mossman, 2005), spotted owls (*Strix occidentalis*; Azuma et al., 1990; MacKenzie et al., 2003), marbled murrelets (*Brachyramphus marmoratus*; Stauffer et al., 1995), fishers (*Martes pennanti*) and martins (*Martes americanus*; Zielinski & Stauffer, 1996; Carroll et al., 1999), and tigers (*Panthera tigris*) including their prey species (Nichols & Karanth, 2002).

Prior to work of MacKenzie et al. (2002 & 2003), detection/non-detection data had been used to estimate abundance using mark-recapture models, with presence signifying a “mark” (Hewitt, 1967; Thompson & Gidden, 1972). Mark-recapture models estimate the number of

animals in a population by capturing a sample of the population, marking each individual, and releasing them back into the population. A second sample is captured some time later, and the proportion of marked individuals in the second sample is assumed to be equal to the proportion of marked individuals in the population, allowing population size to be estimated (Pollock et al., 1990; Nichols, 1992; Pradel, 1996). In order to have reliable estimates of abundance using such models, the probability of detecting a specific individual must be estimated (Yoccoz et al., 2001; Williams et al., 2002; Schmidt, 2003). Although easily achieved for animals with distinct markings (Karanth & Nichols, 1998), it can be difficult for animals lacking markings and otherwise must be done with DNA analysis, resulting in high costs and extensive effort (Lancia et al., 1994; Pollock et al., 2002; MacKenzie et al., 2002).

Obtaining estimates of occupancy, requiring significantly less effort and resources, are commonly viewed as a surrogate to abundance estimates (MacKenzie et al., 2017). Making inferences about abundance from habitat occupancy estimates is often feasible given commonly observed relationships between occupancy and abundance (Zuckerberg et al., 2009). Positive occupancy-abundance (OA) relationships are supported by empirical evidence throughout the study of ecology (Hanski, 1982; Gaston et al., 2000; Blackburn & Gaston, 2004), however, they are not always evident (Fuller et al., 1995; Chamberlain & Fuller, 2001; Blackburn et al., 2006; Reif et al., 2006; Symonds & Johnson, 2006; Van Turnhout et al., 2007; Webb et al., 2007). Abundance may be inferred from occupancy estimates at suitable scales where the two state variables are positively correlated, however, changes in animal density may not correspond to changes in occupancy (MacKenzie & Nichols, 2004).

Chapter 2 demonstrated that grizzly bear habitat occupancy declined from 2004 to 2014 in the Yellowhead population unit (BMA 3), yet there was little change in the central tendency of the occupancy estimates. However, grizzly bear population estimates developed from the same hair snag data set show the population nearly doubled in size from 2004 to 2014 (Boulanger, 2005; Stenhouse et al., 2015). Specifically, 36 individual grizzly bears (14.4 males and 21.6

females) were identified in 2004 and 71.3 in 2014 (37.6 males and 33.7 females) (Stenhouse et al., 2015). Chapter 2 results also demonstrated that occupancy has become less concentrated in the study area, suggesting that individuals were found more broadly throughout the landscape. However, changes in grizzly bear abundance in BMA 3 do not directly translate to changes in occupancy.

Overall, anthropogenic disturbance (hereafter disturbance) has increased throughout the study area between 2004 and 2014, yet it remains unclear how this increased disturbance has influenced grizzly bears spatially, given observed trends in occupancy and abundance. As previously discussed in Chapter 2, disturbance can have varying effects of grizzly bears. Cutblocks and oil and gas infrastructure can provide increased forage (Nielsen et al., 2004, 2017; Denny et al., 2018; Stenhouse et al., 2015; Sorensen et al., 2021); however, increased access and road density can result in increased mortality (Nielsen et al., 2006; Boulanger & Stenhouse, 2014; Lamb et al., 2017; Proctor et al., 2020). Chapter 2 demonstrated disturbance has a negative influence on grizzly bear habitat occupancy, but how occupancy and density differ spatially provides opportunities for further research needed to support continuing conservation efforts of grizzly bears in Alberta. With the interest in monitoring population change, understanding the nature of AO relationships of a population can allow a greater understanding of habitat suitability and large-scale population dynamics (Freckleton et al., 2005), which is particularly valuable for a threatened species such as the grizzly bear in Alberta (Kansas & Festa-Bianchet, 2016). The purpose of this study is to explore the spatial relationship between grizzly bear abundance and occupancy.

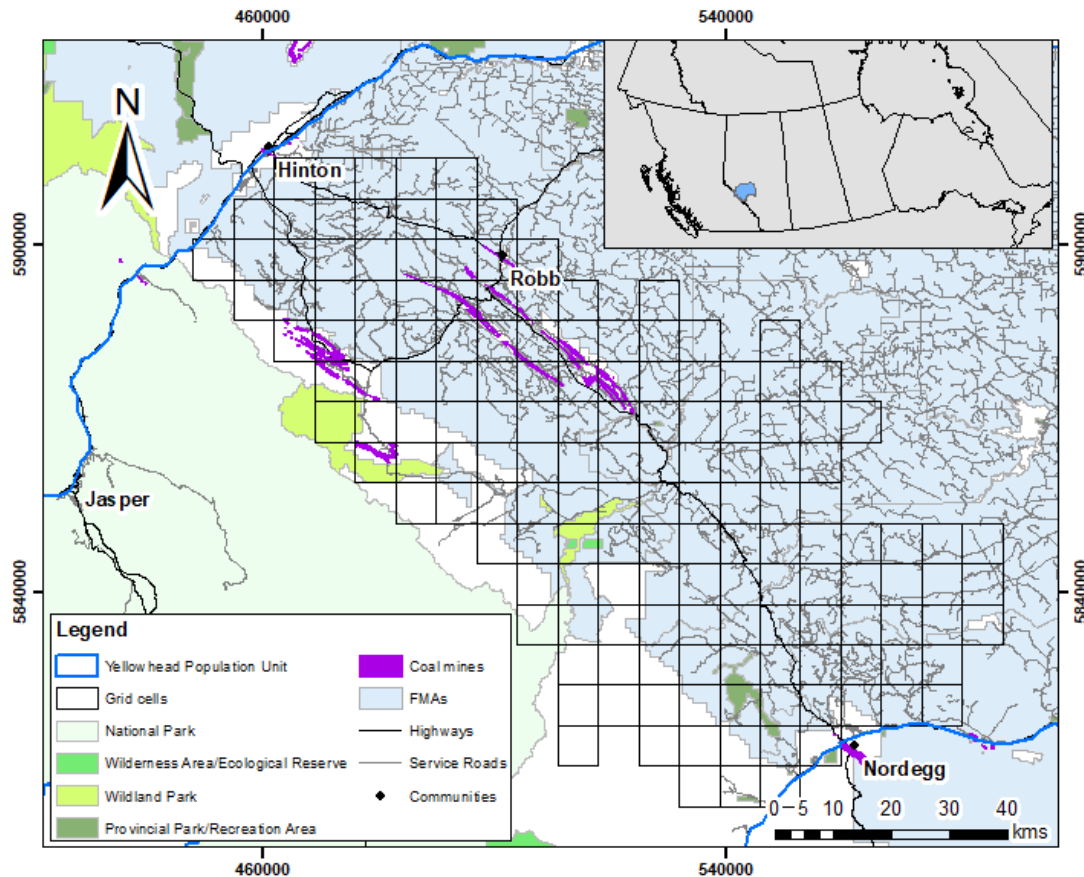
When monitoring ecological variables, it is important to consider spatial structure in order to account for the heterogeneity and functioning of ecosystems (Legendre, 1993). By identifying hot spots or clusters of state variables on the landscape, we can identify patterns to help understand landscape or environmental processes (Ord & Getis, 2001). Here, we can identify what anthropogenic and topographic processes are occurring on the landscape in areas of high

grizzly bear occupancy and density. Specifically, the objectives of this chapter are to 1) identify and compare spatial patterns of grizzly bear occupancy and density using measures of spatial autocorrelation, and 2) quantify relationships between observed spatial patterns of occupancy and density and landscape processes (e.g., disturbance and topography). This study will help inform and direct grizzly conservation and management in Alberta by clarifying spatial relationships between grizzly bear occupancy and abundance, and how landscape processes influence these patterns.

## **3.2 Methods**

### **3.2.1 Study Area**

This study was conducted in the Yellowhead grizzly bear management area (BMA 3) in Alberta, Canada, directly east of Jasper National Park (JNP; Figure 5). Bordered by Highway 16 to the north and Highway 11 to the south, the area occurs primarily in the eastern foothills of the Rocky Mountains in central Alberta. The topography throughout BMA 3 ranges from rugged and mountainous with subalpine and alpine regions in the west to foothills and plains in the east. The study area includes subalpine forest and boreal-cordilleran transition zones, characterized by complex vegetation structure (Moss, 1955). The landscape is heterogeneous, which influences resource availability for grizzly bears (Denny et al., 2018), as a result of widespread resource extraction activities that have increased substantially in the past few decades (Linke et al., 2013). Anthropogenic activities include forestry, oil and gas exploration, and mining, serviced by a large network of roads and seismic lines (Nielsen et al., 2006). Apart from JNP, there are various other provincial parks and protected areas throughout the study area, including multiple Provincial Recreation Areas, which exclude resource development and allow for recreational use. Additionally, there are two Wildland Provincial Parks, which provide remote access backcountry recreation, and a small Ecological Reserve, where foot access only is permitted.



**Figure 5:** Study area in west-central Alberta, showing the grid cells where sampling occurred, parks and protected areas, coal mines, forest management areas (FMAs), highways (which includes secondary roads), service roads, and local communities.

### 3.2.2 Field methods

Site set-up took place between May 25 and June 1 in 2004 and between May 27 and June 4 in 2014. Once sites were established, grizzly bear hair collection took place over the course of four 14-day sampling sessions. The area was surveyed by fRI Research as part of grizzly bear DNA inventory studies, which included 180 cells in 2004 and 197 cells in 2014. Cells that were sampled in both years were included in this study, resulting in 148 49 km<sup>2</sup> cells. Barbwire corrals were built around trees, surrounding a bait pile made of woody debris, which was baited with a scent lure. For detailed description of site selection processes and field methods, see section 2.2.2, Boulanger et al. (2005) and Stenhouse et al. (2015).

### 3.2.3 Data

Our analysis includes grizzly bear occupancy probabilities, grizzly bear density estimates, and landscape variables in 148 49-km<sup>2</sup> grid cells. First, occupancy probabilities were developed (see Chapter 2) using single-season occupancy models (MacKenzie et al., 2002), which utilized grizzly bear hair snag samples as presence/absence data separately for males and females. Second, male and female grizzly bear density estimates, developed by Boulanger et al. (2018) using the same hair-snag data set, were included for grid cells that matched the occupancy estimates. Spatially explicit mark-recapture methods (Efford, 2004, 2011; Efford et al., 2004) were used to model movements and detection probabilities for unique bears with repeated detections, allowing for the estimation of home range centers (Boulanger et al., 2018). Density surface models were then fit using mask points (i.e., systematic points that cover the areas that may contain home range centers of sampled individuals) as a function of resource selection function (RSF) habitat values (Nielsen et al., 2006) and risk (Nielsen, Herrero, et al., 2004) to estimate density across the landscape (Boulanger et al., 2018).

Landscape variables used in this analysis were generated and provided by fRI Research using the Alberta Biodiversity Monitoring Institute (ABMI) Human Footprint Inventory and the Alberta Application Dispositions (DIDS). They include cutblocks (of all ages), mines (open-pit coal), pipelines and well sites, all disturbance (cutblocks, mines, pipelines, and well sites combined), roads, and mean terrain ruggedness index (TRI). All disturbance variables are measured in percent area of the grid cell, with the exception of roads, which are measured in density (km/km<sup>2</sup>). Mean TRI was derived (Riley, 1999) using data from the Canadian Digital Elevation Model (CDEM) from Natural Resources Canada, and was included based on its influence on grizzly bear occupancy observed in Chapter 2.



### 3.2.4 Statistical analysis

To compare spatial patterns of grizzly bear occupancy and density from 2004 and 2014, we examined patterns of spatial autocorrelation of each parameter in BMA 3. Spatial autocorrelation, the measure of similarity among values across geographic space, is commonly observed in ecology at various scales (Legendre, 1993). Global measures of spatial autocorrelation identify general patterns of positive (i.e., clustered) and negative (i.e., dispersed) spatial autocorrelation in a study area, while local measures of spatial autocorrelation identify clusters (i.e., similar values) and outliers (i.e., dissimilar values) among feature attributes based on spatial relationships (Anselin, 1995). For this study, the global and local Moran's I statistics were used to quantify patterns of spatial autocorrelation in grizzly bear occupancy and density using the *spdep* package (version 1.1.5; Bivand, 2015). Spatial neighbourhoods were defined using Queen's case adjacency (i.e., the eight neighbouring contiguous cells) of the grid cells.

The global Moran's I statistic, a commonly used global measure of spatial autocorrelation for quantitative or continuous variables, was calculated to provide a single index of positive and negative patterns of spatial autocorrelation in both abundance and density estimates (Diniz-Filho et al., 2003). The local Moran's I, a local indicator of spatial association (LISA; Anselin, 1995), was calculated to identify clusters and outliers of occupancy and density estimates. Clusters are areas where values are similar among neighbours, and can be defined as either high-high (HH), where cells of high occupancy/density are surrounded by cells of high occupancy/density, or low-low (LL), where cells of low occupancy/density are surrounded by cells of low occupancy/density. Spatial outliers are cells surrounded by dissimilar values and indicate heterogeneous patterns of occupancy and density at local scales. Spatial outliers are defined as either high-low (HL), where cells with high occupancy/density are surrounded by cells with low occupancy/density, or low-high (LH), where low occupancy/density are surrounded by cells with high occupancy/density. Significance of the Moran's I statistics were

tested using 999 Monte Carlo permutations. This approach determines if Moran's I value is statistically different from a spatially random pattern (Besag & Diggle, 1977).

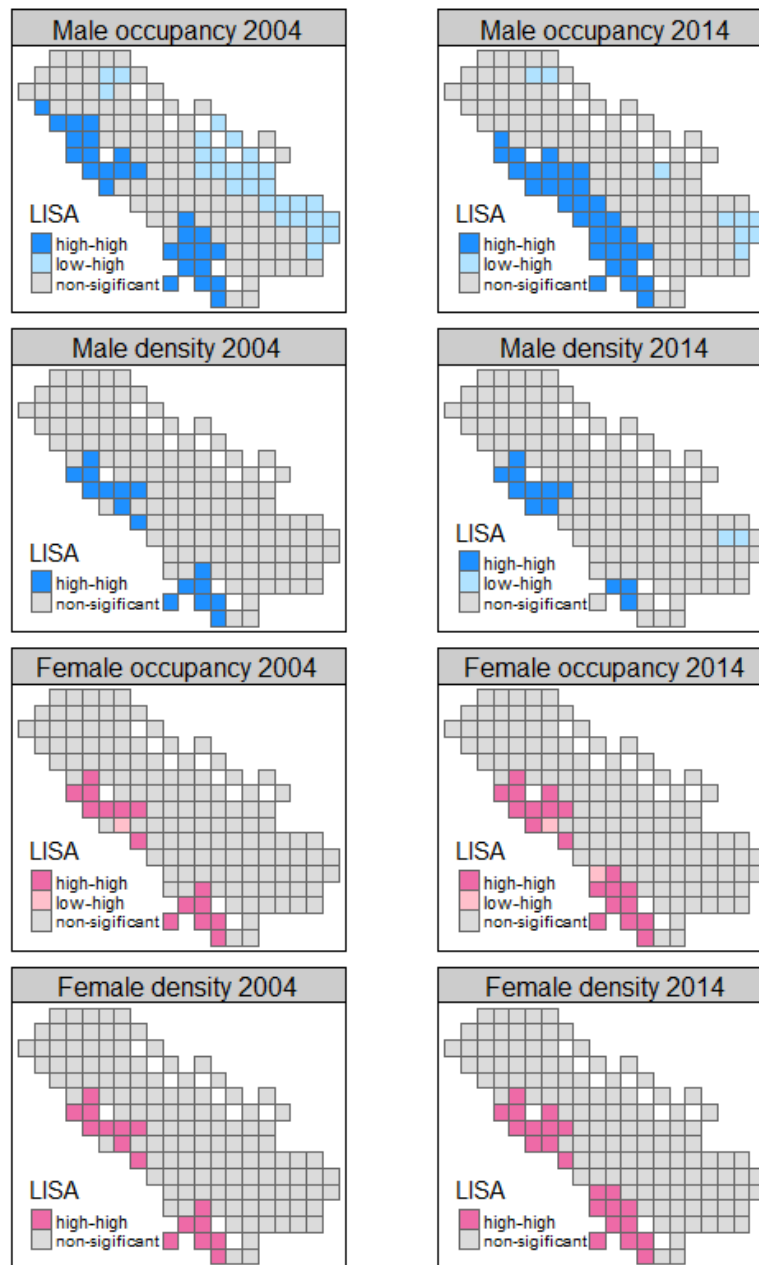
A Mann-Whitney U test was used to compare the mean values of the disturbance and landscape variables among the local Moran's I spatial cluster and outliers. Finally, the Wilcoxon signed-rank test, a non-parametric alternative to the paired Students t-test (McDonald, 2014), and Levene's test (1960) were used to compare the mean and variance of disturbance values from 2004 and 2014. Combined, the statistical tests provide evidence of spatial differences in landscape processes associated with spatial patterns of grizzly bear occupancy and density.

### **3.3 Results**

#### **3.3.1 Spatial autocorrelation**

The global Moran's I statistic showed significant spatial autocorrelation for both occupancy and density of grizzly bears in BMA 3. Specifically, male occupancy exhibited relatively strong positive autocorrelation in both 2004 and 2014 ( $I=0.69$ ,  $p<0.05$ ; and  $I=0.79$ ,  $p<0.05$  respectively), and male density exhibited moderate positive spatial autocorrelation in both 2004 and 2014 ( $I=0.44$ ,  $p<0.05$ ; and  $I=0.44$ ,  $p<0.05$  respectively). Female occupancy exhibited moderate positive spatial autocorrelation in 2004 and 2014 ( $I=0.56$ ,  $p<0.05$ ; and  $I=0.59$ ,  $p<0.05$  respectively), as well as female density ( $I=0.46$ ,  $p<0.05$ ; and  $I=0.61$ ,  $p<0.05$  respectively). The majority of the study area has relatively local homogenous occupancy probabilities and densities, shown by the grey grid cells in Figure 6. The local Moran's I revealed patterns of positive spatial autocorrelation (e.g., HH clusters) for both male and female occupancy and density, primarily in the western portion of the study area (Figure 6). There were few spatial outliers overall (e.g., LH cells), with the exception of male occupancy in 2004 and 2014. Spatial outliers for male grizzly bear occupancy (in 2004 and 2014) and density (in 2014 only) all occurred along the eastern edge of the study area whereas spatial outliers for female

occupancy (in 2004 and 2014) occurred adjacent to the HH cluster. No spatial outliers were found for male density (in 2004) or female density (in 2004 or 2014).

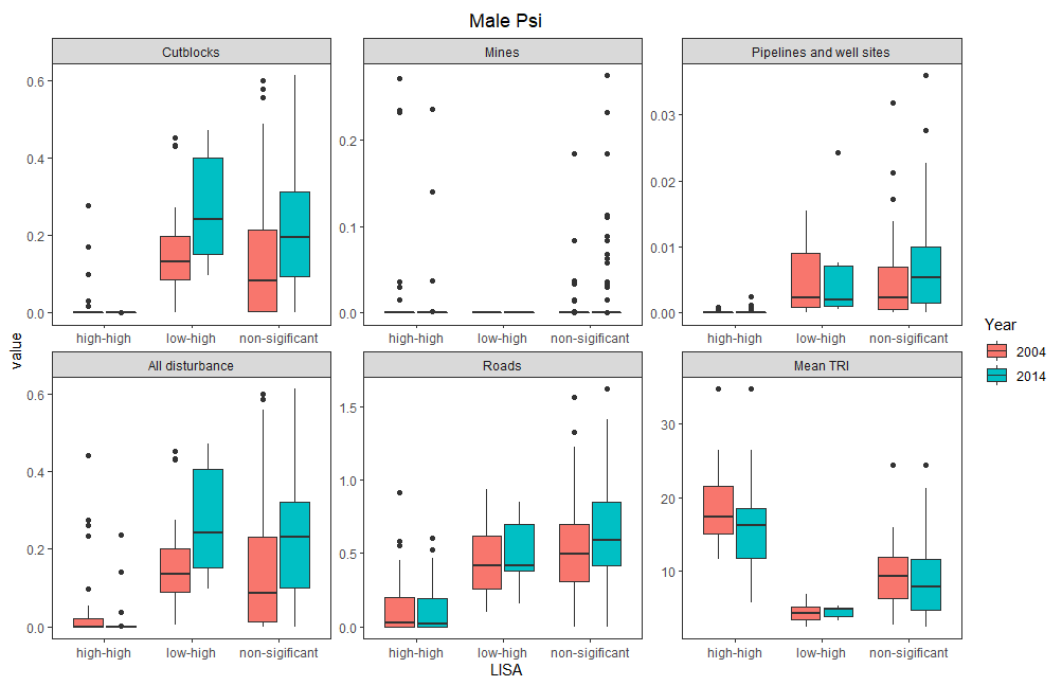


**Figure 6:** Spatial clusters of male and female grizzly bear occupancy and density in BMA 3 for 2004 and 2014. High-high indicates spatial clusters of similar values of high occupancy or density, low-high indicates spatial outliers with low values of occupancy or density that are surrounded by areas of high values, and non-significant indicates grid cells that have no significant spatial autocorrelation with neighbouring grid cells. White cells indicate areas where no sampling was conducted.

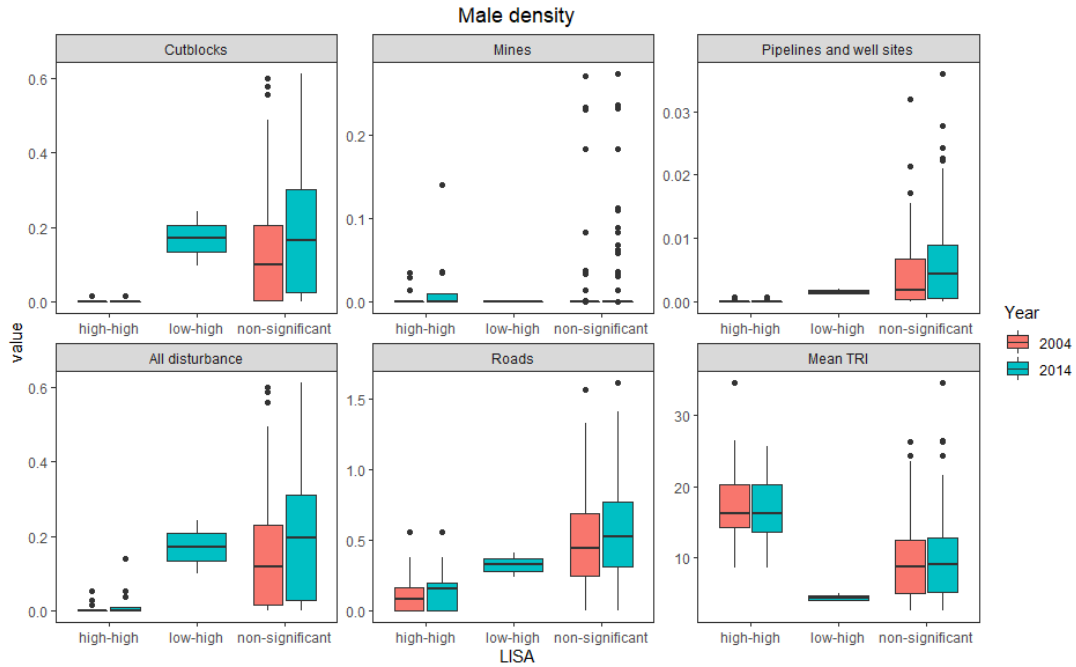
Results indicate that the areal extent of disturbance is lower in HH clusters of grizzly bear occupancy compared to LH and non-significant cells. Mann-Whitney U tests indicate that in clusters of HH grizzly bear occupancy, cutblock percent cover is statistically lower compared to non-significant cells for males (Figure 7) and females (Figure 9) in 2004 and 2014 ( $p < 0.05$ ; Table 6), and statistically lower compared to LH cells for males in 2004 and 2014 and females in 2014 ( $p < 0.05$ ). Cutblock percent cover is also statistically lower in clusters of HH grizzly bear density compared to non-significant cells for males (Figure 8) and females (Figure 10) in 2004 and 2014 ( $p < 0.05$ ), and statistically lower compared to LH cells for males in 2014 ( $p < 0.05$ ). Mine percent cover is statistically lower in clusters of HH bear occupancy compared to LH cells for males in 2004 ( $p < 0.05$ ). Pipeline and well site percent cover is statistically lower in HH clusters of bear occupancy compared to non-significant cells for males and females in 2004 and 2014 ( $p < 0.05$ ), and statistically lower compared to LH cells for males in 2004 and 2014 ( $p < 0.05$ ). Pipeline and well site percent cover is also statistically lower in clusters of HH bear density compared to non-significant cells for males and females in 2004 and 2014 ( $p < 0.05$ ), and statistically lower compared to LH cells for males in 2014 ( $p < 0.05$ ). All disturbance is statistically lower in clusters of HH bear occupancy compared to non-significant cells for males and females in 2004 and 2014 ( $p < 0.05$ ), and statistically lower compared to LH cells for males in 2004 and 2014 ( $p < 0.05$ ). All disturbance is also statistically lower in clusters of HH bear density compared to non-significant cells for males and females in 2004 and 2014 ( $p < 0.05$ ), and statistically lower compared to LH cells for males in 2014 ( $p < 0.05$ ). Road density is statistically lower in clusters of HH bear occupancy compared to non-significant cells for males and females in 2004 and 2014 ( $p < 0.05$ ), and statistically lower compared to LH cells for males in 2004 and 2014 ( $p < 0.05$ ). Road density is also statistically lower in clusters of HH bear density compared to non-significant cells for males and females in 2004 and 2014 ( $p < 0.05$ ).

Contrary to the disturbance features, mean TRI is typically highest in areas of HH grizzly bear occupancy and density, and higher in non-significant cells compared to LH cells. Mean TRI

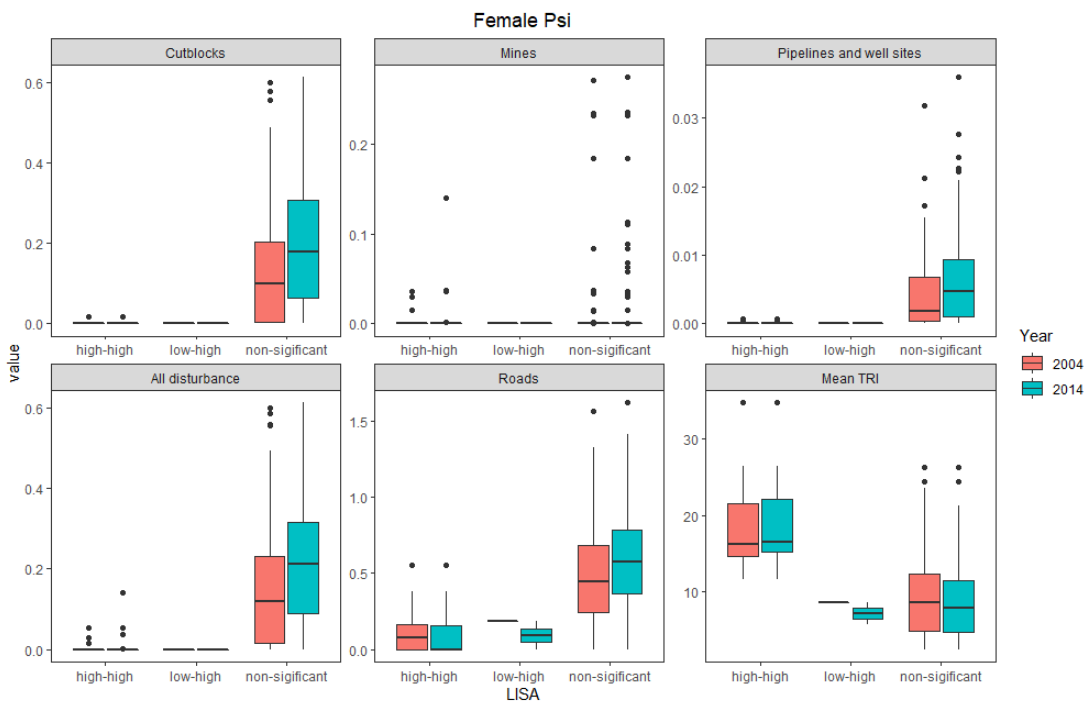
is statistically higher in HH clusters of grizzly bear occupancy compared to non-significant cells for males and females in 2004 and 2014 ( $p<0.05$ ), and statistically higher compared to LH cells for males in 2004 and 2014 and females in 2014 ( $p<0.05$ ). Additionally, mean TRI was significantly higher in non-significant cells compared to LH cells for males in 2004 and 2014 ( $p<0.05$ ). Similarly, mean TRI is statistically higher in clusters of HH bear density compared to non-significant cells for males and females in 2004 and 2014, and statistically higher compared to LH cells for males in 2014 ( $p<0.05$ ).



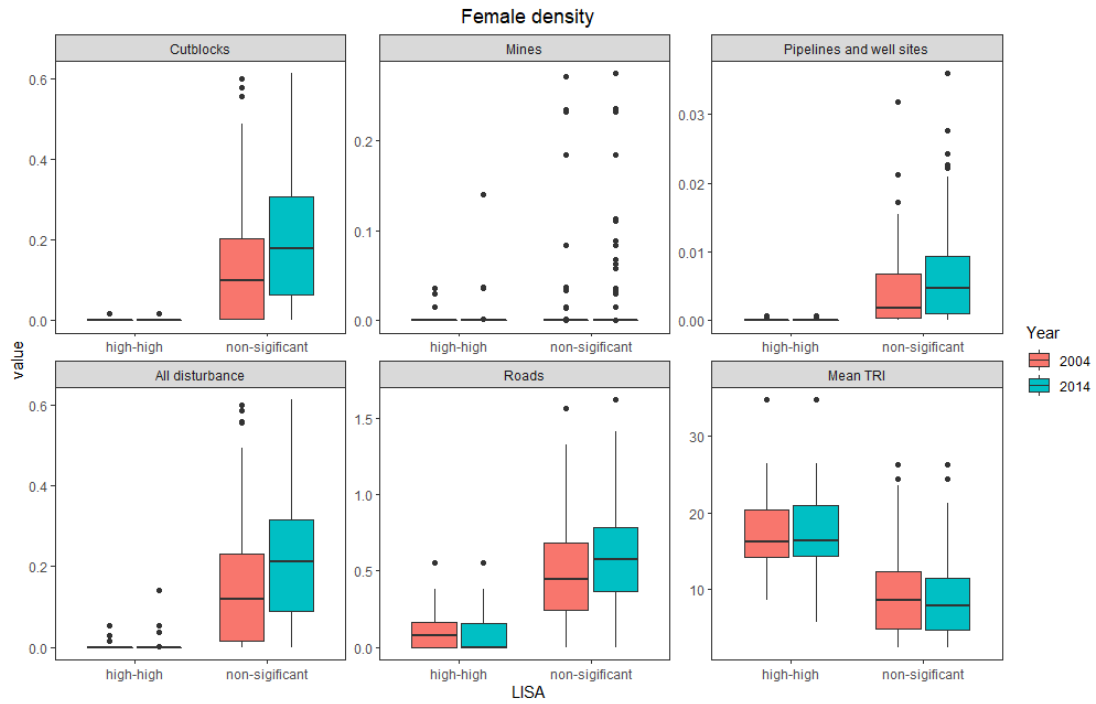
**Figure 7:** Values of disturbance variables and mean terrain ruggedness index (TRI) within LISA statistic clusters compared to those in spatial outliers and non-significant grid cells for male grizzly bear occupancy.



**Figure 8:** Values of disturbance variables and mean terrain ruggedness index (TRI) within LISA statistic clusters compared to those in spatial outliers and non-significant grid cells for male grizzly bear density.



**Figure 9:** Values of disturbance variables and mean terrain ruggedness index (TRI) within LISA statistic clusters compared to those in spatial outliers and non-significant grid cells for female grizzly bear occupancy.



**Figure 10:** Values of disturbance variables and mean terrain ruggedness index (TRI) within LISA statistic clusters compared to those in spatial outliers and non-significant grid cells for female grizzly bear density.

**Table 6:** Results of the Mann-Whitney U test results to determine if disturbance and terrain variables are significantly different inside LISA clusters, in outlier cells, and non-significant cells. Results are separated into male grizzly bear occupancy and density, and female grizzly bear occupancy and density.

	Male grizzly bear occupancy											
	2004						2014					
	HH & LH		HH & non-significant		LH & non-significant		HH & LH		HH & non-significant		LH & non-significant	
	W	p	W	P	W	p	W	p	W	p	W	p
<b>Cutblocks</b>	68	<0.05	451	<0.05	1453	0.15	0	<0.05	115.5	<0.05	562	0.27
<b>Mines</b>	462	<0.05	1342.5	0.08	1106	0.08	162	0.28	1569	0.61	382.5	0.19
<b>Pipelines &amp; wells</b>	37	<0.05	288	<0.05	1333.5	0.51	13	<0.05	258.5	<0.05	376.5	0.38
<b>All disturbance</b>	114	<0.05	535	<0.05	1437.5	0.19	5	<0.05	114	<0.05	535	0.41
<b>Roads</b>	117	<0.05	365	<0.05	1039	0.21	31	<0.05	236.5	<0.05	535	0.41
<b>Mean TRI</b>	756	<0.05	2265	<0.05	262	<0.05	288	<0.05	2812	<0.05	190	<0.05

	Male grizzly bear density											
	2004						2014					
	HH & LH		HH & non-significant		LH & non-significant		HH & LH		HH & non-significant		LH & non-significant	
	W	p	W	P	W	p	W	p	W	p	W	p
<b>Cutblocks</b>	-	-	246	<0.05	-	-	0	<0.05	178.5	<0.05	134	0.93
<b>Mines</b>	-	-	1104.5	0.29	-	-	16	0.42	922	0.78	112	0.6
<b>Pipelines &amp; wells</b>	-	-	245	<0.05	-	-	0	<0.05	198	<0.05	91.5	0.49
<b>All disturbance</b>	-	-	222.5	<0.05	-	-	1	<0.05	231	<0.05	120	0.87
<b>Roads</b>	-	-	280.5	<0.05	-	-	3	0.11	226.5	<0.05	69	0.26
<b>Mean TRI</b>	-	-	1787	<0.05	-	-	24	<0.05	1306	<0.05	43	0.11



Female grizzly bear occupancy												
	2004						2014					
	HH & LH		HH & non-significant		LH & non-significant		HH & LH		HH & non-significant		LH & non-significant	
	W	p	W	P	W	p	W	p	W	p	W	p
<b>Cutblocks</b>	8	1	232	<0.05	14	0.18	21	0.87	181.5	<0.05	17	<0.05
<b>Mines</b>	9	0.75	1047	0.24	57.5	0.77	24	0.55	1274	0.54	104	0.58
<b>Pipelines &amp; wells</b>	9	0.75	234	<0.05	11	0.16	24	0.55	201.5	<0.05	15	<0.05
<b>All disturbance</b>	10.5	0.53	216	<0.05	6.5	0.13	28	0.32	169	<0.05	6	<0.05
<b>Roads</b>	3	0.37	262.5	<0.05	18	0.22	17.5	0.8	163	<0.05	10	<0.05
<b>Mean TRI</b>	15	0.13	1725	<0.05	62	0.98	40	<0.05	2261	<0.05	101	0.7

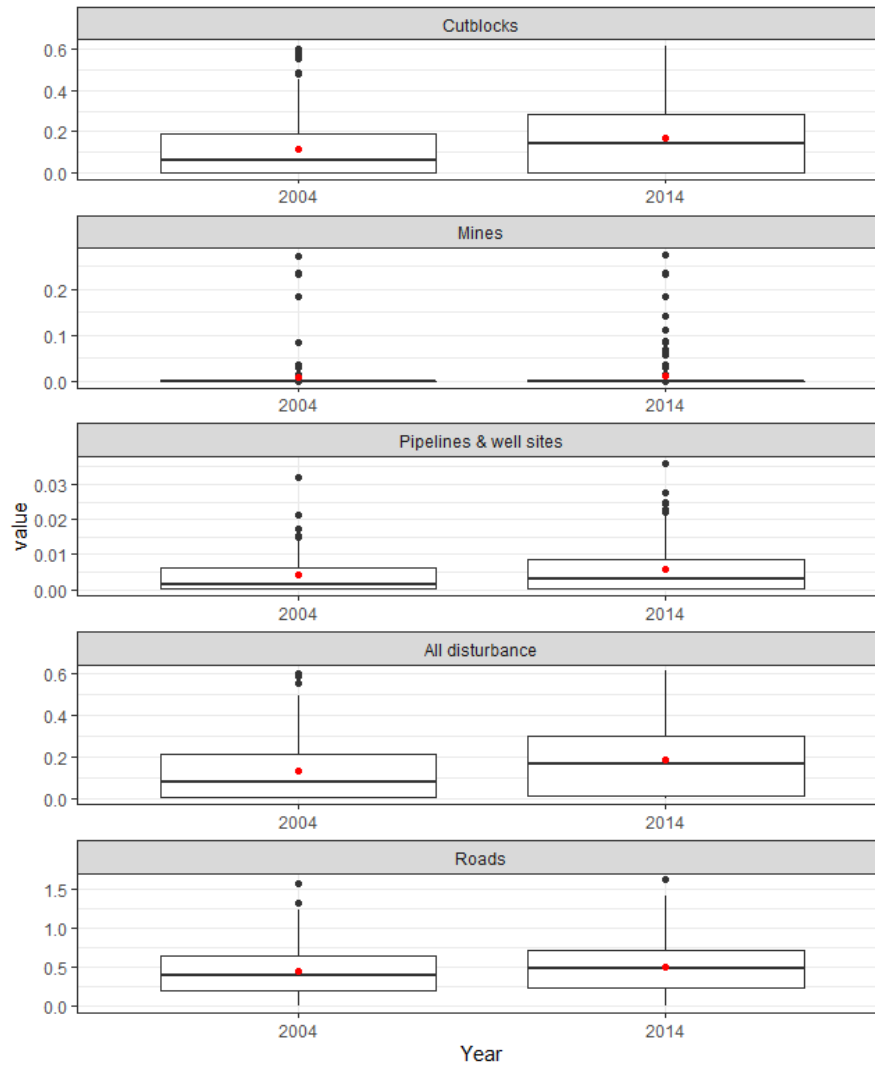
  

Female grizzly bear density												
	2004						2014					
	HH & LH		HH & non-significant		LH & non-significant		HH & LH		HH & non-significant		LH & non-significant	
	W	p	W	P	W	p	W	p	W	p	W	p
<b>Cutblocks</b>	-	-	246	<0.05	-	-	-	-	198.5	<0.05	-	-
<b>Mines</b>	-	-	1104.5	0.29	-	-	-	-	1379	0.67	-	-
<b>Pipelines &amp; wells</b>	-	-	245	<0.05	-	-	-	-	216.5	<0.05	-	-
<b>All disturbance</b>	-	-	222.5	<0.05	-	-	-	-	175	<0.05	-	-
<b>Roads</b>	-	-	280.5	<0.05	-	-	-	-	173	<0.05	-	-
<b>Mean TRI</b>	-	-	1787	<0.05	-	-	-	-	2362	<0.05	-	-

### 3.3.2 Disturbance change

Cutblocks exhibited a significant change in mean percent area ( $W=9355$ ,  $p<0.05$ ) which increased from 0.12 in 2004 to 0.17 in 2014, as well as all disturbance percent cover ( $W=9182$ ,

$p < 0.05$ ) which increased from 0.13 in 2004 to 0.18 in 2014 (Figure 11). The percent area of mines did not increase from 2004 to 2014 ( $W=10773.5$ ,  $p=0.26$ ) and had a mean percent area of 0.01 in both years. However, it is important to note that data used is based off Mineral Surface Lease boundaries, rather than the actual footprint of disturbance. Considering that both the Cheviot and the Coal Valley mines had expansions within the time period of this study, it is likely that the footprint of these operations was not fully captured by the data. Pipelines and well site percent area showed no significant difference in mean values ( $W=9993.5$ ,  $p=0.09$ ), and increased slightly from 0.0058 in 2004 to 0.0065 in 2014. Similarly, mean road density increased from  $0.45\text{km}/\text{km}^2$  in 2004 to  $0.51\text{km}/\text{km}^2$  in 2014, although the change was not significant ( $W=9977$ ,  $p=0.09$ ) (Figure 3). The Levene's test indicated unequal variances between 2004 and 2014 for cutblock percent cover ( $F=4.7$ ,  $p=0.064$ ), mine percent cover ( $F=2.6$ ,  $p=0.405$ ), pipeline and well site percent cover ( $F=4.6$ ,  $p=0.122$ ), all disturbance percent cover ( $F=4.6$ ,  $p=0.055$ ), and road density ( $F=0.47$ ,  $p=0.501$ ). For all disturbance variables, the variance was higher in 2014 compared to 2004.



**Figure 11:** Values of disturbance features in 2004 and 2014 per cell in BMA 3. Cutblocks, mines pipelines and well sites and all disturbance are measured in percent area and roads are measured in density ( $\text{km}/\text{km}^2$ ). Mean values are indicated by the red dot.

### 3.4 Discussion

This chapter explored how grizzly bear occupancy and density differ spatially between two time periods (i.e., a decade) to help inform monitoring of grizzly bears in Alberta. Our results show that both occupancy and density were moderately to strongly positively auto-correlated for both males and females, meaning that overall, as occupancy and density increase, higher values of occupancy and density are seen in neighbouring cells (i.e., cells sharing a border,

including diagonals). Occupancy and density had similar patterns, exhibiting a random distribution throughout the vast majority of the study area with clustering of high values for both males and females in the western portion of the study area, directly adjacent but outside of Jasper National Park (JNP), where TRI is higher and disturbance is limited. Clustering was demonstrated in both years, and for both male and female occupancy and density, a HH cluster occurred within and around the cells containing portions of the Whitehorse Wildland area. The Whitehorse Wildland area shares its border with JNP and is mountainous compared to the foothills to the east (Nielsen et al., 2006). Despite the presence of humans throughout the area, vehicle access is limited and there is lower recreational use compared to the neighbouring Banff National Park, meaning lower human presence throughout the park (Nielsen, et al., 2004a; 2006). Past research has highlighted the area as important for grizzly bear conservation in Alberta, which is classified as a core conservation area, meaning that the area has high grizzly bear occupancy and low mortality risk (Nielsen et al., 2006). Our research corroborates these findings, showing that grizzly bear occupancy and density are higher in the Whitehorse Wildland area compared to the surrounding landscape, which suggests that it could be a potential refuge for wildlife in the region and highlights the importance of maintaining and managing these core grizzly bear areas and surrounding habitat.

We also explored how disturbance features and terrain ruggedness differed in clusters of high occupancy and density (i.e., HH) compared to areas with random distributions (i.e., non-significant cells). We found that cutblock, pipeline and well site, and all disturbance percent cover, as well as road density, were all significantly lower in clusters of HH grizzly bear occupancy and density in both 2004 and 2014. These values were all very close to zero with the exception of a few outliers. Mean TRI was significantly higher in HH clusters compared to areas outside of the clusters for both years. Overall, male and female grizzly bear occupancy and density follow the same pattern, where clusters occur in areas with low disturbance and high TRI, suggesting that they are responding positively to terrain ruggedness and negatively to

disturbance. The HH clusters all occur outside or along the western edge of the Forest Management Area boundaries within BMA 3 in lands that are not open to any forest harvesting, further highlighting the importance of areas lacking anthropogenic disturbance for grizzly bear persistence. Outside of these clusters, we are seeing grizzly bears more broadly across the landscape, however, occupancy and density are randomly distributed across the vast majority of the study area, where various disturbance features create a heterogeneous landscape, which has been shown to be an important factor for grizzly bear habitat use (Denny et al., 2018b). From an east to west gradient, occupancy and density increases towards mountainous areas with low disturbance.

Food availability is an important predictor of grizzly bear habitat selection (Nielsen et al., 2010) and as anthropogenic disturbance has intensified throughout grizzly bear habitat, there are more opportunities to obtain resources (Nielsen et al., 2004b; Munro et al., 2006; Larsen et al., 2019). Despite a population that doubled from 2004 to 2014 (Stenhouse et al., 2015), recent research suggests that BMA 3 is still well below carrying capacity, and that food resources are significantly more abundant throughout the eastern portion of the study area compared to west where grizzly bear occupancy and density is high (McClelland et al., 2021). While the grizzly bear population doubled in size (Stenhouse et al., 2015), the highest observed density values remain aggregated in similar patterns. Terrain ruggedness influences the placement of roads (Roever et al., 2008), which in turn can limit human access (Roever et al., 2010). Despite the potential for backcountry recreational access (e.g., in the Whitehorse Wildland area), areas of HH grizzly bear occupancy and density have high mean TRI values and essentially no roads, which ultimately means less human presence and lower mortality risk. Although Chapter 2 results did not show a relationship between road density and grizzly bear occupancy, road density has been shown to have a negative relationship with grizzly bear density (Boulanger et al., 2014; Lamb et al., 2018).

The link between grizzly bear mortality and human access is well documented (Benn & Herrero, 2001; Nielsen et al., 2004; Schwartz et al., 2006, Boulanger & Stenhouse), as well as changes in movements, distribution, and behaviour in response to roads (Roever et al., 2008a & 2008b; Graham et al., 2010; Northrup et al., 2012). Roads have also been shown to impact stress (Bourbonnais et al., 2013), body condition, and survival of grizzly bears within BMA 3 (Boulanger et al., 2013; Bourbonnais et al., 2014), and have the potential to genetically isolate populations (Proctor et al., 2012). Previous research has suggested that grizzly bears select habitat for security by limiting exposure to roads at the home range scale (Mattson et al., 1987; McLellan & Shackleton, 1988; Bourbonnais, 2018), and that grizzly bear density is impacted by avoidance of human-caused mortality risk rather than habitat type (Ciarniello et al., 2007). Our results indicate similar, broad-scale patterns of preference for areas of low disturbance and limited human access, where food resources are likely widely available.

At finer spatial scales, roads are selected by grizzly bears for ease of movement (Roever et al., 2010) and food availability (Roever et al., 2008a; Bourbonnais, 2018). Selection for roads may be related to selection of cutblocks (Roever et al., 2010), as cutblocks provide various bear foods (Nielsen et al., 2004b; Stewart et al., 2012; Larsen et al., 2019). Additionally, grizzly bears have been shown to select other disturbance related to resource extraction, such as pipelines and well sites (Laberee et al., 2014; Sorensen et al., 2021), and reclaimed mine sites (Cristescu et al., 2016). Specifically, edge habitat resulting from these resource extraction activities presents an opportunity for increased food availability, including berries, herbaceous forage, and ungulates, in Alberta (Forman, 1999; Ries et al., 2004). Grizzly bear food availability (including berries, herbaceous forage, and ungulates) has widely been correlated to edge habitat throughout Alberta (Nielsen et al., 2004 & 2017; Munro et al., 2006; Roever et al., 2008a; Stewart et al., 2012; Bourbonnais, 2018). As resource extraction activities continue within grizzly bear range, there is potential for increased grizzly bear food production; however, access and selection of these resources come with increased mortality risk for bears.

Ecological traps occur when selection for habitat quality results in reduced fitness (Dwernychuk & Boag, 1972). Grizzly bears have been shown to be susceptible to ecological traps in areas of disturbance that provide food resources but also increase risk of human-caused mortality (i.e., a mortality sink; Nielsen et al., 2006; Northrup et al., 2012; Lamb et al., 2017). To reduce mortality risk, the Alberta government has set road density targets of 0.6 km/km<sup>2</sup> in core grizzly bear conservation areas and 1.2 km/km<sup>2</sup> in secondary conservation areas (Nielsen et al., 2009). More recently, the Alberta government has mentioned managing road densities in secondary conservation areas to 0.75 km/km<sup>2</sup> according to their 2016 Draft Grizzly Bear Recovery Plan (Alberta Environment and Parks, 2016) based on research suggesting that road densities >75 km/km<sup>2</sup> are associated with sink habitats, above which female grizzly bear survival decreases (Boulanger & Stenhouse, 2014). The core threshold value is consistent with our results in areas of HH grizzly bear occupancy and density for both males and females where road densities were generally below 0.6 km/km<sup>2</sup>. It is estimated that within secondary grizzly bear habitat in Alberta, 57% has either moderate (0.75-1.25) or high road densities (>1.25) (Boulanger & Stenhouse, 2014). This is consistent with our results, which show road densities occurring above 1.25 throughout non-significant cells east of HH clusters (i.e., in secondary conservation areas).

Maintaining the road density thresholds is particularly important as grizzly bears are expanding into these riskier environments, shown by the changes in occupancy spatial patterns demonstrated in Chapter 2. Although we observed no statistically significant increase in road densities, road densities have increased and, there was a significant increase in cutblock percent area and all disturbance percent area. As these activities continue, so does the risk of human-caused mortality and despite a growing population, grizzly bear survival rates are strongly influenced by human development (Benn & Herrero, 2001b; Boulanger & Stenhouse, 2014; Lamb et al., 2017). In areas of high habitat quality with availability of important food resources and with road densities that surpass 0.6 km/km<sup>2</sup>, evidence shows that the detrimental

effects of roads on grizzly bears can be mitigated by managing motorized access (Proctor et al., 2019). This involves decommissioning and reducing vehicle access on roads, and has particular value for threatened populations and if utilized at scales to benefit females (Proctor et al., 2019). Additionally, in the context of these threats, it is important to continue to monitor grizzly bear populations in regions where resource development occurs.

Occupancy can be an appropriate proxy for abundance in certain situations, for example when sampling units are approximately the same size as territories, and where abundance is low (Nielsen et al., 2005; Negrões et al., 2010; Clare et al., 2015; MacKenzie et al., 2017). In these scenarios occupancy can provide insight into population abundance, however, this study has shown that for grizzly bears in BMA 3, occupancy does not equate perfectly with abundance. When there is a non-linear relationship between occupancy and density, occupancy is undiscerning in high density areas, and fails to account for individual space use (Clare et al., 2015), which is often associated with habitat quality and resource availability (Gill et al., 2001; Freckleton et al., 2006). Spatial patterns of grizzly bear occupancy and density show similar concentrations in areas with complex terrain and limited human presence. However, population abundance is not captured by occupancy estimates alone. Grizzly bears have large overlapping ranges, particularly in areas with widely distributed and extensive resources including food and shelter from risk and heat (Stirling & Derocher, 1990; Waller & Mace, 1997; Pigeon et al., 2016). A non-positive AO relationship can also result from low colonization ability (Freckleton et al., 2005), and despite knowing that grizzly bears are colonizing previously unoccupied eastern portions of the study area (Chapter 2), it is unknown if bears are persisting in those regions in the face of high mortality risks.

Occupancy modelling incorporating multi-season observational data is increasingly used to quantify habitat dynamics and changes in occupancy (i.e., population vital rates, or colonization and local extinction) simultaneously (Martin et al., 2010; Mackenzie et al., 2011; Falke et al., 2012). This can not only help quantify the rate of change in habitat occupancy as a



function of landscape change, but it can also help to project future changes in occupancy (MacKenzie et al., 2017). With sampling occurring a decade apart in BMA 3, rates of colonization and extinction are not overly meaningful at such a broad temporal scale. Because of this, we were unable to identify spatial-temporal occupancy patterns that could be occurring at shorter time intervals. More frequent monitoring would allow for investigations of colonization and local extinctions of grizzly bears to allocate conservation efforts in a timely manner. Additionally, occupancy was predicted in Chapter 2 using proxies for food availability (e.g., forest edge density, and shrub and herb cover); however, these may not directly translate to resources available on the landscape. Food availability is important for predicting occupancy-abundance in grizzly bears (Nielsen et al., 2010), and, selection for resources can occur at finer spatial scales than the 49 km<sup>2</sup> grid cell used for this research.

Positive OA relationships are of particular value in large-scale population dynamics and can be instrumental for monitoring populations (Freckleton et al., 2006). However, there is still value in using habitat occupancy for population monitoring in the absence of an OA relationship. For example, this research has shown that changes in grizzly bear abundance are likely not captured by occupancy modelling; however, the use of an occupancy framework provides insight on changes in spatial-temporal patterns of species distribution. Additionally, our results show that spatial patterns of grizzly bear occupancy are comparable to spatial patterns of grizzly bear density. This is particularly useful for monitoring species that occur at the periphery of their geographic range, such as the BMA 3 population that occurs on the edge of remaining grizzly bear range in Canada. Additionally, grizzly bears have large home ranges and are elusive and solitary outside of breeding season (Mace & Waller, 1997; Graham & Stenhouse, 2014), which makes them a good candidate for occupancy modelling as a means for monitoring their distribution and presence in a given landscape or habitat given appropriate spatial sampling scale (Lindberg & Schmidt, 2008). As OA relationships can change depending on spatial and temporal sampling scales (Steenweg et al., 2018), there is opportunity for further research to

better understand the relationship between occupancy and density in grizzly bears. Our research demonstrates that grizzly bear occupancy and density follow similar spatial patterns in BMA 3 and despite changes in habitat occupancy probabilities not being reflective of changes in population size and resulting density, occupancy can still help identify spatial patterns of relative density.

The grizzly bear population of BMA 3 nearly doubled in size from 2004 to 2014, increasing from 36.0 (14.4 males and 21.6 females) to 71.3 (37.6 males and 33.7 females) (Stenhouse et al., 2015). However, this increase was not reflected by changes in occupancy probabilities for the region, which decreased from 0.35 in 2004 to 0.34 in 2014, but rather by the spatial change in occupancy pattern, with previously unoccupied cells in the east becoming colonized. Male occupancy decreased from 0.37 to 0.27 and female occupancy decreased from 0.17 to 0.12, whereas estimated average male density per cell increased from 1.6 to 4.6, and average female density per cell increased from 2.3 to 3.6. A lack of relationship between occupancy and density is likely the result of non-random distribution throughout the study area and overlapping ranges of conspecifics resulting from ample food resource availability.

This study supports existing research that suggests grizzly bears tend to utilize habitat with complex terrain and limited disturbance. They are more likely to occur in higher densities in areas with low human footprint, suggesting that spatial dynamics of occupancy and density are influenced by human access. Throughout the vast majority of the study area, where disturbance is common and terrain complexity is low, grizzly bear occupancy and density occur in a random distribution. The western portion of the study area, directly adjacent to Jasper National Park and containing the Whitehorse Wildland area, shows concentrated occupancy and density. These results highlight the importance of maintaining and managing these areas for grizzly bear persistence as they expand into areas of greater anthropogenic use with a higher risk of human caused mortality.

Habitat occupancy is a useful state variable for monitoring grizzly bear populations in Alberta based on the observed similarities in spatial patterns of occupancy and density. Occupancy can be used to explore geographic changes in the distribution of populations and help mitigate potential risks that increase the likelihood of extirpation or extinction (Harris & Pimm, 2008). Over large spatial scales and fine temporal scales, occupancy modelling can identify small changes in population trends (Steenweg et al., 2016a), and is a useful tool for monitoring elusive species such as large carnivores (Long & Zielinski, 2008). Given ongoing habitat loss from natural resource extraction (Huang et al., 2010), biodiversity loss (McCallum, 2015), and climate change, it is critical to adopt efficient monitoring approaches that can help prioritize conservation efforts (Soule and Kohm, 1989). As a cost-effective alternative to mark-recapture efforts, occupancy modelling provides a robust and flexible framework for monitoring change in wildlife populations.

## Chapter 4

### Conclusions

#### 4.1 Summary of research

Understanding the impacts of anthropogenic disturbances is a major focus in wildlife conservation (Gill et al., 1996; Abbitt et al., 2000; Underhill & Angola, 2000). Advances in occupancy modelling has provided a flexible framework for researchers to investigate anthropogenic impacts on ecological processes (Bailey et al., 2014; MacKenzie et al., 2017). Occupancy modelling is an attractive approach for wildlife monitoring as it can be cost-effective and uses non-invasive sampling methods (e.g., hair snags and increasingly camera traps) (MacKenzie et al., 2002). Occupancy estimates can be used to examine range size, metapopulations dynamics, and geographic distributions, or alternatively as a proxy for abundance estimates (MacKenzie & Nichols, 2004). The positive relationship between occupancy and abundance is a fundamental aspect of ecology (Gaston et al., 2000; Zuckerberg et al., 2009). In many systems, substituting occupancy for abundance is ecologically feasible (Hanski, 1982; Gaston et al., 2000; Blackburn & Gaston, 2004); however, it remains unclear if the relationship between occupancy and abundance is applicable for solitary, wide-ranging species with overlapping ranges.

This research explored the application of occupancy modelling for monitoring a threatened population of grizzly bears (*Ursus arctos*) in Alberta, Canada where there is ongoing anthropogenic disturbance and habitat change. In Chapter 2, changes in occupancy of grizzly bears in the Yellowhead population unit (BMA 3) were quantified using single-season occupancy models to test hypotheses of how anthropogenic disturbance and habitat characteristics influence grizzly bear occupancy dynamics. Spatial patterns of occupancy indicate that grizzly bears are expanding their range in BMA 3, with eastern cells that were unoccupied in 2004 becoming occupied in 2014 (10 additional cells by males and 3 additional

cells by females). Despite spatial patterns indicating an increase in the geographic extent of grizzly bear occupancy, overall occupancy probability decreased for both males and females. However, the central tendency of occupancy probability did not change significantly over a decade.

Two habitat features consistently influenced male and female occupancy in both 2004 and 2014: mean terrain ruggedness index (TRI) and proportion of wetland cover. Grizzly bear occupancy is positively associated with TRI, which has been well documented in Alberta and British Columbia as rugged topography that inhibits human access is positively correlated with grizzly bear detection and habitat selection and use (Apps et al., 2004; Proctor et al., 2015; Apps et al., 2016; Boulanger et al., 2018; Bourbonnais, 2018). Grizzly bear occupancy was found to be negatively associated with proportion of wetland cover, which suggests that grizzly bears may avoid these areas due to a lack of high quality foods and resistance to movement (Nielsen et al., 2004, 2006; Roever et al., 2008). While cutblocks can be associated with grizzly bear selection (Nielsen et al., 2004, 2006), we found a negative association between grizzly bear occupancy (for all bears and males in 2014) and cutblocks, as well as a negative relationship with total anthropogenic disturbance (for males in 2014). While harvested areas are associated with grizzly bear foods (Souliere et al., 2020), many areas with extensive cutblocks are associated with human access and activities (Apps et al., 2004), which may result in increased risk and avoidance of these areas (Gibeau et al., 2002). Additionally, food availability is strongly linked to stand disturbance age, with early seral stages of recovery providing greater abundance of resources (Nielsen et al. 2004; Souliere et al. 2020). Our analysis incorporated a relatively coarse (i.e., 49 km<sup>2</sup>) metric of harvest in a grid cell and finer scale patterns of disturbance age and recovery may be influencing observed occupancy dynamics.

Disturbance variables were only influential in all grizzly bear and male grizzly bear occupancy models suggesting that male occupancy is impacted by anthropogenic disturbance. Other studies have demonstrated avoidance of anthropogenic features by male grizzly bears

compared to females (McLellan & Shackleton, 1988; Roever et al., 2008b; Stewart et al., 2013; Cristescu et al., 2016). The observed differences may reflect learned behaviour among females who use areas with anthropogenic activity, which may reduce risk and competition with male conspecifics (Rode et al., 2006), and may reduce risk of infanticide for females with cubs (Libal et al., 2011; Steyaert et al., 2013; Elfström et al., 2014). However, it should be noted that infanticide has not been readily observed in the Alberta grizzly bear population (Graham & Stenhouse, 2014) and our data did not include offspring information. Alternatively, it is also possible that female grizzly bears are displaced into riskier or lower quality habitat by males (Mattson et al., 1987; Wielgus & Bunnell, 1995; Steyaert et al., 2013).

The influence of anthropogenic disturbance was greater in 2014 compared to 2004, suggesting there is an increasing effect of anthropogenic disturbance on occupancy over time. Even though unique anthropogenic disturbance types (e.g., cutblocks, roads) may not appear to impact wildlife, cumulative effects can have significant influences on individual behaviour and populations (Theobald et al., 1997; Johnson et al., 2005). Here, the cumulative footprint of disturbance (i.e., all disturbance) had a negative influence on occupancy probability, compared to the influence of individual anthropogenic disturbances such as pipelines and mines. Resource development alters the structure of forested landscapes and decreases ecological integrity (Nitschke, 2008), and in areas with cumulative anthropogenic pressures, avoidance behaviour, changes in population dynamics, and altered habitat use and occupancy can be detrimental to wildlife (Erb et al., 2012). Despite the potential for increased food availability resulting from anthropogenically driven landscape heterogeneity (Denny et al., 2018), increasing anthropogenic disturbance has the potential to discourage occupancy.

Abundance estimates from BMA 3 suggest the grizzly bear population nearly doubled from 2004 to 2014 (36.0 to 71.3, respectively; Stenhouse et al., 2015). Despite this increase, Chapter 2 demonstrated a decrease in overall occupancy probability using the same detection data. However, there was no significant changes in mean occupancy and density per grid cell.

To better understand the relationship between occupancy and abundance of grizzly bears in Alberta, spatial patterns of grizzly bear occupancy and density were compared in Chapter 3 using measures of spatial autocorrelation (Anselin, 1995). The local Moran's I statistic revealed a notable cluster of high occupancy and density in the western portion of the study area, where the landscape is more rugged, and lower occupancy and density in the east. The west-east gradient in occupancy is consistent with other research on grizzly bear density in Alberta (Boulanger et al., 2018), and supports the range position hypothesis, which suggests that density and occupancy should decline near the boundaries of a species range (Brown, 1984; Lawton, 1993; Volis & Kark, 1994). Given that the eastern border of BMA 3 is at the geographic limit of grizzly bear range in Canada (Rovang, 2013), lower densities in the east are expected. However, there is a clear distinction between landscape characteristics in clusters of high occupancy and density compared to surrounding habitat.

To further explore relationships identified in Chapter 2, anthropogenic disturbance and topography within identified clusters of grizzly bear occupancy and density were compared to conditions in surrounding cells. Generally, TRI was higher in clusters of high occupancy and density compared to cells outside of clusters, and cutblocks, roads, and pipelines and well site densities were lower. Again, the results are consistent with other research, which demonstrate a positive relationship between grizzly bear distribution and density with increasingly rugged terrain where anthropogenic activities are limited (Apps et al., 2004, 2016; Proctor et al., 2015; Boulanger et al., 2018; Bourbonnais, 2018). This study adds to the body of research that demonstrates avoidance of anthropogenic disturbance by grizzly bears, and more broadly, by wildlife. Specifically, fragmentation resulting from anthropogenic activity and disturbance has been shown to negatively impact occupancy of avian species (Bolger et al., 1991; Boulinier et al., 2001; Hames et al., 2001; Ferraz et al., 2007; Zipkin et al., 2009; Collier et al., 2012) and several mammalian species including sloth bears (Das et al., 2014), tigers (Pillay et al., 2011), tapirs (Rivera et al., 2020), fishers (Fuller et al., 2016), and corsac foxes (Lkhagvasuren et al.,

2016). Anthropogenic pressures not only influences individual species behaviour and habitat use, but can alter predator-prey dynamics by modifying predation success (Burr et al., 2017) and by displacing predators and prey at different times (Thomas et al., 2019). These studies highlight the complex relationships between anthropogenic activities and disturbance and wildlife distributions, behaviour, and habitat use. These relationships are multifaceted, and as our results demonstrate, can change over time.

This research showed grizzly bear occupancy probabilities do not capture changes in population density and as a result may not be a reliable substitute for monitoring abundance. Ultimately, occupancy modelling cannot fully replace genetic hair-snag surveying, as it does not provide researchers with information regarding DNA that can be used to identify individuals and estimate density and abundance (Boulanger et al., 2006; Croose et al., 2019). If occupancy-based methods are used to monitor wildlife populations, practitioners must accept that reliable inferences regarding abundance are limited as each variable addresses different aspects of a population (MacKenzie et al., 2017). However, occupancy is still a valuable state variable for monitoring sensitive species, as species distribution is a reliable predictor of extinction risk (Harris & Pimm, 2008).

While this research focused on a single large-bodied mammal, the occupancy modelling approach is applicable to other long-term wildlife monitoring programs. Occupancy modelling is particularly valuable for monitoring changes in species and population distribution over time in rapidly changing environments resulting from climate change, habitat loss, fragmentation and over-exploitation (Brown et al., 1996). Application of broad-scale occupancy modelling used here can identify shifts in species distributions (Whittington et al., 2015), and for detecting elusive large carnivores (Noon et al., 2012; Steenweg et al., 2016), which can help inform proactive and adaptive wildlife management.



## 4.2 Contributions and management implications

Occupancy modelling is an alternative to costly mark-recapture studies needed for estimating density and can be used as a tool to help inform wildlife management decisions (Fuller et al., 2016; MacKenzie et al., 2002, 2017). Occupancy and density are closely related, with both parameters requiring an estimate of the portion of patches (or cells) that contain one or more individuals. However, density requires the probability of detecting specific individuals whereas occupancy requires the probability of detecting any individual at various sites (MacKenzie et al., 2017). As a result, reliable density estimates require multiple detections of individuals (Yoccoz et al., 2001; Williams et al., 2002; Schmidt, 2003), which requires high-quality genetic samples that are difficult and costly to collect at landscape scales (Noon et al., 2012; Boulanger et al., 2006; Steenweg et al., 2016a). For example, average costs for laboratory analysis of grizzly bear hair samples (as of 2018) needed for density estimates was \$65 per hair sample (Phoebus et al., 2020). Unlike density estimates, occupancy modelling does not require identification of specific individuals (Waits, 2004), significantly reducing costs associated with monitoring (Noon et al., 2012).

A positive relationship between occupancy and abundance is often observed for many species based on life history attributes and sampling design (Brown, 1984; Gaston et al., 2000; Zuckerberg et al., 2009). For example, occupancy is closely related to the number of individuals or pairs of territorial animals when sampling units approximate the territory size (Azuma et al., 1990; MacKenzie & Nichols, 2004; MacKenzie et al., 2003). As a result, predictions of occupancy can be used to draw conclusions regarding abundance (Tempel & Gutiérrez, 2013; Casner et al., 2014). However, reliable inference of abundance from occupancy estimates requires a clear understanding of the species life history and a sampling design that matches multi-scale processes that influence abundance and occupancy, which may not be possible. In the absence of a clear relationship between occupancy and abundance, occupancy modelling can still be used as a reliable approach for analyzing habitat use and population distributions

(Noon et al., 2012; Tempel & Gutiérrez, 2013; Casner et al., 2014). Occupancy modelling is particularly promising for monitoring sensitive, rare, or elusive species, which are difficult to monitor using abundance estimates, as occupancy detection probabilities can be used to understand how landscape conditions influence presence and distribution of the species over time (Noon et al., 2012; Dibner et al., 2017).

Long term non-invasive monitoring of large carnivores is rare, and as a result it is uncommon to have the ability to estimate occupancy where density estimates are also available (Webb & Merrill, 2012). Here, spatial patterns of occupancy and density estimates were directly comparable as they were developed from the same genetic hair-snag data. This study has demonstrated that grizzly bear occupancy and density are independent in BMA 3, as changes in abundance were not reflected in occupancy probabilities. However, previously unoccupied cells in the east were colonized between 2004 and 2014 and over the same period the population nearly doubled (Stenhouse et al., 2015). Although increases in abundance did not translate to increases in occupancy probabilities, increased abundance may instead reflect changes in the spatial extent of occupancy.

In areas with high resource availability and habitat quality (Gill et al., 2001; Freckleton et al., 2006), occupancy may not be a reliable indicator of density because it is a single state estimate of presence and does not account for individual space use (Clare et al., 2015). Grizzly bears exhibit considerable home range overlap in areas with high habitat quality and resource availability compared to areas with moderate habitat quality (Mcloughlin et al., 2000). Defensive behavior is energetically costly, and for solitary, omnivorous species such as grizzly bears, the cost of defending a food source is not a feasible trade-off when resources are widely available (Mcloughlin et al., 2000). Furthermore, occupancy and abundance may be influenced by extrinsic factors, including resource availability, landscape conditions, and anthropogenic activities, as well as intrinsic factors, including survival, reproduction, and individual physiological state, that vary across scales of space and time (Dibner et al., 2017). It is possible

that if occupancy data collection in HH clusters occurred at finer scales to capture food availability, changes in abundance may be detected. However, at the scale utilized in this study, increases in abundance are not evident in an occupancy framework in the west where habitat quality is high (Nielsen et al., 2006). For grizzly bears, occupancy is likely to be strongly driven by resource availability, which occurs at relatively fine scales (Bourbonnais, 2018).

Occupancy is frequently used as a criteria in wildlife recovery monitoring (e.g., Alberta Grizzly Bear Recovery Plan 2008-2013, 2008; U.S. Fish and Wildlife Service, 2016), and can help wildlife managers understand how habitat conditions and anthropogenic activities influence species presence. This study has shown that monitoring occupancy over a decade can allow understanding of how distributions of animals change in response to anthropogenic landscape change. Used as a criteria for monitoring, occupancy is useful for identifying changes in population distribution over long periods of time. Occupancy modelling also can be used over smaller time periods to explore population vital rates (i.e., the rate of change in local extinction or colonization; MacKenzie et al., 2003), which can identify drivers of occupancy at a finer temporal scale and allow for timely conservation initiatives.

#### **4.2.1 The need for ongoing monitoring**

This study showed that in western cells, where terrain ruggedness is high and anthropogenic disturbance is low, grizzly bear occupancy and density is consistently high compared to the rest of the study area. Areas such as the Whitehorse Wildland area are prime examples of important grizzly bear habitat characterized by high occupancy acting as source habitats producing individuals that disperse into unoccupied habitat (Nielsen et al., 2006). Despite the increase in population size observed from 2004 to 2014 combined with the expansion of grizzly bear occupancy shown here, which indicate a positive trend for the threatened grizzly bear population in Alberta, conservation and management challenges remain.

An active source-sink dynamic is present in BMA 3 (Boulanger et al., 2018). Attractive sinks occur in areas where high animal occurrence or habitat selection is coupled with high mortality risk (Nielsen et al., 2004; Nielsen et al., 2006). Human-caused mortality is particularly threatening to peripheral grizzly bear populations, including BMA 3 (Benn and Herrero, 2002). Despite observed increases, grizzly bear occupancy and density remain low in BMA 3, and with continued human access and increasing road density, pressures on reproduction and recruitment combined with human-caused mortality remain high (Schwartz et al., 2006, 2010; Boulanger et al., 2014).

In areas with high mortality rates, vacant habitat is often colonized by juvenile males (Cooley et al., 2009; Lamb et al., 2017), who disperse further than females (McLellan & Hovey, 2001). Juvenile males dispersing into the eastern portion of the study area face high mortality risks resulting from extensive road networks servicing industrial activities and agriculture (Nielsen et al., 2006). If dispersing males survive to sexual maturity, it is unlikely they will encounter a female given the low female grizzly bear occupancy observed in this study. Ultimately, there is low reproductive potential and survival in the east and population persistence is unlikely. To ensure population persistence in unoccupied grizzly bear habitat, a balance between mortality and recruitment is needed where mortality risk is managed allowing individual bears to colonize, survive and reproduce (Boulanger et al., 2018). With the goal of reducing mortality risk, the Alberta government has set road densities thresholds of 0.6 km/km<sup>2</sup> in core habitat and 1.2 km/km<sup>2</sup> secondary habitat areas in the east (Nielsen et al., 2009). However, research has shown that road densities >75 km/km<sup>2</sup> are associated with sink habitats and approximately 57% of secondary grizzly bear habitat in Alberta has either moderate (0.75-1.25 km/km<sup>2</sup>) or high (>1.25 km/km<sup>2</sup>) road densities. As a result, successful and persistent grizzly bear colonization, survival, and reproduction in secondary habitat remains unlikely. By managing motorized access (i.e., decommissioning and limiting vehicle use of resource roads),

the detrimental effects of roads on grizzly bear population persistence can likely be mitigated (Proctor et al., 2019), but monitoring is still required to assess the state of the population.

Annual monitoring in the east is needed to determine whether colonization and occupancy are persistent or intermittent for both males and females and to understand how anthropogenic factors are creating sink dynamics. Further, monitoring is also necessary in western portions of the study area to ensure these areas continue to act as a population source. Chapter 2 results showed a decrease in habitat occupancy in the western portion of the study area from 2004 to 2014, suggesting that habitat occupancy in core areas declined despite increases in density and geographical extent of occupancy. Given the occupancy patterns in the west observed here over a decade (i.e., high occupancy relative to the rest of the study area), monitoring efforts may not be required as frequently. However, it is critical to ensure that high mortality in peripheral eastern regions are not confounded by decreasing source populations in the west (Guisan & Thuiller, 2005).

#### **4.2.2 Alternative occupancy monitoring techniques**

Hair-snag genetic surveys (Woods et al., 1999), exemplified by the non-invasive approaches used in this research, are widely employed for monitoring grizzly bear populations (Mowat & Strobeck, 2000; Boulanger et al., 2001, 2005; Stenhouse et al., 2015). Hair-snag surveys are perhaps the most effective method for monitoring changes in occupancy over time for grizzly bears (Nielsen et al., 2009), especially when compared to radio collaring which is both expensive and highly invasive (Gompfer et al., 2006). Hair-snag genetic surveys provide an opportunity to estimate population vital rates (Schwartz et al., 2007), assess regional population connectivity (Dixon et al., 2006; Proctor et al., 2004, 2005), and can be used to obtain health markers for quantifying long-term stress and reproduction (Koren et al., 2002; Accorsi et al., 2008; Bourbonnais et al., 2013). Nielsen et al. (2009) suggested semi-annual sampling

using a systematic grid design or habitat-based stratified sampling in each watershed for grizzly bear population monitoring. However, considering that large-scale sampling has only occurred every decade, it is unlikely that sufficient resources are available for monitoring using genetic surveying for the Alberta grizzly bear population. Large-scale DNA mark-recapture studies using hair-snag surveys for monitoring grizzly bears can cost millions of dollars (Alberta Grizzly Bear Recovery Plan 2008-2013, 2008), which can limit their application for long-term population monitoring needed in Alberta (Steenweg, 2016).

Camera traps are becoming an increasingly popular approach for wildlife monitoring, as they offer low cost, non-invasive detection data, and can capture rare and understudied species (Burton et al., 2015; Steenweg et al., 2017). Cameras have been used to detect occupancy trends in carnivore species in the Rocky Mountains (Ellis et al., 2014; Steenweg, 2016, 2019), and can be used to assess changes in occupancy, producing results comparable to DNA-based mark-recapture methods (Steenweg et al., 2016b). Due to the large number of detections produced over time, camera trap detection data have been used in multi-state hierarchical occupancy models (Nichols et al., 2007) to assess spatial patterns of reproductive success of grizzly bears in different land-cover types in the Rocky Mountains, with individuals classified as either *single* or *breeder* (i.e., female with cubs; Fisher et al., 2014). Detection probabilities using camera trap data varied based on reproductive success, and by employing multi-state models spatial heterogeneity in detection probabilities can be accounted for (Fisher et al., 2014), which can help reduce bias in occupancy estimates (MacKenzie et al., 2017).

A primary goal of wildlife population surveys is to maximize detection probabilities (Bailey et al., 2007). Attractants, or lures, are often used in camera trap monitoring programs to increase detection probabilities (Burton et al., 2015; Buyaskas et al., 2020). Recent research has highlighted the importance of species-specific approaches for wildlife detection surveys (Steenweg et al., 2019). For example, the use of lures can be more effective for detecting black bears (*Ursus americanus*) and sites lacking lures can be ineffective for detecting carnivores

(Buyaskas et al., 2020). However, it is important to note that the use of lures may have implications for site and detection independence (Burton et al., 2015), as lures may result in geographic closure violation by drawing animals into the sampling area (Gerber et al., 2012). Additionally, lures must be reapplied regularly which may not be logistically feasible (Steenweg et al., 2016b) and individuals may become habituated to lures over time causing detection probabilities to decrease regardless of reapplication (Fisher et al., 2014). If it is not feasible to reapply lure frequently, there are alternative ways to increase statistical power, including increasing sampling time. By leaving cameras out for longer periods of time, detection probabilities are increased. However, occupancy may be better interpreted as use, as closure assumptions are less likely to be met over longer periods of time (Steenweg et al., 2016b).

Scat surveys are commonly used as detection methods for carnivore species (e.g., Gompper et al., 2006; Long et al., 2011; Schregel et al., 2012, 2018), and could be used in conjunction with camera traps or alone to assess occupancy. A recent study comparing hair-snag and scat sampling as a monitoring approach for grizzly bears determined that scat surveys provided better coverage within grid cells compared to the hair snag design and resulted in more detections and better discrimination of species (Phoebus et al., 2020). While both methods can identify sex, hair samples allowed for more successful genotyping to the individual level. However, the hair-snag method reduced costs by approximately 30% (Phoebus et al., 2020). Further, Phoebus et al. (2020) caution that the scat-survey approach has the potential to be biased against road-avoidant bears (Graham et al., 2010), but conclude that scat surveying has promise for grizzly bear monitoring.

#### **4.2.3 Modelling approaches**

The use of multi-scale models can also improve inference of detection and occupancy (Nichols et al., 2008a). The application of multi-scale models to quantify spatial-temporal

patterns of grizzly bear occupancy would be highly informative, given that grizzly bear occupancy and density are influenced by bottom-up habitat and environmental conditions and top-down anthropogenic factors (Nams et al., 2006; Apps et al., 2016; Bourbonnais, 2018). Traditional occupancy models consider two levels of information, the survey units and the surveys within the units that are replicated either spatially or temporally. Instead, multi-scale models consider additional levels of information which can be either spatial or temporal (MacKenzie et al., 2017). For example, information can include multiple detection methods (e.g., hair-snags and camera traps; Nichols et al., 2008a), which can be used to test the efficacy of detections methods, detect multiple species, or detect different life history stages for a single species (Bailey et al., 2014).

Multi-scale occupancy models can be useful for wide-ranging mammals, including grizzly bears, which are influenced by landscape characteristics at different scales (Sunarto et al., 2012). Multi-scale models can help characterize complex habitat interactions for vulnerable species in disturbed landscapes to identify restoration and conservation priority areas (Deere, 2018). Camera trap surveys combined with multi-state occupancy models would be useful for monitoring grizzly bear populations in Alberta, particularly in boundary areas of the population range where sink habitats are prevalent, to develop a better understanding of occupancy dynamics related to reproductive success and survival. Multi-scale, multi-state occupancy models are also available (Miller et al., 2011), providing an opportunity to combine the use of camera traps and scat to explore scale dynamics and breeding success simultaneously. However, increasing model complexity potentially can result in weaker inferences and poorer precision (Bailey et al., 2014).

To fully understand population dynamics, a study should systematically sample populations to infer changes in patterns in response to extrinsic conditions (MacKenzie et al., 2003; MacKenzie & Nichols, 2004). A limitation of this study is the length of time (i.e., a decade) between hair-snag sampling efforts, which were primarily designed for population abundance



estimates. As a result, the sampling protocol could not capture finer-scale patterns of occupancy (e.g., colonization and extinction) that are likely present throughout most of the study area where human-caused mortality remains high. Due to much of the area being a mortality sink, it is probable that occupancy changes are dynamic and changing at finer temporal scales. Future efforts could employ dynamic occupancy models to monitor population vital rates overtime smaller time intervals to address this limitation (MacKenzie et al., 2003, 2017) and to quantify occupancy trends and rates of change (Kéry et al 2010, Adams et al 2013, Weir et al 2009, 2014).

Incorporating fine-scale detection data (e.g., multi-seasonal and inter-annual) would refine grizzly bear colonization and local extinction rates related to seasonal changes in snow cover (Berman et al., 2019), and phenology and resource availability (McClelland et al., 2020), as well as a multi-annual or decadal anthropogenic disturbance and landscape change as demonstrated here. This approach would allow for timely management of the species and grizzly bear habitat, and can be implemented using camera traps or scat surveys, or a combination of both. In a previous study, the use of camera traps and dynamic occupancy models detected small changes in grizzly bear population occupancy between two sampling years (Steenweg et al. 2016), and would be a feasible approach for monitoring populations more frequently, as opposed to large-scale population abundance studies using genetic hair-snag surveys (as suggested by Nielsen et al. 2009).

Occupancy modelling is also useful for multi-species monitoring (Dorazio & Royle, 2005; Kéry & Royle, 2009), where developing abundance estimates is impractical due to extensive effort and high costs associated with multi-species mark-recapture (Noon et al., 2012). Multi-species occupancy models can be used to simultaneously monitor local extinction and colonization of multiple species, to investigate species interactions and potential effects of competition or predation, and to improve inferences of species that are influenced by the presence of other species (MacKenzie et al., 2017). Communities can be monitored over large

time periods and geographic areas using dynamic (i.e., multi-year) multi-species occupancy models (Dorazio et al., 2010), which can help understand population responses to changes in land use and habitat characteristics (Goijman et al., 2015), catastrophic events (Russell et al., 2015), and climate (Tingley & Beissinger, 2013).

#### **4.2.4 Insights on spatial scale for occupancy modelling**

Choosing an appropriate spatial scale for monitoring initiatives is a key consideration for wildlife conservation (Nams et al., 2006). From a management standpoint, sampling at a fine geographic scale can create an unfeasible workload, while using too coarse a scale may mask ecological processes. When selecting a spatial scale for sampling, researchers must consider how processes governing habitat characteristics and wildlife behaviour, as well as relationships among habit variables measured at different scales (Nams et al., 2006). For occupancy modelling, the probability values are intrinsically linked to the scale at which sampling units have been defined (MacKenzie et al., 2017). Sampling scales should therefore be selected based on specific research objectives. For example, if the purpose of an occupancy study is to determine specific variables that influence species presence, such as habitat type, then sampling units should be defined at a scale where habitat type is homogeneous within the unit (MacKenzie et al., 2017). However, reducing the size of sampling units can result in a violation of the closure assumption for wide-ranging species, changing the definition of occupancy (MacKenzie et al., 2017). Additionally, using variables defined at varying scales can help determine which spatial scales are the best predictors of occurrence (MacKenzie et al., 2017).

Sampling units can be defined based on management objectives (e.g., the grid system used here) or can be defined using naturally occurring habitat units (e.g., forest patches; MacKenzie et al., 2017). The 49 km<sup>2</sup> scale used here is commonly employed to monitor grizzly bear populations in Alberta (Boulanger, 2005; Boulanger et al., 2006; Stenhouse et al., 2015),

as grizzly bears habitat selection likely occurs close to this scale (Apps et al., 2016). Alternatively, watershed units (Boulanger et al., 2014), or approximate female home range (Alberta Environment and Parks, 2016), may be used to define sampling scale, which may better reflect animal biology. Using home-range or territory size to define sampling unit size has been suggested for occupancy studies in continuous habitat (as opposed to discrete habitat types; Jathanna et al., 2015; O'Connell & Bailey, 2011; Karanth & Nichols, 2010). The use of territories or home ranges is often employed to define sampling units not being used by multiple individuals or to infer abundance from occupancy (MacKenzie et al., 2017). However, the use of discrete territories is not a biologically realistic approach for grizzly bears, as they have overlapping ranges in areas with widely available resources (Stirling & Derocher, 1990; Waller & Mace, 1997). Additionally, defining sampling units based on home ranges or territories is not necessary if the research goal is to understand species presence (MacKenzie et al., 2017).

Although occupancy did not directly translate to abundance in this study, occupancy-abundance relationships are scale-sensitive (Royle & Dorazio, 2008; Steenweg et al., 2018). This research used a 49 km<sup>2</sup> spatial scale, and considering grizzly bears select for certain habitat features (e.g., food sources) at much finer scales (Ciarniello et al., 2007; Nielsen et al., 2010; Rovang, 2013; Bourbonnais, 2018), it is possible that at a finer spatial scale a occupancy-abundance relationship would exist. Additionally, the use of finer sampling scales might refine estimates of colonization and extinction and help identify landscape conditions that influence these processes, which may have been unidentifiable based on the heterogeneous nature of the cell size used here. A finer scale, for example a 5 x 5 km cell, which was found to have the highest detection probabilities in a meta-analysis of grizzly bear mark-recapture techniques in British Columbia (Boulanger et al., 2001), might provide better opportunities to understand occupancy-abundance relationships for grizzly bears.

### 4.3 Future research

The relationship between grizzly bear occupancy, anthropogenic disturbance, and habitat condition is complex both spatially and temporally. As anthropogenic disturbance and habitat loss increase organisms may no longer be able to respond, regulate, or adapt to changing conditions, reducing their overall fitness (Battisti et al., 2016). Identifying these 'disturbance thresholds' (i.e., tipping points) is complex and represents an important area of research for monitoring threatened wildlife populations. In Alberta, occupancy modelling can be used to determine if grizzly bears are persisting in the eastern portion of the study area, which is recommended based on the sink potential of the area. Currently, it is unknown whether extensive anthropogenic disturbance and activities occurring in the eastern portion of BMA 3 are creating suitable habitat conditions that will allow grizzly bears to persist over time. To better understand the relationship between grizzly bears and anthropogenic disturbance, future research should consider:

- 1) Multi-state occupancy models (Nichols et al., 2007) could be used to assess reproductive success (Fisher et al., 2014), which would be particularly useful in eastern regions where female occupancy was low. Detection probabilities using camera traps can be increased using scent lures, which are particularly important for carnivores (Buyaskas et al., 2020).
- 2) The relationship between abundance and occupancy dynamics of grizzly bears in Alberta should be further explored to understand patterns of population size and habitat occupancy (Freckleton et al., 2005). Future research should consider the use of camera traps and scat surveys that will provide finer-scale detection data that can be related to seasonal variability in resources and environmental conditions that also influence population status. Multi-scale models (Nichols et al., 2008b) are specifically valuable for grizzly bears, who are influenced by both top-down and bottom-up processes (Nielsen et al., 2010).

- 3) A parameterized occupancy model could be used to identify disturbance thresholds that result in shifts in occupancy by predicting occupancy probabilities across disturbance gradients (Frey et al., 2012). This framework would provide a predictive tool for evaluating potential outcomes of varying landscape and population management strategies.
- 4) In this study, landscape and disturbance variables were defined at the same sampling scale used to detect bears (i.e., 7km x 7km). Modelling occupancy as a multi-scale process would provide opportunities to understand how spatial scales of resource availability, anthropogenic disturbance, topography, and even climate influence grizzly bear occupancy patterns.
- 5) Dynamic occupancy models (i.e., multi-season models; MacKenzie et al., 2003) should be used to understand seasonal as well as inter-annual changes in grizzly bear occupancy. Grizzly bears are highly responsive to seasonal change in resource availability and landscape conditions. Dynamic models would help differentiate areas of seasonal habitat use and areas of permanent occupancy and population persistence.

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