INCORPORATING VISUAL AND AUDITORY PERCEPTION INTO UNDERSTANDING GRIZZLY BEAR BEHAVIOURAL RESPONSES TO ROADS IN ALBERTA, CANADA

by

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Abstract

Anthropogenic disturbances, including roads, are known to influence animal habitat selection and mortality. However, little is known about the role of sensory perception in animal responses to disturbance. The goal of this thesis was to investigate the effect of visual and auditory perception around roads on grizzly bears (*Ursus arctos*) in Alberta, Canada. As an apex predator, the greatest threat to grizzly bear populations in my study area is human-caused mortality near roads, yet grizzly bear behavioural responses to roads are not fully understood. In this thesis, detailed topographic and land cover data from airborne Light Detection and Ranging (lidar) and Landsat imagery were used to estimate visibility and audibility around roads. Using a modified semivariogram approach with data on step lengths from GPS-collared grizzly bears, I found that grizzly bears responded to roads at slightly further distances when roads were perceptible (80 m) than when roads were imperceptible (60 m). I extended the analysis of grizzly bear response by modelling habitat selection as a function of road perception and other environmental variables using integrated step selection analysis. I also assessed mortality risk in visible areas by comparing habitat selection between grizzly bears that died and grizzly bears that survived. Grizzly bears were less likely ($p < 0.05$) to select visible areas when moving slowly or resting, suggesting that road visibility is perceived as a risk. However, bears were more likely ($p < 0.05$) to select visible areas when moving quickly, which may indicate that grizzly bears use roads as travel conduits. Results suggested no difference in selection for visible areas between grizzly bears that survived and grizzly bears that died. However, an exploratory analysis showed that grizzly bear mortalities commonly occurred in visible areas. From a management context, maintaining 20 m wide vegetative buffers along roadsides may decrease visibility, allowing grizzly bears to use travel corridors associated with roadways and access cut blocks for forage

while reducing human-induced risk. Collectively these findings highlight the importance of sensory perception in understanding animal behaviour.

Lay Summary

Roads and other human disturbances have profound impacts on wildlife behaviour and survival, and many studies have examined how wildlife respond to disturbances. However, little is known about how perception of a disturbance by sight or sound affects wildlife behaviour. In this thesis, I studied the effect of perceptibility on grizzly bear behaviour and mortality in Alberta, Canada. I found that grizzly bears responded to roads at further distances when they could see or hear them than when roads were imperceptible. In addition, I found that grizzly bears preferred areas visible to roads when travelling, but avoided visible areas when resting. This suggests that grizzly bears are risk averse when resting, but that they use road corridors for travelling. This research highlights the importance of perception in understanding animal behaviour and has important management implications for reducing risk around roads.

Preface

The body of this thesis is made up of two scientific papers written for peer review for which I am the lead author and investigator, as listed below. The framing questions for this research were developed through discussions with Dr. Nicholas Coops and Dr. Trisalyn Nelson. I was primarily responsible for refining the research objectives, developing and implementing the methodology, analysing and presenting results, and preparing manuscripts for submission. Gordon Stenhouse provided access to grizzly bear data and guidance in matters of bear ecology, as well as editorial assistance for Chapters 1, 2, 3, and 4. Dr. Sean Kearney provided programming and statistical assistance as well as editorial comments on Chapter 4. Dr. Nicholas Coops, Dr. Cole Burton, and Dr. Trisalyn Nelson provided guiding feedback and suggestions throughout the development of the research as well as editorial assistance on all thesis chapters.

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List of Abbreviations

AB - Alberta

AIC - Akaike Information Criterion

ALS - Airborne Laser Scanning

Aud - Road Audibility

BC - British Columbia

BMA - Bear Management Area

CHM - Canopy Height Model

CI - Confidence Interval

COSEWIC - Committee on the Status of Endangered Wildlife in Canada

DEM - Digital Elevation Model

DSM - Digital Surface Model

Edge - Absolute distance to forest edge

Elev - Elevation

Food - Food rating

Insol - Solar Insolation

iSSA - Integrated Step Selection Analysis

lidar - Light Detection and Ranging

Ln(sl) - Natural Log of Step Length

N.S. - Not Significant

Percep - Road Perceptibility

Rd - Distance to Road

RSS - Residual Sum of Squares

SRTM - Shuttle Radar Topography Mission

TOD - Time of Day

TWI - Terrain Wetness Index

Vis - Road visibility

ZOI - Zone of Influence

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Dedication

This thesis is dedicated to my parents, Steve and Janice Arndt, who instilled in me the love of science, discovery, and wilderness.

Chapter 1: Introduction

1.1 Grizzly bears in North America and Alberta

Grizzly bears (*Ursus arctos*) were once widespread across North America, ranging from the northwestern corner of the continent south as far as Mexico and east to the Mississippi River (Schwartz et al. 2003). Grizzly bears are also found in parts of Europe and Asia, where they are known as brown bears (Festa-Bianchet 2010). However, grizzly bear populations worldwide have been increasingly threatened by anthropogenic activity and habitat loss and extirpated from much of their range (McLellan et al. 1999). Grizzly bears were nearly extirpated from the contiguous United States, but persist in a few remnant populations in the northwestern states. Southern BC and Alberta are at the edge of historical range contractions, while grizzly bears remain relatively common in northern BC, the Canadian territories, and Alaska (Schwartz et al. 2003). In Canada, grizzly bears are designated as a species of "Special Concern" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and are designated "Threatened" in Alberta as of 2010 (although this designation was originally recommended in 2002) (Alberta Environment and Parks 2016). Reasons for designation in Alberta included low population size (less than 1000 adults), frequent human-caused mortality, and habitat decline (Alberta Environment and Parks 2016, Coogan et al. 2018). There is approximately 112 000 km^2 of grizzly bear habitat in Alberta, supporting a population estimated to be about 900 grizzly bears (Festa-Bianchet 2010, Proctor et al. 2020). Portions of the Alberta population of grizzly bears are genetically connected to larger populations in British Columbia and Montana, although topographic features including ice fields and mountains provide natural barriers to dispersal in some areas (Proctor et al. 2012).

Grizzly bears can also be divided into subpopulations within Alberta. Although grizzly bears across Alberta share some gene flow, major highways limit movement between subpopulations (Proctor et al. 2005, Festa-Bianchet 2010). For grizzly bear management purposes, the province has been divided into seven bear management areas (BMAs) between which dispersal is limited (Alberta Environment and Parks 2016). The most recent provincial grizzly bear recovery plan delineated two types of conservation areas with each BMA (Alberta Environment and Parks 2016). Core areas were identified where high quality habitat was found along with low density of open access roads, which is used as a surrogate for reduced risk of human-caused mortality. Secondary areas were put in place adjacent to these core areas, but had higher road densities (Alberta Environment and Parks 2016).

1.2 Grizzly bears, anthropogenic activity, and roads

Alberta's Rocky Mountains and foothills, which support the highest concentration of grizzly bears in the province, are in many places being highly altered by industrialization and natural resource extraction, particularly forestry, mining, and oil and gas operations (Nielsen et al. 2009). Grizzly bears are omnivore generalists, and they are able to adapt to using disturbed areas associated with natural resource extraction so that habitat loss is minimal (Stewart et al. 2012). However, these activities require extensive road networks which greatly increase human access into grizzly bear habitat (Ladle et al. 2019). These roads are also frequently used for recreational purposes long after extraction operations cease.

Besides intraspecific predation, grizzly bears have no natural predators, thus most grizzly bear mortalities result from interactions with humans (Nielsen et al. 2004b, Boulanger and Stenhouse 2014). Although a sport hunting moratorium was enacted in Alberta in 2006, human-caused mortality is still common due to poaching, being mistaken for black bears, real or perceived defense of life or property, management actions against “problem” bears, and rail or road kills (Festa-Bianchet 2010). In fact, Boulanger & Stenhouse (2014) found that of 22 mortalities recorded for radiocollared bears between 1999 and 2013 in Alberta, 16 were human-caused, one was natural, and five were unknown.

According to the most recent status report for grizzly bears in Alberta, the expanding road network allowing motorized access into grizzly bear habitat poses the single greatest threat to recovering grizzly bear populations (Festa-Bianchet 2010). In a review of grizzly bears and roads in BC and Alberta, Proctor et al. (2020) found that roads affected grizzly bear populations by causing mortality, displacement, and habitat loss. For example, Boulanger and Stenhouse (2014) reported that 86% of mortalities recorded for radiocollared bears were within 500 m of a road. Roads also act as barriers to movement between subpopulations of grizzly bears, as bears avoid crossing major highways (Proctor et al. 2005, Coogan et al. 2018). Grizzly bears have lower population densities when road densities are high; the highest grizzly bear densities are found in large areas with few or no roads (Lamb et al. 2018).

Road-associated mortality is especially concerning for grizzly bears because roads are often associated with high quality habitat. Grizzly bear distributions are largely resource driven, based on the presence of five main food groups: grasses, sedges, and rushes, forbs and roots, seeds and berries, mammals, and insects (Munro et al. 2006). Several of these resources are concurrent with roads, for example, grasses, sedges, and rushes are primarily found in low elevation valleys where roads are commonly situated (Munro et al. 2006, Roever et al. 2008b). In addition, roadside openings and adjacent regenerating forest, including cut blocks, provide increased production of forage plants, as well as earlier fruiting of berry plants in the spring due to greater light availability (Roever et al. 2008b, Pollock et al. 2017, Larsen et al. 2019). Roads may provide additional attractants including road-killed animal carcasses or garbage (Alberta Environment and Parks 2016). Grizzly bears may also use roads as travel corridors as has been found in other large carnivores (James and Stuart-Smith 2000, Roever et al. 2010). Some studies have found that grizzly bears use roads at higher frequencies than expected, even when compared to road-like habitats such as low elevation valleys (Nielsen et al. 2006, Roever et al. 2008a, Graham et al. 2010). In fact, roads that are associated with grizzly bear foods are considered a primary sink for grizzly bears – an area that is attractive to grizzly bears but is associated with unsustainably high mortality (Machutchon and Proctor 2015, Nielsen et al. 2017). Grizzly bear behaviour around roads varies by age and reproductive class (Graham et al. 2010), as well as traffic levels (Northrup et al. 2012). Table 1.1 provides a summary of several studies on the influence of roads on grizzly bears in Alberta.

Table 1.1 A selection of studies on the influence of roads on grizzly bears in Alberta

Reference	**Study Area**	**Major Findings**
Nielsen et al. 2004b	Central Rockies, AB	Grizzly bear mortality risk increased near roads
Roever et al. 2008a	Yellowhead, AB	Grizzly bear selection of roads was greater than selection of road-like habitats
Roever et al. 2010	Yellowhead, AB	Grizzly bears selected for areas near roads and increased movement rates near roads
Graham et al. 2010	Yellowhead, AB	Grizzly bear road selection and crossing behaviour depended on season, sex, and age class
Northrup et al. 2012	Southwestern AB	Grizzly bears selected for low traffic roads but avoided high traffic roads
Boulanger and Stenhouse 2014	Western AB	Grizzly bear survival and population growth was negatively correlated with road density
Kite et al. 2016	Kakwa and Yellowhead, AB	Grizzly bears' spatial scale of response to roads based on movement patterns ranged from 35 - 90 m
Whittington et al. 2019	Banff National Park, AB	Temporal road closures significantly increased road use by grizzly bears

1.3 Grizzly bear management strategies in Alberta and BMA 3

Grizzly bears have low reproductive rates which limit population growth, thus high survival, particularly for adult females, is crucial for population recovery (Schwartz et al. 2003). Alberta has taken several actions to promote grizzly bear recovery in the province, the most notable being the sport hunting moratorium put in place in 2006. In the six years before the hunting moratorium (2000 – 2005) there was an average of 26 known grizzly bear deaths in Alberta per year, and this declined to an average of 14 known deaths per year in the three years following the moratorium (2006 – 2008) (Festa-Bianchet 2010). However, from 2009 to 2018 there was an average of 23 known grizzly bear deaths per year and 92% of these were human caused (Government of Alberta 2019), indicating the need for further reductions in human caused mortality.

Beyond the hunting moratorium, grizzly bear recovery action in Alberta is largely focussed on access management. Reducing road density has been correlated to population increases (Lamb et al. 2018), and where roads cannot be decommissioned, closing roads to public use may be effective to increase grizzly bear security (Proctor et al. 2020). The 2016 draft Grizzly Bear Recovery Plan recommends that for population recovery open road density should be limited to less than 0.6 km/km^2 in Core habitat and 0.75 km/km^2 in Secondary habitat (Alberta Environment and Parks 2016, Proctor et al. 2020). However, these guidelines are not consistently met; for example, within BMA 3 36.4% of Core areas and 71.4% of Secondary grizzly bear habitat exceeds recommended thresholds (Alberta Environment and Parks 2016), therefore work on achieving these goals continues.

Some BMAs within Alberta appear to be experiencing population growth in grizzly bears. For example, the population estimate for BMA 3 was 74 (95% Confidence Interval 56 - 98) bears in 2014, whereas the previous population estimate in 2004 was 36 bears (95% Confidence Interval 29 – 45), thus representing a population increase averaging 7% per year (Stenhouse et al. 2015). However, it is difficult to elucidate whether local increases are due to management actions or movement of grizzly bears (Stenhouse et al. 2015). In particular, translocations of bears involved in human-bear conflicts may influence rates of population change; between 2004 and 2014, 30 bears were translocated into BMA 3. Further research regarding the effectiveness of management actions on grizzly bear recovery is needed.

While the relationship between grizzly bears and roads in Alberta has been researched extensively, the role of perception is largely unknown.

1.4 Animal perception and behaviour

One factor that may influence grizzly bear habitat selection and movement decisions around roads is sensory perception. Animal distributions and movement are functions of intrinsic constraints, including an animal's physiological movement methods and speed, extrinsic constraints, such as topographic or anthropogenic barriers, and habitat selection (Martin et al. 2008). Habitat selection results from individual animal movement decisions, which are based on the animal's knowledge of the landscape (Avgar et al. 2013, Spiegel et al. 2017). However, landscape awareness is rarely included in behavioural models (Avgar et al. 2013, Fagan et al. 2017). Most models either assume animals have complete knowledge of the entire landscape (e.g. optimal foraging theory) or only knowledge of the landscape immediately around them (Fagan et al. 2017). Aben et al. (2017) stress that an essential component of understanding animal behaviour is quantifying an animal's ability to perceive its environment. Perception is a key factor influencing animal decisions about foraging (Fagan et al. 2017) and breeding strategies (Aspbury and Gibson 2004), and also affects predator-prey relationships including habitat selection and flight distances (Ndaimani et al. 2013, Olsoy et al. 2015, Davies et al. 2016b). However, while animal responses to human activity are often comparable to predator-prey responses (Frid and Dill 2002), little work has been done on how the perception of anthropogenic disturbances influences wildlife behaviour (Brown et al. 2012a).

Visual and auditory perception depend on distance as well as topography, land cover, and vegetation height and density (Skov-Petersen and Snizek 2007, Reed et al. 2012). While in the past, studies of perception have been limited by often subjective field-based estimates of cover or broad spatial resolution elevation data ignoring vegetation (Camp et al. 1997, Loarie et al. 2013), advances in remote sensing technology allow us to build more accurate depictions of what is perceptible to an animal (Loarie et al. 2013, Aben et al. 2018).

One way to measure perception is by considering what is visible to an animal. Although traditionally used for landscape planning and aesthetics, viewsheds have been increasingly used in wildlife studies. Studies summarized in Table 1.2 demonstrate that visibility can be used to describe animal habitat selection for hunting, denning, resting, and breeding display sites, as well as to evaluate the effects of human disturbances. Most studies use a Digital Elevation Model (DEM) to compute viewsheds, which allows landscape visibility to be modelled based on topography but without vegetation (Aspbury and Gibson 2004, Alonso et al. 2012). However, many studies also acknowledge the importance of vegetation in blocking visibility. Vegetation may be incorporated by using a Digital Surface Model (DSM) that includes vegetation height (Loarie et al. 2013, Davies et al. 2016b), or by adding a layer with estimated vegetation heights to a DEM (Montgomery et al. 2012, Costello et al. 2013). Some studies are beginning to use horizontal measures of vegetation such as Terrestrial Laser Scanning to estimate not only vegetation height but gaps below the canopy as well (Olsoy et al. 2015).

Table 1.2 Selection of studies using viewshed analysis to predict animal movement or behaviour

Authors	**Species**	**Viewshed Data**	**Purpose**
Camp et al. 1997	Golden eagle	DEM	Provide an alternative management area to buffer zones
Aspbury and Gibson 2004	Greater sage grouse	30 m DEM	Investigate selection of courtship display areas
Hopcraft et al. 2005	Lion	DEM (triangular irregular network)	Investigate hunting distributions
Alonso et al. 2012	Great bustards	5 m DEM	Investigate selection of courtship display areas
Montgomery et al. 2012, 2013	Elk	10 m DEM plus vegetation raster	Describe movement around roads
Costello et al. 2013	Black bear	10 m DEM plus vegetation raster	Evaluate response to path construction
Loarie et al. 2013	Lion	1.12 m DSM	Compare hunting and resting sites between sexes
Ndaimani et al. 2013	Sable antelope	30 m DEM	Explain flight behaviour
Jiang et al. 2014	Amur tiger	1 km DEM	Determine distribution patterns and factors driving range loss
Olsoy et al. 2015	Multiple	Terrestrial Laser Scanning point cloud	Calculate predator/prey sightlines to evaluate predation risk
Davies et al. 2016a	African wild dog	1 m DSM	Investigate den selection
Davies et al. 2016b	Lion	1 m DSM	Predict kill sites

Hearing, or sound, is also an important component of animal perception (Table 1.3). “Technophony”, or anthropogenic noise, has been shown to have significant effects on animal fitness and behaviour (Shannon et al. 2016, Munro et al. 2018). Although anthropogenic noise is most commonly evaluated as an effect on birds and marine mammals that use vocalizations for long-distance communication (Shannon et al. 2016), several studies have found that technophony influences the behavioural responses of a variety of terrestrial mammals (Table 1.3). In fact, traffic noise has commonly been studied as one of the furthest reaching impacts of road disturbances, using many different methods of estimating sound propagation (Coffin 2007, Munro et al. 2018). Sound may be measured directly using recording devices, or be modelled from road and topographic variables. For example, Brown et al. (2012a) used recording devices on their field vehicles to assess traffic noise levels when observing behavioural patterns of ungulates, whereas Iglesias et al. (2012) employed sound models typically used for road planning when researching the effects of traffic noise on wildlife underpass use.

Table 1.3 Selection of studies using soundscape analysis to assess the effects on traffic noise on terrestrial mammals

Authors	**Species**	**Soundscape Data**	**Purpose**
Archibald et al. 1987	Grizzly bear	Sound level meter transects	Assess effect of logging traffic on space use
Byrnes et al. 2012	Three rainforest mammals	Traffic noise simulators	Determine traffic noise influence on movement and behaviour
Brown et al. 2012a	Elk and pronghorn	Portable recording device on vehicle	Assess effects of road activities on behaviour
Iglesias et al. 2012	Eight vertebrate species	Predictor Type 7810 sound model	Evaluate effects of traffic noise on use of underpasses
Shannon et al. 2014	Prairie dog	Sound level meter	Assess traffic noise influence on foraging and vigilence
Iglesias-Merchan et al. 2018	Roe deer	Predictor Analyst sound model	Assess effect of traffic on stress levels

1.5 Grizzly bear perception

Very little is known about the importance of visual perception to grizzly bear behaviour. Grizzly bear eyesight is generally thought to be similar to that of humans (Macpherson 1966), and they have been recorded to observe moving objects at up to 2 km (Schwartz et al. 2003). Some studies, although not evaluating the importance of sight from the perspective of the grizzly bear, have looked at the importance of vegetative cover to provide concealment for grizzly bears (Oldershaw 2001, Ordiz et al. 2009). For example, when in hiding cover, grizzly bears have shorter flight responses and are less likely to be disturbed by human activity than in open areas (Mclellan and Shackleton 1973). Some studies of grizzly bears and roads have also recommended reducing visibility around roads to reduce human-bear conflicts, but the effectiveness of this has not been studied (Roever et al. 2010).

Research on noise effects on bears is also limited (Amec Americas Limited 2005). In a study on bear repellents on four captive grizzlies, most sounds, including bells, shouting, and growling, were ineffective, while sudden loud noises such as a thunderflash and a cap-chur gun were effective at causing bears to retreat (Miller 1980). In addition, denning grizzly bears have increased heart rates in response to seismic blasts (Reynolds et al. 1983). In a movement study, Archibald et al. (1987) measured sound levels around active hauling sites and noted that grizzly bears avoided areas where noise exceeded 60 dB(C). Additional research on grizzly bear responses to noise disturbance did not directly measure sound, but grizzly bears have been reported to respond to loud disturbances such as aircraft overflights, roads, gas development, and other human activities (Amec Americas Limited 2005). However, grizzly bears are known to habituate quickly to noise disturbances such as acoustic deterrent devices (Amec Americas Limited 2005).

1.6 Research objectives

The goal of this thesis was to investigate the research question "How can measures of perception including sight and sound be used to better understand the effects of disturbance on wildlife, specifically, roads on grizzly bears?" To do so I address two sub-questions:

Sub-question 1: How does road perception affect zones of influence around roads for grizzly bears?

Sub-question 2: How are grizzly bear movement, behaviour, and mortality influenced by road perception?

1.7 Thesis overview

This thesis is made up of five chapters: an introduction, information on the study area and data used, two research chapters, and a conclusion.

Chapter 2 describes the study area used for analyses in Chapters 3 and 4 and introduces environmental and grizzly bear datasets.

Chapter 3 addresses sub-question 1 and builds viewsheds and soundscapes around roads using detailed remotely sensed landscape data. Semivariograms are used to investigate the use of measures of animal perception in creating zones of influence measuring the spatial extent of disturbances.

Chapter 4 addresses sub-question 2 by modelling grizzly bear habitat selection around roads using integrated step selection analysis with the viewsheds and soundscapes developed in Chapter 3 and grizzly bear movement data. Selection for perception variables is compared between grizzly bears that have died and grizzly bears that have survived.

Chapter 5 provides a summary and conclusions for the analyses in Chapters 3 and 4. It also discusses management implications, limitations of the study, and avenues for further research.

Chapter 2: Study area and data

2.1 Study area

My focus area is Alberta's Bear Management Area 3 (BMA 3), which is the Yellowhead region of the eastern foothills of Alberta's Rocky Mountains (Figure 2.1). The area of BMA 3, excluding Jasper National Park for which environmental data were unavailable, is 21632 km^2. Of this area, 11590 km^2 are considered 'Core' or 'Secondary' grizzly bear habitat, whereas the remaining area is used occasionally by grizzly bears. BMA 3 is bordered by Highway 16 to the north, Highway 11 to the south, and the BC-Alberta border to the west (Graham and Stenhouse 2014). To the east the study area has a higher density of humans and increasing agricultural use, corresponding with a decrease in grizzly bear densities (Festa-Bianchet 2010). Terrain varies from mountains in the west to rolling foothills in the east, with elevation between 766 m and 3369 m. Most of the study area is covered with coniferous forests, mainly lodgepole pine (*Pinus contorta*) and secondarily spruce (*Picea* spp) and fir (*Abies* spp.). The landscape also contains mixed forests with trembling aspen (*Populus tremuloides*) and Balsam poplar (*P. balsamifera*) as well as bogs and meadows (Graham and Stenhouse 2014).

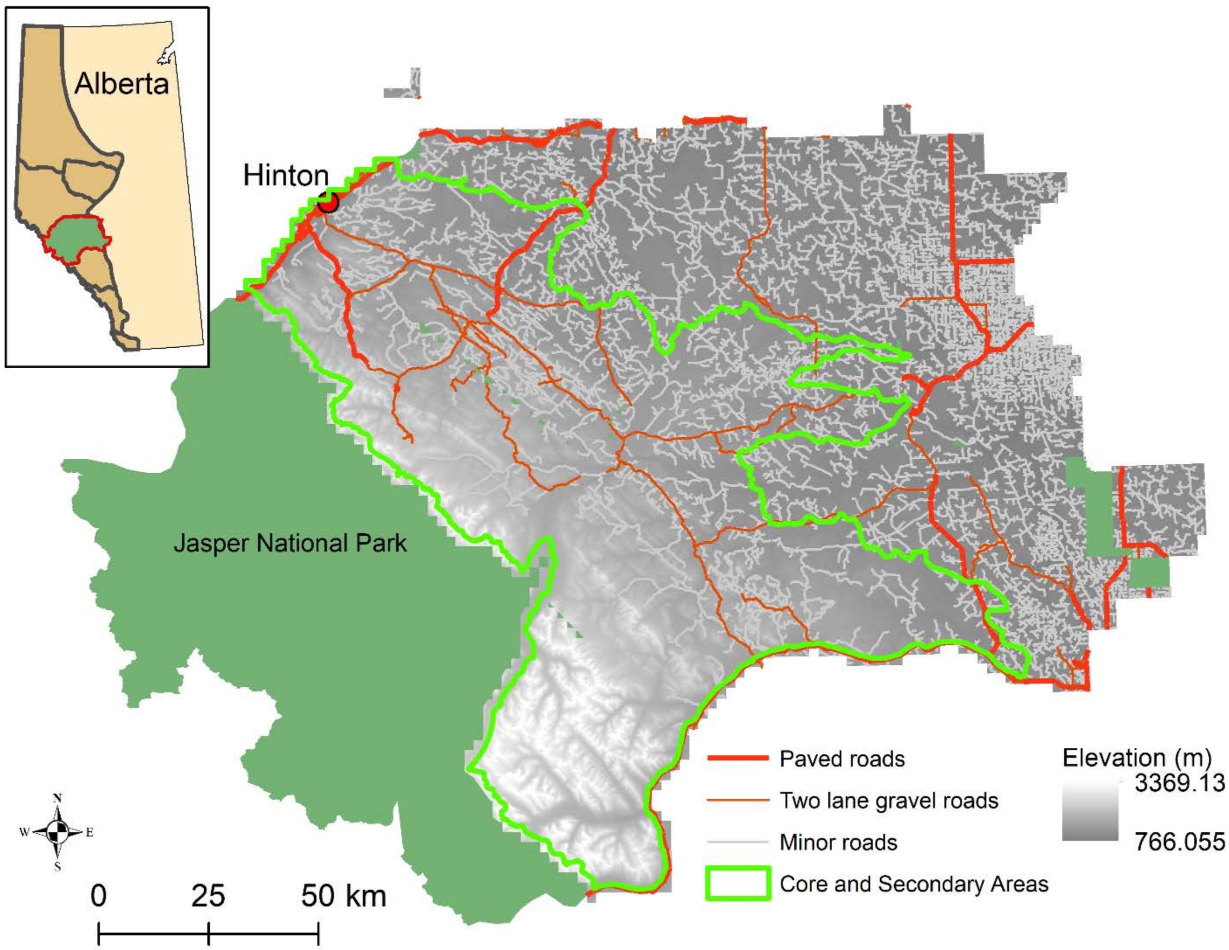

Figure 2.1 Study area

2.1.1 Disturbances

Historically, the study area experienced frequent fires resulting in a mosaicked landscape of successional stages; however, modern fire suppression has led to decreased natural openings within the area and increased homogenous, late successional forests (Nielsen et al. 2004). Natural openings are partially replaced by those resulting from anthropogenic activities including open-pit coal mines, oil and gas extraction, and timber harvest. BMA 3 is also used heavily for recreation such as motorized offroad vehicles, mountain biking, camping, and hiking (Ladle et al. 2018). An extensive road network supports natural resource extraction activities and recreation. The study area contains 14244 km of roads: mostly unimproved or unclassified roads used for industry (8947 km) and gravel roads (4490 km) with few paved roads mostly on the outskirts of the study area (815 km). The overall linear density of roads in Core and Secondary grizzly bear habitat within the study area of 0.52 km/km^2 is within the recommended density threshold, however, density varies widely over the study area (Figure 2.1; Alberta Environment and Parks 2016).

2.2 Remote sensing data

Remotely sensed Airborne Light Detection and Ranging (lidar) data was acquired for the study area in 2007. Lidar provides detailed information on topography and vegetation and is increasingly being used to calculate viewsheds for ecological studies (Davies et al. 2016; Aben et al. 2018) and, more commonly, transportation studies to inform road placement and safety (Jung et al. 2018). The data had an average first return point density of 11.6 points/m^2. A 10 m Digital Elevation Model (DEM) was created based on returns classified as "ground", and a 10 m Digital Surface Model (DSM) was created from first returns, representing vegetation (see Coops et al. (2016) for details on data processing). For the sound analysis, I used a 10-class land cover layer including upland and wetland trees, upland and wetland herbs, shrubs, water, barren ground, snow or ice and cloud and shadow produced by McDermid et al. (2005). I used annual data on stand replacing disturbances including fire and harvesting as well as forest cover data derived from remotely sensed Landsat imagery from 2006 to 2017 to determine areas that experienced substantial landscape changes between the time of lidar collection and recorded grizzly bear presence. Details on the collection, processing, and classification of Landsat imagery can be found in Hermosilla et al. (2016, 2017, 2018). I used the official Alberta road layer for 2009 to 2016 obtained from the Government of Alberta web portal (https://geodiscover.alberta.ca/). Despite obtaining the most current information available, resource roads are dynamic within the study area as new roads are frequently built and some roads are decommissioned or overgrown, thus our analysis may include some roads that were not in use for the entire study period (Kearney et al. 2020).

2.3 Grizzly bear data

Grizzly bear movement data was obtained from GPS locations of grizzly bears collected through the fRI Grizzly Bear Program from 2006 to 2017. Bears were captured using culverts or aerial darting with helicopters and fitted with Followit (Lindesburg, Sweden) GPS radiocollars (Televit, Simplex, and Tellus models) in compliance with the American Society of Mammologists (Cattet et al. 2013). Annual permits from the University of Saskatchewan Animal Care Committee (#20010016) and University of Alberta Animal Care (AUP00000436) authorized capture. GPS data with a sampling interval of one hour was used. The mean location accuracy of GPS collars was < 10 m (K. Graham, personal communication, November 27, 2019). GPS data from 2007 to 2014 were used for Chapter 3 analyses, and data from 2006 – 2017 were used for Chapter 4 analyses.

2.3.1 Grizzly bear mortality data

Grizzly bear mortality data was used for Chapter 3 analyses. Information on grizzly bear mortalities was collected in two primary ways. First, deaths of radiocollared grizzly bears are suspected when the GPS signal remains stationary for long periods of time outside of denning season, and mortalities were confirmed by fRI Research field crews. Of 39 radiocollared bears used in Chapter 3 analyses, 10 had died as of the end of the study period in 2017. Secondly, I acquired mortality data for grizzly bears without radiocollars that were reported by hunters (before the sport hunting moratorium) or by the public. Information was obtained about the location of all known deaths of collared and uncollared grizzly bears in the Yellowhead region between 2000 and 2017 from the fRI Research Grizzly Bear Program. There were 69 recorded deaths, but only 22 deaths had exact location of mortality. Most exact mortality locations were investigated by fRI Research crew members or Fish and Wildlife Officers and recorded with handheld GPS units.

Chapter 3: Building a perceptual zone of influence for wildlife: delineating the effects of roads on grizzly bear movement

3.1 Introduction

Anthropogenic disturbances have major impacts on shared landscapes, influencing both land management and wildlife conservation. Tracking anthropogenic disturbances is essential for understanding and mitigating the impact of human activity (Burton et al. 2014); researchers and managers are increasingly using a range of geospatial tools, including remote sensing technologies, to map and monitor rapid landscape changes (Bolton et al. 2019). However, the ecological effects of spatially fixed disturbances - such as roads, mines, well sites, or other human infrastructure - are rarely limited to the specific area disturbed, but typically extend to affect the surrounding landscape. This area around the disturbance is known as the zone of influence, defined as the furthest extent that a disturbance affects the surrounding habitat and wildlife (Wilson 2016). The extended effects that delineate a disturbance's zone of influence can be divided into two categories: 1) environmental effects, for example, chemical run-off, exotic plant invasion, or dust and 2) effects on wildlife health and behaviour, such as changes in movement patterns or bird songs (Coffin 2007). Health and behavioural effects can spread well beyond the spatial extent of detectable environmental changes and can vary with species (Wilson 2016, Medinas et al. 2019).

Whether measuring environmental or behavioural effects, the resulting zone of influence is most often delineated as a simple buffer zone around the disturbance feature based on the calculation of a Euclidean distance threshold (Shanley and Pyare 2011, Boulanger et al. 2012). A drawback to the buffer approach to managing disturbances is that zones of influence are not constant widths but are context-specific (Kite et al. 2016). For example, zones of influence around roads for desert tortoises (*Gopherus agassizii*) have been estimated to extend less than 200 m from roads in some studies but over 3 km from roads in others, depending on the criteria used (Boarman and Sazaki 2006). In reality, the boundaries of a zone of influence are irregular, extending to varying degrees from a feature depending on the characteristics of the disturbance, surrounding landscape, and the species of interest (Forman and Deblinger 2000, Coffin 2007, Shanley and Pyare 2011). In fact, the Canadian Environmental Assessment Agency recommends that practitioners consider flexible boundaries when estimating the zone of influence for environmental impact assessments (CEAA 2012). Recent literature demonstrates a move towards more mechanistic methods of building zones of influence, by, for example, investigating changes in animal distributions or movement (Boulanger et al. 2012, Kite et al. 2016).

One way to improve our understanding of the mechanisms of animal response to disturbance is to study sensory detection (Tablado and Jenni 2017); animal decision making depends on collecting data via sight, sound, or chemosenses (Fagan et al. 2017). While disturbances may also influence wildlife behaviour via undetected secondary effects, quantifying an animal’s ability to perceive a disturbance increases our ability to make inferences about their subsequent behaviour. Visual or auditory perception may be estimated by modelling viewsheds (sight propagation) and soundscapes (sound propagation) around the disturbance. While constant buffer zones of influence do not consider the dynamic nature of either the geographical or the biological context, viewshed and soundscape modelling incorporate both of these aspects. The type, structure and configuration of vegetative, geological and edaphic conditions in a landscape influence sight and sound propagation, and the resulting perception of that signal is essential to animal movement and behaviour.

Past research has used viewsheds and soundscapes to assess zones of influence around disturbances, but for largely different purposes. Although zones of visual impact are common for human aesthetic purposes (Wood 2000), they are rarely used for wildlife except to assess visibility as a measure of risk (Montgomery et al. 2012, Buchanan et al. 2014). Conversely, sound has often been considered an important part of the zone of influence for wildlife (Shannon et al. 2016). Studies of sound disturbance commonly examine how anthropogenic noise disrupts animal communications (Shannon et al. 2016), and noise has been found to negatively affect widlife abundance and body condition (Ware et al. 2015, McClure et al. 2017). However, few studies have used sight or sound as measures of perceptibility – how detectable the disturbance is (Brown et al. 2012a). Understanding how perception affects the zone of influence is an important avenue for new research.

To investigate the role of perception in understanding the effects of disturbances on wildlife, I developed a case study using grizzly bears (*Ursus arctos*), a threatened species in Alberta, Canada (Festa-Bianchet 2010). The negative effects of roads on grizzly bears have been addressed in various regions by either limiting road densities or limiting public access to roads (Festa-Bianchet 2010, Boulanger and Stenhouse 2014). However, the variety of responses observed by grizzly bears to roads makes it difficult to generalize management decisions across landscapes. Proctor et al. (2020) reported estimates of road impacts on grizzly bear behaviour and survival extending between 100 m and 1 km, settling on 500 m as the minimum distance for habitat to be classified as “secure” (unaffected by the road). However, more research into the spatial extent of road disturbance is needed (Proctor et al. 2020).

In this chapter, I addressed two objectives. My first objective was to estimate perception of roads using viewshed and soundscape modelling with detailed remotely sensed landscape data. My second objective was to demonstrate how this perception data could be used with wildlife movement data to estimate context-specific zones of influence (or “road-effect zones”) using data from grizzly bears in Alberta, Canada. I hypothesized that the zone of influence would extend further in areas where roads are perceptible than in areas where roads are imperceptible.

3.2 Methods

Detailed landscape and road data were used to model a visual zone of influence (viewshed) and auditory zone of influence (soundscape), which were combined to create a perceptual zone of influence (Figure 3.1). The modelled perception layers were then related to grizzly bear movement data using modified semivariogram models to create a behavioural zone of influence specific to grizzly bears, as described in the diagram below (Figure 3.1).

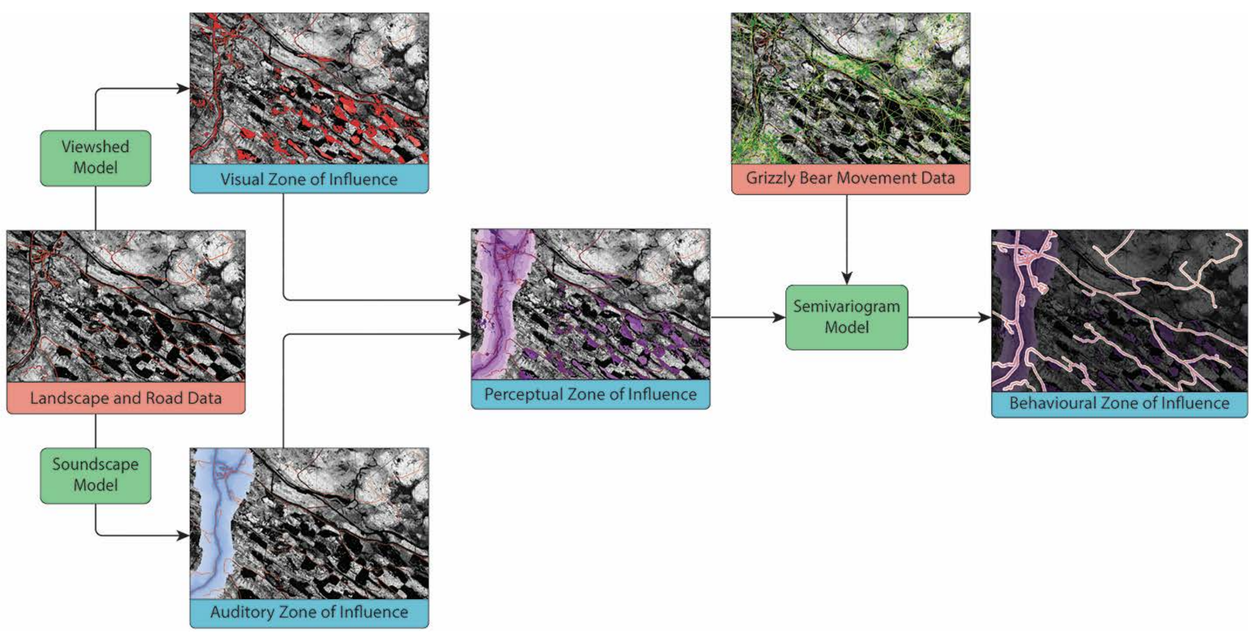

Figure 3.1 Flow diagram of approach to building perceptual and behavioural zones of influence

3.3 Perception analyses

3.3.1 Viewsheds

Viewsheds can be used to approximate visual perception using 3D topographic and vegetation data at an x, y, z (height above ground) location (Aben et al. 2018). To create viewsheds, lidar data was resampled to a 10 m resolution. Viewsheds are usually considered intervisible, assuming that if Point B is visible from Point A then Point A must also be visible from Point B (Llobera 2003). Therefore, I modelled viewsheds at points along roads at 10 m intervals then assessed where a given bear relocation was in relation to the viewshed, rather than calculate the viewshed for each bear point and look for a road within it. All locations with clear sightlines to a road were assigned as within the viewshed. Since most studies of grizzly bear selection and survival agree that the zone of influence around roads for grizzly bears is less than or equal to 1 km (Proctor et al. 2020), the analysis was limited to within this buffer.

I performed two viewshed analyses for comparison: one using the DEM, representing a bare landscape, and one using the DSM. DSMs, which incorporate natural and anthropogenic features on the landscape such as trees and buildings, are useful for characterizing forested landscapes (Aben et al. 2018). DSMs do not account for forest permeability and gaps at resolutions coarser than individual trees, potentially resulting in false negatives, where visible areas are classified as invisible (Murgoitio et al. 2013). However, for my analyses it was assumed that forests block most lines of sight, which is reasonable for roadside forest in BMA 3. Oldershaw (2001) did field tests of visibility in Alberta forest interiors, finding that maximum visibility averaged 18 m for Engelmann spruce forests and 26 m for lodgepole pine forests. It can be assumed that visibility is even lower when looking in from a road, as forest edges are often denser than the interior due to greater light availability and increased shrub presence, eventually forming a closed side canopy blocking light penetration (Matlack 1994).

A challenge to using the DSM for viewshed analyses is that the model runs as if observers are standing on top of trees and buildings. To address this, an additional output of the visibility analysis was used: the Above Ground Level (AGL). The AGL is zero for all visible cells, but for invisible cells provides the height the cell would need to be raised to be visible. I combined this with the canopy height model (CHM). If the CHM > 1 m, the approximate grizzly bear eye height, visible cells were reclassified to invisible as the grizzly bear would be standing within the trees rather than on top of them. For invisible cells, if CHM + AGL was less than 1 m it was assumed a grizzly bear would be able to see above the vegetation and it was reclassified as visible.

Viewsheds are most often considered as a binary response: visible or invisible (Davies et al. 2016). However, clarity decreases with distance, so that objects on the edge of a viewshed are much less obvious than objects near the viewer (Fisher 1994). Several models of non-binary viewsheds have been proposed (Table 3.1); however, for this thesis I used a simple distance decay of 0.975 per 25 m (visibility = $0.975^{distance/25}$) (Skov-Petersen and Snizek 2007) making viewsheds comparable to the built in modelled decay of the soundscapes. The distance decay was applied separately for each road point, as the nearest road point to a cell is not necessarily the nearest point to which it is visible. The minimum visibility for areas within the viewshed was 0.36 at a distance of 1 km.

Table 3.1 Review of viewshed methods

Method	Description	References	Software
Binary Viewshed	Points are intervisible if a straight line connecting them is always above the surface	De Floriani and Magillo 2003	Built into ArcGIS (Spatial Analyst Visibility with OBSERVERS as Analysis type)
Cumulative viewshed	Counts how many times a point is visible	Chamberlain and Meitner 2013	Built into ArcGIS (Spatial Analyst Visibility with FREQUENCY as analysis type)
Probable Viewshed	Monte Carlo simulation of DEM error to account for uncertainty	Fisher 1994, Rášová 2014	ArcGIS Desktop toolbox developed by Rášová (2014) https://www.arcgis.com/home/item.html?id=9645d482c2f341fba27890c6346a097b
Fuzzy viewshed	Visibility decreases with distance decay function (usually exponential)	Kumsap et al. 2005, Ogburn 2006, Rášová 2014	ArcGIS Desktop toolbox developed by Rášová (2014) https://www.arcgis.com/home/item.html?id=5e9cb4fd73fe4288a4cf534cc5a119aa; see also Alberti (2017)
Higuchi viewshed	Visibility is divided into 3 zones: perfect clarity, decaying clarity, and background	(Wheatley and Gillings 2000, Rášová 2014)	ArcGIS Desktop toolbox developed by Rášová (2014) https://www.arcgis.com/home/item.html?id=5e9cb4fd73fe4288a4cf534cc5a119aa
Visual Magnitude	Proportion of an observer's field of view calculated from distance, slope, and angle	Fabrizio and Garnero 2013, Chamberlain and Meitner 2013	ArcGIS Pro toolbox developed by (Chamberlain and Meitner 2013) https://github.com/czechflek/VisualMagnitude

Table 3.2 Sample of sound propagation models used in ecological soundscape modelling

Method	Description	References	Software
SPreAD-GIS	Developed for modelling noise from outdoor recreation	Reed et al. 2012, Keyel et al. 2017	ArcGIS Desktop toolbox developed by Reed et al. (2012) http://sarahreed.squarespace.com/tools/
CadnaA	Models traffic noise using count data	Barber et al. 2011, Bastián-Monarca et al. 2016	Commercial software available from https://www.datakustik.com/en/products/cadnaa/
NMSim	Developed for aviation	Fleming et al. 2005, Keyel et al. 2017	ArcGIS Desktop toolbox developed by Reed et al. (2012) http://sarahreed.squarespace.com/tools/
ISO 9613-2	International standard for noise propagation; older model	Schomer 2003, Keyel et al. 2017	ArcGIS Desktop toolbox developed by Reed et al. (2012) http://sarahreed.squarespace.com/tools/
Predictor Analyst	Designed for environmental noise mapping	Iglesias-Merchan et al. 2018	Commercial software available from https://www.bksv.com/en/News/Predictor-LimA-latest-version

3.3.2 Soundscapes

Soundscapes can be created by modelling sound propagation from noise sources over a landscape, taking into consideration land cover and elevation data (Reed et al. 2012). A single averaged sound level is highly inadequate to describe sound around the road network in rural Alberta, as traffic varies by season and industrial activity, which can change considerably from year to year. Unfortunately, real-time sound data is unavailable for previously collected GPS locations. Therefore, I only modelled roads where traffic levels were sufficient that relatively constant noise emission could be assumed. Although several models of traffic noise have been developed (Table 3.2), I used SPreAD-GIS which is specially designed for rural areas such as BMA 3 (Reed et al. 2012). Soundscapes were modeled at 30 m intervals along roads using 30 m resolution land cover and elevation data. A resolution of 30 m is recommended by Keyel and Reed (2017) as an acceptable trade off between detail and processing time for sound modelling. Sound was modelled at one third octave frequency bands between 400 and 2000 Hz and then weighted and reported as db(A). In the absence of sound data around roads, input sound levels for traffic were taken from Harrison et al. (1980) as recommended by Keyel and Reed (2017). Input sound levels varied by frequency between 60 and 68 dB at 15 m from the source. The decay function depended on frequency, elevation, vegetation type, and weather conditions (Table 3.3; Reed et al. 2012).

Table 3.3 Input values used for SPreAD-GIS sound modelling

Inputs	**Temperature**	**Humidity**	**Wind Direction**	**Wind Speed**	**Seasonal Conditions**
Value	20°C	50%	200°	6 km/h	Clear, calm summer day

Because sound levels are additive when there are multiple sources, a road with many vehicles will propagate sound further than a road with few vehicles. Therefore, for busier paved roads I converted frequencies to acoustic energy and summed the energy from each point to create the soundscape, so that each cell on the landscape was receiving sound from multiple road points at once. For two lane gravel roads, the model was built taking only the maximum energy value from a single point for each cell, assuming one vehicle present on a road segment at a time. Sound was not modelled for unimproved roads (i.e., single lane gravel and dirt roads) because I assumed that sound emitted by lower traffic volumes was inconsistent.

A predetermined audio perception threshold was used to calculate areas within hearing of bears. I used 25 dB as the threshold, which represents approximate ambient sound levels in undisturbed wilderness; ambient sound levels vary from approximately 20 dB in barren landscapes to 29 dB in coniferous forests (Kelly 2013).

The DSM viewshed and soundscape were combined to estimate a “perception zone” where bears could see or hear a road. Sight and sound layers were both scaled between 0 and 1 and then each cell value was summed to represent the combined perceptibility of sight and sound, with a maximum perception value of 2.

3.3.3 Movement analyses

I used grizzly bear GPS data as described in Chapter 2 in a modified semivariogram analysis. For the analyses described in this chapter, GPS data was limited to those collected between 2007 and 2014 (Figure 3.2).

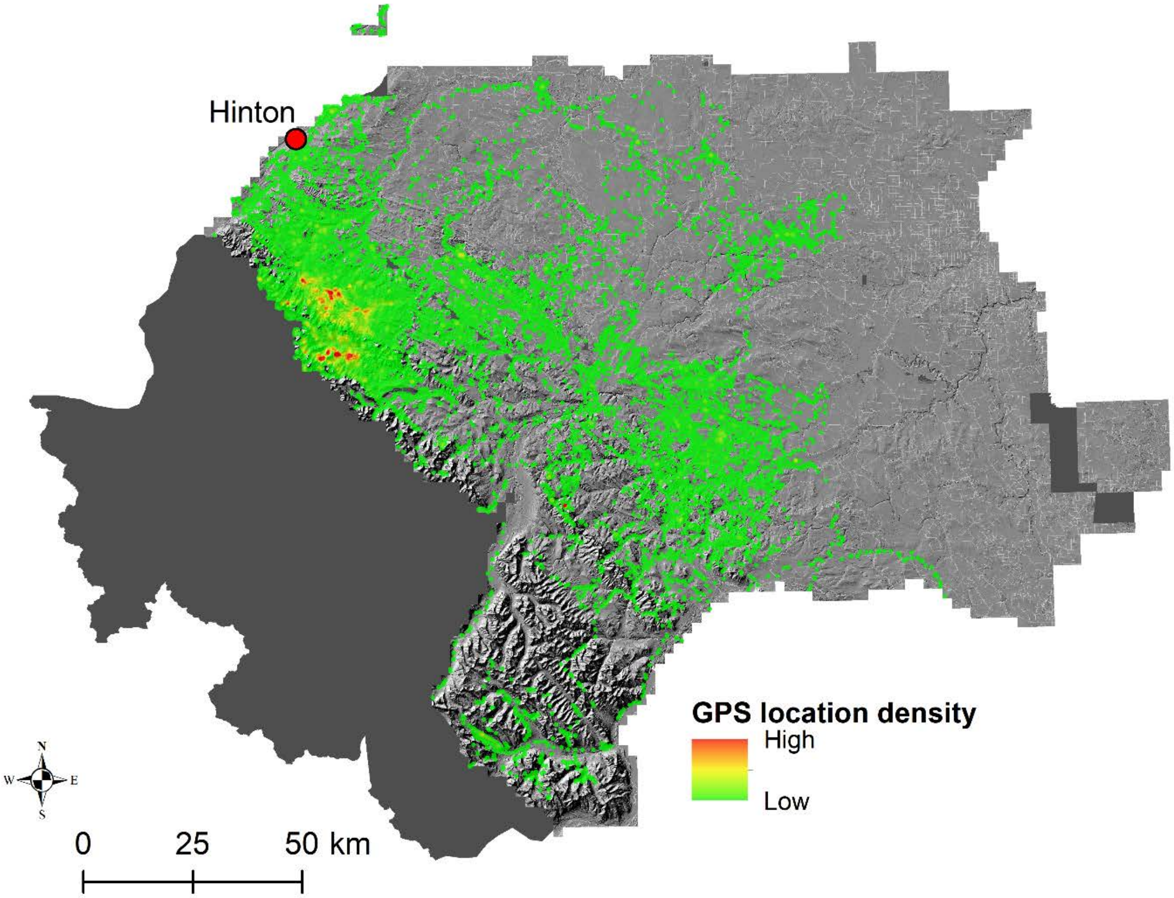

Figure 3.2 Density heat map of grizzly bear GPS locations from 2007 to 2014

To account for changes occurring on the landscape between 2007, when lidar data was collected, and 2014, any GPS points recorded in areas where Landsat imagery indicated significant changes such as clear-cutting or growth had occurred were removed. Omissions represented less than 10% of the original dataset. All data was cropped to the extent of the lidar coverage. Data was limited to within 500 m from the road because of insufficient data from perceptible areas at greater distances and because results from Kite et al. (2016) suggested response distances well under 500 m. After filtering, models were built on 39482 data points from 28 individual bears and 54 bear years. Of these, 36.9% of the data came from 10 adult females (breeding = 21.4%, nonbreeding = 15.4%), 22.9% of the data came from 8 sub-adult (age less than 5 years) females (breeding = 7.7%, nonbreeding = 15.2%), 20.4% came from 8 adult males (breeding = 10.6%, nonbreeding = 9.8%), and 19.9% came from 8 sub-adult males (breeding = 9.8%, nonbreeding = 10.0%). Some bears had data as both sub-adults and adults. The number of points per individual ranged from 28 to 5038.

I used a modified semivariogram approach to test for differences in response distances between areas perceptible (either by sight or by sound) and imperceptible to a road. Semivariograms assess autocorrelation between points by visualizing the variance in an attribute at increasing binned distances (Turner and Gardner 2015). The distance where variance levels off gives the range, where locations are no longer autocorrelated (Turner and Gardner 2015, Kite et al. 2016). Semivariograms can be modified so that instead of plotting the variation in attributes between pairs of points, the coefficient of variation in groups of points is plotted at increasing distance bins from a feature (Kite et al. 2016). In this case, the range represents the distance at which a feature no longer influences that attribute. I followed a similar approach to that outlined by Kite et al. (2016) by using the range of modified semivariograms of grizzly bear step lengths (natural log transformed) to assess mechanistically at what distances bears respond to roads. Step lengths, the distance between two consecutive GPS fixes, are commonly linked to animal behaviour; for example, long step lengths may indicate searching for new forage patches, whereas short step lengths could indicate within-patch foraging (Morales et al. 2004) or mating behaviour (Graham and Stenhouse 2014). By plotting variance in step lengths with distance to roads and determining where variance levels off, the response distance where roads no longer impact grizzly bear behaviour can be inferred.

Grizzly bears have previously been found to have different movement patterns between day and night (Nielsen et al. 2004a, Graham and Stenhouse 2014). In addition, perceptibility is expected to change based on light availability and time-dependent traffic levels. Grizzly bear GPS locations were divided into areas perceptible to a road (perceptibility > 0) and those imperceptible to any road (perceptibility = 0), as well as into daytime locations (5 AM to 10 PM) and nighttime locations (10 PM to 5 AM). While Kite et al. (2016) subsetted bear locations into classes based on sex, age, and season, previous research has suggested that there should be at least 30 - 50 points per distance bin (Babish 2000) resulting in insufficient data within some categories for my analysis. Therefore, data was pooled in a population level model. Distance bins of 10 m were used to match the scale of the viewshed data. I fit curves to the semivariograms using least squares regression and chose the curve with the lowest residual sum of squares as the best fit. The range, or response distance, was found by calculating the cumulative sum of differences between the average slope and the slope for each lag; the maximum cumulative sum value identifies where variation stops increasing and becomes random (Kite et al. 2016).

I used the maximum response distances determined by the semivariograms for imperceptible and perceptible areas to determine a combined behavioural zone of influence for grizzly bears that accounts for visual and auditory perception. I also examined how perceptibility influenced average step lengths near roads.

3.3.4 Comparing zones of influence

To assess how the perceptual zone of influence compares to the standard distance-based zone of influence I calculated the area within the binary perceptual zones of influence compared to the most accepted distance buffer of 500 m (Mattson et al. 1987, Proctor et al. 2020). The zones of influence using the DSM and DEM viewsheds were also compared by calculating the percent change in area, in order to estimate how forestry practices or other vegetation disturbances may influence the perceptual zone of influence. Finally, the behavioural zone of influence was compared with all other options.

3.3.5 Software

The viewshed analysis was conducted using the arcpy tool “Visibility” within the spatial analyst extension. Soundscape modelling was carried out using SPreAD-GIS from the ArcGIS Sound Mapping Toolbox (Reed et al. 2012), run through arcpy. Semivariogram modelling and area calculations were performed in R (R Core Team 2019). Maps were created in ArcGIS.

3.4 Results

3.4.1 Perception analyses

My approach resulted in the generation of four perception-based zones of influence (Figure 3.3).

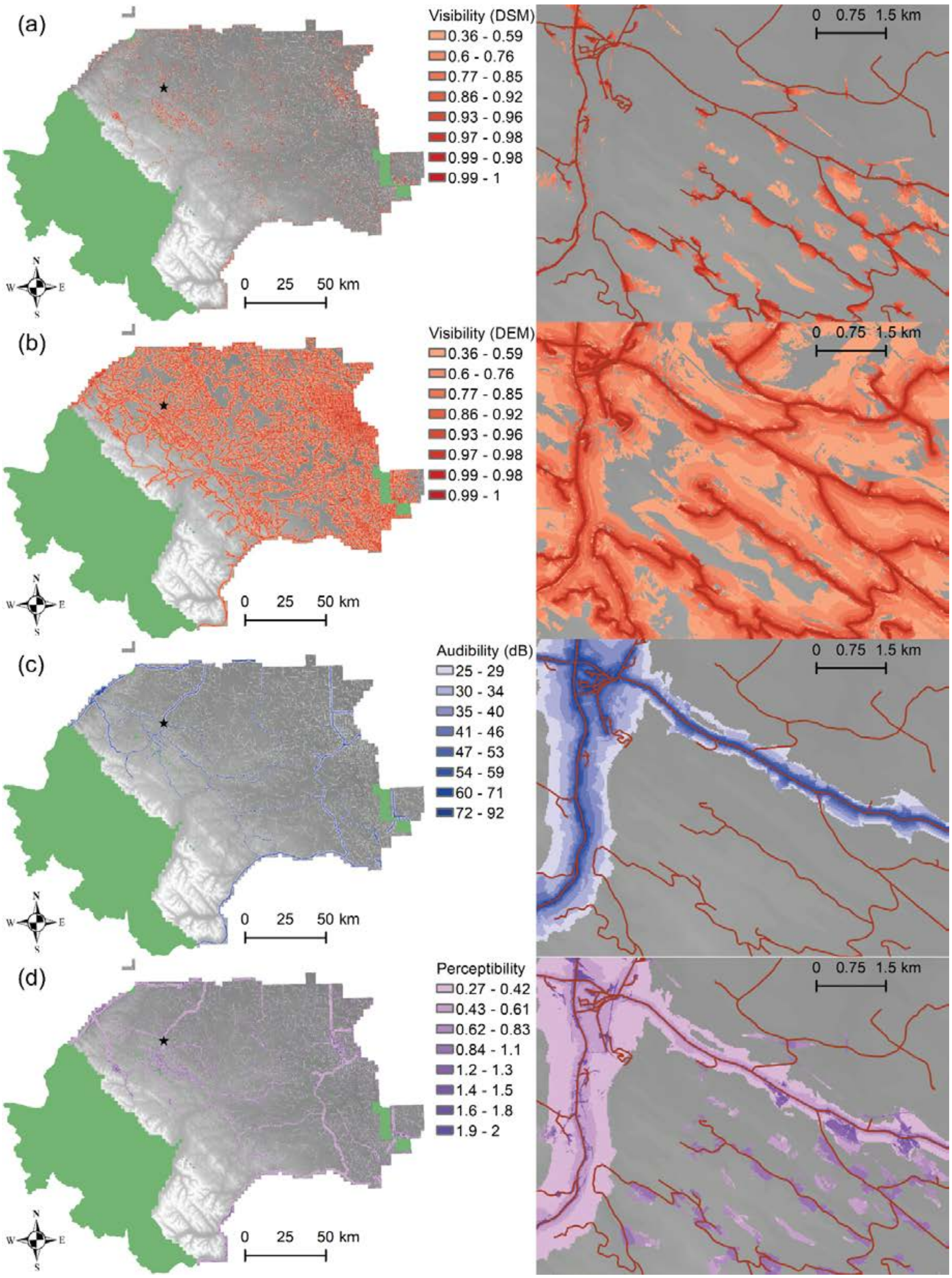

Figure 3.3 Model outputs for a) Visual Zone of Influence (DSM), b) Visual Zone of Influence (DEM), c) Auditory Zone of Influence, d) Perceptual Zone of Influence, combining DSM visibility and scaled audibility. The star marks the location of the magnified panel

The distance decayed viewshed had a maximum value of 1.0 (perfect visibility) and a minimum value of 0.36 at 1000 m (Figure 3.4 a-b). The soundscape was cut-off at a minimum of 25.0 dB and rose to a maximum of 92.0 dB adjacent to the road (Figure 3.4 c). Scaled, this layer had a minimum value of 0.27 and a maximum value of 1.0. Perceptibility, combining the scaled audibility and visibility, ranged between 0.27 and 2.0, with most values falling below 1.0 (Figure 3.4 d).

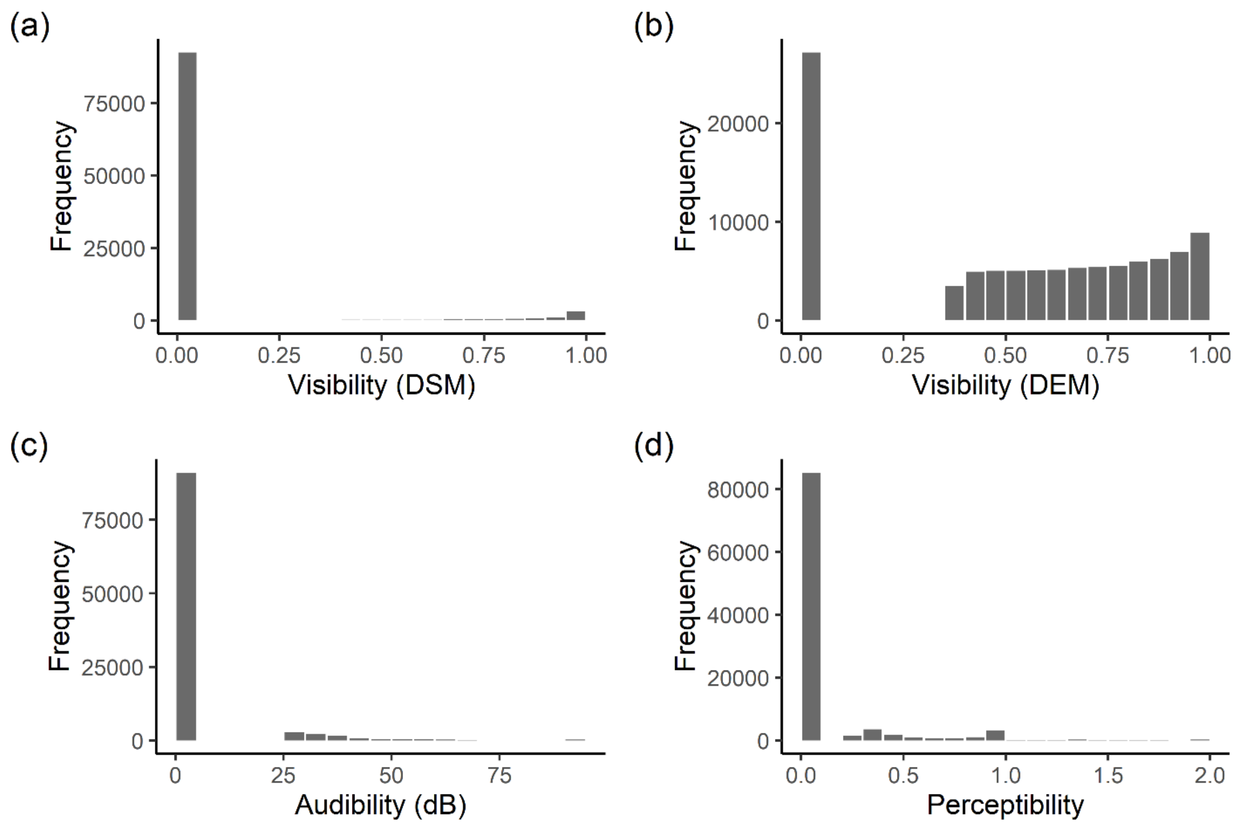

Figure 3.4 Histograms of a) Visibility (DSM), b) Visibility (DEM), c) Audibility, d) Perceptibility. Histograms were based on 100 000 pixels sampled within 1 km of a road

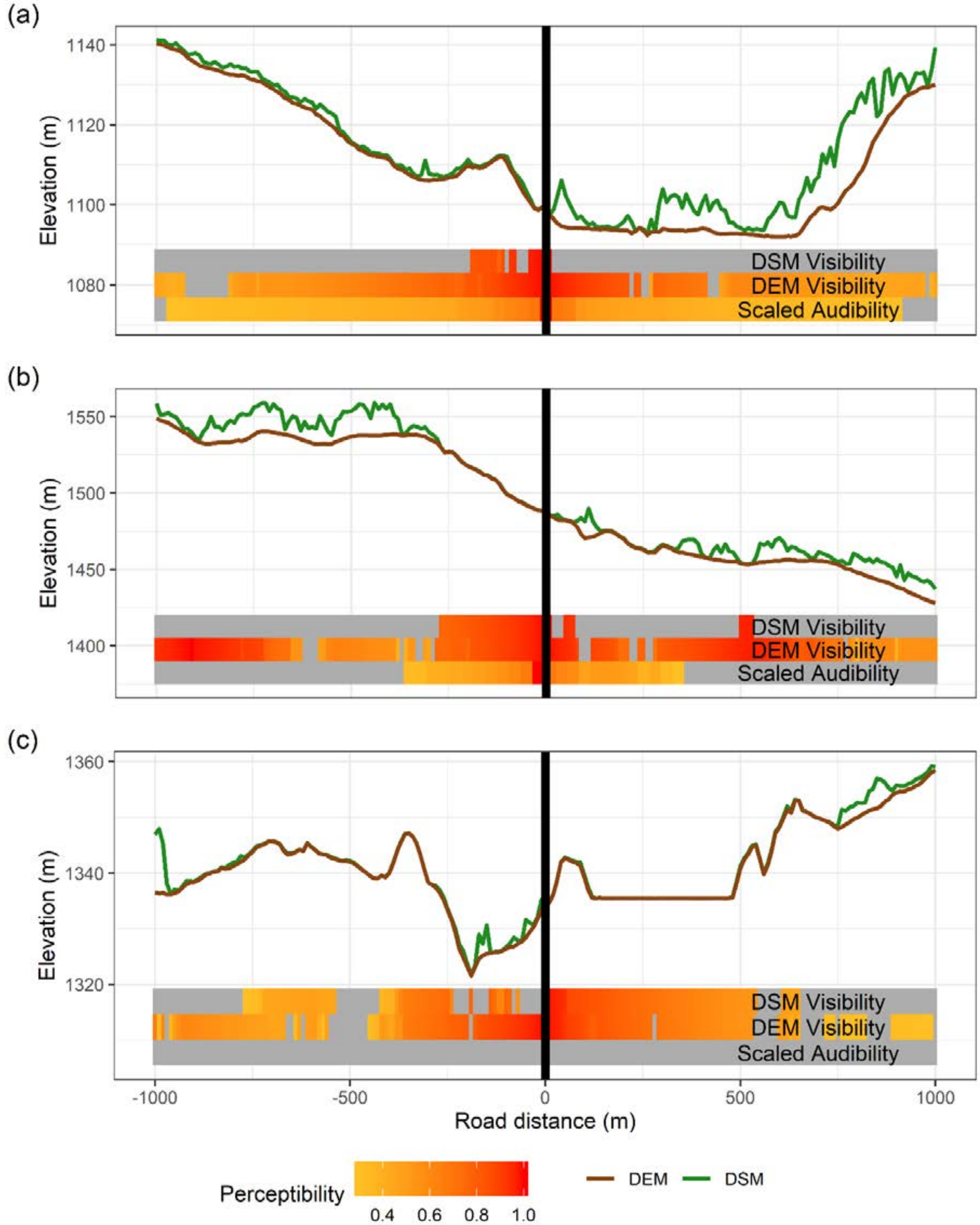

Figure 3.5 Profile plot showing changes in perceptibility for an example a) paved road, b) two lane gravel road, and c) unimproved road at increasing distances from the road, dependent on DEM and DSM. Grey areas represent 0 perceptibility. Note that although the x-axis shows distance from a single point, perceptibility may be influenced by other road sections. Negative and positive numbers represent increasing distances on opposite sides of a road

Audibility depends primarily on distance, and secondarily on topographic and land cover features, including hills and forests, which may block signal propagation (Figure 3.5 a-b). Both measures of visibility also depend on distance, but are more affected by topography and, for the DSM visibility, canopy height (Figure 3.5).

3.4.2 Movement analyses

I found that grizzly bears displayed altered movement patterns at greater distances from perceptible roads than imperceptible roads for daytime movements (Figure 3.6 a, b; Table 3.4). In addition, step lengths increased near roads in all areas, but step lengths were longer within the perceptible portion of the zone of influence (mean = 199 m, ln ~ 5.3) than the imperceptible portion (mean = 179 m, ln ~ 5.2) (Figure 3.6 c).

Table 3.4 Outcomes of semivariogram models for 28 grizzly bears from 2007 to 2014 for daytime and nighttime movements. N is number of step length observations in each subset, Med N/bear represents the median and range of the number of step length observations per bear, Function represents the best fitting semivariogram curve, RSS is the residual sum of squares, and distance is the range found by the modified semivariogram

Subset	**N**	**Med N/bear (range)**	**Function**	**RSS**	**Distance (m)**
Day (Imperceptible)	12580	274 (6 - 1564)	$Y \sim a + b/X$	0.037	60 m
Day (Perceptible)	9701	218 (1 - 1419)	$Y \sim a + b/X^{0.5}$	0.120	80 m
Night (Imperceptible)	8817	225 (17 - 1283)	$Y \sim a + b/X$	0.025	60 m
Night (Perceptible)	8384	172 (3 - 1276)	$Y \sim a + b/X$	0.186	60 m

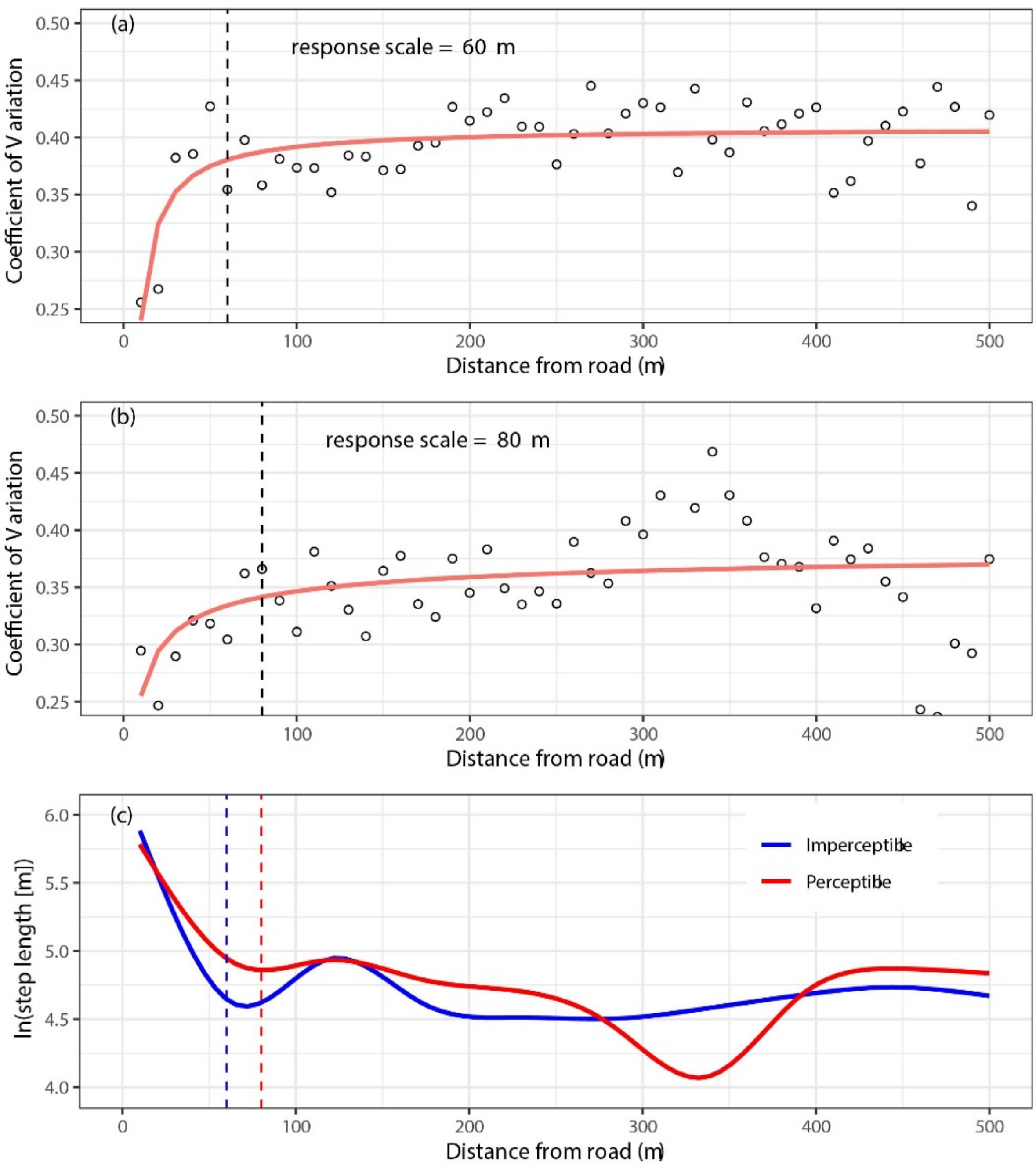

Figure 3.6 Modified semivariogram model using all daytime grizzly bear step lengths for a) imperceptible and b) perceptible areas. The y-axis is the coefficient of variation in step lengths grouped within distance bins from the road. Panel c) shows how daytime step lengths change with distance to road when perceptible and imperceptible with reference response scales

I used the 80 m response distance for perceptible areas and 60 m response distance for imperceptible areas to create a behavioural zone of influence (Figure 3.7). A response distance of

80 m represents a decayed visibility value of approximately 0.922/1, a sound level of around 40 – 60 dB depending on road type and topography, and a combined perception value of approximately 1.5/2 where perceptible by both sight and sound.

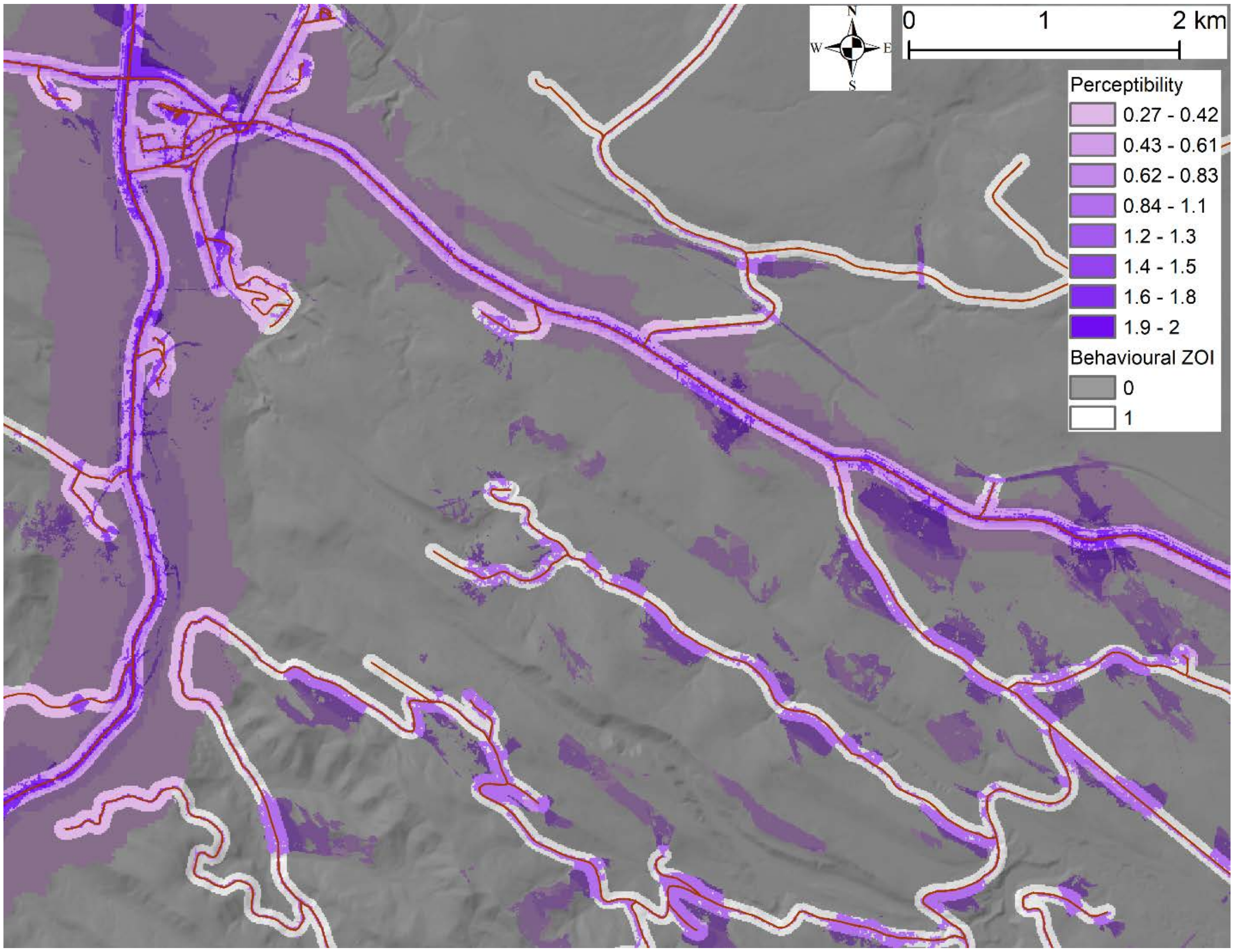

Figure 3.7 Subset of the study region showing the behavioural zone of influence (light) using 60 or 80 m buffers depending on perceptibility, overlaying the perceptual zone of influence

3.4.3 Comparing zones of influence

The smallest zones of influence are the treed viewshed and the soundscape (representing only improved roads) (Table 3.5). The treed viewshed covers 10% of the bare earth viewshed (Figure 3.8).

Table 3.5 A comparison of the area occupied by seven methods of delineating a zone of influence (ZOI)

	500 m buffer	**Visual ZOI (DSM)**	**Visual ZOI (DEM)**	**Auditory ZOI**	**Perceptual ZOI**	**Behavioural ZOI**
Area (km^2)	10501	1110	11112	1363	2241	1785
% 500 m buffer	100	10.6	105.8	12.98	21.34	16.99
% Study Area	48.9	5.1	51.4	6.3	10.4	8.2

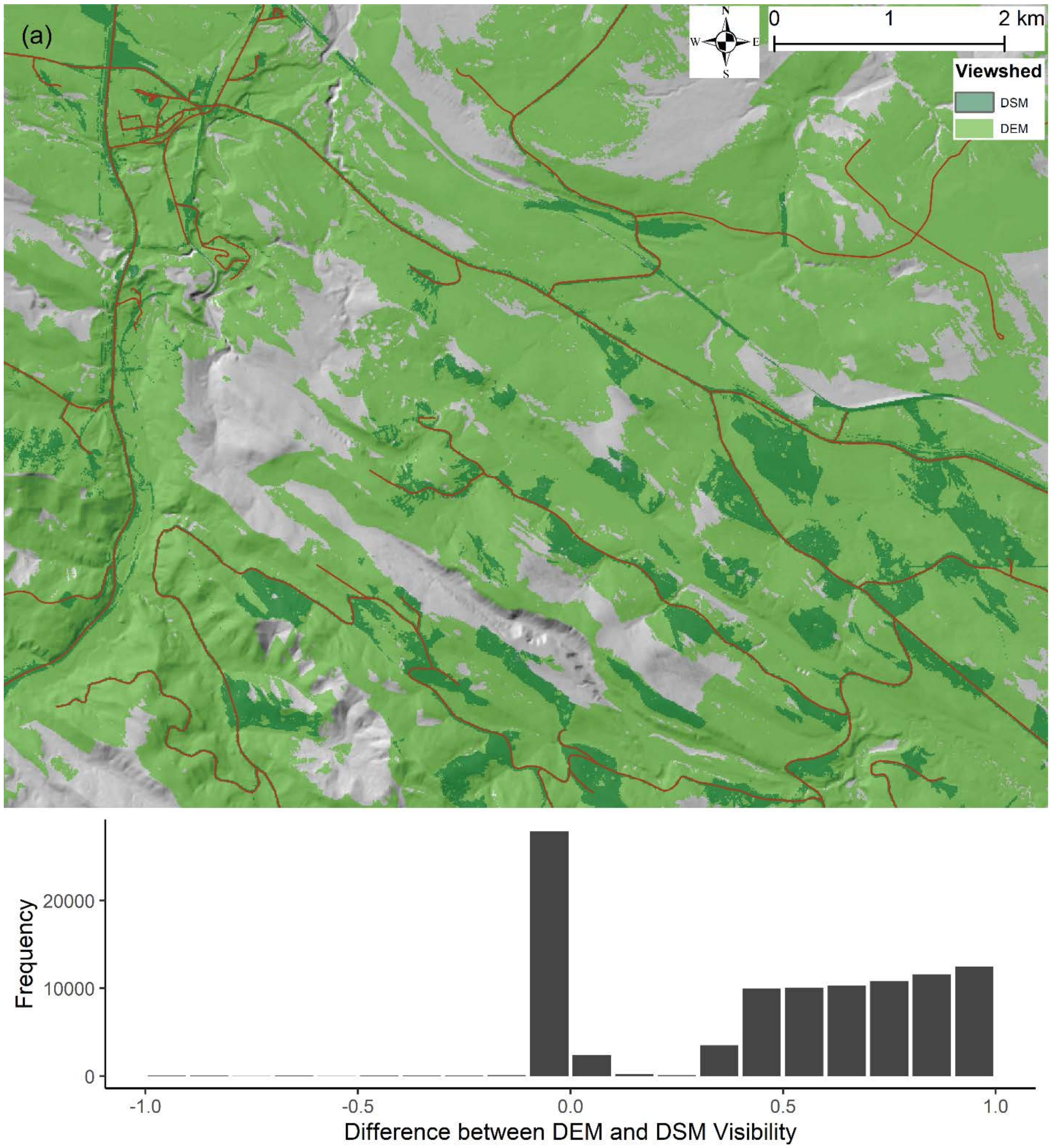

Figure 3.8 Comparison of viewsheds created using DSM (treed) and DEM (bare) landscapes; a) the DSM viewshed shows logged areas, and b) DEM visibility is much greater

3.5 Discussion

Understanding the influence of disturbances is essential to conservation. The analyses in this chapter demonstrate how landscape data may be combined with wildlife movement data to create a biologically and topographically relevant zone of influence around disturbances, using perception as the mechanistic bridge linking disturbance stimuli with behavioural response. This research aims to contribute to understanding the effects of disturbance by taking into consideration the surrounding landscape and species-specific movement behaviour (Medinas et al. 2019). Previous work has shown how changes in distributions, movement behaviours, and population dynamics can be used to estimate the zone of influence (Polfus et al. 2011); my work on perception provides one of the underlying mechanisms of these behavioural responses (Avgar et al. 2013, Tablado and Jenni 2017).

Several studies have investigated the use of sight or sound in understanding animal responses to disturbances; for example, Montgomery et al. (2012) used visibility interacting with distance to understand elk use around roads, and Brown et al. (2012a) studied the impact of anthropogenic noise on ungulate behaviour. However, few studies have considered sight and sound together. A notable exception is Clevenger and Wierzchowski (2006), who used both viewsheds and soundscapes in their model of animal movement around the Trans-Canada highway, finding that incorporating these and other fine-scale spatial databases significantly improved model reliability. In another study, Gnieser (2000) used a 200 m sound buffer plus an 800 m viewshed to determine a visitor exclusion area that minimized both auditory and visual disturbances on nesting golden eagles. My research is one of the first to incorporate sight and sound as well as wildlife movement data to create improved zones of influence.

Although limited research on perception is available for disturbances, the importance of perception is becoming widely acknowledged in predator-prey analyses (Aspbury and Gibson 2004, Loarie et al. 2013, Lawson et al. 2019). For example, viewsheds are important to determining both lion kill sites (Davies et al. 2016b), and lek selection of great bustard (Alonso et al. 2012), highlighting the importance of perception for both predator and prey. Wildlife encounters with human disturbances have been compared to predator-prey interactions (Frid and Dill 2002), supporting the incorporation of perception into understanding disturbances as well.

The response distances estimated by modified semivariogram models are comparable to those found by Kite et al. (2016), who reported response distances between 25 and 90 m for grizzly bears to roads in west central Alberta. My initial hypothesis that the zone of influence would extend further in areas where roads are perceptible than where roads are imperceptible was supported. This result corroborates previous work suggesting that wildlife avoid human disturbances at further distances in open areas than forests due to increased visibility (Benítez-López et al. 2010). However, I found that the difference between perceptible and imperceptible areas was small and only for daytime movements. The lack of differentiation between perceptible and imperceptible areas at night may correspond to low visibility and low traffic levels resulting in limited nighttime perception. In addition, visualisation of step length results showed that step lengths increased in perceptible areas more than in imperceptible areas within the zone of influence. Previous work has shown increased movement rates near roads (Roever et al. 2010), and this chapter suggests that this response is heightened when the road is perceptible. My findings are comparable to previous studies finding that animal flight distances are reduced when visually shielded (Camp et al. 1997, Ndaimani et al. 2013).

The response distance of 80 m based on variation in step lengths is very near to the road, even when only including areas perceptible to roads. This response distance represents mostly areas rated as highly perceptible by either sight or sound, suggesting that bears may not perceive roads as a risk worth changing behaviours for except at near distances and high perceptibility. These findings are consistent with previous research showing that animal responses start at sound levels above 40 dB (Shannon et al. 2016) and that the impact of visibility is highly dependent on distance (Montgomery et al. 2012).

In addition to showing that not all areas perceptible to a road influence grizzly bear movement behaviour, modified semivariogram models demonstrated that movement behaviour is affected in areas imperceptible to roads. This result implies a minimum response distance to roads, even when not visible or audible. A response may be caused by perception that was not picked up in my model, such as occasional traffic noise on roads where sound was not modelled, glimpses of a road through gaps in trees, or a bear having recently passed through an area where it could perceive the road. Grizzly bears may also be responding to olfactory cues, which were outside of the scope of this study. Alternatively, responses to roads may be unrelated to perception, but due to differences in vegetation and topography near roads, or memory (Avgar et al. 2013). Grizzly bears are known to become habituated to human disturbances (Roever et al. 2008a, Penteriani et al. 2016), thus grizzly bears may be less likely to respond to disturbances which they have encountered before regardless of perceptibility. Future work could compare movement patterns between recently translocated bears and bears within their home range to investigate the relationship between perception and habituation. Grizzly bears may also alter movement patterns around roads based on attractive food resources such as regenerating vegetation along roadsides (Roever et al. 2008a).

Semivariogram model results can be sensitive to changes in model parameters including bin distance or maximum distance cut-off, limiting the confidence in the exact estimates. In addition, differences between perceptible and imperceptible areas were low, representing only two distance bins. The results may have been affected by limited data in some distance bins (e.g., very few imperceptible areas immediately adjacent to roads), unaccounted for changes in the landscape between the creation of the perception layer and the grizzly bear movement data, intermittent sound on unimproved roads, or because of additional unmeasured variation in bears or the landscape. Grizzly bears have been found to differ in their responses to road based on sex, age, and season (Roever et al. 2010), as well as traffic levels (Northrup et al. 2012). For example, female grizzly bears with cubs have been suggested to use areas with higher levels of human disturbance to avoid infanticidal males (Cristescu et al. 2016b), and also have overall lower movement rates than other grizzly bears (Schwartz et al. 2003), making it difficult to generalize responses at the population level. Sensitivity to additional factors should be considered when making management decisions. Future research could also consider the influence of visual and auditory perception separately, as animals may respond differently to different types of perception. For example, while either sight or sound may alert an animal to the presence of a disturbance, it may be that the animal associates one of these signals with risk but not the other. My findings that perception influenced grizzly bear movement variability and speed suggest that the role of perception in animal response merits further research.

Chapter 4: Road perception influences habitat selection by grizzly bears (*Ursus arctos*)

4.1 Introduction

The study of animal behaviour is incomplete without considering the overarching effects of human activity on the landscape. Few wildlife populations are untouched by human activity; in particular, roads are considered the largest global anthropogenic disturbance and continue to expand at rapid rates (Brady and Richardson 2017). Roads have many detrimental effects on wildlife populations, such as causing direct mortality through vehicle collisions and acting as a barrier to movement, resulting in road avoidance by many species (Coffin 2007). However, some wildlife display selection of roads and roadsides, possibly because roads can act as food sources or travel corridors (Dickie et al. 2020). Habitat selection around roads has been studied extensively, however, many studies use simple distance-to-road metrics without considering how the environmental context around roads may affect animal behaviour (Montgomery et al. 2012). As improvements in remote sensing technology increase the availability of fine-scale landscape data, I can develop more nuanced explanations of animal responses and better mitigate the effects of disturbances.

In the previous chapter I created viewsheds and soundscapes and demonstrated how perception data may be used with wildlife data to make inferences about zones of influence. In this chapter I take a closer look at how visual and auditory perception may influence both grizzly bear behaviour and risk.

Visibility may influence not only a bear's awareness of the landscape, but also how it interacts with people. While a grizzly bear hearing road traffic will not affect whether it is detectable by humans, visibility is usually considered two-way, thus how visible a road is to a grizzly bear is equivalent to how visible a grizzly bear is to someone travelling along the road. Therefore, visibility may influence not only animal behaviour but also human-caused risk around roads. Several studies of grizzly bear behaviour around roads have suggested that visibility may increase the likelihood of negative human-bear interactions around roads, recommending leaving buffer strips of forest to reduce visibility between forage-rich cut blocks and roads when forest harvesting occurs (Graham et al. 2010, Roever et al. 2010, Kite et al. 2016). However, no known research is available linking grizzly bear mortality around roads to visibility.

4.1.1 Research aim

The objectives of this chapter were to investigate the role of perception in grizzly bear habitat selection and mortality around roads. I hypothesized that road perception increases perceived and actual risk of human-caused mortality for grizzly bears resulting in modified habitat selection and mortality in visible areas. I addressed three specific hypotheses: 1) Models of grizzly bear habitat selection including road perception will improve upon models without road perception. 2) Grizzly bears will be more likely to select areas near roads, as has been found previously, but will be less likely to select areas perceptible to roads. 3) Grizzly bears that have died during the study period will be more likely to select road visibility than grizzly bears that have survived. I tested my hypotheses by evaluating selection coefficients from models of grizzly bear movement using integrated step selection analysis and viewsheds and soundscapes derived from remote sensing data. The second hypothesis was evaluated using only the perception variable found to be the most useful in modelling habitat selection based on the results of the first hypothesis.

4.2 Materials and methods

Integrated step selection analysis (iSSA) was used to evaluate grizzly bear responses to road perception. First, I used iSSA on individual bears and years and selected the best model describing grizzly bear movement and habitat selection using corrected Akaike Information Criterion (AICc). Then, the best model was used to create a population level model and bootstrapped selection coefficients were calculated to assess population responses. To assess whether road visibility influenced mortality risk, selection coefficients were compared between bears that survived and bears that died. Finally, I compared the locations of grizzly bear mortalities with GPS locations of live bears and landscape availability to explore whether mortalities were more frequent when visible to roads.

4.2.1 Study area

For the second stage in the analysis I limited my study area to grizzly bear core and secondary areas within BMA 3, an area of 11 590 km^2 as described in Chapter 2.

4.2.2 Grizzly bear movement data

Grizzly bear movement data between 2006 and 2017 as described in Chapter 2 was used. Any grizzly bears with less than two weeks of data (672 observations) were removed from the analysis, leaving 39 individual bears (18 females and 21 males) and 69 bear-years.

4.2.3 Creation of landscape variables

Ten landscape variables were created from remotely sensed data for inclusion in iSSA models (Table 4.1). These variables were chosen to represent terrain, resource availability and risk, which are expected to influence grizzly bear habitat selection patterns (Nielsen et al. 2010). I used the perception layers as described in Chapter 3 as predictors of interest. To evaluate potential landscape changes in canopy height occurring between the time of lidar collection and the later grizzly bear data for the visibility layer, I consulted annual disturbance and forest cover data derived from remotely sensed Landsat imagery (Hermosilla et al. 2016, 2017, 2018). When evaluating potential changes, I reclassified visible areas to invisible if a location changed from open in 2007 to forested at the time of grizzly bear movement, and if sufficient time had passed for growth of greater than one meter to occur. Invisible areas were reclassified to visible if a stand-replacing disturbance occurred and if the location was visible when modelled using a DEM (bare landscape). Visibility was estimated to change for only 3.8% of grizzly bear locations and running models with and without estimated changes was not found to alter model inferences, therefore I retained all original data. Elevation and absolute distance to edge were also derived from lidar data. Absolute distance to edge describes the distance from the forest edge either from or within a forested stand > 2m in height.

Food layers were created for ten bi-monthly periods from the beginning of May to the end of September based on the modelled distributions of important grizzly bear foods, compiled and weighted to provide a rating between 0 and 100 where 100 is the maximum food value, as described in Nielsen et al. (2010). Food models were available annually from 2014 onward, and the 2014 model was used for grizzly bear data collected before 2014. Solar Insolation and Terrain Wetness Index were derived from the NASA Shuttle Radar Topography Mission

(SRTM) digital elevation model. Solar Insolation uses terrain variability to estimate the amount of solar energy reaching the Earth's surface, and terrain wetness index describes the distribution of surface water.

Distance to road was calculated as Euclidean distance to the nearest road using road layers downloaded from the Government of Alberta web portal (https://geodiscover.alberta.ca/).

4.2.4 Integrated step selection analysis

An extension of Resource Selection Functions, iSSA is commonly used to model animal behaviour, allowing selection to be modelled as a result of movement and habitat variables simultaneously (Prokopenko et al. 2017, Scrafford et al. 2018). Availability in iSSA is defined on a stepwise basis: each observed step, or set of two consecutive data points, is compared to possible steps with the same origin. Thus, availability is relative to the probability of an animal taking a step in the absence of habitat selection (Avgar et al. 2016, Prokopenko et al. 2017).

Five random available steps were generated for each observed step, based on the distributions of observed step lengths (Euclidean distance) and turning angles (angular deviation in direction). Predictor variable information was extracted from the end of each observed and available step. Continuous predictor variables were standardized by subtracting the mean and dividing by the standard deviation, and checked for Pearson's Correlation. All pairwise correlation coefficients were less than 0.5.

Table 4.1 Predictor variables used in step selection modelling with references indicating relevance to grizzly bear habitat selection

Predictor Variable Name	Spatial Resolution	Reference
Natural $\log_e$ of step length (Ln(sl))	n/a	Munro et al. 2006
Time of Day (Tod)	n/a	Munro et al. 2006
Food rating (Food)	30 m	Nielsen et al. 2010, Larsen et al. 2019
Elevation (Elev)	10 m	Nielsen et al. 2004b, Nielsen 2005
Solar Insolation (Insol)	30 m	Nielsen et al. 2004a, Nielsen 2005
Terrain Wetness Index (TWI)	30 m	Nielsen 2005
Absolute distance to edge (Edge)	30 m	Nielsen et al. 2004a, Stewart et al. 2013
Distance to road (Rd)	10 m	Roever et al. 2010, Boulanger and Stenhouse 2014
Visibility (Vis)	10 m	n/a
Audibility (Aud)	30 m	n/a
Perceptibility (Percep)	10 m	n/a

4.2.4.1 Model Selection

To address the first hypothesis that accounting for road perception improves model performance, I created conditional logistic regression models of grizzly bear movement to determine how adding road perception affects model performance (Table 4.2). The Core model included variables selected based on previous research on grizzly bear habitat selection, but did not include any road variables (Table 4.1; Table 4.2). Additional models included either distance to road or a perception variable, or both. Step length was included to allow for differences in selection based on movement speed. Time of day was divided into day (reference category), twilight (including dawn and dusk), or night based on the sunrise/sunset calculator from the National Oceanic & Atmospheric Administration (NOAA; https://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html). In addition to the additive effects among predictor variables, I included an interaction between step length and time of day, and between step length and distance to road, to accommodate previous observations that grizzly bear movement changes with time and proximity to roads (Roever et al. 2010, Prokopenko et al. 2017). An interaction was also included between step length and perception variables.

Two rounds of modelling were completed. The first round of modelling was used to determine whether and which perception variables were important to grizzly bear habitat selection, thus I compared equivalent models including either distance to road, road audibility, road visibility, or combined road perception to each other and a core model (Table 4.2). In the second round of modelling, I added a model including both the best perception variable and distance to road. Perception variables that were not found to be important in the first round of modelling were excluded from further analyses.

Individual grizzly bear behaviour is highly variable (Northrup et al. 2012, Hertel et al. 2017), therefore each grizzly bear was modelled separately to determine the best model. I used similar methods to Prokopenko et al. (2017) and Ladle et al. (2018) to fit each model on each bear-year and calculated AICc and AICc weight to determine the best model for each bear-year. I summed the AICc tally (i.e. number of times a model had the lowest AICc) and averaged AICc weights across all bear-years to identify a best performing model that was used for further analyses (Prokopenko et al. 2017, Berman et al. 2019). I checked whether the results were biased by bears with multiple years by performing the tally using only the first year of data for each bear and results remained qualitatively similar (analysis not shown); therefore, I retained all bear-years. To determine the most important variables and consistency among grizzly bear responses I tallied the number of times each variable was significant within the best model for each bear-year and counted the number of bear-years that matched the population trend (either likely or unlikely to select) for each predictor variable.

4.2.4.2 Best Model Outputs

I predicted probability of use based on the best model as a function of road perception and distance to road using methods developed by Avgar et al. (2017). Probability of use plots are a useful visualization tool for observing patterns of selection, where selection is averaged over the range of values for other predictor variables and relative to the most suitable resource unit. For this chapter, I pooled the fitted model outputs for all available (random) steps from each of the 69 bear-years. Grizzly bear responses to road variables were divided into three movement modes; hourly step lengths of less than 10 m (ln ~ 2.30) were classified as resting (n = 64772), step lengths from 10 m - 390 m (ln ~ 5.97) were classified as foraging (n = 278040), and steps greater than 390 m were classified as travelling (n = 133720) (Hunter 2007).

To address the second hypothesis that grizzly bears will select areas near roads but avoid areas perceptible to roads, I obtained selection coefficients for the population, creating a population level model including all bears and years using the best model as determined by the AICc tally and weights. Confidence intervals for selection coefficients were calculated using 2000 bootstrapped iterations (Prokopenko et al. 2017). I used a simple cluster bootstrap clustering on individuals (n = 39), so that each bear had an equal probability of being included in a resample, regardless of the amount of data for that individual. Separate models were also created for adult males (n = 14), sub-adult males (n = 11), adult females (n = 8), sub-adult females (n = 12), and females with cubs (n = 5) to allow for differences in selection between age and reproductive classes. Sub-adults were less than five years old. Some individuals sampled in multiple years were included in more than one age or reproductive class.

4.2.4.3 Additional Interactions with Visibility

I was interested in how road visibility may interact with additional ecologically important variables, so I created two additional models for an exploratory post-hoc analysis. First, to the Distance + Visibility model (Table 4.2) I added interactions between road visibility and food availability, and between road visibility and time of day to investigate the relationships between these variables. Second, I investigated the role of road visibility at the start of the step to see whether seeing a road alters grizzly bear decisions about future habitat selection and movement. To do this, road visibility was extracted at the beginning of each step. Road visibility at the start and at the end of steps were correlated, so they were not included in the same model. Instead, I used the Distance model (Table 4.2) and added an interaction between road visibility at the beginning of the step and distance to road at the end of the step, and an interaction between beginning road visibility and step length. For both new models population level coefficients and confidence intervals were calculated using cluster bootstrapping as described above.

4.2.5 Mortality analysis

To address the third hypothesis that grizzly bears that died will be more likely to select road visibility, I compared the selection coefficients between bears that had died during the study period (2006 - 2017) with bears that survived to see whether bears that spent more time in visible areas had higher mortality. The data were divided into bears that died (n = 10) and bears that survived (n = 29), and the best model was fitted to each group using simple cluster bootstrapping. I obtained and compared selection coefficients and confidence intervals for each group.

Finally, I performed an exploratory analysis with known locations of grizzly bear deaths within the study area between 2000 and 2017. Of exact locations, 91% (20 locations) of data were within 500 m of a road, so I limited analyses to within this buffer. I compared the proportion of visible locations between mortality locations, used grizzly bear steps, and the overall landscape within 500 m of a road. Sample size was low, so the data were visualized without testing for significance.

4.3 Software

Data organization and analysis was primarily carried out in R (R Core Team 2019) using the packages “amt” version 0.0.6 (Signer et al. 2019) and “mclogit” version 0.6.1 (Elff 2018). ArcGIS was used for map creation and variable processing.

4.4 Results

4.4.1 Model selection

In the first round of selection, the Visibility model performed significantly better than competing models, and was the best model for almost half of the bear years (Table 4.2). The Audibility model performed worse than the Distance model with no perception variables and the Perceptibility model performed only slightly better than the Distance model. Therefore, the Audibility model and Perceptibility model incorporating both sight and sound were discarded for the second round of model selection and were not included in any further analyses. In the second round of model selection, the Distance + Visibility model was most commonly selected as the best model according to the lowest AICc across 69 bear-years. According to average AICc weights, the Distance + Visibility model was 44 times more likely [0.654/0.015] to be the best model than the Core model with no road variables, and 9 times more likely to be the best model than the Distance model [0.654/0.072] (Table 4.2). The Distance + Visibility model was used for remaining analyses.

Table 4.2 Model descriptions and AICc tally and average AICc weight for 69 bear-years

Model	Variables	Tally (round 1)	Weight (round 1)	Tally (round 2)	Weight (round 2)
Core	Ln(sl) + Food + Ln(sl):Tod + Elev + Insol + TWI + Edge	0	0.006	1	0.015
Distance	Core + Rd + Rd:Ln(sl)	14	0.202	4	0.072
Visibility	Core + Vis + Vis:Ln(sl)	34	0.477	17	0.259
Audibility	Core + Aud + Aud:Ln(sl)	3	0.046	NA	NA
Perceptibility	Core + Percep + Percep:Ln(sl)	18	0.269	NA	NA
Distance + Visibility	Core + Rd + Rd:Ln(sl) + Vis + Vis:Ln(sl)	NA	NA	47	0.654

4.4.2 Best model outputs

The variables that were significant for the most bear-years in the Distance + Visibility model were step length, step length interacting with time of day, and step length interacting with visibility (Table 4.3). Effect direction was determined as selection coefficients greater than one indicating more likely to select (+) and selection coefficients less than one indicating less likely to select (-), and was consistent over individuals for these variables. The selection coefficient for road visibility was not significantly different from one, indicating that at mean step length (96 m), visibility was neither selected nor avoided at the population level. However, a coefficient greater than one for step length interacting with visibility indicated that when bears had shorter than average step lengths, bears were less likely to select areas with higher road visibility. As step lengths increased, bears were more likely to select road visibility.

Table 4.3 Mean and 95% confidence intervals of selection coefficients (β) estimated from the Distance + Visibility iSSA model including all 69 bear-years (i.e. population level) model and direction of the population effect (N.S. indicates that confidence intervals overlap with one). Also shown is the number of times across 69 individual bear-year models that estimated coefficients were consistent with the direction of the population effect and number of times each variable was significant ($p < 0.05$) using the Distance + Visibility model

Predictor	Population Mean (95% CI)	Effect Direction	Effect Agreement (/69)	Significant (/69)
Ln(sl)	1.289 (1.238,1.341)	+	67	63
Food	1.022 (0.993,1.05)	N.S.	NA	29
Elev	0.829 (0.695,0.964)	-	47	39
Insol	1.037 (1.005,1.068)	+	39	37
TWI	1.007 (0.987,1.027)	N.S.	NA	19
Edge	0.783 (0.735,0.831)	-	63	49
Ln(sl):Night	0.582 (0.522,0.641)	-	66	61
Ln(sl):Twilight	0.845 (0.773,0.917)	-	45	30
Rd	0.950 (0.919,0.981)	-	43	30
Vis	1.000 (0.965,1.035)	N.S.	NA	37
Ln(sl):Rd	0.942 (0.930,0.954)	-	55	30
Ln(sl):Vis	1.143 (1.119,1.167)	+	65	54

Probability of use plots were used to illustrate trends around visibility, roads, and movement modes. As suggested by selection coefficients, when travelling, bears were more likely to use areas of high road visibility, whereas they were less likely to use visible locations when resting (Figure 4.1). No clear pattern in probability of use was observed when moving at foraging speeds. Grizzly bears were much less likely to use areas near roads at resting speeds when roads were visible, whereas there was no clear pattern in probability of use for distance to road while resting when not visible from roads (Figure 4.2). Bears were slightly more likely to use locations near roads when foraging, but were more likely to use invisible areas as they approached roads. Locations close to roads were most likely to be used when grizzly bears were travelling, with little differentiation between visible and invisible areas. Narrow confidence intervals may be attributed to the high number of available steps used for probability of use plots.

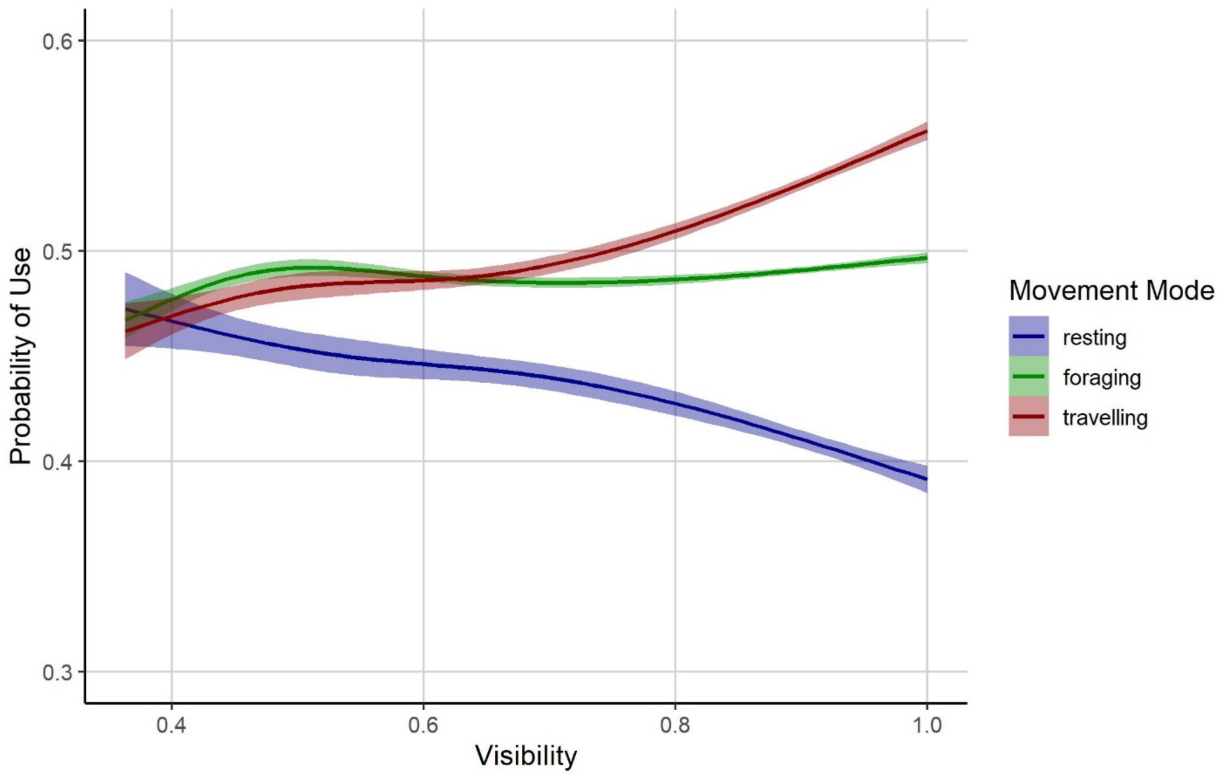

Figure 4.1 Probability of use as a function of visibility and movement mode based on the Distance + Visibility model for 69 bear-years. Lines were fitted using a cubic spline function with four knots and visualized with 95% confidence intervals. This figure only includes areas with sightlines to a road

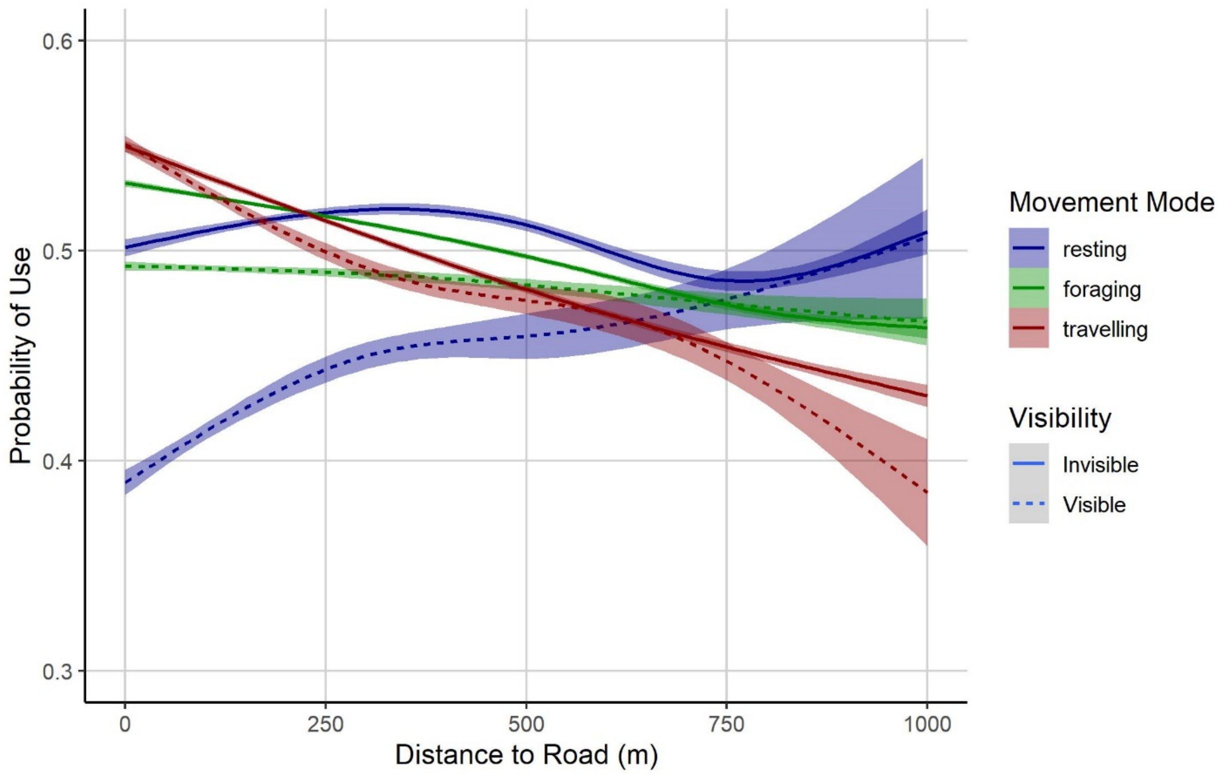

Figure 4.2 Probability of use as a function of distance to road, binary visibility, and movement mode based on the Distance + Visibility model for 69 bear-years. Lines were fitted using a cubic spline function with four knots and visualized with 95% confidence intervals

Selection coefficients for road visibility were not significantly different between age and reproductive classes (Figure 4.3). However, there was an indication that adult females were less likely to select road visibility than males and sub-adults (although confidence intervals overlapped). The selection coefficient for females with cubs was significantly less than one ($p <$ 0.05), indicating they were less likely to select road visibility at average movement speeds.

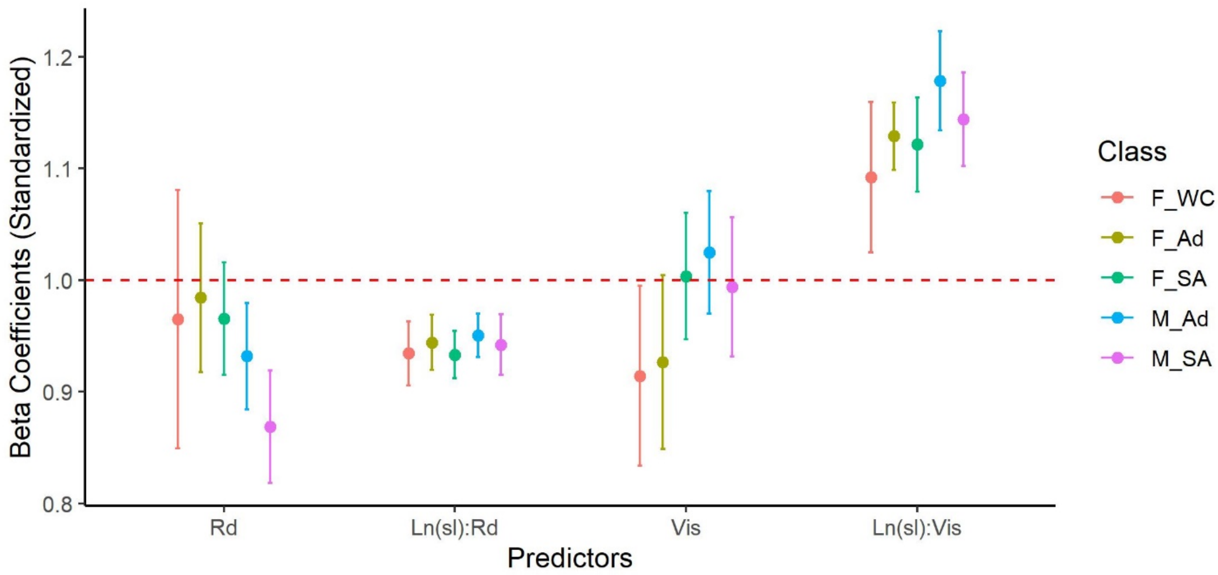

Figure 4.3 Selection coefficients based on 2000 bootstrapped samples, clustering on individual, for grizzly bear age and reproductive classes. Predictors are defined in Table 4.1. (F_WC = Female With Cubs; F_Ad = Female Adult (solitary); F_SA = Female Sub-Adult; M_Ad = Male Adult; M_SA = Male Sub-Adult). The dotted line represents no selection

4.4.3 Additional interactions with visibility

Adding interactions did not significantly ($p < 0.05$) change selection coefficients for variables already in the best model. Grizzly bears were more likely to select areas of high visibility when food rating was also high and vice versa (Table 4.4). No difference in selection for visibility was observed between day and night. Grizzly bears were overall less likely to select road visibility at twilight, however, this interaction was significant for very few individual bear years. When road visibility at the beginning of a step was high, grizzly bears were more likely to select areas near roads and take longer steps.

Table 4.4 Selection coefficients (β) mean and confidence intervals for additional interaction terms not included in model selection process and direction of the population effect (N.S. indicates that confidence intervals overlap with one). Also shown is number of times coefficients were consistent with the direction of the population effect and number of times each variable was significant ($p < 0.05$) for 69 individual bear-years

Predictor	Population Mean (95% CI)	Effect Direction	Effect Agreement (/69)	Significant (/69)
Vis:Food	1.022 (1.003, 1.041)	+	39	17
Vis:Night	0.977 (0.950, 1.005)	N.S.	NA	12
Vis:Twilight	0.960 (0.931, 0.990)	-	39	4
Rd:Vis(start)	0.962 (0.941,0.984)	-	44	20
Ln(sl):Vis(start)	1.116 (1.083,1.148)	+	62	48

4.4.4 Mortality analysis

Patterns of selection for most predictor variables were similar between bears that died and those that survived during the study period (Figure 4.4). There was a significant difference (non-overlapping CI) in selection for distance to road; bears that died were more likely to select areas nearer the road. No significant difference was observed in road visibility coefficients between bears that died and bears that survived.

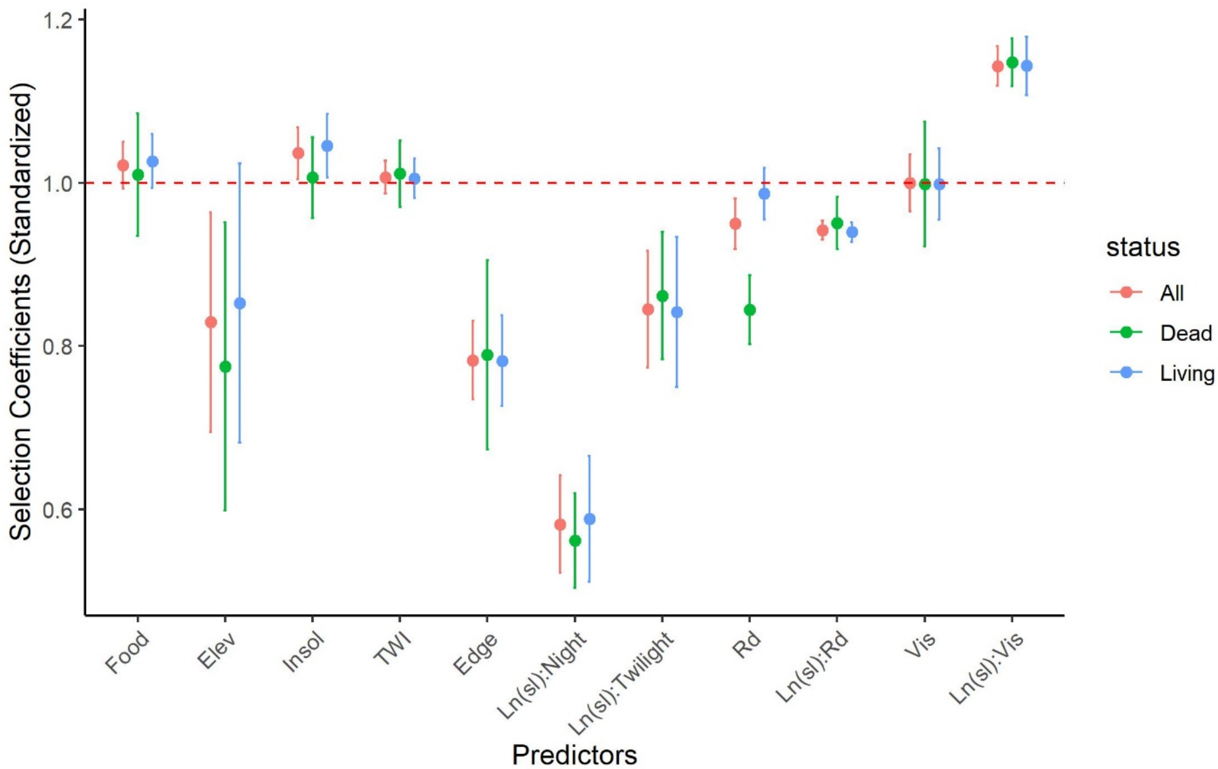

Figure 4.4 Selection coefficients for the Distance + Visibility model based on 2000 bootstrapped samples, clustering on individual, for dead and living bears. Predictors are defined in Table 4.1. The dotted line represents no selection. Population level coefficients are shown for reference

Our exploratory analysis suggests that grizzly bear mortalities occurred disproportionately in areas visible to roads; 40% of all mortalities (8 of 20) occurred in visible areas, whereas only 24% of used locations (19907 of 84404) were visible to roads and only 10% of the available landscape was visible (10436222 of 101967060 cells) (Figure 4.5).

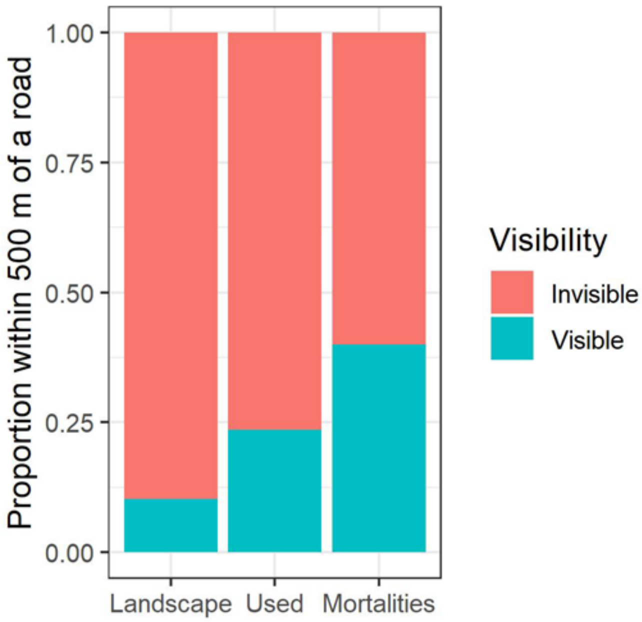

Figure 4.5 The proportion within 500 m of a road of invisible and visible points for: landscape cells representing availability (n = 101967060), GPS collar relocations of live bears (n = 84404), and known locations of grizzly bear mortalities (n = 20)

4.5 Discussion

In this chapter, I used iSSA to investigate grizzly bear habitat selection and mortality around roads. While I originally explored the influence of both audible and visual perception, audible perception was not found to be important to habitat selection around roads so only road visibility was used in further analyses. Incorporating road visibility improved models of habitat selection, providing evidence of the importance of visual perception in understanding animal behaviour. In addition, behaviour (inferred from movement) was important to understanding grizzly bear selection of road visibility, and bears selected for road visibility when travelling but against road visibility when resting. I did not find a link between selection of road visibility and mortality; however, only a limited sample size was available.

4.5.1 Road perception and habitat selection

Models including road visibility outperformed models of grizzly bear habitat selection including road audibility or combined perceptibility. Although my results may be limited by a lack of traffic data providing fine tuned information about sound, this suggests that grizzly bear responses to roads do not primarily depend on being aware of the road, which sound would indicate. Instead, the importance of visibility suggests that bears may respond to the more direct contact of being able to both see and be seen from roads.

4.5.2 Road visibility and habitat selection

My first hypothesis that models of grizzly bear selection including road perception would improve upon models without road perception was strongly supported for visibility and was consistent across bear-years, suggesting that road visibility is an important factor in animal habitat selection. Replacing road distance with road visibility substantially improved model AICc, and the model including both distance and visibility to roads was clearly the best model in terms of both the AICc tally and weights. My work is consistent with previous work done by Montgomery et al. (2012, 2013) on elk (*Cervus elaphus*), where binary visibility interacting with distance to road better explained elk space use than distance to road alone.

My second hypothesis, that grizzly bears would be less likely to select areas perceptible to roads, was explored with respect to road visibility with mixed results. While this chapter did not find an overall avoidance of road visibility at the population level, grizzly bears were less likely to select visible areas when moving at below average speeds, which is consistent with the theory of risk avoidance. However, grizzly bears were also more likely to select road visibility when moving at greater than average speeds. Thus, although visibility’s main effect was insignificant, the interaction with step length was one of the most important variables explaining selection across bear-years. These results demonstrate the importance of evaluating habitat selection concurrently with movement, allowing us to detect relationships that would otherwise pass unobserved (Scrafford et al. 2018).

Previous research has shown that grizzly bear selection and movement varies by time of day; for example, Graham & Stenhouse (2014) found that grizzly bears moved fastest in the morning and evening and slowest at night. In addition, grizzly bears have been found to avoid high traffic roads more during the day than at night when traffic is lighter (Northrup et al. 2012). I used an interaction between time of day and road visibility to see whether time of day explained the variation in movement patterns. However, no difference in selection for road visibility between day and night time was observed, and although grizzly bears were overall less likely to select road visibility at twilight, this pattern was significant for very few bears. Therefore, the evidence does not suggest that differences in selection of road visibility are explained by time of day alone.

Roever et al. (2010) also found longer step lengths associated with roads, suggesting that grizzly bears may increase speeds either because roads elicit a flight response or because roads are used as travel conduits. I found increased step lengths associated with road visibility at both the beginning and the end of steps, which could support either a flight response (long step lengths associated with high visibility at the start of steps) or a travel response (long step lengths associated with high visibility at the start and end of steps). Prokopenko et al. (2017) similarly found increased step lengths in elk near roads and concluded that they increased movement rates as an indication of being disturbed. However, while flight responses would be expected to be away from a road, I found that grizzly bears were more likely to select areas nearer roads when a road was visible at the beginning of a step. In addition, selection for road visibility suggests that grizzly bears may follow roads and visually orient themselves along them, supporting the travel hypothesis. Alternatively, visible areas are open with low vegetation and may allow for greater ease of movement for grizzly bears, contributing to the observed patterns of selection for road visibility when travelling.

Another common explanation for grizzly bear selection of roads is that they are foraging for roadside vegetation (Roever et al. 2008b). I found that grizzly bears were slightly more likely to select areas near roads at intermediate speeds, such as those used when foraging, but that they were less likely to use visible areas as they approached roads. These results support the foraging hypothesis, but suggest that grizzly bears are more wary when using areas near roads for feeding than when travelling. This is consistent with migratory theories observing that wildlife prioritize the path of least resistance while moving, but choose areas that reduce predation risk when foraging and resting (Saher and Schmiegelow 2005). I also found a slight positive interaction between road visibility and food rating, suggesting that grizzly bears may be attracted to areas of high visibility near roads where forage is also visible.

Grizzly bears were less likely to rest in locations visible to roads. This response implies a risk associated with visible areas, as was anticipated. Although my study is the first, to my knowledge, to investigate grizzly bear response to road visibility, visibility depends largely on cover, as all visible areas in the study were in open habitat. Cover has been previously discussed in terms of concealment and security for brown bears. Bears in open habitat are more likely to be involved in human-bear conflict resulting in bear mortality, and grizzly bear flight responses to humans are further and more frequent in open habitats than within hiding cover (Mclellan and Shackleton 1973, Oldershaw 2001). Cover also influences bear behaviour; Nielsen et al. (2004a) observed that grizzly bears stayed near the edge of forest harvesting areas and were more likely to use open areas at night. In addition, bears have been found to forage in open areas but select greater concealment at den sites (Libal 2011), and resting sites (Munro et al. 2006, Ordiz et al. 2011, Pigeon et al. 2016). Cover may also be selected while resting to avoid heat in open areas (Nielsen et al. 2004a). The results in this chapter may partially reflect a general selection of grizzly bears for covered, secure areas when resting and open areas when foraging and travelling that is not dependant on road visibility. However, previous studies were limited to using cover or concealment as a proxy for risk avoidance, without specifying the risk to be avoided. Including road visibility provides an added association between open areas and anthropogenic risk, allowing a mechanism explaining why concealing vegetation may be selected. Because grizzly bears have no natural predators besides other grizzly bears (Hertel et al. 2016), the use of concealing cover may be an adaptive response to avoid human encounters in an increasingly human dominated landscape.

Patterns of selection around roads and visibility were similar between age and reproductive classes, with no significant differences in selection coefficients observed. However, females with cubs were more likely to select against road visibility at average step lengths, a response that was not observed at the population level. Although previous research has found that females with cubs select areas with greater human disturbance, possibly to avoid male grizzly bears which can pose a danger to cubs (Graham et al. 2010, Cristescu et al. 2016a), my research suggests greater wariness around roads in females with cubs. Female grizzly bears with cubs have been found to travel less and have smaller home range sizes, which may be a strategy to increase cub security (Schwartz et al. 2003, Graham and Stenhouse 2014). Cristescu et al. (2016b) also found that while females with cubs were frequently found in active mining areas, they selected for tree islands that provide hiding cover. Decreased selection for areas visible to roads in females with cubs supports my hypothesis that visibility increases perceived risk around roads for grizzly bears.

4.5.3 Road visibility and mortality

My analysis found that grizzly bears that were more likely to select areas near roads have higher mortality as has been found previously (Nielsen et al. 2002, Boulanger and Stenhouse 2014). However, I did not find statistical support for a relationship between selection of road visibility and grizzly bear mortality as predicted by my third hypothesis. This may be due to low sample size in my analysis (n = 10 collared grizzly bear deaths). However, in the exploratory analysis including all known locations of grizzly bear mortalities, mortalities were located in visible areas more frequently than expected based on used or available locations within 500 m of a road. This pattern may be largely attributed to the relationship between visibility and distance to road, and was based on very few data points. However, a high proportion of mortalities in visible areas suggests that further research into the risk of visibility is warranted.

Chapter 5: Conclusion

5.1 Overview addressing main research question

My overarching research question was "How can measures of perception including sight and sound be used to better understand the effects of disturbance on wildlife, specifically, roads on grizzly bears?" I answered this question by first, using remote sensing data to create viewsheds and soundscapes around roads in the Yellowhead region of Alberta, and secondly, using these models along with grizzly bear movement data to create zones of influence and model habitat selection.

In chapter 3, perception was estimated around roads using detailed remotely sensed data. Viewsheds were created at a 10 m resolution from topographic and vegetation data around roads and soundscapes were created at a 30 m resolution using topographic and land cover data. I combined the viewshed and soundscape layers to create an overall perception zone. Finally, I used grizzly bear GPS data to create a species-specific zone of influence, finding that during the day grizzly bears responded at slightly further distances when roads were perceptible than when roads were imperceptible.

In chapter 4, I investigated the role of perception in grizzly bear habitat selection by performing further analyses using grizzly bear GPS data and the modelled perception around roads. During my model selection process, I found that of three variables - visibility, audibility, and perceptibility - visibility was the most useful in modeling grizzly bear habitat selection, therefore I focused the remainder of my analyses on visual perception. I found that a model including both road distance and road visibility was the best model (lowest AICc) for explaining habitat selection and that grizzly bears were more likely to select areas visible to roads when travelling but less likely to select areas visible to roads when resting. I also found that female grizzly bears with cubs were overall less likely to select areas visible to roads, suggesting that bears in these vulnerable demographic classes are more risk averse. I did not find a difference in selection coefficients for road visibility between grizzly bears that survived and those that died ($p < 0.05$), however, an exploratory analysis demonstrated that grizzly bear mortalities may occur more frequently in visible areas.

In answering my research question, I determined that perception can be used to better understand the effects of disturbance using a case study with grizzly bears and roads. In particular, perception was able to make more precise estimates of the zone of influence. Perception was also used to clarify our understanding of when and why grizzly bears use areas near roads, and thus suggest better management. My results did not confirm a relationship between perception and mortality risk for grizzly bears; however, I suggest that further research is warranted to examine linkages between the observed behavioural responses and population outcomes.

5.2 Significance of research and key findings

In this thesis, I used perception as the cognitive link between the spatial pattern of grizzly bear movement and the underlying processes of grizzly bear behaviour and their responses to anthropogenic disturbances (Nathan et al. 2008, Spiegel et al. 2017). In Chapter 3, I developed a novel method of evaluating the site- and species-specific zone of influence for a disturbance by including perception by sight and sound and behaviour, resulting in irregular zones of influence around roads. I used detailed remote sensing data including lidar, which allows fine scale modelling of vegetation height. Incorporating lidar based vegetation is significant because many previous studies, having no vegetation data available, have relied on elevation data alone to model viewsheds, which overestimates visibility (Murgoitio et al. 2013). The inclusion of vegetation not only increases the accuracy of visibility models, but also provides a connection between visibility and human activity such as forest harvesting. This research demonstrates how advances in remote sensing technology can contribute to the fields of animal ecology and natural resource management. I found that, during the day, grizzly bears responded at further distances to roads when the road was estimated to be perceptible than when the road was estimated to be imperceptible, indicating that efforts to reduce sight and sound propagation around human activity may be one way to reduce the zone of influence of a disturbance. Increasing our understanding of the zone of influence, which is commonly used in anthropogenic impact mitigation, can aid in landscape planning and remediation efforts to minimize the effects of human activities and developments.

In Chapter 4, I highlighted the importance of accounting for perception in understanding animal habitat selection, particularly around anthropogenic disturbances. While sound was not found to be important to grizzly bear habitat selection in my models, I found that models that included road visibility better explained grizzly bear habitat selection than models using only distance to road. Grizzly bears were more likely to select road visibility when moving quickly, supporting the hypothesis that roads are used as travel conduits for grizzly bears. However, grizzly bears were less likely to select visible areas when moving slowly or resting, suggesting that road visibility is also perceived as a risk. With these findings, I demonstrated how using perception along with movement data can be used to explain animal behaviour. Finally, I demonstrated how perception may be used to explore relationships between anthropogenic disturbances and not only animal behaviour but mortality risk. In my analysis, no difference in selection for road visibility was detected between surviving and dead grizzly bears, and the sample size of known bear mortalities was insufficient to determine whether the probability of grizzly bear mortality was statistically higher in areas visible from roads. However, I provide a framework for future work to take into account the potential role of visibility in increasing animal risk around roads either by comparing selection for visible areas between animals that died and those that survived or by testing whether mortalities are more likely to occur in visible areas.

5.3 Management implications

The work in Chapter 3 provides a framework to use advances in remote sensing data to model wildlife perception over the landscape. While previous studies have incorporated some aspects of perception into wildlife analyses, few have considered both sight and sound together or used broad landscape scales. The viewshed and soundscape modelling approaches described may be used as management tools to understand animal behaviour and responses in various contexts. For example, perception modelling may be used to explore animal space use in response to hunting or tourist activity, or to explore the effects of habitat modification on animal behaviour. Perception models may be used in spatial planning including choosing the location of crossing structures or designing wildlife corridors and protected areas.

Specifically, in this chapter I suggest a novel method of estimating zones of influence for current or proposed disturbances using perception modelling and semivariograms. My results suggest that the zone of influence should be wider in areas where disturbance perceived by the animal may be higher due to greater propagation of sight and sound; however, these methods allow for behavioural zones of influence to vary by context. Viewsheds and soundscapes may be used not only to define zones of influence for roads, but also for diverse disturbance types including mining or oil and gas operations. In this study, perceptual zones of influence and behavioural zones of influence varied widely from the standard 500 m buffer zone (Proctor et al. 2020). I do not suggest that the behavioural zone of influence estimated here for grizzly bears be used to replace larger buffer zones, as altered behaviour derived from step lengths is only one possible effect of disturbances; grizzly bears may experience increased health and survival risks from roads at much greater distances than those at which they change movement patterns. When making zones of influence for management purposes, multiple scales and metrics of response should be considered. While my study examined perception and behaviour at very fine scales, species abundance may be affected at much greater scales (Torres et al. 2016). However, incorporating animal perception and movement would allow priority to be placed on areas with the highest perceptual - and thus behavioural - impact when making management decisions.

My methods may be broadly applied to any stationary disturbance for which remote sensing data is available, as well as used for land planning and development. The perceptual zone of influence does not require field observations and can effectively be created for proposed developments or forestry operations to determine configurations that will minimize the perceptual zone of influence or avoid predetermined key wildlife habitats. In addition, perceptual and behavioural zones of influence can be tailored to species of interest, such as woodland caribou (*Rangifer tarandus caribou*), which have been found to be negatively affected by various human activities (Vors et al. 2007). While GPS location data is useful for evaluating movement responses, semivariograms may also be applied to other types of numerical data such as song amplitude in birds.

My results suggest possible ways to decrease the zone of influence, particularly for forest harvesting disturbances. Along with my results in Chapter 3 showing that grizzly bears respond to roads at greater distances when perceptible to roads, Chapter 4 provided further evidence of the effects of road visibility on grizzly bears. Although my study did not reveal a relationship between selection of road visibility and mortality, an exploratory analysis demonstrated that a higher proportion of grizzly bear mortalities occurred in areas visible to a road than expected based on grizzly bear use of visible areas. In addition, the avoidance of areas visible to roads by vulnerable demographic classes (females with cubs), and during more vulnerable behaviours (resting vs travelling), suggests that road visibility is perceived as a risk to grizzly bears. In an increasingly human-dominated landscape where natural disturbances are infrequent, grizzly bears have adapted by accessing forage in human-caused disturbances such as cut blocks (Roever et al. 2008b, Kearney et al. 2019). Bears have also been found to alter space use patterns by time of day to avoid human activity (Machutchon and Proctor 2015, Ladle et al. 2018). Wildlife operate within trade-offs between obtaining resources and avoiding risks (Davies et al. 2016a), and my research suggests that an additional adaptive strategy employed by grizzly bears is using areas not visible to roads to reduce risk while foraging and resting. Recent changes to forestry practices in North America have focussed on creating harvesting patterns that mimic natural disturbances, in an effort to reduce human impact on wildlife (Nielsen et al. 2008, Larsen et al. 2019). Another innovation that may facilitate continued coexistence between grizzly bears and people is implementing measures to reduce visibility around roads. The comparison of DSM (treed) versus DEM (bare) viewsheds in Chapter 3 illustrates the effectiveness of vegetation in reducing viewshed size, thus visibility may be minimized by maintaining vegetative buffers between roads and adjacent harvesting sites, a practice that is also used to reduce visibility of cut blocks along roads for aesthetic reasons (Wing and Johnson 2001). Field tests in Alberta found that, on average, visibility extended up to 18 m in Engelmann spruce forests and 26 m in lodgepole pine forests (Oldershaw 2001). Therefore, leaving forested buffers at least 20 m wide on the edge of cut blocks could allow grizzly bears to use travel corridors associated with roadways and access cut blocks for forage while reducing human-induced risk. Providing visual cover allows humans and grizzly bears to coexist in closer quarters, facilitating shared landscapes (Mclellan and Shackleton 1973; Oldershaw 2001). While grizzly bears cannot be prevented from using the roads intruding into their habitat, actions can be taken to reduce encounters with humans and thus increase grizzly bear security.

5.4 Limitations

5.4.1 Limitations in modelling perception

One limitation to modelling perception in my study was that it did not incorporate temporal aspects. Time is especially important for modelling traffic noise, which depends on the number of vehicles on a road at a time and varies by road, season, and time of day. For this thesis, I did not have access to detailed traffic data and roads were assumed to have constant traffic levels depending on road class, a simplification that may not have accurately represented sound perception for grizzly bears. Visibility is also not static, but depends on vegetation cover and height, which may change seasonally and annually. In addition, road networks change annually as new roads are built and old roads are decommissioned. Therefore, my study was limited in that I could not be sure whether a road was perceptible at the time of grizzly bear passing.

An additional limitation to modelling perception was processing time. In this thesis, visibility was modelled at a 10 m resolution and audibility was modelled at a 30 m resolution. Data were available at much finer resolutions; however, fine scale modelling was prohibitively computationally expensive due to the large extent of the study area and many kilometers of roads. Processing time also limited opportunities for modelling different scenarios, for example daytime or nighttime traffic or simulated changes in vegetation over time.

5.4.2 Limitations in modelling grizzly bear responses

Another limitation to the study was the moderate fix rate available for grizzly bear GPS relocations. Visibility occurs in fine scale patterns over the landscape, and a bear could pass through multiple visible and invisible areas in the space of one hour. In addition, analysis of the risks facing grizzly bears would benefit from more detailed data collection around grizzly bear mortalities, as less than a third of known deaths within the study area had accurate location data. Finally, I only analysed the influence of road perception on grizzly bear selection and mortality. Visibility or audibility may also affect grizzly bear stress, health, and reproduction, indirectly affecting population fitness. For example, viewshed at den sites has been found to be an important predictor of litter size in African wild dogs (*Lycaon pictus*) (Davies et al. 2016a).

5.4.3 Model uncertainty

It is also important to acknowledge the inherent uncertainty in ecological modelling. In my study, there was uncertainty at both the perception level of modelling and the wildlife level of modelling. Uncertainty in ecological modelling may be due to measurement or observation errors (Cressie et al. 2009); in the case of my study, observation error may have occurred in both landscape and wildlife data. Advanced remote sensing technology is increasingly accurate

(Hilker et al. 2010), however, errors may occur in both collection and processing or classification of remote data. In addition, although GPS collars were found to have on average high accuracy (K. Graham, personal communication, November 27, 2019), even a 10 m error in location accuracy could cause a GPS location to be classified incorrectly as visible or invisible, particularly as grizzly bears often select for forest edges (Larsen et al. 2019) where visible and invisible areas would be adjacent. Uncertainty is amplified as both the temporal and spatial resolution increases. For example, simplifying lidar vegetation heights into 10 m grid cells eliminates small forest gaps, which could influence visibility. In addition, uncertainty is introduced in the modelling process for step selection analysis. Along with uncertainty associated with the temporal resolution used, user choices around the method of generating and the number of available steps, as well as how to model individuals within populations may have significant effects on model outcomes (Holloway and Miller 2014). Individual variation is especially important to grizzly bears, which have been found to exhibit strongly individualistic behaviour (Hertel et al. 2017). Overall, my models suggested that incorporating perception was useful to explaining grizzly bear habitat selection and movement, however, accurately predicting grizzly bear decisions remains beyond the modelling scope of this work.

5.5 Future work

I recommend that future work incorporate temporal variation in traffic, vegetation and land cover, and roads in modelling perception. For example, Kearney et al. (2020) developed algorithms based on satellite imagery to update road networks and detect temporal changes due to new roads and road reclamation. Additional work could also be done to allow updating lidar data on vegetation heights based on satellite land cover data that can be collected at more frequent intervals. Temporal variation in traffic noise could also be estimated from traffic counts, mobile big data, or from noise detectors placed along roadways (Barber et al. 2011, Shannon et al. 2014). Alternatively, the addition of acoustical recording devices (Lynch et al. 2013) or even cameras (Patel et al. 2017) to GPS tracking devices could provide real-time information on animal perception.

Future work should continue to build on GIS applications to improve processing efficiency over large areas, which would allow perception to be modelled at finer spatial scales. For example, some studies have used lidar point clouds to create detailed three dimensional viewsheds; however, so far these studies have focussed on much smaller areas (Murgoitio et al. 2014).

To further explore the relationship between perception and grizzly bear behaviour, future work would benefit from more frequent data on grizzly bear movement. In addition, while I used only step lengths to estimate when grizzly bears were resting, foraging, or travelling, accelerometer data could provide detailed activity data to improve dividing grizzly bear locations into behavioural modes (Abrahms et al. 2016). For instance, two sequential GPS locations in close spatial proximity may indicate either resting or intense foraging (Brown et al. 2012b), which can be determined using accelerometers. I also recommend further research employ a more nuanced approach to understanding fitness responses in grizzly bears and other wildlife. For example, hormones collected from animal hair can be used to determine stress levels (Heimbürge et al. 2019), thus future analyses could evaluate relationships between time spent in areas perceptible to roads and grizzly bear stress.

Additional work may also consider other aspects of perception, such as olfaction. While odour is more difficult to measure or model than sight or sound, previous research has evaluated the effect odours have on human perception of roads (Jiang et al. 2016), and grizzly bears and many other animals rely extensively on their sense of smell (Schwartz et al. 2003). Grizzly bears are also known to become habituated to human disturbances (Roever et al. 2008b, Penteriani et al. 2016), and future work may consider whether grizzly bear perception and behaviour is influenced by memory, for example by comparing models between recently translocated bears and bears within their home range. Perceptual ability also varies by species and even individuals (Fagan et al. 2017), and evaluating animal responses in light of these differences would be beneficial.

Finally, as remote sensing technology becomes increasingly available, it opens new possibilities for studies of animal behaviour to more easily incorporate new variables such as perception. I recommend that my methods be developed further for use with new disturbance types, landscapes, and species.

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