Multiscale Habitat Selection and Road Avoidance of Elk on their Winter Range

by

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Abstract

Roads are a prevalent, ever-increasing form of human disturbance on the landscape. In many places in western North America, energy development has brought human and road disturbance into seasonal winter range areas for migratory elk. In this population, I studied individual habitat selection relative to road proximity at two scales to quantify factors influencing among- and within-home-range selection of winter range. Further, I sought to evaluate predictions from the risk-disturbance hypothesis when studying fine-scale movement and selection response to roads during winter. I outlined availability extents for 107 individual elk-years based on observed fall migration distance, and with a minimum convex polygon around winter telemetry relocations. To model the response by elk to road disturbance, I fit a resource selection model to each elk-year, and examined population-level and individual variation in the movement response. In addition, I evaluated the relationship between inferred selection at the two scales and the functional response in selection. In addition, I used integrated Step Selection Analysis (iSSA) to evaluate four alternative hypotheses regarding the influence of roads on space-use behaviour across 175 elk-years of elk telemetry data, and I quantify both population and individual variation in responses. Road proximity and crossing were used to evaluate these behaviours, which offered a rare comparison between two common measures of roads. Roads had a ubiquitous influence on elk across scales. Elk, individually and as a population, avoided roads when migrating to their winter range and within this home range. Individual elk that avoided roads more strongly relative to the population did so at both scales of analysis. Our results thus support bottom-up habitat-selection patterns, where the underlying behaviours are not scale-dependent. Further, I demonstrated, for the first time, how iSSA can be used to marry movement analysis in a refined approach to habitat selection. Elk responded to roads as they would natural predation risk. Elk selected areas farther from roads at all times of day with avoidance being greatest during twilight. In addition, elk sought cover and moved more when in the vicinity of roads. Road crossings were generally avoided, but this avoidance was weakest during daytime when elk were both moving and closer to roads. Energy development is transforming landscapes in western North America with the proliferation of roads, which I show is having substantial and multifaceted negative effects on elk behaviour across multiple scales. Consequently, any new road construction or increases in existing road-use intensity would have detrimental effects on migratory elk populations by restricting space-use.

Preface

This thesis is an original work by Christina Marie Prokopenko. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Title "Effects of Access Management on Habitat Use, Movement, and Survival of Elk in SW Alberta", NO. AUP#00000009. Chapters 2 and 3 have been formatted for *Landscape Ecology* and *Journal of Applied Ecology* prior to final submission of this thesis. M.S. Boyce and T. Avgar were the supervisory authors involved in the formation of concepts and composition of those manuscripts.

Dedication

This thesis is dedicated to Hugh.

And you ask 'what if I fall?'
Oh but darling, what if you fly?
- Erin Hanson

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List of Abbreviations

iSSA

integrated Step Selection Analysis

NDVI

Normalized Difference Vegetation Index

RSA

Resource Selection Analysis

RSS

Resource Selection Strength

SSA

Step Selection Analysis

CHAPTER 1: PROLOGUE

Road networks affect wildlife populations across taxa and geographic regions (Trombulak and Frissell 2000). Understanding the complex effects of roads and other forms of human disturbance on wildlife populations has been a long-term area of research, the findings of which can have direct management implications. There is some evidence for anthropogenic disturbance having a positive influence on species. For some species, anthropogenic features can promote movement (Latham et al. 2011), can provide refuge from predators (Muhly et al. 2011), might enhance vegetation quality in the nearby area (Beyer et al. 2013), could favour efficient hunting behaviour (Meunier et al. 2000), or provide scavenging opportunities (Kawashima 2016). However, the effects of roads on most species are negative (Fahrig and Rytwinski 2009). Indeed, roads cause mortality through wildlife-vehicle collisions or incidentally through hunter access (Hayes et al. 2002, Frair et al. 2008, Orlowski 2008). In addition, development creates barriers to wildlife movement and fragments populations (Dyer et al. 2002, Nellemann et al. 2003, Andrews and Gibbons 2005, Shepard et al. 2008). Further, habitat loss can occur literally through removal and fragmentation, or functionally when areas are avoided by animals (Forman and Alexander 1998).

There are some shared features between species that are negatively affected by road disturbance. For example, large-bodied mammals with greater movement capacity and lower reproductive rates often experience negative consequences of road features (Rytwinski and Fahrig 2012). Nevertheless, within a species there can be contradictory responses to human disturbance. For example, the same prey species might use a human-shield against predators in one system (Berger 2007), while humans in another area could be perceived as predators themselves (Frid and Dill 2002). In systems where humans are a source of mortality it is intuitive that the effects of human presence on prey species could be identical to that of predators (Frid and Dill 2002). Indeed, stronger behavioural responses to humans are observed in hunted populations (Stankowich 2008).

For populations that respond negatively to human disturbance, the form of this response can vary. Avoidance of these areas is a generally supported pattern in ungulates (Rowland and Wisdom 2005, Laurian et al. 2008, Dussault et al. 2012). Further, fine-scale changes to movement rates (Leblond et al. 2013, Beyer et al. 2013), forage selection (Van Dyke et al. 1996),

and vigilance (Ciuti et al. 2012b) has been documented in relation to road disturbance. These responses are sensitive to the spatial interaction with vegetation surrounding the road (Meisingset et al. 2013) and to the temporal aspect of human use (Gagnon et al. 2007, Northrup et al. 2012, 2015). Consolidating the various expected impacts of roads into one body of work for one study population gives insight into the extent of road influence on wildlife behaviour, as I have done in my work.

The elk (*Cervus elaphus*) is a gregarious large herbivore found across North America. The ~180 elk in the study population range mostly in Southwestern Alberta but their distribution extends to Southeastern British Columbia and Northwestern Montana. The Rocky Mountains border the study area to the west. To the east, rolling slopes give way to open prairie. The area is a mosaic of public, private and Crown land with Waterton Lakes National Park, a portion of an international peace park, situated in the Southwestern corner of Alberta.

To humans, the elk is a model species for scientific work, an agricultural nuisance, an attraction for tourists, and a natural resource for hunters. Human use in in this region consists of agriculture, recreation, and industry. In terms of recreation, this region experiences considerable ATV use during the warmer seasons. In addition, hunting was the dominant source of mortality for elk in this study; natural predation was negligible because wolf abundance was low and remaining packs predominantly consumed cattle (Morehouse and Boyce 2011). Waterton Lakes National Park offers respite from hunting, but is intensely used for non-consumptive recreation in the spring and summer. Lastly, natural gas wells and ancillary access roads occur in the area.

Elk in Southwestern Alberta have shown indications of changing their behaviour in response to human disturbance. Vigilance-foraging trade-off shifted towards vigilance when distance to road decreased and traffic volume increased, and notably, vigilance was not affected by natural factors such as predation or female reproduction (Ciuti et al. 2012b). As well, there is evidence that human disturbance can influence habitat use in this system. Indeed, elk favoured foraging in areas farther from roads (Seidel and Boyce 2015, 2016). To date, research on this population has not included analysis focusing on winter-range behaviour.

Biologically, winter is a critical time for elk. Elk migration to low-elevation winter ranges is driven by snow depth and thus vegetation access (Boyce 1991, Boyce et al. 2003). This population is largely migratory (~75% migrants; as identified by Killeen et al. 2014) and migrants travel east during the fall to their winter ranges. In this system, the population

aggregates into approximately eight herds during winter. The winter season is energetically demanding because of movement through snow and thermoregulation (Parker and Robbins 1984, Sweeney and Sweeney 1984). Further, forage availability is limited by snow, making energy acquisition challenging (Wickstrom and Robbins 1984, Christianson and Creel 2007).

Practically, understanding the influence of disturbance on elk during winter was of importance because of the winter-range regulations that are in place from December to March. These management guidelines limit development and access in core winter range. Documenting elk responses to road disturbance on their winter range can educate future management decisions and mitigate their negative effects.

Habitat selection modelling is a technique that is widely used to describe the relationship between landscapes and wildlife. In resource selection analysis (RSA), the habitat determined to be available is the reference from which we determine selection through the comparison to used habitat (Boyce and McDonald 1999, Manly et al. 2002). Flexible definitions of availability allow questions regarding wildlife selection behaviour to be dynamic. In RSA, available locations can be generated at various extents which allows for conclusions regarding habitat selection behaviours at different scales (McLoughlin et al. 2002, van Beest et al. 2010). Further, altering how we define availability has led to additional methods being developed to investigate selection. Step selection analysis (SSA) is a form of RSA that examines the linkage between movement and selection by generating available steps (a step is the line between consecutive points), based on outlined movement parameter distributions or maximum values (Fortin et al. 2005, Avgar et al. 2016).

However, the sensitivity of our analysis to availability should be cautionary. The resolution of availability determines if the landscape is adequately sampled, while the extent determines which behaviours are captured, or fail to be captured (Northrup et al. 2013). Often, in ecology the scale of measurement impacts resulting inferences (Hobbs 2003). Indeed, the discussion of scales is not limited to habitat selection literature, but exists throughout ecology (Levin 1992). This work addresses the subjects of availability domain and scale, which are both longstanding topics of study in habitat selection literature.

The culmination of this work provides a comprehensive investigation of the response of elk to road disturbance on their winter range. The following chapter seeks to detail winter range selection at two scales (selection of home range and selection within the home range) with a

focus on the influence of roads on selection. In addition, I determine the effect of availability on our inferences through using two availability domains to consider two scales of winter range selection, subsequently comparing these scales, and considering the change in selection across changing availability (i.e. the functional response). In the third chapter, I formulate hypotheses regarding fine-scale responses to roads, which were tested by incorporating movement into the definition of availability, and by integrating movement and selection into the modeling approach. Basal winter movement and selection behaviours are outlined in this analysis, and the utility of two road metrics used in habitat selection and movement studies are assessed as well. In conclusion, this thesis is primarily a study on elk ecology but can also be viewed as an illustration of the importance of availability domains to our habitat selection analysis, and how the decision to sample available habitat at different extents can result in helpful perspectives about a system.

CHAPTER 2: EXTENT-DEPENDENT HABITAT SELECTION IN A MIGRATORY LARGE HERBIVORE: ROAD AVOIDANCE ACROSS SCALES

Introduction

Wildlife select habitats at multiple scales; from coarse-scale selection in the form of migration to fine-scale site-level plant selection (Senft et al. 1987, Fryxell et al. 1988, Owen-Smith et al. 2010). Conservation and management recommendations often are based on conclusions drawn from habitat selection work done at disparate scales (Hobbs 2003). Resource selection analysis, hereafter RSA, is a common tool used to study wildlife behaviour and informs the management of many populations worldwide. RSA contrasts the habitat used by an animal against the habitat available on the landscape to determine what is selected (Manly et al. 2002, Johnson et al. 2006). The relationship between inferred resource selection and the scale of analysis is a crucial consideration in wildlife studies (Johnson 1980, Boyce et al. 2003, Boyce 2006a). However, most studies on habitat selection do not include multiple scales in their analysis (McGarigal et al. 2016). Thus, from both theoretical and management perspectives, thoughtful application, and not solely acknowledgment, of scale in RSA is paramount.

Johnson (1980) defined a hierarchy of selection, termed "orders of selection," where the higher orders depend on those below it and the coarser scale restrict the finer availability. The species range is the first order and coarsest scale of selection, the among-home-range of habitat selection is the placement of a home range (among-home-range), and the third order is a finer scale of habitat use within the available home range area (within-home-range; Johnson 1980). Rettie and Messier (2000) postulated that the most influential limiting factors on fitness are selected or avoided at the coarsest scale. Thus, an effect of these factors at finer scales might not be apparent. Selection can be scale-dependent when fitness consequences of the behaviour act at distinct scales (Orians and Wittenberger 1991). Conversely, behaviour at fine scales may be the foundation for patterns observed in coarse-scale selection, generating a positive relationship between the selection at different scales (Levin 1992, Owen-Smith et al. 2010).

To document habitat selection at multiple scales various methods have been employed. For example, scales can be analyzed separately to then be compared post-hoc (McGreer et al. 2015). Often however the design is nested, where the used area at coarser scales are defined as the available area at the finer scales (McLoughlin et al. 2002, van Beest et al. 2010). Altering both the availability and use domains creates difficulty when interpreting the response, as

varying availability alone can alter the magnitude and direction of selection coefficients when use remains the same (Beyer et al. 2010). Defining the domain of availability is integral to studies of habitat selection because it is the reference from which we calculate selection (Manly et al. 2002, Johnson et al. 2006). The availability samples can be altered in both intensity of sampling, in addition to the resolution and the extent that is sampled. However, there is not a single correct extent because behaviours can be evident at different scales, in fact there are benefits to analyzing multiple scales for this reason (Northrup et al. 2013).

Here we fitted the same RSA with both among- and within-home-range availabilities (i.e., 2nd and 3rd orders of selection respectively). In previous work, among-home-range availability has been outlined using the entire study area, defined by the extent of the landscape sampled during the study (McLoughlin et al. 2002, van Beest et al. 2010), the area around the study population when multiple herds were sampled (Bastille-Rousseau et al. 2015), or by buffering identified home ranges of individuals in a study population (Ciarniello et al. 2007). Alternatively, population ranges determined from historical data have been used to define among-home-range availability (DeCesare et al. 2012). To our knowledge, little work has been done where among-home-range availabilities were identified for each individual separately.

Availability at the third order is bounded by home-range area. However, definitions of home-range extent and what should be considered available in the home range varies widely. Previous within-home-range availability definitions were based on a 100% Minimum Convex Polygon, hereafter MCP (Ciarniello et al. 2007), 95 % MCP (van Beest et al. 2010), and a MCP with an added buffer determined by average movement distance (Laforge et al. 2015). A more confined measure of home range can be created by defining utilization distributions using Kernel Density Estimators (Nielson and Sawyer 2013). Instead of relocations, movement paths can be used to define an available area (DeCesare et al. 2012). Within-home-range selection also can be analyzed using a more restricted extent by using movement speed and time between consecutive used locations to define available area (Arthur et al. 1996, McLoughlin et al. 2002, Boyce et al. 2003, Ciarniello et al. 2007). Additionally, Brownian bridges have been used to incorporate movement patterns to determine availability (Horne et al. 2007). Lastly, step selection analysis is a form of RSA that details the link between movement and selection further by generating available steps (lines between consecutive points), based on observed movement characteristics

(Fortin et al. 2005, Avgar et al. 2016). Here we use the simplest of these approaches, the 100% MCP encompassing all individual locations during a particular time.

Consideration of scale can be exceptionally important when studying migratory populations, due to the interplay of coarse-scale drivers of migration and fine-scale forage and risk pressures. For elk, migration to higher elevation in spring is driven by phenology whereas autumn migration to lower elevation is driven by snow depth and forage availability (Boyce 1991, Boyce et al. 2003, Bischof et al. 2012). Resource acquisition during winter is an important factor for elk winter-range selection and survival as the variety and quantity of resources are limited due to depletion, and large areas can be inaccessible due to snow (Wickstrom and Robbins 1984, Christianson and Creel 2007).

In our study system, natural predation is not a significant limit on individual fitness due to low wolf abundance and reliance on domestic cattle by existing packs (Morehouse and Boyce 2011). Hunting by humans is however a dominant cause of mortality, and has been shown to influence elk movement and selection behaviour (Ciuti et al. 2012a). The response to, and the perception of, disturbance created by human activity is thought to be comparable to that of natural predators (Frid and Dill 2002). The stresses imposed on elk during winter means it is a critical period to understand and properly manage human activity. In southwestern Alberta, and across western North America, human activity in the form of energy extraction, road creation and traffic is increasing and encroaching into core elk winter range areas (Naugle 2010). Despite all this, no work has yet directly addressed winter-range habitat selection in our study population in southwestern Alberta (Ciuti et al. 2012b, 2012a, Killeen et al. 2014, Seidel and Boyce 2015, 2016).

In general, we expected drivers of among-home-range selection in our study to be akin to previously found migration drivers, while within-home-range selection will reflect fine-scale influences. On our study area we expected elk to select winter ranges in lower elevation because snow accumulation in these areas is lower (Boyce 1991, Boyce et al. 2003). Migrating to low elevation areas will drive elk into areas of higher road density resulting in the absence of avoidance or even apparent selection of roads at the coarse scale. To clarify, ideally elk would avoid roads at both scales, but we expected abiotic effects (elevation) to override this.

Within their home range elk were expected to select foraging habitats, such as deciduous forest, shrublands, and grasslands (Gude et al. 2006, Jenkins et al. 2007, Sawyer et al. 2007) as

well as elevated regions, such as slopes and hilltops, due to improved winter forage access (Sawyer et al. 2007). We expected that elk will perceive roads as risky and will avoid them within their home range (Rowland and Wisdom 2000, Sawyer et al. 2007, Rogala et al. 2011).

On the aspect of scale dependency, we expected the response to foraging areas will be scale independent and positively related between scales. Conversely, selection for elevation should be scale dependent because of the contrasting processes occurring across scales (Bailey et al. 1996, Boyce et al. 2003). Due to the changes in selection for elevation across scales, and the relationship between elevation and road density in the study area where there are fewer roads at high elevation, we expected road avoidance to be scale dependent as well. Overall, our objective was to determine the influence of road avoidance on elk winter range selection in context of multiscale selection, so as to develop multiple perspectives regarding elk winter range management in southwestern Alberta.

Methods

STUDY AREA

We studied elk in the Pincher Creek area (49.4856° N, 113.9482° W) in southwestern Alberta. The ~5000-km^2 study area had wide variation in vegetation, topography, and human use. The Rocky Mountains border the west side of the study area, providing areas of recreation both within Waterton Lakes National Park in the most southwest corner and outside of it in a combination of private land and public Crown land. At low elevations, coniferous and deciduous forests transition to open grasslands. To the east, rolling hills are present throughout the landscape and are used predominantly for agriculture. Some natural gas extraction occurs on the landscape, and wells and access roads are scattered throughout the area. Road disturbance is present throughout the area, with the density and intensity of vehicular use increasing from west to east and south the north (Northrup et al. 2012). Predators of elk in the area include wolves (*Canis lupus*), cougars (*Puma concolor*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*). In addition to elk, large herbivores in the area include moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*).

ELK DATA

GPS relocations from 180 elk were collected from 2007 to 2013 at two-hour intervals. Potentially erroneous relocations (e.g. locations leading to unreasonable speeds or round-trips) were removed prior to analysis. Each unique individual-year combination ('elk-year') was analyzed separately. Elk-years with 200 or more relocations during winter season (January to March) were used, resulting in 107 elk-years.

AVAILABILITY EXTENTS

MCPs were created for each elk-year for both winter and summer (June to August) to define seasonal home ranges. To study selection at the among-home-range scale we defined the area available to an animal using the fall migration distance. The distance between the centroid of the summer range to the furthest edge of the following winter range was calculated in ArcGIS 10.1. The resulting "fall migration distance" was used as the radius defining a circle of among-home-range availability (Figure 1). The entire winter home range for an elk-year was defined as available for habitat selection at the finer scale. Available points were generated uniformly across each availability domain at a density of one point per 90 m using the fishnet tool in ArcGIS 10.1. Used points were identical across the two extents - the relocations for that respective elk-year.

RESOURCE SELECTION ANALYSIS

Logistic regression was used to estimate a resource selection function of the form $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 \ldots + \beta_n x_n)$ at the among- and within-home-range scales, with vegetation, elevation, and distance to roads as predictor covariates (Johnson et al. 2006). Habitat-selection models and all subsequent analysis were completed in R version 3.2.2.

MODIS-based Normalized Difference Vegetation Index (NDVI; indicative of live green vegetation) values were obtained via the Land Processes Distributed Active Archive Center at the U.S. Geological Survey Earth Resources Observation and Science Center (temporal resolution - 16 days, spatial resolution - 250 m pixels) and were subsequently averaged within the winter season for each year. These values ranged from -2,000 to 10,000 but were rescaled (by subtracting the minimum, dividing by the range, and multiplying by 100%), so values used were between zero and 100. Both a linear and a squared term for winter NDVI were included in the model to allow for non-monotonic responses to NDVI (Figure 2), where, during winter, we

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would expect a peak in selection at intermediate values (deciduous forest, shrub lands, grasslands) with a decrease in selection towards lower NDVI values (barren open areas with little forage) and higher NDVI value (coniferous forests with low forage value).

Elevation above sea level (in meters) was included as the third covariate in our model. A Digital Elevation Model (DEM) layer at a 30 m resolution was obtained directly from Alberta Environment and Parks, and from the online GIS resources provided by British Columbia and Montana.

Road layers for Alberta, British Columbia, and Montana (from online government GIS repositories) were merged to cover the entire study area. The resulting road layer was separated into three categories based on the descriptions provided with the original road layers and the traffic data collected for a subset of southwestern Alberta (Northrup et al. 2012). The first category included highways and main roads, the second was medium-use roads, and the third was low-use roads and trails. Distance to the nearest of each road class was calculated across a 25 m raster using ArcGIS 10.1. Distance to the nearest road for each road category was included in our model as natural logarithm transformed distance +1 (lnRoadDist), to incorporate the decay in elk response to road proximity as distance from road increases.

We estimated the same exponential habitat-selection models (with the above 6 covariates) for each elk-year and at each of the two scales. To determine a population-level pattern, the mean and the confidence interval was calculated by bootstrapping the coefficients using package 'boot' with equal weighting for each elk, so that elk with multiple years were not sampled unequally. This two-step approach was used to deal with autocorrelation issues within individuals (Fieberg et al. 2010). The proportion of elk following the population level pattern was calculated for each coefficient at each order (the number of elk with the coefficient following the population selection direction out of 107 elk-years used in the analysis) to consider variability in individual model outputs.

RELATIONSHIP BETWEEN SCALES AND FUNCTIONAL RESPONSE

To investigate the relationship between habitat selection at the two different scales, the variation in within-home-range habitat selection coefficients was modeled as a function of among-home-range habitat selection coefficients, as well as mean covariate availability (calculated within each winter MCP), with elk ID and year included as separate random effects to account for pseudoreplication. To model NDVI, the squared term was combined with the

linear term in the form $w(NDVI) = \exp(\beta_1 NDVI + \beta_2 NDVI^2)$ and was calculated for each individual elk-year at both scales. Here β_1 is the coefficient for the linear NDVI coefficient and β_2 is the coefficient for the squared term. The result was an individual selection value at an intermediate value of normalized NDVI (=22%; see results for details) for each elk-year at both scales. Mean availability for the environmental covariates used in the models were calculated for each elk-year using the 100% MCP at the within-home-range scale. The full model included both availability and among-home-range selection with the random effects of elk and year. Three other models were evaluated using one of the fixed effects with the random effects separately, and finally the two random effects alone as the null model. These models were fitted using function *lmer* in the R package lme4. The most parsimonious model was selected using Akaike Information Criterion (AIC; Akaike 1973).

Results

The 95% confidence intervals obtained from bootstrapping individual among-home-range selection coefficients did not overlap zero for any of the covariates included in the models. On average, elk selected NDVI with a peak occurring at intermediate values, avoided high elevation, and selected areas further from all classes of roads (Table 2.1). There was positive selection for intermediate values of NDVI demonstrated in 85% of the individual elk-year models, whereas 95% of elk-years selected lower elevations when placing their range. Primary, secondary, and tertiary roads were avoided by 66%, 80% and 83% of elk-years in our sample, respectively.

At the fine-scale, based on the bootstrapped population mean and confidence intervals, NDVI coefficients were positive for the linear term and negative for the squared term, yielding an intermediate maximum in selection. Elk selected high elevation, as well as areas further from primary and secondary roads (The 95% confidence intervals for the selection for lnRoadDist for tertiary roads overlapped zero; Table 2.1). Across individual elk-years, the pattern for NDVI within-home-range selection had more variation, with 63% selecting for NDVI and demonstrating a peak in selection at intermediate levels. Remaining elk-years had a linear or slightly curve-linear NDVI selection pattern. Elk that selected for higher elevation within their home range made up 71% of individual elk-years. A large proportion of elk-years (89%) avoided secondary roads within their home range but only 57% of elk-years avoided primary roads and 61% of elk avoided tertiary roads.

To quantify the spatial extent of road effects in our system we calculated the Relative Selection Strength (RSS; a measure of effect size for used-available RSA; Avgar and Boyce, submitted manuscript), of one position over another, where the two differ solely by their distance to road. First, we calculated the natural-log transformed RSS of a location that is 5 km from a road (the average maximum distance an elk was found from a road) relative to each raster cell (Figure 3). We also calculated, for each road class at each availability extent, the distance from a road at which moving 25 m further (the resolution of our distance to road raster) would result in 1% increase in selection strength (i.e., where RSS = 1.01). The resulting among-home-range road-effect extents are 703 m from primary roads, 1122 m from secondary roads, and 1923 m from tertiary roads. The within-home-range road effect extents are 335 m from a primary road, 1165 m from a secondary road, and 360 m from a tertiary road.

On average, NDVI selection peaked at a normalized NDVI value of 22% (within-home-range) and 23% (among-home-range; Figure 2). From this, a normalized NDVI value of 22% was chosen to calculate selection for all elk using their unique coefficients for the linear term and the squared term. The variation in the within-home-range magnitude of selection for this intermediate value was best described by the among-home-range variation (Table 2.2). Elk that selected higher NDVI when placing their home range also selected higher NDVI within this range (Figure 4).

Within-home-range selection for elevation varied with among-home-range selection of elevation, as well as with within-home-range availability (mean elevation with the home range; Table 2.2). Elk that most strongly selected higher elevations within their home range were also those least strongly avoiding high elevation when placing their home range, and this selection decreased as mean elevation within the home range increased (Figure 2.4).

Within-home-range avoidance of primary roads was not described well by either among-home-range avoidance or home-range availability (Table 2.2). Within-home-range avoidance of secondary and tertiary roads increased with among-home-range avoidance (Table 2.2; Figure 2.4). Within-home-range tertiary roads avoidance was further influenced by availability, where selection for areas farther away from tertiary roads decreased as these roads became more prevalent within an individual elk winter range (Table 2.2; Figure 2.4).

Discussion

We used two availability extents, derived directly from individual space-use patterns, to study elk habitat selection and road avoidance during the winter. By using the fall migration distance to outline among-home-range availability, we essentially addressed endpoint selection of fall migration. In addition, we studied fine-scale within winter range selection. Amid the strong consistent signal of road avoidance, elk responded to road classes differently between and within the two scales. Elk that avoided roads more strongly at the coarse scale, did so at the finer scale. Further, the functional response in selection for tertiary roads, and not other classes, reinforced the idea that elk responded to differences in intensity of use on these features.

We predicted that selection for lower elevation due to snow accumulation would drive elk into area burdened with higher road density resulting in weak or absent road avoidance at the coarse scale. Contrary to this prediction, however, roads of all classes were avoided by the majority of elk when selecting their home ranges, indicating the importance of anthropogenic disturbance to elk at the migration scale. Within their home range, elk avoided roads as expected but less so for primary and tertiary roads. Surprisingly, the general signal for avoidance across the three road classes was weaker within the home range. Weaker selection does not imply that roads were not important, but instead indicates the variability that can exist among road features due to their varied qualities (including feature size, prevalence, and most importantly intensity of use).

The elk is a well-studied species and its habitat selection patterns are consequently well described. This prior knowledge provides a useful benchmark in to assessing the utility of conducting habitat selection analysis using multiple extents of availability. Elk seek lower-elevation ranges and slopes during winter (Boyce 1991, Sawyer et al. 2007). In agreement with this, elk in our system avoided higher elevations at the migratory among-home-range scale but selected higher elevations within the extent of their low-elevation home ranges, again following our expectations. Therefore, the two availability extents captured the opposing selection behaviour that occurred in response to topography. Indeed, elk selection responses are found to differ between scales when there is high variation in topography and elevation across the landscape (Boyce et al. 2003). During winter elk selected deciduous forests, shrubland, and grasslands (Gude et al. 2006, Jenkins et al. 2007, Sawyer et al. 2007). Overall, elk selected intermediate NDVI values (indicative of these aforementioned areas) as predicted although, the

strength in the pattern differed between scales. Almost all elk exhibited this pattern at the coarse scale but the response to NDVI was weaker and more variable at the within-home-range. Overall, our results corroborate previous findings regarding winter range habitat selection in elk, thus landing support to the usefulness of using two extents of availability to understand multiscale selection drivers in other, lesser known systems.

Migration may be considered habitat selection at a coarse scale (Fryxell et al. 1988, Avgar et al. 2014). Following this idea, our definition among-home-range availability matched migration movement, and so, our inference at the coarse scale of analysis can describe winter home range selection in our migratory population of elk. Certainly, some seasonal home range shifts have been argued as within home range habitat selection behaviour when animals follow resources and do not develop separate or stable home ranges (Gaudry et al. 2015). However, across the spectrum of migration, space-use goals are similar to those within home ranges; even when one seasonal home range is departed for another, an animal aims to reduce predation risk and increase forage access (Bischof et al. 2012, Hopcraft et al. 2014, White et al. 2014). In fact, there is evidence for the link between migration and within home range selection in the form of trade offs between the scales. For example, elk can change migration or within-range behaviour in attempts to reduce predation risk (Hebblewhite and Merrill 2007). Thus, migration is often not a disconnected leap in space but a manifestation of the same space use behaviour that is seen within home ranges (Avgar et al. 2014). Practically, our course scale selection analysis can outline which features determine where migration ends, as we have demonstrated in this work. Further, with the decline in ungulate migration across the globe (Berger 2004, Hebblewhite et al. 2006), the consideration of habitat selection of migratory species across multiple scale becomes especially vital.

Elk habitat selection inferences at the migration (among-home-range) extent were strongly related to the within-home-range scale, indicating that, overall, individuals seek the same resources at both scales. Elk that avoided secondary and tertiary roads more strongly at one scale did so at the other, whereas the coarse-scale response to primary roads was not related to the fine-scale selection. This could indicate some elk were able to escape the proximity of these high-use roads during migration. This is consistent with Rettie and Messier (2000) argument that such a release effect is likely to happen with the most limiting landscape features. Interestingly, elevation selection coefficients were positively related across extents despite the clear switch in

direction of selection. Elk that selected higher elevations when placing their home range demonstrated this pattern within their home range as well. This pattern is likely indicative of a true scaling-up effect where within-home-range selection behavior percolates up to affect our among-home-range inference. Similarly, we found NDVI selection was related between scales. In previous work, detailed measures for vegetation such as species composition and biomass quantity were used as independent variables when the responses were found to be scale dependent or trade-offs between scales existed (Johnson et al. 2001, van Beest et al. 2010). NDVI is a more general measure of vegetation and forage availability and its ecological significance is more likely to be consistent between scales. The agreement of selection responses between scales of observation is relatively scarce in the literature (with exception to McGreer et al. 2015) and direct comparisons between scales should be done more frequently to test the generality of patterns in habitat selection. The majority of studies finding selection coefficients that differ between scales (*i.e.* scale dependent) varied both the availability and used domains for different scales (Orians and Wittenberger 1991, Johnson et al. 2001, McLoughlin et al. 2002, van Beest et al. 2010, DeCesare et al. 2012). Our study is distinct by changing availability domains alone. Overall, our findings support the bottom-up notion that habitat-selection patterns do not show abrupt scale-dependent shifts but rather gradually evolve across spatial scales.

A common pattern is a decrease in selection of a habitat type as it becomes more common on the landscape (Mysterud and Ims 1998, Herfindal et al. 2009). As identified by Mysterud and Ims (1998), this 'functional response' (in the habitat selection sense) shares similarities with functional response in the predator-prey sense, where satiation or switching patterns might arise as a result of changing availability. Availability can be quantified as binary categories or, more frequently, as continuous mean availability within the domain (Mysterud and Ims 1998, Hebblewhite and Merrill 2008, Beyer et al. 2010). In our study, mean availability was included in the best models for elevation and tertiary roads and in both cases, selection (or avoidance) decreased with increasing availability within the home range. Elk selecting intermediate elevation during the winter can explain the pattern observed with elevation. Specifically, if elk occupied a high-elevation home range they selected lower elevation within their home range, or if their home range was relatively low elevation, they select for higher elevation within it. In essence, we are seeing 'satiation' in the functional response generated

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from intermediate elevation use on their winter range. Often a decrease in avoidance of human features has been interpreted as a signal of habituation to human disturbance (Knopff et al. 2014). In our system, elk switching their avoidance for road proximity as density increased was only supported for low-use roads. Thus, when road density increases, elk continue to avoid high-use roads, while placing themselves closer to low-use roads. Indeed, there is a decreased ability to select areas away from roads when roads are saturating the landscape and deducting useable habitat (Rowland and Wisdom 2000, Hebblewhite and Merrill 2008).

Road avoidance was a prevailing pattern across scales, with a footprint that extended far beyond the linear feature itself (Figure 3). Elk avoid road proximity most for tertiary roads at the coarser scale, possibly reflecting the risk associated with these roads during the hunting season when elk place their winter ranges. In addition, elk avoid roads proximity least for primary roads at the fine-scale, possibly reflecting release from their effect at a coarser scale. Regardless of road type or scale, our findings indicate elk space-use may be severely limited by roads even when situated hundreds of meters away. That said, decreased avoidance of tertiary roads as they increase on the landscape may indicate that elk are to some degree capable of adjusting their space-use to low-use roads. We thus recommend that, whereas limiting road construction on winter ranges would be ideal, controlling traffic on existing roads can serve as an effective alternative solution when roads are deemed necessary.

To have a chance of elucidating the mechanisms occurring at different scales, the choice of scale (resolution or extent) should be done with biological justification (Mayor et al. 2009). Unfortunately, often the decision of scale is arbitrary, in fact, only 29% of all studies (45% of mammal studies) provide biological reasons for the choice (Wheatley and Johnson 2009). In our work we defined among- and within-home-range availability using individually and biologically based metric, fall migration distance and winter home range areas. Regardless of its simplicity, changing the extent of availability in this way supplied further insight about our system than if we had only considered one scale in our analysis.

Table 2.1. Mean beta coefficients and 95% confidence intervals (CIs) from resource selection analysis completed at the within-home-range scale and among-home-range scales. Population mean and CI values were calculated by bootstrapping coefficients for all individuals, with the probability of sampling weighted equally among elk to account for elk with multiple years of data. Values in bold indicate mean population coefficient estimates with a 95% CI that did not overlap zero.

| Covariate | Within-Home-range | | | Among-Home-Range | | |
	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI
Elevation	**0.0018**	0.0009	0.0028	**-0.0078**	-0.0088	-0.0069
Normalized NDVI	**0.2698**	0.1723	0.3804	**0.8514**	0.6807	1.0386
Normalized NDVI^2	**-0.0062**	-0.0083	-0.0043	**-0.0178**	-0.0218	-0.0141
lnPrimaryRoadDist	**0.1283**	0.0021	0.2680	**0.2749**	0.1680	0.3941
lnSecondaryRoadDist	**0.4590**	0.3788	0.5368	**0.4417**	0.3393	0.5489
lnTertiaryRoadDist	0.1386	-0.0336	0.3098	**0.7605**	0.6039	0.9255

Table 2.2. Akaike Information Criterion (AIC) scores for models explaining the variation in selection coefficient obtained in the within-home-range RSA. Bold values indicate the top model for each covariate.

	Elevation	lnPrimary RoadDist	lnSecondary RoadDist	lnTertiary RoadDist	Normalized NDVI
Fixed effects: Among-Home-Range Coefficient + Within-Home-Range Availability Random effects: Elk + Yr	**-842.39**	232.49	73.77	**243.88**	642.99
Fixed effects: Among-Home-Range Coefficient Random effects: Elk + Yr	-838.22	233.57	**72.72**	291.84	**641.00**
Fixed effects: Within-Home-Range Availability Random effects: Elk + Yr	-830.25	231.28	113.26	297.50	740.30
Random effects: Elk + Yr	-831.81	**231.62**	111.42	299.92	740.58
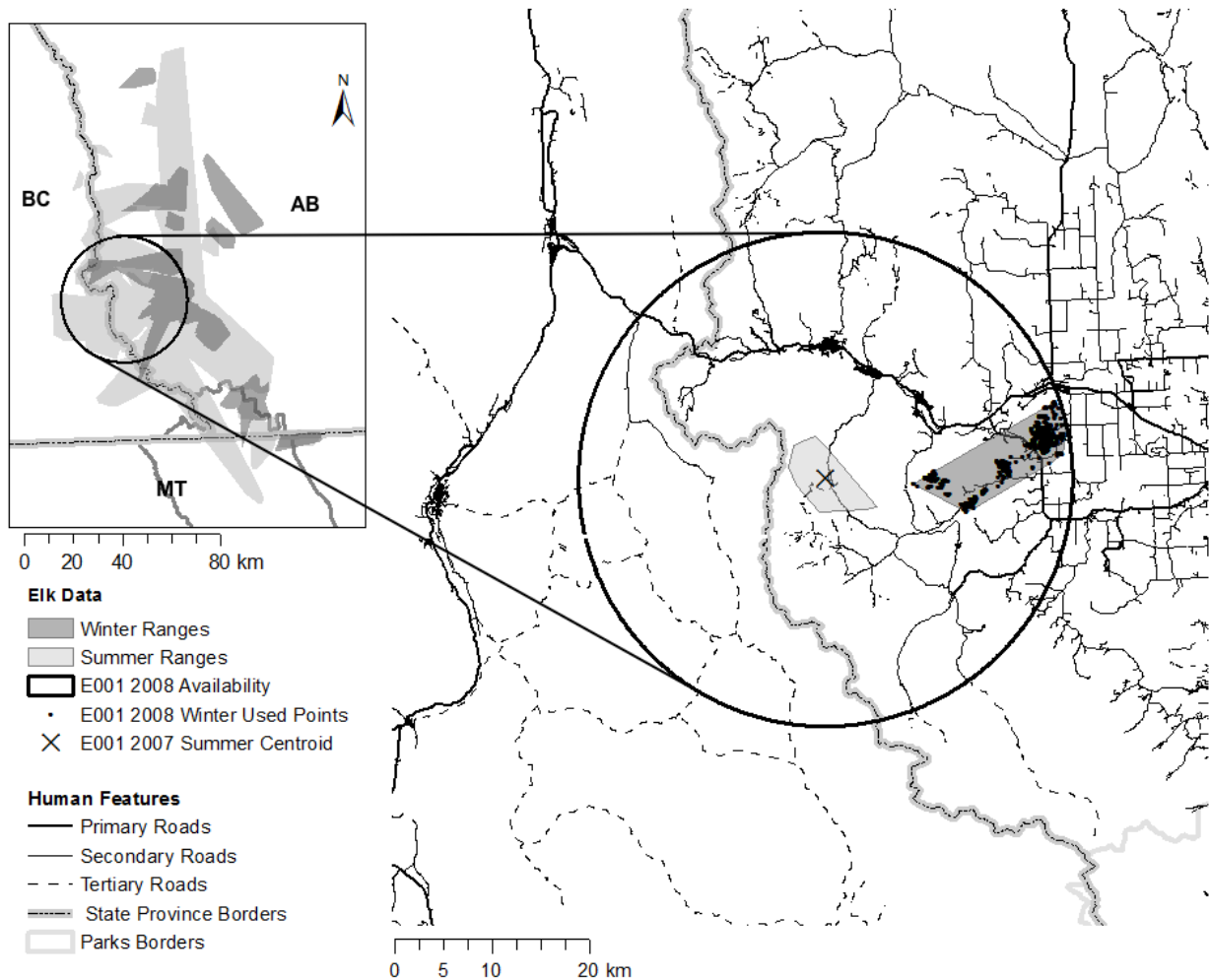
Figure 2.1. Map of study area with individual elk-year 100% MCPs for the summer (light grey) and winter (dark grey). Inset: Example of availability extents (using Elk 001 winter of 2008) at the both scales. Among-Home-Range availability circle (black circle) was created using the fall migration distance as the radius; the distance from the centroid (×) of the previous summer range (light grey) to the edge of the winter home range area. Within-home-range availability was the 100% MCP for the winter (dark grey) calculated using winter used points for that year. The used domain for both analyses was the used relocations, depicted as black points.
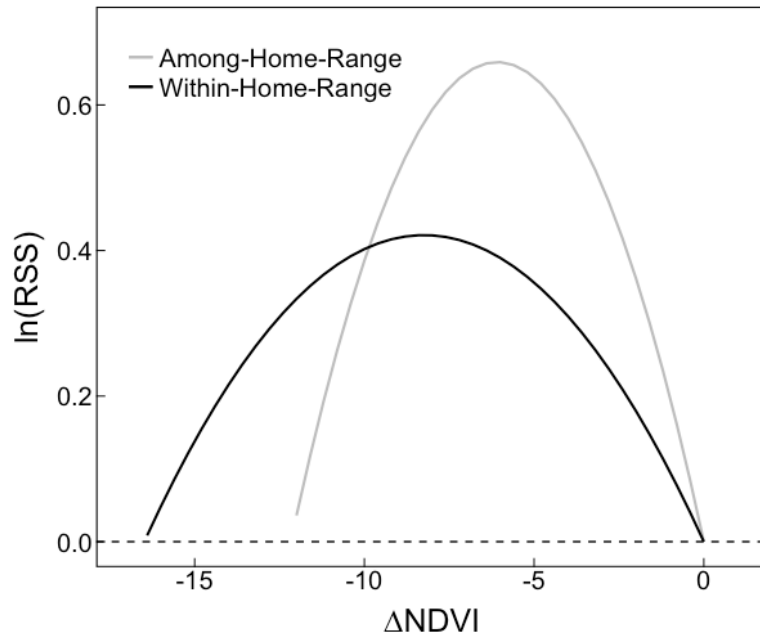
Figure 2.2. Ln-transformed relative selection strength (log-RSS; Avgar and Boyce, submitted manuscript) for a location with a normalized NDVI values of 30% relative to a location with ΔNDVI less NDVI. Curves were calculated using the bootstrapped mean linear NDVI coefficients (β_i) and the mean quadratic NDVI coefficient (β_{i2}) at for within-home-range (black) and among-home-range (grey) selection.

	Primary	Secondary	Tertiary

Linear Feature
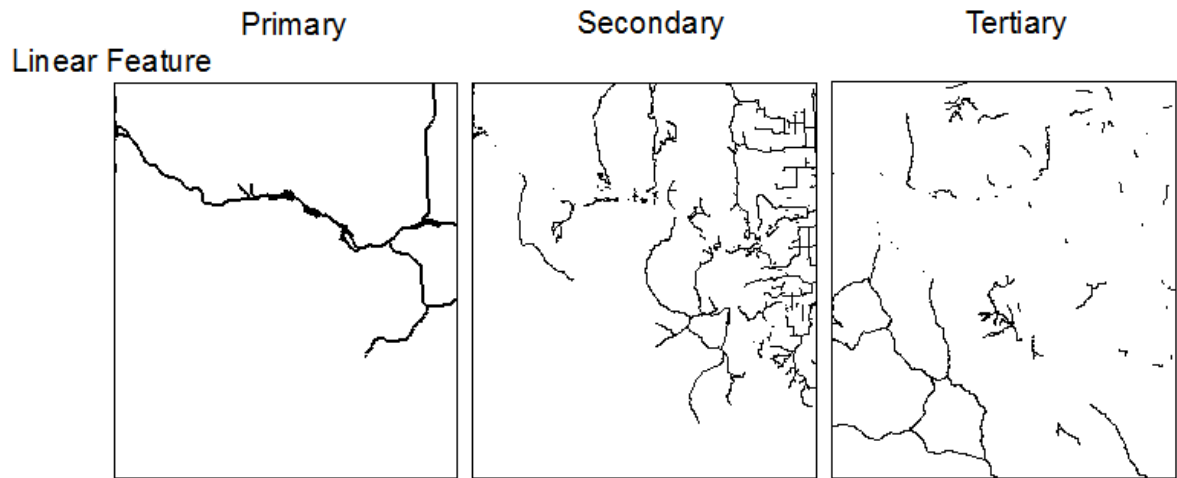
Within-Home-Range Effect Distance
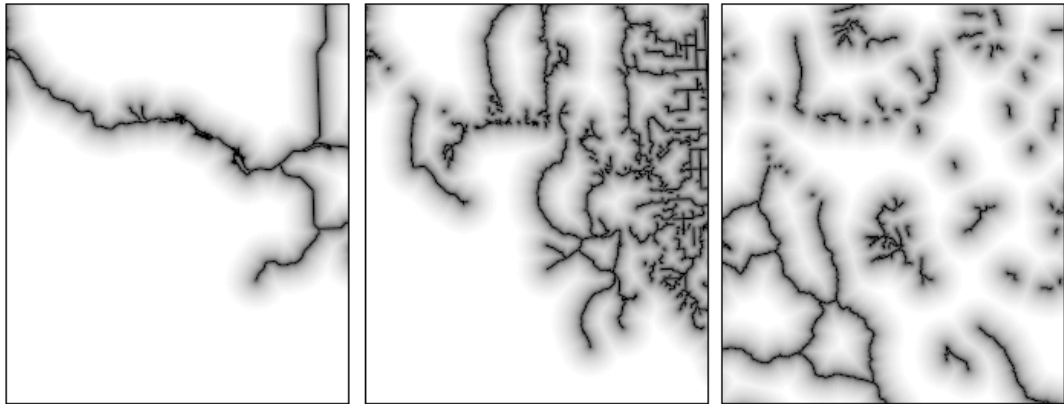
Among-Home-Range Effect Distance

0   55 110   220 km
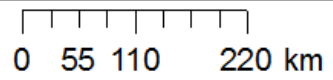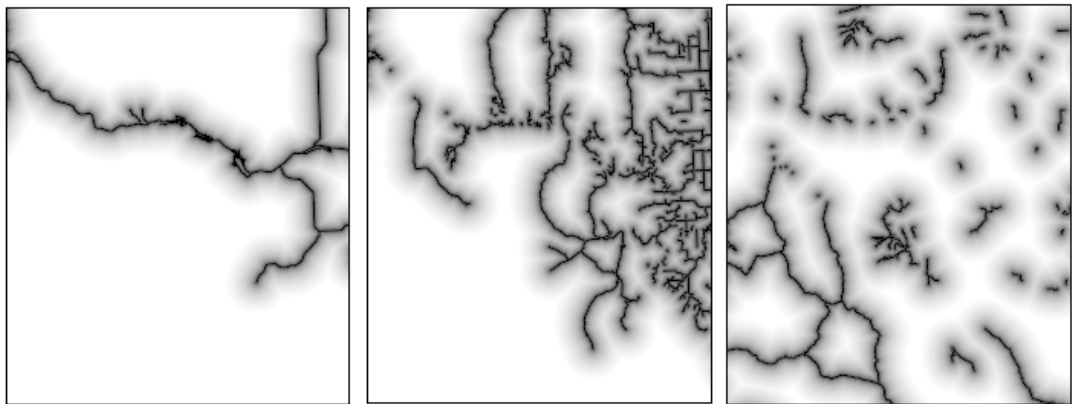
Figure 2.3. The spatial extent of road-avoidance. Ln-transformed relative selection strength for a location 5 km from a road in relation to another (the local distance to road in the 25 m pixel) projected across a portion of the study area (centered on the winter range of elk E001 in 2008). Grey scale reflect the strength of avoidance (in relation to a reference 'refuge' located 5 km away from the road). RSS was calculated using the bootstrap mean lnRoadDist coefficients (β_i).
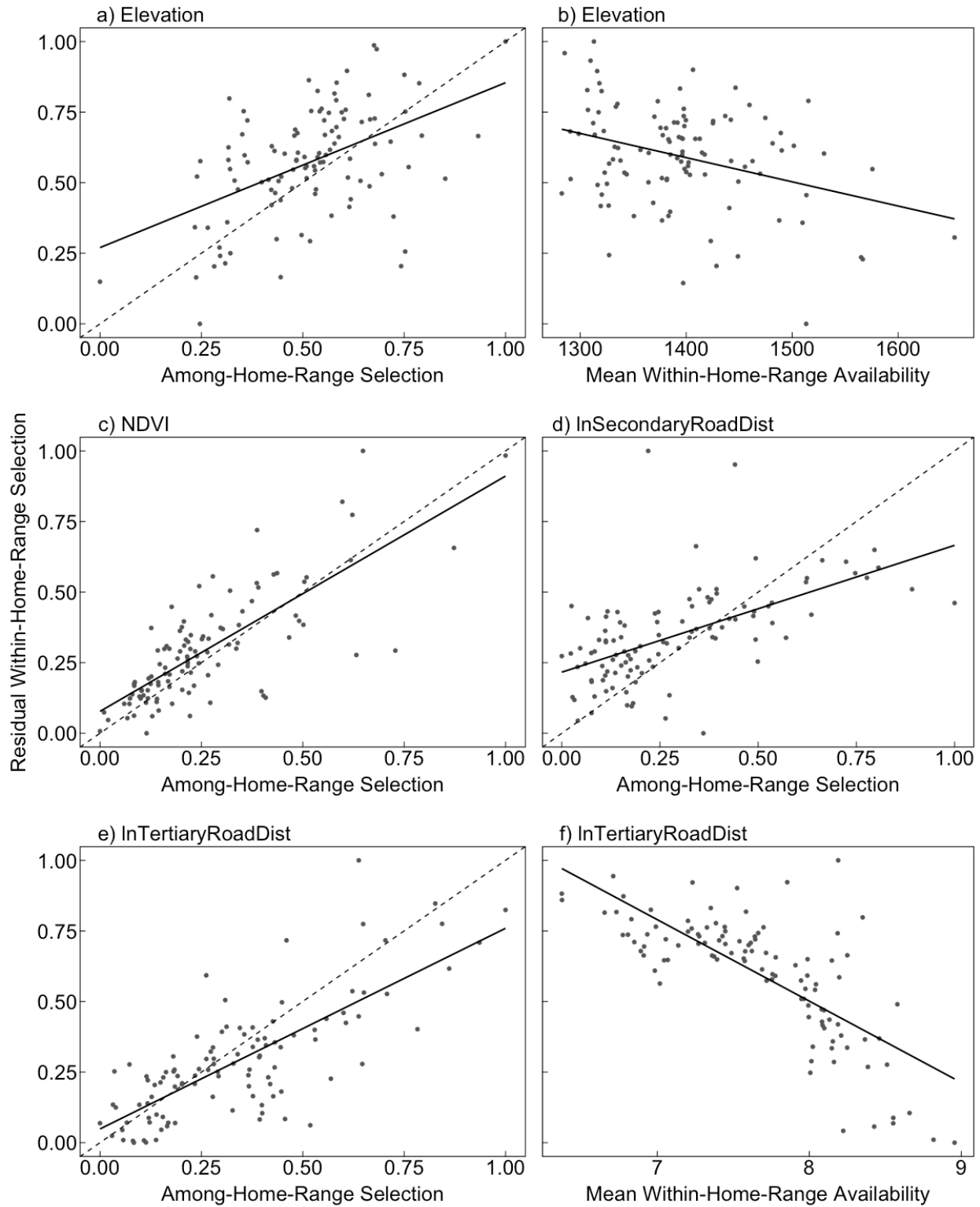
Figure 2.4. Partial residual plots of variation in within-home-range selection coefficients. Residual within-home-range selection, after removing the variation explained by random effects and within-home-range availability, plotted against among-home-range selection coefficients for (a) elevation, (c) NDVI (as an exception, selection strength was calculated for an NDVI value of 22%), (d) lnSecondaryRoadDist, (e) lnSecondaryRoadDist. The dashed line represents the predicted 1:1 relationship between the two scales. Residual within-home-range selection coefficients, after removing the variation explained by random effects and among-home-range selection, plotted against the mean within-home-range (b) elevation, (f) and lnTertiaryRoadDist. In both plots, each point represents a unique elk-year, and the solid black line represents the line of best fit.

CHAPTER 3: THE ROAD LESS TRAVELLED: CHARACTERIZING WILDLIFE BEHAVIOURAL RESPONSES TO ROADS USING INTEGRATED STEP SELECTION ANALYSIS

Introduction

Road networks have far-reaching, and frequently negative, ecological effects on landscapes and wildlife (Forman and Alexander 1998, Forman et al. 2003, Fahrig and Rytwinski 2009). There can be mortality effects resulting from road networks, mainly through increased predator/hunter access and direct vehicle collisions, but also behavioural changes caused by this disturbance (Trombulak and Frissell 2000, Kociolek et al. 2011). These disturbance-induced behavioural adjustments can have costs to individuals, and ultimately populations (Shepard et al. 2008, Fahrig and Rytwinski 2009). The perception of, and response to human disturbance is thought to be equivalent in impact to predation risk (risk-disturbance hypothesis; Frid and Dill 2002).

Animals respond to predation risk by adjusting their behaviour in multiple ways. First, wildlife avoid unfavourable areas and this avoidance of predators occurs at multiple scales (Hebblewhite and Merrill 2009, Dussault et al. 2015). The complete avoidance of risk is however unattainable in most systems, and animals have been shown to selectively use habitats that provide refuge (e.g., thick vegetation cover) when exposed to risk (Fortin et al. 2005, Hebblewhite and Merrill 2009, Ciuti et al. 2012a). Similarly, animals are often thought to reduce the time spent in risky areas by increasing their movement rates (Frair et al. 2005). Elk (*Cervus elaphus*), for example, responded to wolf (*Canis lupus*) and human predation risk by increasing their movement rate (Proffitt et al. 2009). However, from a temporal rather than a spatial perspective, increased movement rates may act to increase the probability of encountering a predator (Avgar et al. 2011, 2013, Vander Vennen et al. 2016). Overall, we might expect a negative response towards roads to manifest itself as direct avoidance of roads, and indirectly through increased selection for cover and increased movement rate in the vicinity of roads.

Our study focuses on the effects of roads on the behaviour of elk in southwestern Alberta where road construction has accelerated due to energy development. Elk mortalities due to natural predation are uncommon in our study area because wolf abundance is low (Morehouse and Boyce 2011). The main cause of mortality is hunting by humans, and behavioural response to hunters has been demonstrated in this population of elk (Ciuti et al. 2012a). Thus, areas related

to human use, such as roads, should be perceived as risky. The response of elk to disturbance during the winter (post hunting season) has yet to be studied in this population. Winter is a demanding period of the year when elk face low forage availability coupled with high energetic costs of movement, foraging, and thermoregulation (Parker and Robbins 1984, Parker et al. 1984, Sweeney and Sweeney 1984). Road avoidance and associated behaviours, such as seeking cover when near roads, has been found in other elk populations during the winter (Beck et al. 2013, Buchanan et al. 2014). Thus roads may present another burden during winter. Moreover, energy development in the area brings new human features and continued disturbance into core winter range areas of this migratory population. Collectively, these factors necessitate a fine-scale understanding of the effects of roads on elk winter range behaviour.

Movement and selection are linked, both in the relation to the landscape and their relationship to one another (Avgar et al. 2016). Movement has been incorporated into models of habitat use by adjusting the availability domain. Availability, in the context of habitat selection, is the area an animal could potentially use, and the habitat composition of the availability domain is contrasted against that of the used domain to infer selection. Step selection analysis (SSA) defines availability using the empirical distributions of movement attributes of used steps, where a step is the linear connection between consecutive relocations (Fortin et al. 2005, Thurfjell et al. 2014). Within this availability, random steps are generated and analysis is based on contrasting used versus random steps using conditional logistic regression (Fortin et al. 2005, Thurfjell et al. 2014). Including movement parameters into the analysis itself was found to reduce inferential bias with regards to habitat selection (Forester et al. 2009). The recently developed 'integrated Step Selection Analysis' (hereafter iSSA) incorporates movement and habitat selection by estimating them in the same model while still using conditional logistic regression as in previous SSAs (Avgar *et al.* 2016; for a user guide see Appendix S4 therin).

Here we use iSSA to detect fine-scale direct and indirect spatiotemporal effects of roads on movement and selection simultaneously. We built four alternative models based on the expectation that elk perceive roads as risky. The predicted behaviours were time-dependent avoidance of roads or road crossings, and increased selection for cover and increased movement rate when at the vicinity of roads. We evaluated which of these alternative models was most supported by our data at both the population and individual levels.

Materials and methods

Our study area is situated on the eastern slopes of the Rocky Mountains in southwestern Alberta near Pincher Creek (49.4856° N, 113.9482° W). Coniferous and deciduous forests and grasslands are available to elk during winter, although accessibility is usually limited by snow. Snow accumulation and compaction is highly variable within the area, being heavily influenced by Chinook winds. The greater study area has a wide range in topography, with the Canadian Rocky Mountains to the west and prairies to the east. Elk winter ranges are mostly low in elevation relative to landscapes used during other seasons. Land is a mosaic of private land, much of which is used for agriculture (primarily pasture), and public Crown land, with Waterton Lakes National Park in the southwest. Roads are present throughout the area, being denser with higher traffic in the east. Predators present in the area during winter include wolves and cougars (*Puma concolor*), but natural predation is low, especially during winter. Large wild herbivores in the area, in addition to elk, are bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*).

ELK CAPTURES AND MONITORING

GPS relocations were collected every two hours from a total of 180 elk during 2007 to 2013, capture methods followed University of Alberta Animal Care protocol number AUP0000009. All analyses were completed on steps occurring in winter, January to March, for each year an elk was radiocollared (hereafter 'elk-year'). Elk-years with 500 or more relocations during winter were used in the analysis (for a total of 175 elk-years)
.

INTEGRATED STEP SELECTION ANALYSIS

Step length is the straight-line distance between two consecutive relocations. Available step lengths were sampled from a gamma distribution (where mostly short steps are taken, with occasional longer steps) parameterized based on observed step lengths. Turn angles are the angular deviations between the headings of two consecutive steps. Observed steps that did not have a valid step preceding them were thus omitted from our analysis. Turn angles (in radians) for available steps were sampled from values between -π and π following a uniform distribution

(corresponding to a pure random walk with no directional persistence). For each used point, ten random steps were generated from these step-length and turn-angle distributions (Fig. 1).

Four iSSA models were fitted to each individual elk-year separately. We used the function *clogit* in the *survival* package in R (version 3.2.2) to fit a conditional logistic regression, with start point ID as the strata for these models.

CORE MODEL COVARIATES

A consistent core model that included covariates expected to influence movement and selection regardless of road avoidance, was used as the foundation for the four models designed to test hypotheses related to road disturbance.

Topography can influence movement rate and direction (step length and turn angle), as well as habitat selection (Parker et al. 1984, Boyce et al. 2003). In the fall, elk migrate to low elevation winter ranges due to snow accumulating at higher elevation (Boyce 1991). Within these low elevation winter home ranges, elk use wind-swept ridges of higher elevation in this area which was not expected to place a physiological limit on movement. We expected elk to select high-elevation areas within their winter range as windswept hilltops and slopes often offer improved forage access. Elevation was thus included in the model only as an influence on selection, the elevation at the end of the step. A Digital Elevation Model (DEM; 30 m) was obtained from Alberta Environment and Sustainable Resource Development, and from the online GIS resources for British Columbia, and Montana.

We expected elk to move and select habitats differently throughout the day (Boyce et al. 2010, Ensing et al. 2014). In winter, twilight hours are spent feeding, resting occurs during the day, and there is a mixture of these two behaviours at night (Green and Bear 1990). A time of day category was calculated, where a step is classified as 'Dawn' if the fix was taken anytime between one hour before the onset of civic dawn and sunrise. 'Dusk' was assigned to the step if the starting point was between one hour before sunset and the end of civic dusk. Steps classified as 'Day' occurred between sunrise and one hour before sunset, and steps taken between the end of civic dusk and one hour before the onset of civic dawn were assigned to the 'Night' class. 'Dawn' and 'Dusk' were then combined into 'Twilight' due to a low sample size in the two shorter time periods.

The Normalized Difference Vegetation Index (NDVI; indicative of live green vegetation) at the end of the step was included in the model as both linear and squared terms. The linear term

of NDVI was included as an interaction with time of day to account for potential differences in habitat requirements. Hence, three (linear) NDVI selection coefficients were estimated; Day, Night, and Twilight. From existing literature we expected resting to occur in areas of forest cover, resulting in higher cover selected during the day than at night (Ager et al. 2003, Northrup et al. 2015). Further, areas used for foraging would be selected during twilight (Ager et al. 2003). The squared term for NDVI was included to allow for an intermediate peak in NDVI selection. We expected elk to select intermediate values of NDVI, indicative of winter foraging areas such as grassland, shrubs, and deciduous cover (Gude et al. 2006, Jenkins et al. 2007, Sawyer et al. 2007). Areas of low or high NDVI values represent open areas or closed coniferous canopy, respectively. MODIS-based NDVI was obtained from the Land Processes Distributed Active Archive Center at the U.S. Geological Survey Earth Resources Observation and Science Center (16 days, 250 m pixels). NDVI values were assigned to each used and available points based on position is space (raster cell) and time (the 16-day window during which the step was taken). NDVI values were normalized by subtracting the minimum, dividing by the range, and multiplying by 100, so values used were between 0% and 100%.

The iSSA statistical coefficient of the ln-transformed step length (hereafter ln*StepLength*) is a modifier of the shape parameter of the gamma distribution originally employed to generate the available steps (Avgar *et al*. 2016). We expected temporal activity patterns would translate to differing movement rates, with more movement occurring while foraging during twilight compared to during the day and night (Ager et al. 2003, Frair et al. 2005). Time of day categories were thus included as an interaction with the ln*StepLength* (resulting in three coefficients) to account for behavioural phases that may coincide with times of day. An additional temporally dynamic effect on movement is snow depth, expected to increase friction and hence decrease movement (Parker et al. 1984, Sweeney and Sweeney 1984, Proffitt et al. 2009, Avgar et al. 2013). Projected snow depth values (daily, 40 km) were obtained from the Canadian Meteorological Centre, and the *SnowDepth* value at the start point of each step was included in as an interaction with ln*StepLength* to account for the effect of snow on movement.

The cosine of the turn angle (cos*TurnAngle*) is used to describe directionality of an individual's movement (Turchin 1998, Avgar et al. 2013). Using cos*TurnAngle*, the circular measure becomes a linear correlation factor (between -1 and 1) where a negative value indicates moving backwards from the previous location, zero indicates a random walk, and moving

forward is indicated by a positive value (Benhamou 2006). When cos*TurnAngle* is included in SSA, the beta coefficient is an unbiased estimator of the concentration parameter of the von Mises distribution (Duchesne et al. 2015, Avgar et al. 2016). Our inference on selection is sensitive to the definition of availability (Forester et al. 2009); accounting for directional persistence allowed us to get unbiased inference of habitat selection and road avoidance.

ROAD COVARIATES

We formulated four statistical models to quantify behavioural responses to roads (Table 3.1). The first two models address the direct effect of roads on selection or movement and the following two address indirect effects on behaviour, using either proximity or crossings. Whereas the four hypotheses are not mutually exclusive (elk can display any combination of the four hypothesized behavioural responses), they cannot be assessed within the same model due to high degree of colinearity. Road layers for Alberta, British Columbia and Montana (obtained from online government GIS repositories) were merged to cover the entire study area. Distance to road in metres was calculated as raster (25 m) using ArcGIS 10.1 and was transformed to the natural logarithm of the distance to the nearest road + 1, hereafter ln*RoadDist*, to incorporate a decay in road effect as the distance from road increased. Road crossings were identified by intersecting used and available steps with the road features in ArcGIS 10.1, and were included in models as a binary variable, hereafter *RoadCros*, with 0 being a step that did not cross a road and 1 being a step that crossed at least one road (Fig. 1).

First, we expected that elk would select for areas farther from roads. Road avoidance has been shown to vary between times of day due to traffic patterns and behavioural patterns (Ager et al. 2003, Northrup et al. 2015). Corresponding to this expectation, our Model 1 included the core model components with an additional interaction between ln*RoadDist* at the end of a step and time of day, resulting in a ln*RoadDist* selection coefficient for Day, Night, and Twilight. Similarly, we predicted that elk would avoid taking steps that crossed roads and that the response would be sensitive to the time of day due to traffic patterns and behaviour (Gagnon et al. 2007, Meisingset et al. 2013, Beyer et al. 2013). Thus, Model 2 included, in addition to the core model components, the interaction between *RoadCros* and time of day. Traffic is heaviest during the day, followed by twilight and low at night, and we expected elk road avoidance (proximity and crossing) to rank accordingly.

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When exposed to risk, one common response is to seek cover (Fortin et al. 2005, Hebblewhite and Merrill 2009, Ciuti et al. 2012a). To incorporate this into our analysis, Model 3 included the interaction between ln*RoadDist* at the step's start-point and the linear NDVI value at the end of the step. Likewise, the interaction between *RoadCros* and the linear NDVI value at the end of the step was added to the core covariates in our fourth model. We expected heightened NDVI (cover) selection when steps began near roads or crossed roads. We expect movement rate to increase when in risky areas (Proffitt et al. 2009). The interactions between ln*StepLength* and, either ln*RoadDist* value at the start of the step, or *RoadCros*, were thus included in Model 3 and Model 4, respectively (Table 3.1).

EVALUATION AND APPLICATION OF iSSA

After fitting each of the four iSSA formulations to each elk-year, population averages of beta coefficients from each of the four model formulations were obtained by bootstrapping coefficients. Each sample was weighted by elk i.d. so that the probability of sampling an elk coefficient was equal regardless of the number of years an elk was observed, reflecting that the individual elk (rather than elk-year') is the unit of replication. Further, the variation around each elk-year coefficient was not incorporated into the sampling. Subsequently, the overall mean and confidence interval for the 2000 samples taken was calculated and used as an indicator of the population level results. In addition, the proportion of elk-years following the population trend, as identified by the bootstrapped population mean, was calculated for each covariate.

Movement rate was calculated by multiplying the shape and scale parameter of the gamma distribution of step lengths. We used the iSSA coefficient of ln*StepLength* to modify the shape of the gamma distribution originally employed to generate the available steps, and then multiplied this by the original scale parameter (untransformed step-length was not included in our model, thus the scale parameter remained unchanged; see Avgar et al. 2016). Movement rate was calculated using bootstrapped mean and confidence intervals for three times of day, at different snow depths, at varying distances to roads, and when crossing a road or not ('Day' was the reference time-of-day category for movement rate when calculating effect of snow or roads).

As a measure of effect size, we calculated Relative Selection Strength (RSS) for one location, x_1, over another, x_2, given the difference in the i'th habitat covariate, h_i where all other habitat covariates are the same and the difference in h_i is Δh_i in favour of location 1 [i.e., $\Delta h = (h_i(x_1) - h_i(x_2))$] (Avgar and Boyce, *submitted*).

Finally, we used Akaike Information Criterion (AIC; Akaike 1973) to assess which of the four models described elk behaviour best. The instances of a model having the lowest AIC value were tallied for elk with results for all four models.

Results

CORE COVARIATES

The resulting coefficients of the covariates in the core model largely agreed among the models, thus discussion of the population and individual-level responses for core covariates will be restricted to the top model (but variation in these trends are detailed in Table 3.2 and 3.3).

Selection covariates

Based on the bootstrapped population means there was positive selection for elevation (mean coefficient value = 0.0028, 95 % CI[0.0022, 0.0034]) with 77% of elk-years having positive coefficients for elevation. There was positive selection for NDVI at all three times of day, with a maximum in the selection for NDVI (i.e., a negative coefficient value for squared NDVI; Figure 2). This population-level pattern was demonstrated by 64% of elk-years during the day, 61% during twilight, and 58% during the night. Selection for NDVI was not significantly different between times of day (based on the 95% bootstrapped CI), though the average selection coefficient was greatest for NDVI in the day (0.047, 95% CI[0.033, 0.063]), followed by twilight (0.036, 95% CI[0.021, 0.058]), and night (0.024, 95% CI[0.011, 0.048]). Further, only 35% of elk followed this temporal NDVI selection pattern.

Movement covariates

The population mean of the coefficient for the cos*TurnAngle* was positive (0.23, 95% CI [0.21, 0.24]), indicating significant directional persistence, and almost all (99%) individual elk-years followed this pattern. Movement rate (i.e., the mean of the model-adjusted gamma step-length distribution) differed between times of day. Elk moved fastest during twilight (mean movement rate = 527.8 m/2; h 95% CI [510.2, 545.4]) followed by day (274.3 m/2 h; 95% CI [281.8, 293.7]), and were slowest at night (241.4 m/2 h; 95% CI[233.9,249.7]). In terms of individual elk-years, 86% followed this time of day pattern (Twilight>Day>Night). Expected movement rates were greater than the average of the observed step-length distribution (used for generating random steps) for 99% and 69% of elk-years during twilight and day, respectively.

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For night, 82% of elk-years had movement rate that was lower than the observed average. Snow depth had a significantly negative, albeit weak, effect on movement rate. Snow depth negatively interacted with ln*StepLength* for 76% of elk-years. However, during the day, at 1 m of snow, the movement rate was 273.2 m/2 h (95% CI[272.9, 273.3]), almost the same as with no snow.

ROAD COVARIATES

Influence of roads on selection: proximity to roads

Elk selected for areas farther from roads at all times of day (Figure 3 and 4). Selection for areas farther from roads occurred for 93% of elk-years at twilight, 91% during the day, and 95% at night. Elk selection for areas farther away from roads was greatest during twilight (mean coefficient value = 0.37; 95% CI[0.29, 0.43]), then daytime (0.33; 95% CI[0.30, 0.37]), and least for nighttime (0.22; 95% CI[0.19, 0.25]). However, the temporal pattern of road avoidance was consistent only within 32% of elk-years.

Influence of roads on movement: road crossing

At all times of day, elk avoided taking steps that crossed a road (Figure 3). During twilight 78% of elk years demonstrated negative coefficients for road crossing, 66% of elk-years followed this trend for day, and 77% at night. Avoidance of crossing roads was weakest for daytime (mean coefficient value = -0.35; 95% CI[-0.49,-0.21]), then night (-0.55; 95% CI[-0.66,-0.44]), and greatest for twilight (-0.65; 95% CI[-0.79,-0.50]). This temporal pattern of road-crossing avoidance was maintained in 32% of elk-years.

Influence of roads on NDVI selection: proximity to roads

As the distance from road at the start point of a step increased, selection for NDVI at the end of the step decreased (Figure. 2; -0.0097; 95% CI[-0.013, -0.0066]). The interaction between ln*RoadDist* at the start-point of the step and normalized NDVI value at the end-point of the step was negative for 66% of elk-years.

Influence of roads on NDVI selection: road crossing

Contrary to our expectation, steps that crossed roads had lower NDVI values at the end of the step (Figure. 2; -0.026; 95% CI[-0.0033, -0.0018]). Steps crossing roads had lower selection for normalized NDVI values for 64% of elk-years.

Influence of roads on the movement rate: proximity to roads

As the distance from road at the start point of a step increased, the movement rate decreased (Figure. 5). The daytime movement rate was 421.1 m/2 h (95% CI[419.3, 422.6]) when 1 m from a road, whereas 1 km away the movement rate decreased to 287 m/2 h (95%CI[268.9,302.3]). The coefficient for ln*RoadDist* interacting with ln*StepLength* was negative for 90% of elk-years.

Influence of roads on the movement rate: road crossing

There was no effect of crossing roads on step length indicated by both the bootstrapped confidence intervals of the expected movement rate when crossing a road (mean movement rate = 288 m/2 h; 95% CI[264.14,319.1]), and individual elk-year coefficients.

AIC TALLY

The model that included distance to roads during day, night, and twilight (Model 1) was most frequently the most supported model describing elk road avoidance behaviour (Table 3.1).

Discussion

We studied behavioural responses to road disturbance by formulating hypotheses on the direct and indirect effects and translating those hypotheses into robust statistical models. Using both road crossing and proximity metrics within a powerful iSSA that included movement metrics, we were able to distinguish and characterize movement and selection behavioural responses that could not have been disentangled otherwise.

Elk moved in a directional fashion even at the rather coarse resolution of two hours. Directional movement is often associated with larger distances moved (e.g., during dispersal or migration), while within range or restricted movements are often described by low directional persistence and small distances travelled (Morales et al. 2004, Haydon et al. 2008). Positive directional persistence may enable elk to avoid recently depleted foraging areas, which might be especially important during winter when there is no forage renewal (Seidel and Boyce 2016). Taken together with our findings of distinct temporal patterns in movement rate, these results demonstrate the value of combining movement and habitat selection analysis.

There exist various ways to quantify road features. For example, the distance from a road often has been used to assess wildlife behaviours in proximity to roads (Roever et al. 2010, Ciuti et al. 2012b, Montgomery et al. 2013). Other measures include density of road features in an

area, and the configuration of the road network (Rowland and Wisdom 2000, Frair et al. 2008). Road crossings can be used to determine the permeability or barrier effect of roads on animal movement behaviour (Andrews and Gibbons 2005, Shepard et al. 2008, Northrup et al. 2012, Beyer et al. 2014). Not all road indicators are created equal. For example, road crossing is a binary variable and contains less information than distance to a road, road density, or arrangement. Further, temporal scale influence the accuracy of road crossing designation (Thurfjell et al. 2014). An alternative is to incorporate multiple road metrics into the same analysis (Frair et al. 2008, Montgomery et al. 2013, Beyer et al. 2014). Here we directly compared two of the most common approaches used to measure road effect, distance to roads and road crossings. Elk responded to these metrics differently, and through these differences we learned more about elk behaviour than if we had considered only one metric.

The model that best described elk behaviour demonstrated avoidance of roads at all times of day. During the day, the RSS for moving away vs towards a road is 2 (a twofold increase in the probability of selection) when an elk is situated 320 m from the nearest road. This 'twofold' range decreases at night (272 m) and is greatest during twilight (345 m). Thus, the ecological footprint of roads, at least as they relate to elk ecology, far exceeds mere 'linear features' and may extend several hundreds of metres into the surrounding landscape. Moreover, the spatial extent of elk road avoidance is largest when elk are most active and foraging. Indeed, the trade-off between forage and predation risk has been found at multiple scales; in both broad and fine space-use and fine scale time allocation between vigilance and foraging behaviours (Hebblewhite and Merrill 2009, Ciuti et al. 2012b).

Our results indicate that, when close to roads, elk selected areas of high vegetation cover. Indeed, Hebblewhite and Merrill (2009) found that, when exposed to risk, elk changed their use of vegetation, moving from high-forage quality intermediate vegetation to areas of higher cover. Likewise, Fortin *et al.* (2005) found that elk shifted their selection from deciduous to coniferous habitats when in areas of high wolf use. Further, flight responses occur more frequently in open habitats indicating that these areas perceived as riskier to wildlife (Stankowich 2008). Following similar results Buchanan *et al.* (2014) suggest that tree cover should be maintained near disturbance to preserve the elk in the region. That said, and contrary to our expectations, locations in open habitat were selected when elk crossed a road. This counterintuitive result may make more sense when we consider 'why did the elk cross the road?' Elk might select open areas

to promote visibility or quick movement when crossing a road. Alternatively, elk might cross roads to reach open areas where grasses are exposed on windblown slopes. Similarly, highway crossings increase when the features are in preferred habitat (Gagnon et al. 2007). Further, red deer crossed roads to access foraging areas (Meisingset et al. 2013). Whereas this might seem contradictory to the finding that elk seek closed cover when near roads, our results indicate that elk strongly avoid road crossing and hence most steps starting close to a road would not cross it. Hence, proximity to roads and crossing roads result in distinct habitat selection behaviors. This illustrates the comprehensive inferences we achieved through incorporating both direct and indirect effects of roads while separating distance from roads and roads crossings.

We demonstrated barrier effects of roads on elk movement. In our study, elk avoided crossing roads at all times of day. Similarly, roads have been found to be semi-permeable barriers to movement in other systems (moose - Laurian *et al.* 2008; snakes and turtles - Shepard *et al.* 2008; songbirds - Tremblay and St. Clair 2009; caribou - Leblond, Dussault and Ouellet 2013). Usually traffic along a road is related to permeability of this barrier, previously demonstrated by road crossings occurring more frequently when traffic is low or by increased time to cross a high-traffic barrier (Andrews and Gibbons 2005, Gagnon et al. 2007, Leblond et al. 2013, Meisingset et al. 2013). We found an opposite temporal pattern where most crossings occurred during the busier day time. In view of our other findings however, this should not come as a surprise. To cross roads elk must be both close to the road and on the move. When moose moved faster, road crossings were more frequent, and an increase in road density is related to more frequent road crossings (Beyer et al. 2013). Our results indicate that, in our system, the combination of relatively high movement rates and relatively high road proximity happens most during daytime, hence the relative weak crossing avoidance during that time.

Elk moved faster when closer to roads, as predicted. Other prey species, including moose and caribou, move faster in areas with more roads (Leblond et al. 2013, Beyer et al. 2013). We interpret increased movement rates when near roads as a behavioural indication of disturbance. This disturbance may interrupt resting and feeding behaviour (Naylor et al. 2009). An alternative interpretation of increased movement rates in the vicinity of roads might be that elk use human travel corridors for travelling or that elk forage (hence, most active) along roads. This is unlikely in our system, however, because we observed strong avoidance of roads during foraging and

travel times (*i.e.* twilight). In conclusion, roads restrict elk space use during winter while also acting to increase movement rate, which could translate to an additional energetic cost.

 Our work clearly demonstrates the diverse effect of roads on selection and movement behaviour of this migratory elk population during the winter. Elk avoided being near roads and crossing roads while indirectly changing their vegetation selection and increasing movement rates in response to roads. These road effects have the potential to exacerbate the conditions on elk winter range. To mitigate this, we suggest road closures or traffic management, in addition to protection of tree cover on elk winter ranges. However, it is of utmost importance that further road development is limited in core areas.

Table 3.1. Number of instances that a model had the lowest Akaike Information Criterion score (minimum AIC tally) out of the four models run for each elk-year. All models contained the same core model cosTurnAngle + lnStepLength:TimeOfDay + lnStepLength: SnowDepth + Elevation + NDVI:TimeOfDay + NDVI2 (":" denotes an interaction between two variables; see Methods for details). The models differed in the covariates used with respect to roads (lnRoadDist or RoadCros) and evaluated predictions of the effects of roads on habitat selection and movement. 133 out of 175 elk-years had results for all four models.

	Model	Road Covariates	Minimum AIC Tally
1	Influence of road proximity on selection	Core Model + ln*RoadDist* (end-point) : *TimeOfDay*	63
2	Influence of road crossing on movement	Core Model + *RoadCros* : *TimeOfDay*	25
3	Influence of road proximity on cover selection and movement	Core Model + ln*RoadDist* (start-point) : NDVI (end-point) + ln*RoadDist* (start-point) : ln*StepLength*	15
4	Influence of road crossing on cover selection and movement	Core Model + *RoadCros* : NDVI (end-point) + *RoadCros* : ln*StepLength*	30

Table 3.2. Mean beta coefficient values and 95% CIs from the core model used in the four models to control for basal selection and movement behaviours. Population means and CIs were calculated by bootstrapping coefficients for individual elk-years, with the probability of sampling weighted equally between each elk to account for elk with multiple years of data. Note that ":" indicates an interaction. The covariates added to the core model are as follows: Model 1 – ln*RoadDist* (end-point) : *TimeOfDay*, Model 2 – RoadCros : *TimeOfday*, Model 3 - ln*RoadDist* (start-point) : NDVI (end-point) + ln*RoadDist* (start-point) : ln*StepLength*, Model 4 - Core Model + *RoadCros* : NDVI (end-point)+ *RoadCros* : ln*StepLength*

	Model 1	Model 2	Model 3	Model 4
Total elk-years	175	133	175	162
Movement Parameters				
cos Turn Angle	0.2254 [0.2058, 0.2440]	0.2018 [0.1822, 0.2214]	0.2260 [0.2071, 0.2459]	0.2213 [0.2015, 0.2422]
ln*StepLength*:Day	0.0392 [0.0210, 0.0579]	0.0382 [0.0169, 0.0619]	0.3715 [0.3254, 0.4187]	0.0403 [0.0218, 0.0607]
ln*StepLength*:Night	-0.0710 [-0.0875, -0.0519]	-0.0483 [-0.0682, -0.0256]	0.2464 [0.1993, 0.2931]	-0.0578 [-0.0762, -0.0381]
ln*StepLength*:Twilight	0.5832 [0.5435, 0.6224]	0.6256 [0.5791, 0.6763]	0.9011 [0.8393, 0.9651]	0.6070 [0.5654, 0.6511]
ln*StepLength*:*SnowDepth*	-0.0024 [-0.0032, -0.0017]	-0.0026 [-0.0035, -0.0018]	-0.0025 [-0.0031, -0.0019]	-0.0025 [-0.0033, -0.0018]
Selection Parameters (end-point)				
Elevation	0.0028 [0.0022, 0.0034]	0.0034 [0.0027, 0.0042]	0.0038 [0.0031, 0.0044]	0.0036 [0.0029, 0.0042]
NDVI:Day	0.0473 [0.0328, 0.0628]	0.0671 [0.049, 0.0857]	0.1128 [0.0863, 0.1407]	0.0556 [0.0404, 0.0708]
NDVI:Night	0.0240 [0.0111, 0.0376]	0.0459 [0.0292, 0.0641]	0.0861 [0.0608, 0.1118]	0.0300 [0.0404, 0.0708]
NDVI:Twilight	0.0345 [0.0211, 0.0483]	0.0518 [0.0561, 0.0684]	0.0984 [0.0730, 0.1260]	0.0428 [0.0299, 0.0584]
NDVI^2	-0.0006 [-0.0009, -0.0004]	-0.0009 [-0.0012, -0.0007]	-0.0006 [-0.0008, -0.0004]	-0.0007 [-0.0009, -0.0005]

Table 3.3. Percentage (%) of elk-years following the population level trend established by bootstrapped means each of the covariates included in the core model.

	Model 1	Model 2	Model 3	Model 4
Total elk-years	175	133	175	162
Movement Parameters				
Positive cos*TurnAngle*	98.86	98.50	98.29	98.15
Positive ln*StepLength* : Day	69.14	66.92	87.43	69.14
Positive ln*StepLength* : Night	82.29	76.69	21.14	77.78
Positive ln*StepLength* : Twilight	98.86	99.25	97.71	99.38
ln*StepLength* : Twilight>Day>Night	86.29	81.20	89.71	84.57
ln*StepLength* : *SnowDepth*	76.00	76.44	76.00	74.69
Selection Parameters (end-point)				
Positive selection for Elevation	76.57	75.94	80.57	80.25
Positive NDVI : Day, negative NDVI^2	64.57	70.68	57.14	67.90
Positive NDVI : Night , negative NDVI^2	58.29	66.17	54.86	61.73
Positive NDVI : Twilight, negative NDVI^2	61.14	68.42	54.29	66.05
NDVI : Day>Twilight>Night	34.29	30.08	36.00	31.48
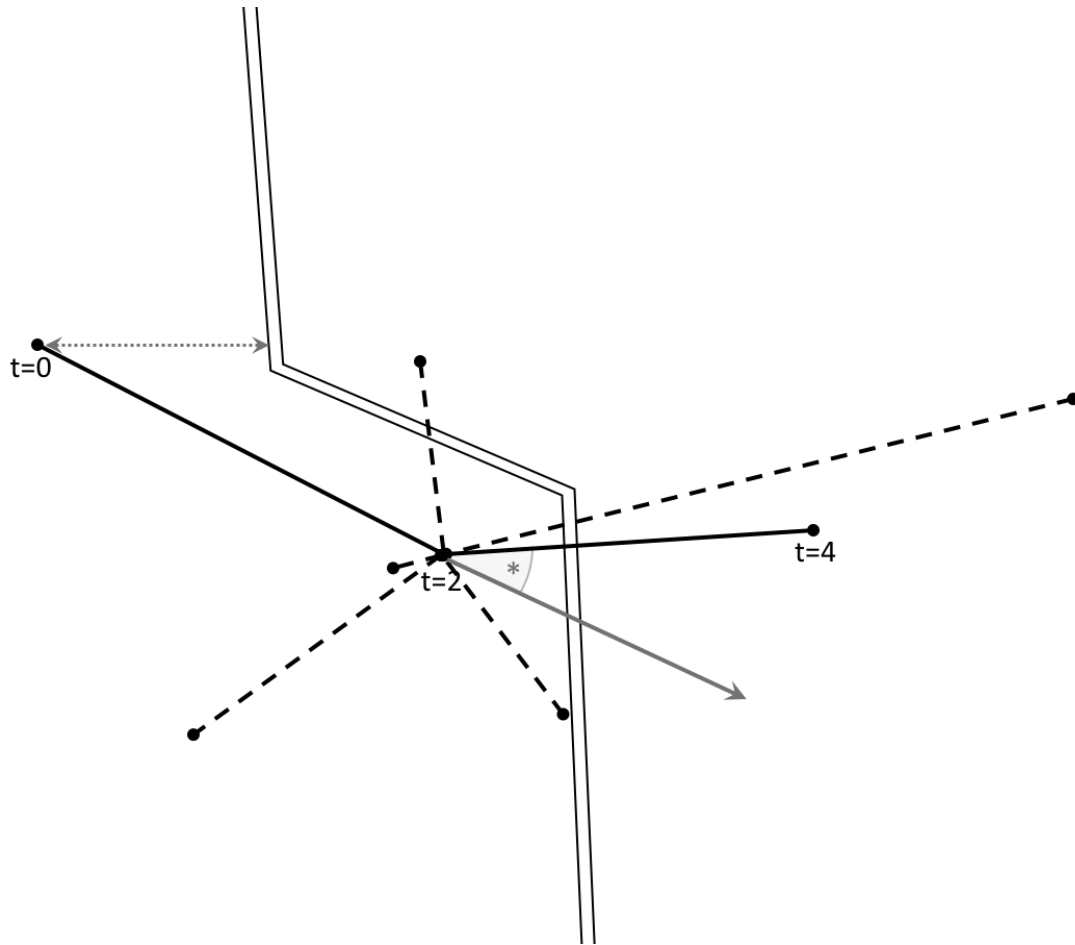
Figure 3.1. Example of three used points and two used steps (black solid lines) in relation to road features (road crossing at t = 2, road proximity at t = 0 indicated by double arrow), "*" notes used turn angle calculated from the previous step heading (grey line) to the used step, step length is the distance between the used start point and the step end point. A subset of five available steps and end points for the used start point at t = 2 (dashed black lines) are shown.
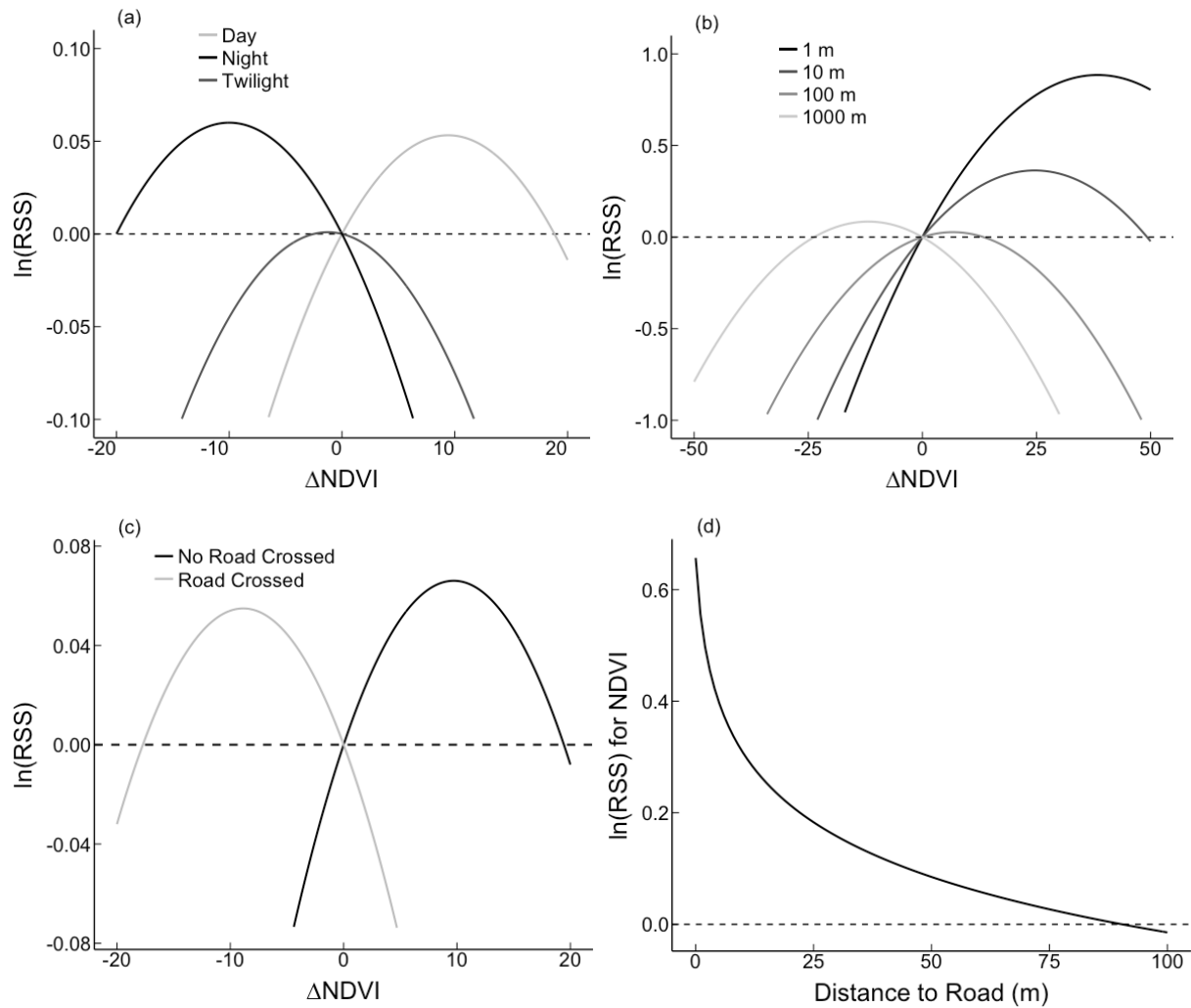
Figure 3.2. (a) RSS of one location over another (differing by ΔNDVI units) at three times of day. The value of NDVI at location 1 was set to 30%. Curves were calculated using the bootstrapped NDVI and NDVI^2 from top model (Model 1). (b) RSS of selecting one location over another given their NDVI difference (NDVI at the first location = 50%), both locations are the same distance from road. Curves were calculated using the mean coefficients from Model 3 for NDVI, NDVI^2, and NDVI:ln*RoadDist*. (c) RSS of one location (with NDVI = 50%) over another (with an NDVI = 50 − ΔNDVI) for steps that crossed a road or did not cross a. Curves were calculated using the mean coefficients from Model 4 for NDVI, NDVI^2, and NDVI: *RoadCros*. (d) RSS of one location (NDVI = 65%) over another (NDVI = 50%) given the distance to road. For all figures, RSS was ln-transformed so that zero indicates indifference.
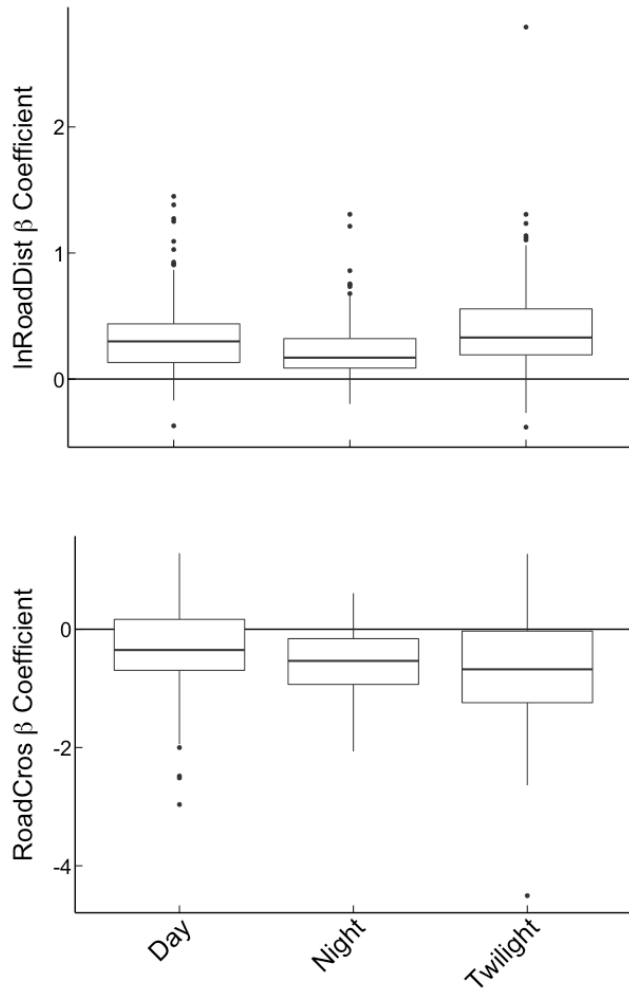
Figure 3.3. Boxplots of the beta coefficients for ln*RoadDist* and for *RoadCros* during day, night and twilight. The boxplots were constructed from the coefficient estimates for each elk-year from Model 1 and 2, respectively.
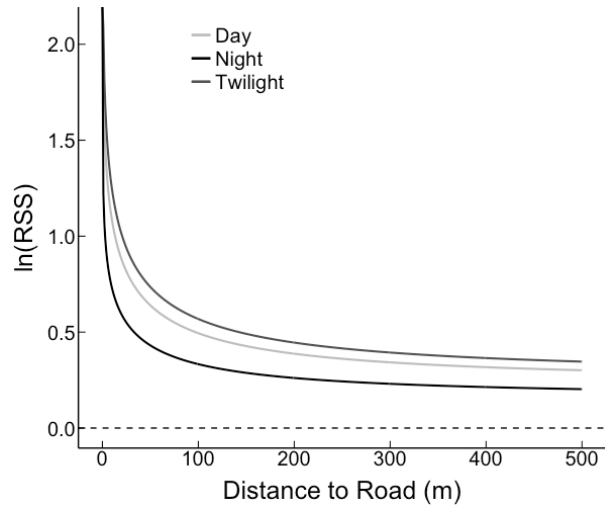
Figure 3.4. RSS for a location further from a road in relation to another as a function of the distance to road of the latter where the difference between locations is 250 m. Curves were calculated using the mean ln*RoadDist* coefficients three times of day Model 1.
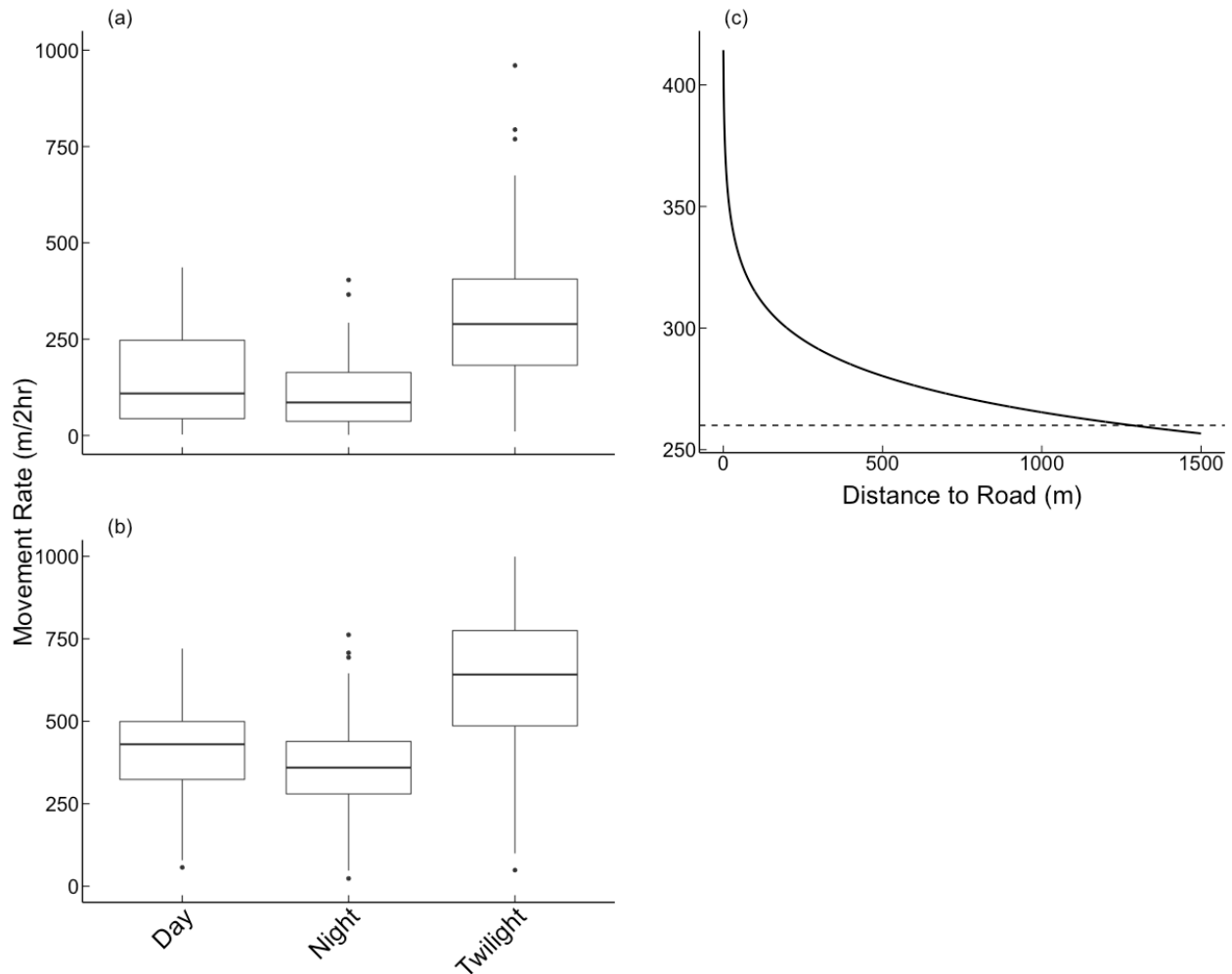
Figure 3.5. Boxplots of expected two-hour step length during day, night, and twilight when the start of the step is (a) 1 km and (b) 1 m from a road. (c) The change in expected movement rate with distance from roads at the start point of a step. The horizontal line represents the observed average movement rate during daytime in winter. Values were calculated based on Model 3 coefficient estimates for each elk-year.

CHAPTER 4: EPILOGUE

In this thesis, I provide a multiscale analysis of elk winter range habitat selection and the effect of roads thereon. In Chapter 2, I highlighted the effect of changing availability in habitat selection analysis. The consistency or variation of a response between scales helped to illustrate the impact of a features presence across the landscape, and the functional response in selection demonstrated the importance of habitat prevalence in the domain of availability. Changing availability to consider different scales of habitat selection supplied further insight about the study system than if I had only considered one scale in this analysis.

In Chapter 3, I completed habitat selection analysis at an even finer scale to detail behaviours in response to roads. Using a contemporary method of step selection analysis that incorporates movement and selection simultaneously allowed me to make detailed conclusions regarding temporal and spatial aspects of these behaviours. Further, I was able to test both direct and indirect behavioural effects of road proximity and road crossing. The leading objective of my thesis was to determine the response of elk to roads on their winter range; however, the importance of scale is a resonating message in my work. In addition, I employ unique methodology to consider individual variation around population trends that deserves attention.

The effect of a road can reach far past the feature itself, the extent of which is important to quantify the amount of habitat affected by human disturbance on a landscape (road-effect zone; Forman 2000). Road effect zones have been previously determined by using categorical distance measures, then subsequently analyzing the relocations or evaluating model results within those extents (Shanley and Pyare 2011, Leblond et al. 2013). The relative probability of moving to a road has been used as a continuous measure of road-effect distance (Fortin et al. 2005). Using Relative Selection Strength, I outlined the road effect for all three of my habitat selection models. The decay in effect was fairly consistent across analyses, with the influence of roads on selection becoming minimal after 500 metres from roads. The effect zone is an important factor to include whenever studying road avoidance. Road-effect distance helps in understanding the degree to which roads influence wildlife, and in evaluating habitat loss resulting from development, both of which can educate mitigation practices.

Another approach to evaluate the magnitude of the effect of a habitat feature is by determining at what behavioural scales animals respond to it. One theory regarding scales of habitat selection suggests the most important habitat components influence selection at larger

scales (Rettie and Messier 2001). However, I would interpret consistent avoidance at all scales as indisputable evidence for a habitat components importance. My work demonstrates that the response of elk to roads occurs across scales of selection. Road avoidance was observed when modeling second and third order resource selection (home range placement and within home range selection). Further, I provide evidence for direct and indirect effects when evaluating fine-scale behavioural processes. Thus, road disturbance is a notable influence on elk behaviour.

Road presence alone can impact animals (Andrews and Gibbons 2005, McGregor et al. 2008), but often the amount of vehicle disturbance on a road better describes observed animal behaviour (Forrest and St. Clair 2009, Ciuti et al. 2012b, Montgomery et al. 2013). Traffic on roads has been evaluated using continuous measures of traffic which vary in space and time (Gagnon et al. 2007, Northrup et al. 2012). Alternatively, roads can be categorized based on size or traffic intensity (Alexander et al. 2005, Montgomery et al. 2013). Each chapter of my thesis incorporates traffic into the analysis, yet differs in the approach to do so.

In my second chapter, I categorized roads intro three classes based on their size, substrate, and traffic level (determined by the traffic model created for this study area, Northrup et al. 2012). Road avoidance was not directly related to traffic intensity; in fact, avoidance was more consistent for secondary roads, than primary roads. Nevertheless, as road density increased the use of areas near tertiary roads increased, providing some support for traffic impacting selection of road proximity.

In my third chapter, I use the temporal pattern of roads to integrate traffic into the models. Elk avoided being close to roads during the day and twilight, both times of higher traffic. These temporal patterns were easier to interpret than the resulting spatial patterns in the first chapter. I would speculate that this is because traffic is less variable between road classes in the winter. When comparing classes, higher traffic on primary roads only occurs during the weekend in the winter. In contrast, weekday daytime traffic levels are equivalent in volume to weekend traffic on primary roads during hunting and summer seasons. Thus, in the winter there is a limited time when the primary and secondary classes truly differ. In summary, the temporal pattern may be more reflective of road avoidance behaviour, especially during the winter in this area. Regardless, I observed both spatial and temporal variation in the response to road networks that supports the inclusion of traffic measures when assessing effect of road disturbance on wildlife behaviour.

Moreover, roads of all classes and at all times of day were avoided be elk, which indicates that they are a significant source of disturbance regardless of traffic. However, when spatial or temporal use was lower, avoidance of roads was less. Further, in areas with higher road density, elk selected to be closer to low use roads. Thus, roads with less traffic could relax the pressure of higher traffic roads. In agreement with this, Montgomery et al. (2013) found that elk selected for closed roads. Even more, grizzly bears in this study area selected for higher density but lower use roads (Northrup et al. 2012). In conclusion, the incorporation of intensity of use in my analyses demonstrates that limiting the development of roads in core areas is key, but once present, reducing traffic can help mitigate their influence.

Together with determining the response to roads, I investigated the response to natural habitat characteristics during the winter. Elevation is an important aspect of winter range selection (Boyce and McDonald 1999, Boyce et al. 2003, Sawyer et al. 2007). Both third order RSA and iSSA indicated elk selected higher elevations within their low-elevation winter ranges and this response was highly reproducible among individual elk-years. In contrast, second order RSA indicates winter ranges were placed in areas of low elevation. Indeed, abiotic factors can have a strong influence on habitat selection at large scales (Bailey et al. 1996, Fortin et al. 2003). Therefore, elevation provides a revealing depiction of scale dependent selection behaviour.

Normalized Difference Vegetation Index (NDVI) is a measure of vegetation productivity, as assessed by infrared reflectance (Pettorelli et al. 2005). This measure has been widely used to investigate topics pertaining to wildlife ecology such as migration, dispersal, habitat selection, space use and body condition (Pettorelli et al. 2006, Hebblewhite et al. 2008, Bischof et al. 2012, Killeen et al. 2014, Avgar et al. 2015). For my purposes, NDVI was used to quantify vegetation selection on elk winter range. During the winter, low NDVI values represent non-vegetated or consistently snow covered areas, while high values represent coniferous forests, neither of which provide winter forage for elk. Thus, a linear and a squared term of NDVI was included to describe the expected non-linear response to vegetation (Avgar et al. 2015, S1). Support for my expectation that elk select for intermediate levels of vegetation was found at all scales of analysis. Further, modelling interactions with the linear NDVI term in the iSSA allowed me to specifically test my predictions regarding over-seeking behaviour. In conclusion, using a squared term for NDVI could improve models which aim to describe wildlife-vegetation interactions.

Scale is important throughout ecological analyses, and habitat selection modeling is no exception (Levin 1992, Hobbs 2003). I studied habitat selection at three scales by using different extents when defining availability domains. In general, patterns are expected to be more conserved at broad scales, whereas fine-scale patterns may provide more variation (Wiens 1989). At the broad domain of availability, termed second order in this analysis (after Johnson 1980), I observed more stability in the patterns observed across individuals and a greater ability to detect trends in the population compared to the third order RSA, and iSSA analysis. However, iSSA indicated strong directional responses for a large proportion of individuals for movement and road coefficients. Perhaps the purely spatial nature of third order analysis did not match the level at which the behaviour occurs, this there was more variation in this analysis. The scale of observation resulted in a different answer to the posed question of how elk responded to natural and anthropogenic covariates. Therefore, different extents have their advantages and considering them in concert offers unique perspectives.

Extent was the focus in my consideration of scale; however, throughout my thesis there exist examples of the relationship between resolution and my resulting observations. Matching the resolution to behaviour is key and the resolution of data limits what can be adequately tested (Boyce 2006b). First, the resolution of habitat attributes effects the resulting functional response, where smaller grain sizes show a stronger signal for a relationship between selection and availability (Laforge et al. 2015). In Chapter 2, I might not have observed a functional response for NDVI because this covariate had the largest resolution (250 metre pixels) of all those included in my analysis (DEM and Road layers occurred at 30 metre and 25 metre pixels, respectively).

Similarly in Chapter 3, despite the temporal variation (16-day) included in this analysis finer-resolution measurements of vegetation might have been required to capture selection differences during the day. Further, snow depth negatively influenced caribou movement at broad scales but not when movement was modeled at fine scales (Avgar et al. 2013, 2015). This result was attributed to lower variation in snow depth at the fine scale (Avgar et al. 2015), but there is large spatial and temporal variation in snow depth at the fine scale in this study area. However, the spatial resolution of the data was inadequate to capture this (40 km pixels). Thus, though snow depth and NDVI were the most temporally variable in the iSSA they demonstrated a weak or variable response, possibly a result of the coarse spatial resolution.

Lastly, the temporal resolution of elk relocations (at a two-hour fix rate) might have been too coarse to represent road crossing behaviour. The direct and indirect response to road crossing was weaker than that of road proximity. Further, the road proximity models were more parsimonious than models that used the road crossing metric. Thurfjell et al. (2014) suggested that GPS relocations be taken at a higher fix rate followed by exploratory analysis of rarified fix rates to determine adequate temporal scale for measuring road crossing. To summarize, there are no absolute answers as to the correct scale of analysis. I will simply reiterate that the scale must match the question and behaviour of interest (Wiens 1989, Boyce et al. 2003, Hobbs 2003, Boyce 2006a, Northrup et al. 2013)

Scale is often discussed on spatial and temporal planes; however, the scale of the analysis for the species of interest, i.e. population level versus individual level, is critical (Clutton-brock and Sheldon 2010, Cristescu and Boyce 2013). When individual differences are sought, they are likely to be found. There is evidence for individual to differences in behaviours including dispersal and movement, habitat selection, risk-assessment and risk-taking, and foraging (Hawkes 2009, Duchesne et al. 2010, Mathot et al. 2012, David et al. 2014).

Individual variation in behaviour can arise for numerous reasons. First, the environment around an individual can influence their response to habitat characteristics in that location (Mysterud and Ims 1998, Knopff et al. 2014). Further, past experience in other environments can shape future responses (Frair et al. 2007). In addition to the external environment impacting behaviour, individuals can differ because of intrinsic qualities (Gillies et al. 2006). Examples of characteristics that have been related to behaviour include sex, age, condition, and genetics (Ciuti et al. 2012a, Dingemanse and Wolf 2013, David et al. 2014). These among-individual differences can then be linked to fitness consequences (Réale et al. 2007). This was illustrated in the this study population, where fast moving, bold elk were had a greater likelihood of being harvested by hunters (Ciuti et al. 2012a).

Mixed-effects modeling approaches, where the individual is fit as a random effect, has been used to account for and quantify individual differences in behavioural studies, including habitat selection work (Duchesne et al. 2010, Dingemanse and Dochtermann 2013). An alternative approach to this is to model individuals separately, which corrects for autocorrelation and allows variation to be quantified free of imposed distributions (Fieberg et al. 2010, Avgar et al. 2016). All analyses in this thesis fit models to individual-elk years for both RSA and iSSA to

capture individual variation. Following the inclusion of individual variation in the modelling approach comes the challenge of determining population trends. I calculated the average population response to habitat covariates through bootstrapping the individual elk-year coefficients. Individual variation was incorporated by determining the proportion of individuals following the population trend. Moreover, modeling of individual elk-years allows for post-hoc modeling to answer further questions related to individual variation in habitat selection. I did this in Chapter 2 to look at the relationships between scales and the functional response. The only individual trait I incorporated was where elk were (i.e. availability) but this method can be employed to look at intrinsic individual traits. In conclusion, modelling individual variation in habitat selection to determine population trends and explore relationships to individual characteristics is a worthwhile endeavor.

In conclusion, I used fundamental and emerging concepts of habitat selection to explore the influence of road disturbance on elk during the winter. In addition to my main findings regarding elk response to road disturbance, my thesis adds to issues surrounding habitat-selection literature, that is, scale, availability, the incorporation of movement, and individual variation. These topics have been strongly emphasized in the past few years as I completed my work, and I believe that they will be integral to future developments in wildlife ecology.

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